Apomictic lines of sugar beet: development and studying

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Создание и изучение апомиктичных линий сахарной свеклы

D. V. SOKOLOVA

N.I. Vavilov All-Russian Institute of Plant Genetic Resources, 42, 44 Bolshaya Morskaya Street, St. Petersburg 190000, Russia
dianasokol@bk.ru

Д. В. СОКОЛОВА

Федеральный исследовательский центр Всероссийский институт генетических ресурсов растений имени Н.И. Вавилова, 190000 Россия, г. Санкт-Петербург, ул. Б. Морская, 42, 44
dianasokol@bk.ru

Background. While working with such cross-pollinated crops as sugar beet, the greatest problem is the fixation of valuable genotypes. Using apomixis to produce breeding material helps to accelerate the breeding process and save the desired combination of genes. **Materials and methods**. The research objects were 110 accessions of sugar beet from the VIR collection. Field experiments and assessments of the resistance to *Cercospora* leaf spot, monogermity, and non-bolting were performed according to VIR's guidelines in 2016–2018 at Pushkin and Pavlovsk Laboratories of VIR and Maikop Experiment Station of VIR. The sugar level in roots was measured using an optical refractometer. **Results.** A comprehensive study of sugar beet accessions resulted in the development of apomictic lines with cytoplasmic male sterility, followed by an evaluation of their economically important characters. An extremely rare occurrence of biotypes with the 0-type sterility (less than 0.5%) was observed in the population. The seeds obtained from apomixis-prone lines demonstrated a significant difference during inbreeding from the seeds of fertile inbred genotypes: no inbreeding depression was observed in apomictic lines. Lines combining sterility and monogermity in their genotype were produced. Testing parent accessions and apomictic forms did not reveal significant differences in the sugar content and root yield, so the resulting forms can be efficiently used in future breeding programs. **Conclusion.** Using apomixis to develop sugar beet lines helped to fixate the sugar content level, biennial plant development cycle, and *Cercospora* leaf spot resistance. Thus, apomixis is promising for ensuring maternal inheritance and preserving the desired combination of genes in sugar beet, thereby accelerating the breeding process.

Актуальность. Наибольшую проблему при работе с перекрестноопыляющейся культурой сахарной свеклы представляет закрепление ценных генотипов. Использование апомиксиса для создания селекционного материала позволяет ускорить селекционный процесс, сохранить желательную комбинацию генов. **Материалы и методы**. Объектом исследования послужили 110 образцов сахарной свеклы из коллекции ВИР. Полевые наблюдения выполнены по единой методике в течение 2016–2018 гг. на научно-производственной базе «Пушкинские и Павловские лаборатории ВИР» и Майкопской опытной станции – филиале ВИР. Изоляцию растений проводили с использованием индивидуальных изоляторов. Уровень сахара в корнеплодах измеряли с помощью оптического рефрактометра. **Результаты.** Экспериментально были созданы и оценены по комплексу хозяйственно важных признаков апомиктичные линии с цитоплазматической мужской стерильностью. Отмечена крайне редкая встречаемость в популяции биотипов 0-типа стерильности – менее 0,5%. Выявлено значимое отличие при инбридинге у полученного потомства склонных к апомиксису линий от инбредных фертильных биотипов: инбредная депрессия у апомиктичных линий не проявлялась. Созданы линии, сочетающие в своем генотипе стерильность и раздельноплодность. **Заключение.** Тестирование родительских образцов и созданных на их основе апомиктичных форм по сахаристости и урожайности корнеплодов значимых различий не выявило, что позволяет в дальнейшем использовать полученные формы в селекции. Получение линий с помощью апомиксиса позволило закрепить показатель сахаристости, двулетний цикл развития и устойчивость к церкоспорозу. Таким образом, путем апомиксиса можно обеспечить материнскую наследственность и сохранить желательный фенотип у сахарной свеклы, ускорив тем самым селекционный процесс.

Key words: *Beta vulgaris* L., genotype, cytoplasmic male sterility, monogermity; inbreeding, seed quality, bolting resistance.

Ключевые слова: *Beta vulgaris* L., генотип, цитоплазматическая мужская стерильность, раздельноплодность, инбридинг, качество семян, устойчивость к цветушности.

Introduction

Sugar beet (*Beta vulgaris* L. subsp. *vulgaris* var. *saccharifera* Alef.) is one of the main industrial crops in Russia, serving as raw material for sugar production. Developing new cultivars and hybrids of this crop with a high sugar content and a set of valuable characteristics is one of the most important tasks for breeders. When breeders are working sugar beet, it is important for them to have well-aligned, well-studied source material. Obtaining homozygous lines by inbreeding is difficult due to a distinctly expressed system of self-incompatibility in most plants (Zhuzhzhalova et al., 2020). By the third inbred generation, plant forms with distinct self-incompatibility are eliminated, and single self-fertile lines with elements of apomictic reproduction remain. The use of apomixis makes it possible to accelerate the breeding process, preserve the desired combination of genes and offspring uniformity, and fixate the effect of heterosis in sugar beet (Bogomolov, 2008).

Apomixis is an exceptional natural phenomenon that promotes clonal seed propagation of plants while preserving the genotype of the parent plant. In such seeds, the embryos do not occur as a result of the fusion of male and female gametes, as it occurs during sexual reproduction, but due to the cloning of the ovum's maternal tissues. The study of this phenomenon is of great importance for agriculture.

