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DEVELOPMENT PECULIARITIES OF BEAN COMMON MOSAIC VIRUS (*Potyvirus*, *Potyviridae*) IN MOSCOW REGION AND INITIAL MATERIAL FOR RESISTANCE BREEDING

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Abstract

Recent years have seen a significant expansion in the distribution area of bean common (*Phaseolus vulgaris* L.) mosaic virus (BCMV) that has become an economically significant disease agent for the non-chernozem part of Russia. As early as 2014, the epiphytotics were observed in the Moscow region, but no BCMV resistance screening in both Russia and foreign bean accessions has been performed yet in these agroclimatic conditions. Thus, the presented study is the first one that has described the features of BCMV development in the Moscow region and defines climatic factors affecting the disease progression. An assortment of bean accessions has been estimated on a level of resistance to BCMV using different techniques including molecular markers. The goal of the study was to find an initial breeding material as a source for development of new competitive BCMV-resistant local yardlong bean cultivars. The research was carried out in the Moscow Province in 2014-2019. The research methods included visual and serological diagnosis and phytopathological monitoring of disease progression of artificial and natural infection. Field testing of disease resistance in accessions of various genetic and geographical origins over time was performed using a four-point scale; the accessions were ranked into resistance groups based on the degree of the disease with regard to the stability of expression of the characteristic in various years. DNA analysis of the main resistance genes, i.e., dominant gene *I* and recessive genes *bc-1²* and *bc-3*, was performed using the respective markers SW13, SBD5, and ROC11, following the developed procedures. The result of the study was the identification of the biological features of the BCMV isolate from the Moscow region affecting *Phaseolus vulgaris* L. and *Pisum sativum* L. from the *Fabaceae* family in biotest. The expression of symptoms and intensity of the disease in indicator plants in a greenhouse and bean accessions in field trials significantly depended on temperature, and the spread of the virus — on the accumulated precipitation. In general, reduced precipitation in combination with elevated temperatures served as a deterrent preventing the pathogen from further spreading in the climatic conditions of the Moscow region. At the same time, this combination facilitated viral infection manifestations on the plant leaf apparatus, especially during the vegetation period. Out of 207 accessions studied, only 6 % demonstrated a persistently high BCMV resistance in the context of epiphytotics. Screening of 30 accessions with different resistance levels showed that recessive genes *bc-1²* and *bc-3* were present in the majority of the accessions and dominant gene *I* only in half of all accessions. Most accessions had genotypes *I*/*bc-1²*/*bc-3* (33 %) and *bc-1²*/*bc-3* (47 %), among which only 1/3 demonstrated a persistently high virus resistance. The plants lacking the genes *I* and *bc-1²* were severely damaged by the virus. The chi-square test (χ^2) revealed a more significant effect of the gene *bc-1²* on the field resistance of common bean accessions to BCMV. Based on the results obtained, as an initial breeding material for developing yardlong bean cultivars with high BCMV resistance we recommend 17 most promising accessions of different origin, including five cultivars (Khavskaya Universalnaya, Rant, Zolushka, Marlinka, Svetlyachok) and two perspective hybrids (SP-232, KP-

84) selected at Federal Research Center for Vegetable Growing that are distinguished by several agronomic characters.

Keywords: *Phaseolus vulgaris* L., green bean, bean common mosaic virus, BCMV, virus resistance, resistance genes, sustainable resistance, DNA-markers, initial material

Common bean (*Phaseolus vulgaris* L.) is the third most important and worldwide grown food legume crop following soybeans *Glycine max* (L.) Merr. and peanuts *Arachis hypogea* L. [1]. Recently, it has been used as a functional food product with a high content of proteins, vitamins, antioxidants and trace elements, and, moreover, with an excellent taste [1, 2]. According to the FAO (Food and Agriculture Organization) report for 2018, vegetable bean is the crop occupying the largest areas in the countries of Latin America, Eastern and Southern Africa [3]. In recent years, the industrial production of this culture has been actively expanding in Russia [4].

Viruses, especially aphid-transmitted, constitute a large group of pathogenic microorganisms infecting *Ph. vulgaris*. To date, about ten viruses are known, among which the *Bean common mosaic virus* (BCMV), *Bean yellow mosaic virus* (BYMV), *Bean common mosaic necrosis virus* (BCMNV) of *Potyviridae* family, and *Bean leafroll virus* (BLRV) of *Luteoviridae* family are the most harmful and wide-spread. Other species are classified as endemic, the appearance of which is due to certain conditions in different countries and regions [1, 5, 6].

BCMV was first discovered in 1917 in the USA [7]. At present, BCMV is the most harmful. In some countries, the epiphytoties caused by BCMV, according to various estimates, annually result in a 50-100% loss of legumes [8-13]. In the Russian Federation, BCMV was first described in the 1980s on meadow clover in the Far East, and a decade later on bean culture in other regions [14, 15].

BCMV is typically transmitted vertically by pollen and seeds. The virus is found in the seed coat, cotyledons, and embryos [6, 8, 9]. The seed infection is significantly influenced by the time of plant infection: the most vulnerable period is the phase of differentiation of flower organs, while during infection after flowering, the probability of seed transmission of BCMV is significantly reduced [16]. Eleven species of aphids are actively involved in the vector transmission of the virus in a non-persistent way form the source of infection. Most of them effectively transmit the virus as winged migrants in a matter of minutes, but they also quickly lose this ability [6, 9, 17]. The range of natural reserves of BCMV is mainly limited to cultivated and wild species of the *Fabaceae* family, the genera *Phaseolus*, *Pisum*, *Trifolium*, and *Vicia* [11, 18-20].