Gametophytic apomixis in sugar beet is one of the mechanisms of inbreeding that leads to genome homozygotization – according to S. I. Maletskii, 42.8% of genes per one generation of reproduction (Maletskii, 1997, 2000). Under natural conditions, the ability of sugar beet to reproduce apomictically is very weak (Bogomolov, 2005). It is considered that sugar beet is predominantly an allogamous crop. Although cross-pollination is common to *Beta vulgaris* L., it has long been noted that individual plants exhibit the ability to self-pollination to varying degrees (Nilsson, 1924). N. I. Vavilov's employee N. V. Favorsky reported it in 1928, describing the formation of nucellar embryos in the ovules of beet flowers (Favorsky, 1928). In the Russian Federation, self-fertile races were first discovered in 1927 at Ivanovo Experiment Station, where the work on sugar beet crops had been underway (Grinko, 1927). Similar forms were also found in the United States. One such line turned out to be a monogerm mutant and served as the basis for producing monogerm cultivars and hybrids (Owen, 1942a; Savitsky, 1950).

Apomicts are produced by a natural or induced technique. Obtaining seeds on isolated plants with cytoplasmic male sterility (CMS) is a method of natural apomixis. To date, all hybrid breeding of sugar beet is based on the forms with CMS. The first female flowering plants were discovered in the 1920s at Belotserkovsky and Ivanovo Experiment Stations (Arkhimovich, 1931; Gelmer, 1939). The American researcher F. V. Owen (1942b) also found plants with functionally female flowers among inbred lines pollinated with irradiated pollen, and described them. Active research on the use of CMS in sugar beet breeding started in Germany in 1953 (Bandlow, 1958), and later in the USSR (Zaykovskaya, 1960, Zosimovich, 1960). Today, using the analysis of segregating populations and applying cytological techniques, the idea has been formed about the three-gene inheritance of the sterility/fertility character (Bliss, Gabelman, 1965; Hjerdin-Panagopoulos et al., 2002). CMS in beets is determined by the sterile *S* cytoplasm, and nuclear *x*, *z* and *rf*^{par} (*restorer of fertility parity*) genes. With the *N*-type cytoplasm (fertile), only fertile pollen is produced. Distinguishing phenotypic characteristics of a sterile plant are listed in Table 1.

Table 1. Sterility types in sugar beet

Таблица 1. Типы стерильности сахарной свеклы

Types of sterility	Idiotype	Phenotype
0	SxxzzRf^{par}rf^{par} SxxZzrf^{par}rf^{par} Sxxzzrf^{par}rf^{par}	Sterile plants: with white transparent, empty anthers.
I	SxxZzRf^{par}rf^{par} SXxzzrf^{par}rf^{par}	Sterile plants: with shrunken semi-empty, non-cracking anthers containing non-viable pollen.
II	SXxZzrf^{par}rf^{par}	They have large bright yellow anthers, partially or completely filled with a mixture of sterile and normal pollen grains. Anthers do not crack.
Semi-fertile	SXxzzRf^{par}rf^{par}	A mixture of sterile and fertile pollen.
Fertile	SXxZzRf^{par}rf^{par}	Fertile plants.

Also, one of the features needed for the development of beet cultivars and hybrids is monogermity (MG). In general, beets tend to form clusters of 2 to 6 closely fused fruits on their inflorescence. Plants with detached flowers appear in a beet population very rarely. The first attempts to produce plant forms with separate flowers were made in the beginning of the last century, but the resulting forms did not find practical application (Towensend, Rittue, 1905). More than 100 years have passed since then, and the entire sugar industry now uses the seed material of monogerm hybrids. The degree of monogermity (monocarpic degree) is important for accurate seeding and mechanized formation of the density of a plant stand. The development and introduction of new monogerm beet cultivars and hybrids that most fully meet the requirements of industrial cultivation technologies is one of the ways to increase the economic efficiency of its production (Sokolova, 2010).

To be able to use the material in the breeding process, it must have a number of traits valuable for the crop, e.g., resistance to diseases, a biennial development cycle, high sugar content, etc. Therefore, assessment of the source material for main agronomic characters is extremely important.

The goal of the presented research was searching for, developing and studying apomictic lines (A_0) of sugar beet for their economically valuable traits.

Materials and methods

The target objects of the study were 110 accessions of sugar beet from the collection of the N.I. Vavilov All-Russian Institute of Plant Genetic Resources (VIR). They differed in their countries of origin, years of placement into the collection, and degrees of monogermity. The production of sugar beet hybrids all over the world is based solely on CMS forms. Domestic and foreign hybrids used in this work were produced on the basis of CMS, which is recorded in the State

Register for Selection Achievements Admitted for Usage in the Russian Federation (State Register..., 2020), on the websites of their originators, and in their descriptive documents when they were placed into the VIR collection.

This makes it possible to classify with absolute certainty all detected sterile biotypes as CMS.