In fact, BCMV is a complex of strains subdivided into eight pathogroups (PG), five for BCMV (PG-1, PG-2, PG-4, PG-5, PG-7), and three for BCMNV serologically related to BCMV (PG-3, PG-6, PG-8) [21]. Recent molecular studies have shown high genetic diversity among all these strains and a large number of identified recombinants [10, 22-25]. The strains are distinguished due to symptoms of infection they cause in vegetable beans with various combinations of seven currently known resistance genes, a single, the main dominant strain-nonspecific gene *I* and six strain-specific recessive genes *bc-u*, *bc-1*, *bc-1*^{2}, *bc-2*, *bc-2*^{2}, and *bc-3* from four independent loci [17, 26, 27].

Breeding vegetable beans with multiple resistance to BCMV is a priority, since such varieties are resistant to various BCMV pathogroups [17, 26]. In order to pyramid genes conferring bean resistance to BCMV in beans, foreign scientists are increasingly combining the *I* and *bc*-3 genes via marker-assisted selection (MAS), which provides wider range of nonspecific protection [9, 28-31].

Alleles of the recessive genes *bc-1* and *bc-2* prevent the systemic spread of the virus. Their combination in plant genome, even in the absence of the dominant gene *I*, can be effective against many BCMV pathotypes. Transfer of resistance genes to susceptible genotypes using indirect selection under the control of DNA markers was performed for loci *I* [32, 33], *bc-3* [31], *bc-1²* [34, 35] *bc-1*, and *bc-u* [36]. For introduction of the resistance gene *I* into susceptible genotypes, the SW13 marker was used [28, 37-39]. SW13 and SBD5 were used in to pyramid the *bc-1²* and *I* genes in a susceptible genotype [35]. For the *bc-3* gene, markers ROC11 and SG6 have been developed, which can also be used in combinations with other markers [31, 40]. Thus, the SW13 marker is linked to the *I* gene, the SBD5 marker to the *bc-1²* gene, the ROC11 and SG6 markers indicate the presence and absence of the *bc-3* allele, respectively. In recent years, the recessive gene *bc-1²* conferring resistance to the most common BCMV and BCMNV pathotypes, the PG-1, PG-2, PG-3, and PG-5 has been involved in breeding programs [13, 34]. It should be noted that molecular methods for marking *R*-genes are deemed auxiliary. MAS application is successful when combined of requires a combination of molecular markers with classical phytopathological methods for assessing plant resistance to artificial and natural infections.

In Russia, bean crop breeding started in 1920 at the Gribovskaya Vegetable Breeding Experimental Station, the precursor of the Federal Research Center for Vegetable Growing (FRCVG). Over the past 100-year period, the breeders have created 45 varieties of beans, or 32% of the total assortment of the State Register of Breeding Achievements approved for use. Most of the previously created bean varieties are universal. In recent years, the creation of asparagus-type green beans that meet market requirements and are highly resistant to diseases is given a priority.

Because of climate change and uncontrolled import and logistics of virus-infected seeds, BCMV was noticed in the more northern regions of the Non-Black Earth Zone and Western Siberia of the Russian Federation [41-45]. After the first epiphytoty in the Moscow region registered in 2014-2015, a local study of the BCMV biology have been initiated in which *Ph. vulgaris* accessions from extensive Genetic collection of the Federal Research Center for Vegetable Growing were involved.

This paper is the first report on BCMV isolates affecting beans in the Moscow region, and on climatic factors influencing the severity of the infection. BCMV resistance of a wide variety of plant beans has been assessed using molecular markers. New genetic sources of bean resistance to BCMV have been identified and involved in breeding programs. The reported DNA marker-based screening of the gene pool of domestic beans for BCMV resistance is the first in the Russian Federation.

The work aimed to search for sources of resistance to bean common mosaic virus (BCMV) to involve these donor cultivars in common bean breeding for asparagus-type with a desirable combination of characteristics.

Materials and methods. Vegetable bean cultivars of different origin, mostly from the USA, the Netherlands, Germany, and the Russian Federation, including cultivars bred at FRCVG were screened for BCMV infection (207 accessions of the FRCVG collection, 45-60 plants per accession, the Federal Research Center for Vegetable Growing, Moscow Province, 2014-2019). Bean common mosaic virus was isolated from the infected plants.

BCMV was detected in plant leaves by sandwich enzyme-linked immunosorbent assay (ELISA Reagent Set for Bean common mosaic virus, Agdia, Inc., USA). The extinction coefficients were recorded (a semi-automatic Stat Fax® 2100 microplate reader, Awareness Technology, Inc., USA, λ = 480 nm). ImmunoStrip® express test (Agdia, Inc., USA) was used to avoid mixed infection with other plant viruses, in particular *Cucumber mosaic virus* (CMV) and *Tobacco mosaic virus* (TMV) causing symptoms similar to BCMV.

To describe symptoms of BCMV infection and assess phenotypic resistance to BCMV in 30 promising bean accessions, pea (*Pisum sativum* L.) variety Zhegalovets plants and bean (*Phaseolus vulgaris* L.) variety Gribovskaya 92 plants were artificially infected with BCMV (a film greenhouse, ten plants of each cultivar in 3 replicates). Seeds were sown in the third decade of April when the average daily temperature in the greenhouse was 20-22 °C, and in the first decade of June when the average daily temperature was 26-29 °C. At the primordial leaf phase plants were inoculated by rubbing crude juice from leaves of the infected plant in 0.1 M phosphate buffer (pH 7.0) with carborundum, as per Mills et al. [46]. The viral infection was confirmed visually and by ELISA test.

In 2014-2019, the accessions were grown in the field (Moscow Province, Odintsovsky District) under natural infection conditions. A scheme of randomized plots allowed plants of each accession to have approximately the same chance to be infected. The severity of viral infection was assessed visually according to a modified scale where 0 means no symptoms on leaves, 0.5 means weak symptoms on some leaves, 1 means less than 10% leaves affected, 2 points stand for 10-30% affected, 3 points for 30-50%, and 4 points mean that more than 50% of the entire leaf surface of the plant is affected. The BCMV resistance of accessions was assessed by the prevalence (disease incidence) P (%), lesion index I (an average score), and disease severity R (%). The estimates were recorded 3 times, at the third true leaves, flowering and technical ripeness. The aggregated estimates were used to differentiate the accessions in susceptibility to BCMV and stability of manifestation of the infection. The accessions were deemed resistant at $R = 0$, relatively stable at $0 < R \leq 10\%$, weakly susceptible at $10 < R \leq 25\%$, and susceptible at $R > 25\%$. The accessions in group I had no signs of lesion, in group II, symptoms of BCMV infection appeared only in the years of epiphytoties, in group III, symptoms were unstable in different years, and in group IV, stable BCMV lesion occurred in all years of investigation.

During the growing season, the valuable traits of the accessions were assessed [47, 48]. Promising accessions were identified based on complex breeding values by accounting for all studied traits.

Among the accessions involved in field trials in 2014-2019, 30 most promising, with varying degrees and stability of field resistance to BCMV, were selected and screened for genes *I*, *bc-1*^{2}, and *bc-3* to reveal donor cultivars for breeding BCMV resistant common bean varieties. In PCR analysis, markers SW13, SBD5, and ROC11 were used.

Tissues of young leaves of individual plants were disrupted in 200 µl CTAB buffer (a ball mill TissueLyser II, Qiagen, Germany) at 26 Hz (1560 oscillations/min) for 1.7 min to a suspension followed by addition of 15 µl of proteinase K. DNA extraction by CTAB method was performed using a set of Sorb-GMO-B reagents (OOO Syntol, Russia) according to the manufacturer's protocol. The final purity and total DNA concentration were determined spectrophotometrically (a Smart Spec Plus, Bio-Rad, USA) ($OD_{260/280}$ = 1.6-1.8 corre-

sponded to a pure DNA preparation).

For 25 µl PCR, 2.5 µl of 10× PCR buffer, 2.5 mM $MgCl_2$, 0.25 mM individual dNTPs, 0.3 µM of each primer, 1.5 U SynTaq polymerase (Syntol LLC, Russia), and 50 ng of individual DNA template were mixed. The primer sequences for the three resistance markers were taken from Hegay et al. [49]: for SW13, the forward primer 5′-CACAGCGACATTAATTTTCCTTTC-3′, the reverse primer 5′-CACAGCGACAGGGGAGCTTATTA-3′; for SBD5, the forward primer 5′-GTGCGGAGAGGCCATCCATTGGTG-3′, the reverse primer 5′-GTGCGGAGAGTTTCAGTGTTGACA-3′; for ROC11, the forward primer 5′-CCAATTCTCTTTCACTTGTAACC-3′, the reverse primer 5′-GCATGTTCCAGCAAACC-3′. PCR was run according to the following program: 2-5 min at 95 °C (initial denaturation); 30 s at 95 °C (denaturation), 30 s at 59 °C, 64.6 °C, and 53 °C (annealed for SW13, SBD5, and ROC11, respectively), 30 s at 72 °C (elation) (35 cycles); 7 min at 72 °C (final elongation) (a C1000 Touch Thermal Cycler, Bio-Rad, USA) The primer annealing temperature was adjusted so that clear single and reproducible fragments were obtained.

Amplification products were separated in 1.7% agarose gel in 0.5× TBE buffer (a Wide Mini-Sub Cell GT horizontal electrophoresis chamber, Bio-Rad, USA). The resulting gels were stained with ethidium bromide and photographed (a ChemiDoc XRS + system, Bio-Rad, USA) followed by image processing (ImageLab software, Bio-Rad, USA). The sizes of the amplified fragments were determined using the GeneRuler100 bp Plus DNA Ladder molecular weight marker (Thermo Fisher Scientific, Inc., USA).

Data were processed using LightCycler® 480 SW 1.5.1 software (Roche Molecular Systems, Inc., USA) and Microsoft Excel 2010. Mean values (*M*), their standard deviations (±SD) and standard mean error (±SEM), the level of significance of differences (p) was assessed, regression, variance, correlation analysis, and Chi-square goodness-of-fit test ($\chi 2$) were performed [51].

Results. The origin of the common bean samples used in the work is shown in Figure 1.