The research was performed at Pushkin and Pavlovsk Laboratories of VIR (Town of Pushkin, St. Petersburg) in 2016–2018, and at Maikop Experiment Station of VIR (Maikop, Krasnodar Territory) in 2018. The length of the growing season was 130 days for the yield of roots, and 150 for that of seeds. All cultivars were studied on a natural background, without fertilization or crop protection against pests and diseases. Observations were made in accordance with VIR's guidelines (Burenin, 1989). Individual isolation cages made of calico were used for inbreeding. A Master 53 alpha/53 Palpha optical refractometer (Japan) was used to measure the sugar level in beet roots. Germination energy and seed germination percentage were assessed in VIR's laboratory using standard methods for Russia (GOST 12038-84..., 2020). Resistance of the beet leaf system to *Cercospora* leaf spot was scored 20 days prior to harvesting employing a 5-point scale: 0 – no damage; 1 – up to 20% of the leaf surface area damaged; 2 – 21% to 40% damaged; 3 – 41% to 60% damaged; 4 – 61% to 80% damaged; and 5 – 81% to 100% damaged.

The experimental data were evaluated with MS Excel 2007 and Statistica 7.0 software.

Results and discussion

A group of accessions representing the diversity of the sugar beet collection held by VIR was selected for screening. The sets of accessions from Russia, Germany and Ukraine were the largest and most diverse (Fig. 1). Ranked by the years of placement into the collection, the accessions varied from earliest entries of 1928, such as 'Barbabictela Zuchero' (Italy) and 'Pervomaysky hybrid' (Russia), to contemporary hybrids from the UK, Denmark, Germany and Russia.

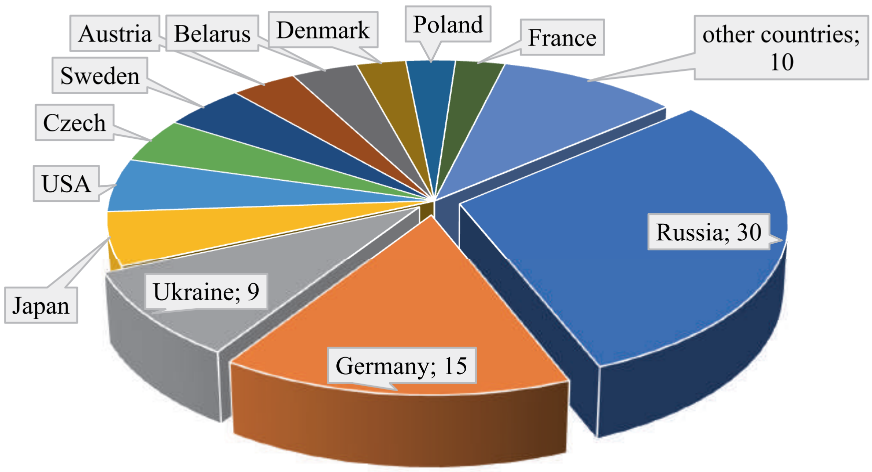

Fig. 1. **Grouping of the tested sugar beet accessions according to their countries of origin**

Рис. 1. **Группировка опытных образцов сахарной свеклы по стране происхождения**

An assessment of the sugar content in roots of the tested accessions showed a significant increase in this character across the years of their placement into the collection, thus evidencing the effectiveness of breeders' efforts around the world (Table 2).

Table 2. **Grouping of the tested sugar beet accessions according to the years of their placement into the collection**

Таблица 2. **Группировка опытных образцов сахарной свеклы по году включения в коллекцию**

Group	Number of accessions in each group	Years	Sugar content in roots, %		
			M ± Sx̄	min	max
1	11	1928–1950	14.3 ± 0.47	12.0	17.5
2	36	1951–1973	15.3 ± 0.22	12.0	17.6
3	50	1974–1994	15.5 ± 0.19	12.1	18.2
4	13	1995–2016	16.2 ± 0.12	15.5	16.9
	110		*15.4 ± 0.13*	*12.0*	*18.2*
$t_{exp} > t_{0.01}$					

The resistance of the tested accessions to the annual development cycle (bolting resistance) was assessed in the environments of Leningrad Province and showed that 94.5% of the accessions were resistant. The highest percentage of bolted plants (5.8%) was observed in the modern domestic diploid single-seeded hybrid 'Kubansky MS 95' (k-3770).

Cercospora leaf spot resistance was assessed in the field under the epiphytotic conditions of 2016. Caused by the fungus *Cercospora beticola* Sacc., this leaf spot is one of the most widespread diseases of beets, affecting both sugar beet and other cultivated beet varieties (Salunskaya, 1959). Resistant lines can be identified by inbreeding among the least affected biotypes (Smith, Gaskill, 1970). Under the 2016 epiphytotics, all sugar beet accessions were more or less susceptible. At the time when the damage was recorded, 98.2% of the accessions had symptoms of *Cercospora* leaf spot at a level from 1 to 4 points (Fig. 2). In most of them (53%), the damaged area of the leaf surface did not exceed 10%. Two accessions manifested 100% resistance under the conditions of field assessment. Those were cultivars of American breeding, 'F 1001' (k-3478) and 'C 562 CMS' (k-3481), included into the collection in 1982. Meanwhile, their sugar content levels were below average (14.0 and 14.5%, respectively).

In 2017, 2,200 beet seed plants (20 plants of each accession) were evaluated for their sterility and monogermity (MG). Individual isolation was provided only for plants with the 0-type sterility, monogerm forms, and 10 plants from each identified accession with fertile pollen (Fig. 3). The desired

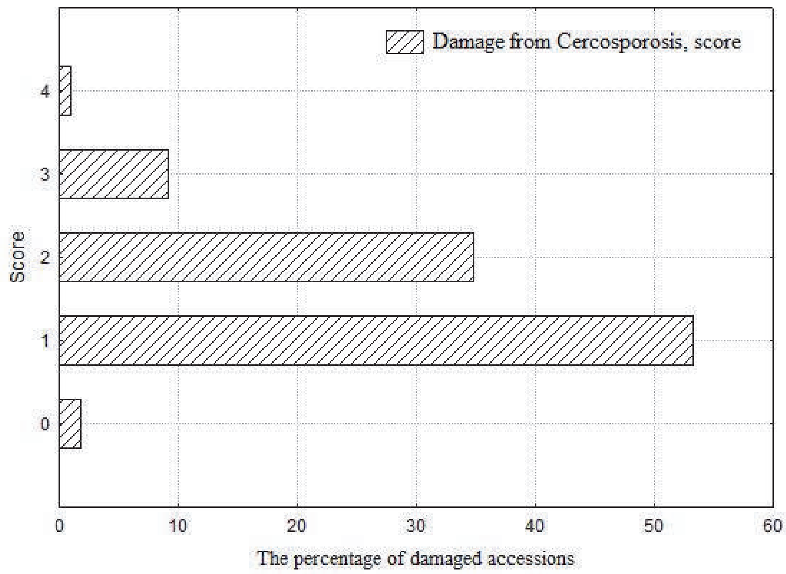

Fig. 2. **Screening of the sugar beet accessions according to their resistance to *Cercospora beticola* Sacc., 2016**

Рис. 2. **Скрининг образцов сахарной свеклы по устойчивости к церкоспорозу (*Cercospora beticola* Sacc.), 2016 г.**

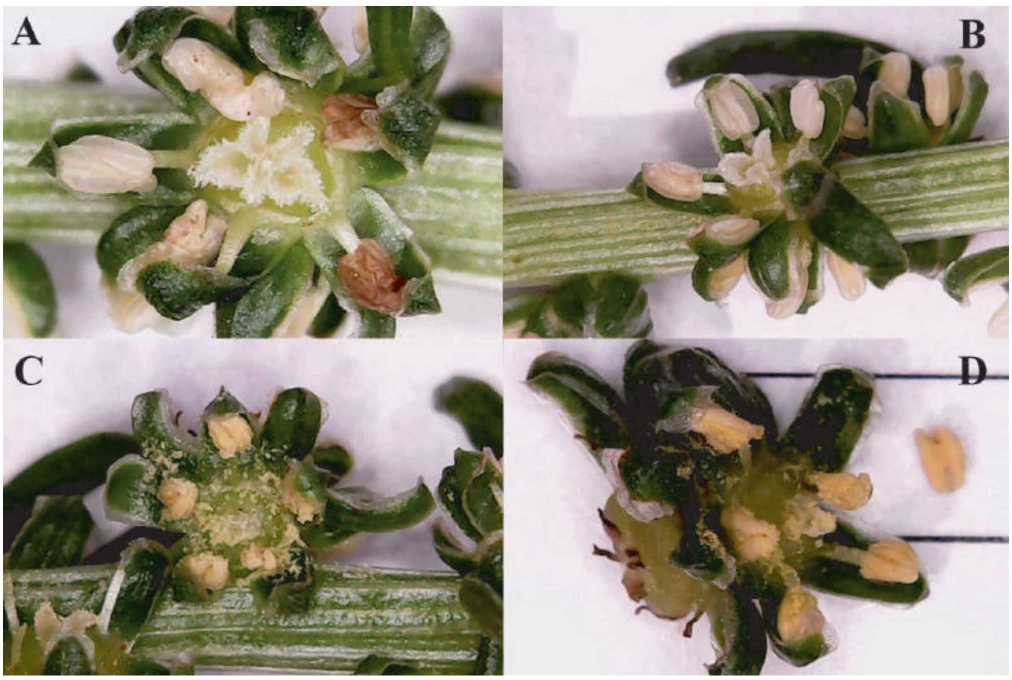

Fig. 3. **Differences between a sugar beet flower with the 0-type sterility (A, B) and a fertile biotype (C, D); Pushkin, 2017**

Рис. 3. **Различия цветка сахарной свеклы с 0-типом стерильности (A, B) и фертильного (C, D); Пушкин, 2017 г.**

biotypes were identified in 9 plants (0.4%) of 7 accessions. The genotype of three of them combined sterility and 100% monogermity. Six accessions, i.e., representatives of contemporary domestic hybrid breeding and the Danish hybrid 'Ventura', showed a low incidence of *Cercospora* leaf spot (1 point) and sugar content from 15.7% to 17.0%. The Czech old-time cultivar 'Wohancova 5' (1947) was characterized by non-bolting, low leaf spot incidence, and extremely low sugar content (12.1%), which allowed us to attribute it to the semi-sugar type. Two plants of the desired biotype were isolated from each of the two hybrids 'Ventura' and 'Kaskad 3'.