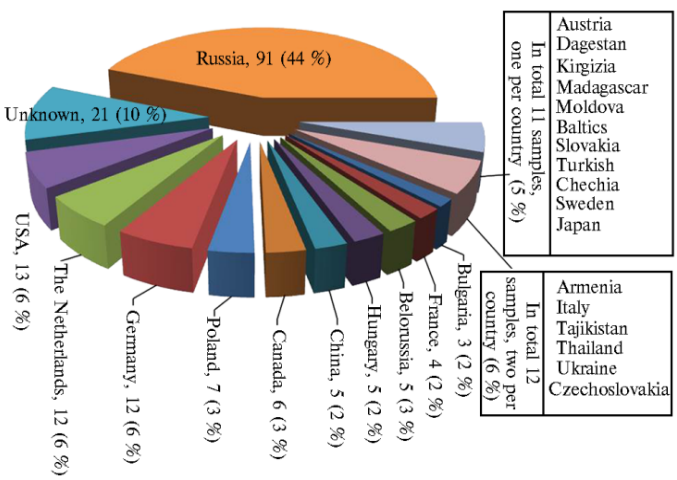

Fig. 1. Origin and number of common bean (*Phaseolus vulgaris* L.) cultivars tested for resistance to Bean common mosaic virus (Genetic collection of the Federal Research Center for Vegetable Growing).

The weather conditions in the years of research differed significantly in the combination of the main climatic factors over growing seasons (Fig. 2), which influenced incidence and severity of the BCMV infection damage.

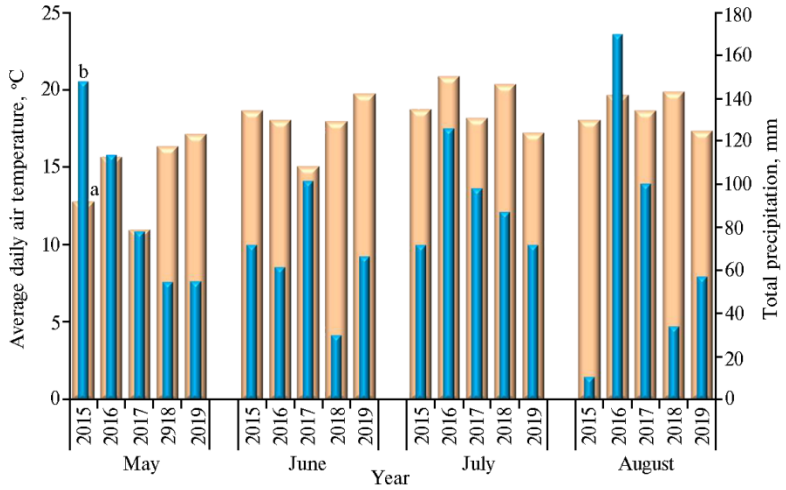

Fig. 2. Average daily air temperature (a) **and total precipitation** (b) **over the years of investigation** (Moscow Province, Odintsovsky District).

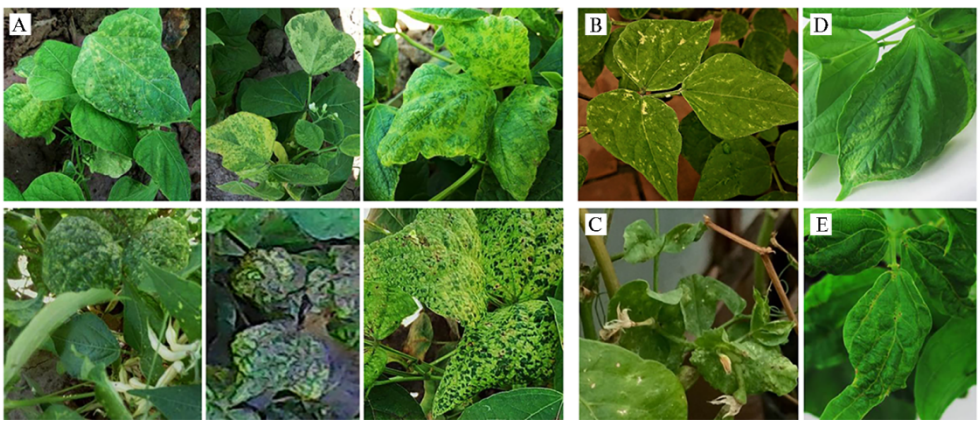

Fig. 3. Symptoms of Bean common mosaic virus (BCMV) **infection in naturally infected common bean (*Phaseolus vulgaris* L.) plants** (A) (Genetic collection of the Federal Research Center for Vegetable Growing, Moscow Province, Odintsovsky District, field surveys, 2014-2019), **and in inoculated test plants of Gribovskaya 92 bean cultivar** (B, C) **and pea (*Pisum sativum* L.) Zhegalovets cultivar** (D, E) (a greenhouse, 2015-2016).

In the Moscow region, bean plants infected by BCMV had typical symptoms of dark green or light green mosaic and leaf deformation (wrinkling and twisting) (Fig. 3, A). ELISA test confirmed the presence of BCMV in plants with different scores of lesions.

In biotests, at temperatures below 26 °C, inoculation with the Moscow BCMV isolate caused weak mosaic of young bean plants. During vegetative phase, a latent (asymptomatic) course of the disease was also noted. However, BCMV had a notable effect on the development of reproductive organs thus reducing plant productivity. At elevated air temperatures (26-29 °C), symptoms typical for BCMV (dark green mosaic, leaf twisting or wrinkling) appeared on susceptible adult plants of Gribovskaya 92 variety followed by leaf necrosis (see Fig. 3, B, C). At the early development, plants of vegetable pea variety Zhegalovets had no symptoms, but, prior the plants entered the flowering stage, a mosaic appeared with subsequent necrosis (see Fig. 3, D, E).