Practical application of inbreeding in beets faces a number of difficulties due to the distinct inbreeding depression exhibited by self-pollinated lines. This is manifested in a decreased number of seeds, deterioration of their quality, reduced germination, growth weakening in young plants, and a decrease in overall productivity (Sokolova, 2010). This is expressed most notably in the first inbred generations. As a rule, the depression stops after reaching a certain plateau. In our experiment, the seed productivity under apomictic reproduction averaged 29 g per plant, and the seed germination percentage was 61.8% (Table 3). At the same time, fertile forms showed symptoms of depression after the first forced self-pollination. Thus, the seed productivity of fertile plants averaged 10 g per plant, and seed germination percentage was 28.9%. It should be noted that all isolated plants were able to form seeds to some extent. Probably, the reproduction system in beets is quite flexible, and, if necessary, it switches from the zygotic mode to the apozygotic one. It is known that some species of *Beta* L. set seeds exclusively in the apozygotic way (Barocka, 1966): for example, representatives of the section *Corollinae* Tran.: *B. lomatogona* Fisch. & C.A. Mey. (2n = 36), *B. corollifora* Zosimovic ex Buttler (2n = 18), *B. trygina* Waldst. & Kit. (2n = 54), and *B. × intermedia* Bunge (2n = 36). Apparently, finding cultivated beet forms with the apomictic reproduction mode is a confirmation of the N. I. Vavilov's universal law of homologous series in variation, which applies to both morphological and reproductive characters.

Differences in the productivity of seed plants are largely related to the architectonics of the seed plant and depend on the number of fruiting stalks, the nature and rate of differentiation in buds, the number of clusters, and the quality of seeds in them. The habitus of the seed plant, in its turn, induces differences in the formation of seeds, which is reflected in their quality. The main mass of seeds (68–99%) is located on the branches of the first and second branching orders, versus 7% to 10% on the central stalks (Kononkov, Balbyshev, 1982). The number of branches, their spatial position, and the expression degree of the main stalk (the leader) are used to characterize beet seed plants. A leaderless plant, with at least 3-4 stalks, is considered the optimal one. Plants of such type are valued for their most harmonious habitus, produce stalks that counterbalance each other in the process of development, usually demonstrate maturation synchrony, yield high-quality seeds, and have high seed yields (Arkhangelsky, 1968). In our experiment, seed plants of the sterile lines 5b from 'Ventura', 9b from 'Kaskad 3' and 12g from 'RO 117' formed a distinctly expressed leading sprout with several first-order branches. This type of bush partly explains their low productivity.

In general, apomixis does not promote adaptability to evolution because it does not affect the spread of new genes in a population and usually serves only to reduce genetic diversity. Many apomictic species retain some ability to reproduce sexually. This apomictic feature allows them to thrive under conditions where pollination is impossible, but they can also resume sexual reproduction when conditions allow. Therefore, apomixis equips a plant species with an enhanced ability to adapt and survive under unfavorable conditions. As shown in Table 3, the inbreeding in fertile biotypes led to a decrease in all seed quality characters: productivity, 1000 seed weight, and germination percentage. Contrariwise, seed setting under the apozygotic mode did not result in a manifestation of inbreeding depression symptoms. The exceptions were two lines: 9b from 'Kaskad 3' and 12g from 'RO 117', with the lowest indicators, which implies that they are not prone to the apomictic mode of seed formation and that, in all likelihood, such biotypes will be completely eliminated in the future.

Of particular interest were three identified lines that combined the 0-type sterility and monogermity (MG). As shown earlier by our experiments on table beet, self-pollination of MG forms leads to a clearly expressed inbred depression, oc-

Table 3. Statistical quality indicators of sugar beet seeds produced by inbred lines of the isolated sterile and fertile biotypes, 2017

Таблица 3. Показатели качества семян сахарной свеклы, полученных в результате инбридинга у стерильных и фертильных биотипов, 2017 г.

Indicators	Inbred form	M	$S\bar{x}$	Cv	LSD (P ≤ 0.05)
Productivity, g/plant	A_0s*	28.97	7.18	74.4	15.6
	I_0f**	10.03	1.61	48.3	
Weight of 1000 seeds, g	A_0s	20.4	1.81	26.7	4.59
	I_0f	16.71	1.17	21.1	
Seed germination, %	A_0s	61.78	9.01	43.7	21.3
	I_0f	27.36	4.46	48.8	

* A_0s – apomictic lines
** I_0f – inbred lines of fertile beet plants
* A_0s – апомиктичные линии
** I_0f – инбредные линии фертильных растений свеклы

currence of teratological changes, and complete elimination of lines (Sokolova, 2010). The analysis of the 2017 data revealed that isolation of monogerm sugar beet forms, both fertile and sterile, mainly affected the overall productivity of a seed bush by reducing it (Fig. 4). At the same time, seed germination percentage as well as germination energy remained at the same level. Thus, the presence of MG genes in the genotype of sterile or fertile plants reduces seed productivity during inbreeding. Minor manifestations of fasciation (less than 1%) were observed on several plants of the fertile biotype.

A comparative test on the obtained apomictic lines (A_0) and the original parent material (P) to assess main economically useful characters was carried out in the beet-growing zone at Maikop Experiment Station of VIR in 2018. The lines with seed productivity below 10 g were not included in the field experiment (Table 4).

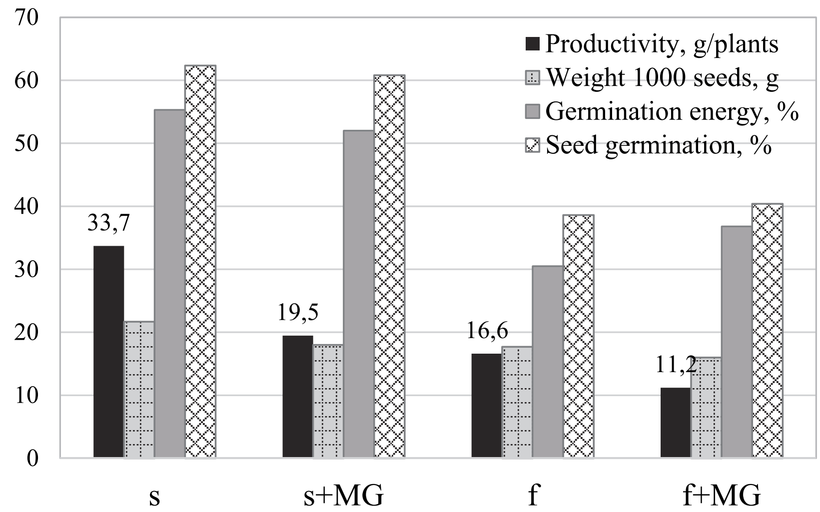

Fig. 4. **Comparative indicators of seed plant productivity and seed quality after inbreeding in different sugar beet genotypes, 2017**

Рис. 4. **Сравнительные показатели продуктивности семенных растений и качества полученных семян инбредных линий сахарной свеклы с различными генотипами, 2017 г.**

Table 4. **Comparative data of economically valuable traits in parent accessions (P) and apomictic lines (A_0) in their first growing season**

Таблица 4. **Сравнительные данные хозяйственно ценных признаков у родительских образцов (P) и полученных на их основе апомиктичных линий (A_0) в первый год вегетации**

Accession name		Weight of one root, kg	Yield, kg/10m²	Sugar content, %	Bolting, %	Damage from *Cercospora* leaf spot, score
Ventura	P	0.74	56.40	16.70	0	1
	A_0	0.69	52.50	16.40	0	1
PMC 120	P	0.96	67.20	15.50	3	2
	A_0	1.18	82.60	16.10	0	1
Kaskad 3	P	1.33	88.40	19.00	3	2
	A_0	0.91	60.40	17.90	1	1
Wohancova 5	P	1.14	79.80	14.40	3	1
	A_0	0.96	68.00	13.70	1	1
Ramoza	P	1.02	69.40	16.80	13	2
	A_0*	1.18	80.20	16.80	0	1
PMC 121	P	0.78	38.90	18.50	2	1
	A_0*	0.80	39.90	17.80	0	1
$F_{emp} < F_{0.05}$						

* – plants combining sterility and monogermity in their genotype

* – растения, сочетающие в генотипе стерильность и раздельноплодность

Statistically significant differences in metric parameters between the obtained lines and the parent accessions were not detected ($F_{emp} < F_{0.05}$). It confirmed the absence of the signs of inbred depression in apomictic lines. The flowering rate of apomicts was lower than that of the parent component, confirming the effectiveness of selection and consolidation of the maternal genotype in apomixis. For example, the line 4g from 'Ramoza' was more productive (80.2 kg/10 m^2) than the parent hybrid, which showed a significant tendency to the annual development cycle under the conditions of Maikop Experiment Station of VIR (bolting was 13%).

Conclusions

As a result of a comprehensive study of 110 accessions from VIR's sugar beet collection, a gradual increase in the sugar content was found in the roots of more recent accessions, attesting to the effectiveness of this breeding trend. The population of sugar beet cultivars and hybrids was observed to incorporate very few forms with the 0-type sterility (less than 0.5%). All identified sterile plants produced viable seeds in different amounts (germination rates varied from 12% to 86%).

Sugar beet hybrids with sterile cytoplasm served as a basis for the development of apomictic lines with CMS, which were evaluated according to a set of economically important characters. Compared with the seeds of inbred fertile biotypes, the quality of the obtained apomictic seeds (1000 seed weight, seed germination percentage, and germination energy) was higher. An assumption can be made that the sugar beet forms with CMS are able to switch quite easily to the apozygotic mode of offspring formation. In contrast to fertile biotypes, there was practically no inbreeding depression in apomictic lines of the first generation.

Comparative evaluation of the parent accessions and apomictic forms isolated from them revealed the absence of significant differences between them in the sugar content and yield. Producing sugar beet lines through apomixis made it possible to fixate the indicators of sugar content, biennial development cycle, and resistance to *Cercospora* leaf spot. This would promote the use of the resulting forms in future breeding programs. Of particular interest are two apomictic lines: 4g from 'Ramoza' and 10v from 'RMS 121', combining the 0-type CMS and 100% monogermity in their genotype.

Thus, the use of apomixis can ensure maternal inheritance in sugar beets and preserve the desired genotype, thereby accelerating the breeding process.

The research was performed within the framework of the State Task according to the theme plan of VIR, Project No. 0662-2019-003 "Genetic Resources of Vegetable and Cucurbit Crops in the VIR Global Collection: Effective Ways to Expand Their Diversity, Disclose the Patterns of Hereditary Variability, and Use Their Adaptive Potential".