Annual monitoring revealed a significantly increased BCMV prevalence in the Moscow region, starting from 2014. In 2015, 2016 and 2019, the disease

reached epiphytotic levels. The maximum number of affected accessions (90% of the total) was noted in 2016. In 2015 and 2019, the proportion was about 50%. The disease prevalence in these years exceeded the threshold of harmfulness, averaging more than 30% of plants with symptoms of damage (34% in 2015, 81% in 2016, and 36% in 2019), with the highest average damage index (2.7 points) registered in 2019.

In 2017 and 2018, there was a sharp decline in the disease incidence and harmfulness. The prevalence did not exceed 10%, the affected accessions amounted to 22 and 13%, respectively, however, the infectious load in 2018 was higher and the lesion index averaged 2.2 points, whereas in 2017 it was less than 1.0 points (Table 1).

1. Characterization of Bean common mosaic virus (BCMV) **infection of common bean (*Phaseolus vulgaris* L.) accessions in the years of investigation** (Genetic collection of the Federal Research Center for Vegetable Growing, field tests, Moscow Province, Odintsovsky District)

Parameters	Year and a sample							
	2016		2017		2018		2019	
	A	B	A	B	A	B	A	B
Infection parameters and loads								
P, %	81	90	9	42	4	33	36	54
I, points	2,2	2,5	0,2	0,9	0,3	2,2	1,0	2,7
R, %	51	57	2	12	2	18	15	40
Proportion of total number of cultivars, %								
Without symptoms	9		78		87		48	
With symptoms	91		22		13		52	
including:			22		13		52	
0 < R < 10%	4		9		6		6	
R = 10-25%	9		11		4		24	
R > 25%	78		1		3		22	

Note. A — the complete sample mean (for all accessions), B — the affected sample mean (infection load); P (%) — prevalence (disease incidence), I — lesion index (an average score), and R (%) — disease severity.

The development of any disease in a specific cultivation zone is known to depend on plant resistance and the environmental conditions. A five-year study of a constant set of accessions revealed a more significant role of weather conditions in BCMV spreading and harmfulness in the Moscow region. Two-way ANOVA showed the 41% contribution of the climatic factor to total variability of the disease development (the aggregate indicator R), with only 17% for the genotype. Moreover, the weather conditions of the year to a greater extent determined BCMV prevalence (73%) as compared to severity (50%).

Based on the effect of climatic factors on BCMV infection, combinations of favorable and unfavorable conditions for the disease development the Moscow region were revealed. The dependences between the average values P and I, on the one hand, and the average daily air temperature (T, °C) and the amount of precipitation ($\sum p$), on the other hand, for each month of the growing season had a complex character and were described by polynomial functions of second and third orders (Fig. 4). However, a number of patterns could be identified. Moderate rainfall together with moderate temperatures in the first half of the growing season ($\sum p \sim 110$ mm, T ~ 15-16 °C in May, $\sum p \sim 70$ mm, T ~ 18 °C in June) and heavy rainfall combined with increased daily air temperatures in the second half ($\sum p > 120$ mm, T > 20 °C) facilitated intensive spread of the virus on bean crops. Decreased precipitation during all periods of plant growth in combination with higher temperatures ($\sum p < 60$ mm, T > 16 °C in May, $\sum p < 70$ mm, T > 18 °C in June, $\sum p < 85$ mm, T > 20 °C in July, and $\sum p < 60$ mm, T > 19 °C in July) as a whole restrained the pathogen spread. However, this combination of factors contributed to more apparent symptoms of

the virus affecting leaves, especially in early growth (see Fig. 4). Thus, a high score of BCMV lesion was noted in years with May average daily temperatures of 16-18 °C and minimum amount of precipitation (2018 and 2019), or with June air temperature of 18-20 °C and moderate rains (2016 and 2019). In the second half of the growing season, the combination of contributing factors was less apparent. It was both cool (T ~ 17.2 °C) and dry ($\sum p$ ~ 72 mm) weather in July 2019 (as compare to average annual rates of 18.8 °C and 81.6 mm), and elevated temperatures (T > 20 °C) with heavy precipitation (Σ~87-126 mm) in 2016 and 2018.

Dry and hot weather in certain periods, mainly in the middle of the growing season, could decrease lesion intensity in relatively stable accessions, as it was in 2015, 2017, and 2019. In 2019, clear symptoms of BCMV lesion appeared in 52% of samples at the beginning of growth (early June), in 36% at the beginning of fruiting, in mid-July when the weather was hot and dry, and in 47% after a cold snap at the end of the growing season. These results are consistent with the observed "masking" of symptoms due to high temperatures. [6, 22]. Therefore, the BCMV infection should be assessed at least twice, in the first and second half of the growing season, and it is the maximum seasonal values of P and I that should be used to rank the BCMV resistance of the sample.