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References/Литература

Arkhangelsky N.S. The study of beetroot seed biotypes (Izucheniye biotipov semennikov svekly). *Doklady TSKhA = Reports of the Timiryazev Agricultural Academy*. 1967;(142):117-119. [in Russian] (Архангельский Н.С. Изучение биотипов семенников свеклы. *Доклады ТСХА*. 1967;(142):117-119).

Arkhimovich A.Z. To the question of the inbreeding method in sugar beet (K voprosu ob intsukht-metode u sakharnoy svekly). *Trudy Belotserkovskoy selektsionnoy stantsii = Proceedings of Belotserkovsky Plant Breeding Station*. 1931;(3):3-62. [in Russian] (Архимович А.З. К вопросу об инцухт-методе у сахарной свеклы. *Труды Белоцерковской селекционной станции*. 1931;(3):3-62).

Bandlow G. Die Pollensterilität der Beta–Rüben und ihre Bedeutung für die Polyploidiezüchtung. *Beiträge zur Rübenforschung*. 1958;34(1);52-68. [in German]

Barocka K.H. Die Sektion Corollinae der Gattung *Beta* (Tournef.) L. *Zeitschrift für Pflanzenzüchtung*. 1966;56(4):379–388. [in German]

Bliss F.A., Gabelman W.H. Inheritance of male sterility in beets, *Beta vulgaris* L. *Crop Science*. 1965;5(5):403-406. DOI: 10.2135/cropsci1965.0011183X000500050009x

Bogomolov M.A. Apomixis and the role of this in sugar beet breeding (Apomiksis i yego rol v selektsii sakharnoy svekly). *Sugar Beet*. 2005;(8):19-21. [in Russian] (Богомолов М.А. Апомиксис и его роль в селекции сахарной свеклы. *Сахарная свекла*. 2005;(8):19-21).

Bogomolov M.A. Features of the use of apomixis in sugar beets when creating a new source material (Osobennosti ispolzovaniya apomiksisa u sakharnoy svekly pri sozdanii novogo iskhodnogo materiala). *Sugar Beet*. 2008;(5):18-20. [in Russian] (Богомолов М.А. Особенности использования апомиксиса у сахарной свеклы при создании нового исходного материала. *Сахарная свекла*. 2008;(5):18-20).

Burenin V.I. Methodological guidelines for the study and maintenance of the world collection of root crops (Metodicheskiye ukasaniya po isucheniyu i podderzhaniyu mirovoy kollektsii korneplodov). Leningrad; 1989. [in Russian] (Буренин В.И. Методические указания по изучению и поддержанию мировой коллекции корнеплодов. Ленинград; 1989).

Favorsky N.V. Materials on the biology and embryology of sugar beet (Materialy po biologii i embriologii sakharnoy svekly) *Doklady VASkhNIL = Reports of the Lenin Academy of Agricultural Sciences*. 1928;(3):3-11. [in Russian] (Фаворский Н.В. Материалы по биологии и эмбриологии сахарной свеклы. *Доклады ВАСХНИЛ*. 1928;(3):3-11).

Gelmer O.F. The main conclusions from the work of the beet section of Ivanovo Station in 1937 (Osnovnye vyvody iz rabot sveklovichnoy sektsii Ivanovskoy stantsii za 1937 g.). In: *The main conclusions of the scientific research work of VNIS in 1937* (*Osnovnye vyvody nauchno-issledovatelskikh rabot VNIS za 1937 g.*). Moscow; Leningrad: Pishchepromizdat; 1939. p.288-292. [in Russian] (Гельмер О.Ф. Основные выводы из работ свекловичной секции Ивановской станции за 1937 г. В кн.: *Основные выводы научно-исследовательских работ ВНИС за 1937 г*. Москва; Ленинград: Пищепромиздат; 1939. С.288-292).

GOST 12038-84. Agricultural seeds. Methods for determination of germination. 2020. [in Russian] (ГОСТ 12038-84. Семена сельскохозяйственных культур. Методы определения всхожести. 2020. URL: http://docs.cntd.ru/document/gost-12038-84 [дата обращения: 03.08.2020].

Grinko T.F. Self-pollinating sugar beet races (Samoopylyayushchiyesya rasy sakharnoy svekly). *Byulleten Ivanovskoy opytnoy stantsii = Bulletin of Ivanovo Experiment Station*. 1927;(4):47-63. [in Russian] (Гринько Т.Ф. Самоопыляющиеся расы сахарной свеклы. *Бюллетень Ивановской опытной станции*. 1927;(4):47-63).

Hjerdin-Panagopoulos A., Kraft T., Rading I.M., Tuvesson S., Nilsson N.O. Three QTL regions for restoration of Owen CMS in sugar beet. *Crop Science*. 2002;42(2):540-544. DOI: 10.2135/cropsci2002.5400

Kononkov P.F., Balbyshev I.F. Influence of the duration of the growing season and the type of branching in table beet seed plants on seed productivity and monogermity (Vliyaniye prodolzhitelnosti vegetatsii i tipa vetvleniya semennikov stolovoy svekly na semennuyu produktivnost i odnosemyannost). *Trudy VNII selektsii i semenovodstva ovoshchnykh kultur = Proceedings of the All-Russian Research Institute for Vegetable Crop Breeding and Seed Production*. 1982;(15):125-132. [in Russian] (Кононков П.Ф., Балбышев И.Ф. Влияние продолжительности вегетации и типа ветвления семенников столовой свеклы на семенную продуктивность и односемянность. *Труды ВНИИ селекции и семеноводства овощных культур*. 1982;(15):125-132).

Maletskii S.I. Linked and unlinked gene inheritance during autosegregation in parthenogenetic plant progenies. *Russian Journal of Genetics*. 1997;33(10):1333-1340.

Maletskii S.I. Biology of sugar beet breeding (Biologiya razmnozheniya sakharnoy svekly). In: S.I. Maletskii (ed.). *Binomial Distributions in Plant Genetic Research* (*Binomialnye raspredeleniya v geneticheskikh issledovaniyakh na rasteniyakh*). Novosibirsk; 2000. p.75-96. [in Russian] (Малецкий С.И. Биология размножения сахарной свеклы. В кн.: *Биномиальные распределения в генетических исследованиях на растениях* / под ред. С.И. Малецкого. Новосибирск; 2000. С.75–96).

Nilsson N.H. Practical beet cultivation according to newer lines at Svalof. *Swedish Seeds Association's Journal*. 1924;5(2):214-226. [in Swedish] (Nilsson N.H. Practisk betforodling enligt nyare linier pa Svalöf. *Sveriges utsädesförenings tidskrift;* 1924;5(2):214-226).

Owen F.V. Inheritance of cross- and self- sterility and self-fertility in *Beta vulgaris*. *Journal of Agricultural Research*. 1942a;64(12):679-698.

Owen F.V. Male sterility in sugar beets by complementary effects of cytoplasmic and Mendelian inheritance. *American Journal of Botany*. 1942b;29:692-695.

Salunskaya V.N. Leaf spot or cercosporosis (Pyatnistost listyev ili tserkosporoz). In: V.N. Salunskaya (ed.). *Cercosporosis. Sugar beet* (*Tserkosporoz. Sakharnaya svekla*). Kiev; 1959. p.221-236. [in Russian] (Салунская В.Н. Пятнистость листьев или церкоспороз. В кн.: *Церкоспороз. Сахарная свекла* / под ред. В.Н. Салунской. Киев; 1959. С.221-236).

Savitsky V.F. Monogerm sugar beet in the United states. In: *The American Society of Sugar Beet Technologists Proceedings of Sixth General Meeting. Vol. 6.* Fort Collins, USA; 1950. p.156-159.

Smith G.A., Gaskill J.O. Inheritance of resistance to *Cercospora* leaf spot in sugarbeet. *Journal of the American Society of Sugar Beet Technologists*. 1970;16(2):170-180.

Sokolova D.V. Demonstration of monogerm character in self-pollinated lines of monocarp table beet. *Sugar Beet*. 2010;(10):26-29. [in Russian] (Соколова Д.В. Особенности проявления признака раздельноцветковости у инбредных линий столовой свеклы. *Сахарная свекла*. 2010;(10):26-29).

State Register for Selection Achievements Admitted for Usage (National List). Vol. 1 “Plant varieties” (official publication). Moscow; Rosinformagrotekh; 2020. [in Russian] (Государственный реестр селекционных достижений, допущенных к использованию. Т. 1. «Сорта растений» (официальное издание). Москва: Росинформагротех; 2020). URL: https://gossortrf.ru/wp-content/uploads/2020/03/FIN_reestr_dop_12_03_2020.pdf [дата обращения: 05.08.2020].

Towensend C.O., Rittue E.G. Die Züchtung von einkeimigen Rubens samen. *Zeitschrift Zuckerindustrie*. 1905;(55):809-845. [in German]

Zaykovskaya N.E. About pollen sterility in sugar beet (O sterilnosti pyltsy u sakharnoy svekly). *Agrobiologiya = Agrobiology*. 1960;(5):778-779. [in Russian] (Зайковская Н.Э. О стерильности пыльцы у сахарной свеклы. *Агробиология*. 1960;(5):778-779).

Zhuzhzhalova T.P., Kolesnikova E.O., Vasilchenko E.N., Cherkasova N.N. Biotechnological methods as a tool for efficient sugar beet breeding. *Vavilov Journal of Genetics and Breeding*. 2020;24(1):40-47. [in Russian] (Жужжалова Т.П., Колесникова Е.О., Васильченко Е.Н., Черкасова Н.Н. Методы биотехнологии как потенциал развития селекции сахарной свеклы. *Вавиловский журнал генетики и селекции*. 2020;24(1):40-47). DOI: 10.18699/VJ20.593

Zosimovich V.P. Pollen sterility and breeding for heterosis in sugar beet (Sterilnost pyltsy i selektsiya na geterozis u sakharnoy svekly). *Byulleten selskokhozyaystvennoy nauki = Bulletin of Agricultural Science*. 1960;(5):40-49. [in Russian] (Зосимович В.П. Стерильность пыльцы и селекция на гетерозис у сахарной свеклы. *Вестник сельскохозяйственной науки*. 1960;(5):40-49).

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ORCID
Sokolova D.V. https://orcid.org/0000-0002-9967-7454