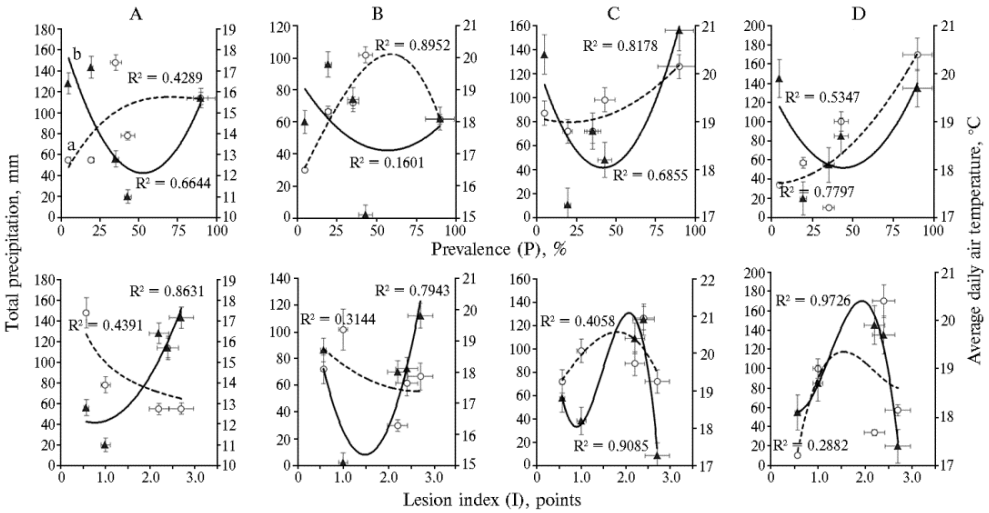

Fig. 4. A relationship between parameters ($M \pm SD$) **of Bean common mosaic virus** (BCMV) **infection of common bean (*Phaseolus vulgaris* L.) plants and climatic conditions** (the complete sample of accessions, Genetic collection of the Federal Research Center for Vegetable Growing)**:** A — May, B — June, C — July, D — August; a, b — polynomial functions of incidence and severity of BCMV infection plotted against the average daily air temperature (°C, triangles) and the total amount of precipitation (mm, circles) (Moscow Province, Odintsovsky District, 2015-2019).

Stability of plant viral resistance in years varying in combination of environmental factors and natural infectious loads should be accounted in searching for sources of resistance. According to this criterion, the collection samples were divided into four groups of stability (Table 2).

The accessions of group I had no BCMV symptoms in all years of investigation. The resistant forms constituted 6% of the complete sample. Most of them were varieties of domestic selection: Zabava (Russia, VIR k-15356), Izunrudnaya (Russia, VIR k-15593), Khavskaya universalnaya (Russia), Mulatka (Russia), Local vegetable beans (Russia, VIR k-15673), Zolotoi nectar (Russia), Zapadnaya Sibir (Russia), Oktava (Belarus), Ryabushka (Russia), Zit 551 RS (the Neth-

erlands, VIR k-15375), Cade 128 (the Netherlands, VIR k-15261), and Alice Sunshine (USA, VIR k-15599).

Susceptible cultivars (group IV, 2% of the complete sample) were stably infected by the virus regardless of the conditions of the year. These were Kirgizskaya Sakharnaya (Kyrgyzstan), Kustovaya (Russia), Zatus (Poland), and Gribovskaya 92 (Russia, VIR k-12200). The prevalence of BCMV in this group averaged 78% over four years (an average lesion index of 2.5 points) and reached 100% in the epiphytotic years (an average lesion index of 3-4 points).

2. Stability of resistance of common bean (*Phaseolus vulgaris* L.) accessions to Bean common mosaic virus (BCMV) (Genetic collection of the Federal Research Center for Vegetable Growing, field tests, Moscow Province, Odintsovsky District, 2015-2019)

Parameters	Stability group				LSD_{05}
	I	II	III	IV	
Averaged infection parameters					
P, %	0	26 (0-100)	38 (0-100)	78 (1-100)	9
I, points	0	0.8 (0-2.6)	1.2 (0-4.0)	2.5 (0.5-4.0)	0.3
R, %	0	17	21	45	6
Proportion of total number of cultivars, %					
Without symptoms	6	0	0	0	6
With symptoms	0	62	30	2	94
including:					
0 < R < 10 %	0	14	1	0	15
R = 10-25 %	0	41	7	1	49
R > 25 %	0	7	22	1	30

Note. I — no symptoms, II — symptoms appeared only in the epiphytotic years, III — unstable symptoms over years, IV — stable lesion occurred in all years of investigations (the range of variation of the indicator between years and samples within a group is indicated in brackets, min-max,); P (%) — prevalence (disease incidence), I — lesion index (an average score), and R (%) — disease severity.

In the largest group II, BCMV infection was recorded in the epiphytotic years 2016 and 2019, with 30% accessions affected in both years, 61% in 2016, and 9% in 2019. Group III showed unstable BCMV resistance. Viral symptoms appeared regardless of the year, including years when the infectious load was low (in 2017 and 2018).

It is worth noting that the four-year mean values of prevalence and lesion indexes in group III were significantly higher compared to group II ($\chi 2 = 3.8$ at $p = 0.05$ and $\chi 2 = 6.6$ at $p = 0.01$, respectively) due to the greater proportion of accessions with R > 25% (see Table 2). However, the average values for 2016 and 2019 indicated that approximately 1% and 4% of the complete sample (in group II and group III, respectively) were highly susceptible to BCMV (R > 75%) during epiphytoties. That is, only in epiphytotic years, it is possible to correctly assess the resistance to BCMV, provided that the combinations of weather conditions in these years differ. Indicators averaged even over several years do not provide reliable estimates. This should be taken into account when selecting valuable samples. In the years with a low infectious load, only negative selection (i.e. culling of susceptible specimens) must be applied.

Primers to the SW13 marker closely linked to the dominant gene *I* generated a 690 bp PCR amplification product, as described [50]. Primers to the SBD5 marker gave a 1300 bp PCR amplification product, indicating the *bc-1²* gene [28, 39]. Primers to the ROC11 marker linked to the *bc-3* gene amplified DNA fragments of 300 bp, whereas in earlier studies it was noted that the size of the product should reach 420 bp [31, 40]. However, other researchers also found deviations in the size of the amplified PCR product when working with this marker [52]. Genetic marking of three resistance genes, *I*, *bc-1²*, and *bc-3* revealed the *bc-3* gene in most of the 30 studied accessions (Table 3).

3. DNA marking of *R*-genes of common bean (*Phaseolus vulgaris* L.) accessions (Genetic collection of the Federal Research Center for Vegetable Growing) **different in stability and field resistance to Bean common mosaic virus** (BCMV)

Stability group	Accessions	Disease severity R, %	Marker (gene)			Extinction coefficient
			SW13 (*I*)	SBD5 (*bc-1²*)	ROC11 (*bc-3*)	
I	Cade 128	0	+	+	+	0
	SP-232	0	–	+	+	0
	Khavskaya universalnaya	0	–	+	+	0
II	Vestochka	2,5	–	+	+	0.115
	Rant	2,9	–	+	+	0.118
	Kit-79	3,3	+	+	+	nt
	Veritsa	7,7	+	+	+	nt
	KP-84	10,7	+	+	+	nt
	Fatima	13,5	+	+	–	0.115
	Montdor	14,0	–	+	+	0.100
	Purpurnaya	20,7	+	+	+	nt
	Holberg	23,3	+	–	–	0.281
	Poroto Evestad	30,0	–	+	+	0.280
	Arion	31,7	+	+	+	nt
	Niagara 776	37,2	+	–	+	0.352
III	SP-164	4,0	–	+	+	nt
	SP-220	5,0	+	+	+	nt
	Zolushka	6,0	–	+	+	0.112
	MBZ 556	11,1	–	–	–	0.250
	Sparzhevaya	11,7	–	+	+	0.114
	Secunda	12,3	–	+	+	0.230
	Rubin	16,2	–	+	+	nt
	Pluto	17,7	+	+	+	0.114
	Kentuky Wander	19,3	–	+	+	nt
	Dilano	20,7	+	+	+	nt
	Rannyaya voskovaya	25,0	+	+	+	nt
IV	Lika	7,8	–	+	+	0.114
	Kustovaya	17,1	–	+	+	0.240
	gribovskaya 92	52,1	–	–	–	0.561

Note. I — no symptoms, II — symptoms appeared only in the epiphytotic years, III — unstable symptoms over years, IV — stable lesion occurred in all years of investigations; nt — not tested. The extinction coefficient is given according to the ELISA test performed to confirm the presence of BCMV in the specimens.

In lab tests, on day 14 after inoculation of 30 promising accessions of various origin with BCMV, typical symptoms (mosaic and leaf deformation) appeared only in plants lacking resistance genes *I* and *bc-1²*. In genotypes harboring these genes, depending on their combination, a hypersensitivity-like response occurred as punctate dry necrosis, yellowing and wilting of infected leaves. Moreover, the gene *I* enhanced wilting which proceeded faster, and on day 10, the infected leaves were practically dry and easily separated from the plant. This was confirmed by significant correlation coefficients between the presence of the gene *I* and the scoring of leaf wilting, *r* from +0.64 to +0.74 depending on the gene combinations. The *bc-1²* in the genome, even in the absence of gene *I*, prevented wrinkling (*r* from –0.59 to –0.73), and reduced the number of necrosis along the veins (r from –0.35 to –0.53).

When comparing the data of field and lab resistance tests, a negative relationship was traced between the degree of BCMV field harmfulness and the intensity of leaf yellowing in seedlings (*r* from –0.52 to –0.85, depending on the gene combinations), as well as a positive relationship with wrinkling (*r* from +0.69 to +0.72). However, we did not reveal a consistently close relationship between the presence of one or another resistance gene and the field resistance of genotypes in different years. Depending on the intensity of the infectious load, it varied from weak to medium or was absent. In some years, there was a relationship between the average score of plant damage and the genes *I* (r from –0.33 to –0.71) and *bc-1²* (*r* from –0.35 to –0.57). Analysis of the average parameters of BCMV infection over all the years of investigation using $\chi 2$ test revealed a significant effect of only the *bc-1²* gene on the field resistance of vege-

table beans in the Moscow region (Table 4).

For all correlation coefficients we obtained, $r_{critical} = 0.36$ at $p = 0.05$.

4. Chi-square-based correspondence between *R*-genes of resistance to Bean common mosaic virus (BCMV) **and field susceptibility to BCMV common bean (*Phaseolus vulgaris* L.) accessions** (Genetic collection of the Federal Research Center for Vegetable Growing, Moscow Province, Odintsovsky District, 2016-2019)

Parameters	*I*	*bc-1²*	*bc-3*	*I* + *bc-1²*	*I* + *bc-1²* + *bc-3*
Number of degrees of freedom	3	3	3	6	8
$\chi^2_{fact.}$ value	0,312	8,334	3,111	10,437	14,844
$\chi^2_{crit.}$ at $p < 0.05$	7,815	7,815	7,815	12,592	15,507
Correspondence at p level	Not found $p = 0.958$	Found $p = 0.040$	Not found $p = 0.375$	Not found $p = 0.475$	Not found $p = 0.875$

Nevertheless, analysis of various combinations of *I*, *bc-1²*, and *bc-3* genes with respect to BCMV infection severity (R) clearly indicates that the resistant forms, which showed no signs of BCMV infection during epiphytoty of 2019, can only be detected among genotypes +/+/+ and –/+/+ (Fig. 5, A, B). They amounted to 40 and 13%, respectively, which confirms the data available in the literature on the enhanced protective functions in plants with a combination of resistance genes *I* and *bc-1²*, although not in all cases this combination guarantees 100% efficiency. In half of the accessions tested, the infection severity was lower (R < 10%); 10% of +/+/+ genotypes and 33% of –/+/+ genotypes showed moderate resistance (R = 10-25%). In the absence of the *bc-3*, combinations +/+/– and +/–/– conferred little field protection. These genotypes turned out to be moderately susceptible, and in the absence of all resistance genes genotypes were moderately and highly susceptible to BCMV.

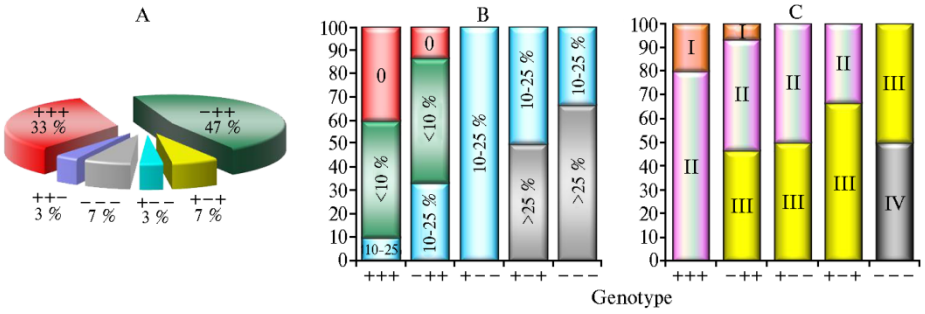

Fig. 5. Combinations of genes *I*, *bc-1²*, and *bc-3* ("+" for presence, "—" for absence the gene) **among 30 promising genotypes of common bean (*Phaseolus vulgaris* L.)** (Genetic collection of the Federal Research Center for Vegetable Growing) (A)**, and their distribution with respect to severity of Bean common mosaic virus** (BCMV) **infection** (R) **in 2019** (B) **and BCMV resistance stability in 2016-2019 in field conditions** (C)**:** R = 0 — resistant, 0 < R ≤ 10 % — relatively resistant, 10 < R ≤ 25 % — low-susceptible, R > 25 % — susceptible; I — no symptoms, II — symptoms appeared only in the epiphytotic years, III — unstable symptoms over years, IV — stable lesion occurred in all years of investigations (Moscow Province, Odintsovsky District).

Involvement of nonspecific resistance genes *I* and *bc-3* in breeding programs worldwide resulted in the emergence of new BCMV strains that overcoming plant resistance that these genes confer, also, the closely related BCMNV virus is spreading which affects BCMV-resistant varieties [9, 22]. In 2018, Feng et al. [22] showed that the use of the recessive resistance genes *bc-1* and *bc-2*, alone or in combination (even without the dominant gene I) is effective in breeding for resistance to a number of BCMV pathotypes. These genes do not affect replication and cell-to-cell movement of the virus, but they affect its systemic spread. We have found that a particular combination of genes does not always

5. Characterization of agronomically valuable genotypes of common bean (*Phaseolus vulgaris* L.) (Genetic collection of the Federal Research Center for Vegetable Growing) **resistant to Bean common mosaic virus** (BCMV) **in the conditions of Moscow region** (2016-2019 годы)

Name (origin)	A	B	C	Pods (technical maturity), *M*±SEM						Seeds (biological maturity), *M*±SEM			
				D	E	F	G	H	I	J	K	L	M
Resistant (group I)													
Izumrudnaya (Russia)	0	3	10.5±0.8	dg	0	12.5±1.2	0.9±0.1	0.85±0.07	90±4.1	w	4.5±0.2	250±14.5	20±1.5
Zapadnaya Sibir (Russia)	0	3	13.0±1.2	y	0	12.5±1.1	0.9±0.1	0.82±0.08	96±4.5	w	4.3±0.2	289±13.7	19±1.2
Zabava (Russia)	0	3	10.5±1.0	g	0-1	10.0±0.9	0.8±0.0	0.65±0.05	82±3.7	w	4.1±0.2	279±15.2	18±1.3
Khavskaya universalnaya (Russia)	0	3	10.1±0.9	g	0-1	9.8±0.8	1.0±0.1	0.90±0.07	82±3.4	w	3.9±0.2	235±13.4	15±1.1
Mulatks (Russia)	0	2	14.5±1.3	v	0-1	13.5±1.2	1.0±0.1	0.85±0.06	91±3.6	lb	5.1±0.3	302±17.5	26±2.1
Oktava (Belarus)	0	2	11.5±0.9	g	0	13.8±1.2	1.4±0.1	1.05±0.09	95±3.9	bl	4.4±0.2	204±12.3	16±1.3
Ryabushka (Russia)	0	3	10.5±0.8	y	0-1	14.2±1.3	1.5±0.1	0.70±0.05	71±3.2	bl	4.3±0.2	250±15.4	15±1.2
Zit 551 RS (the Netherlands)	0	3	11.5±0.8	g	0-1	9.5±0.7	1.3±0.1	0.80±0.04	74±3.5	w	3.9±0.2	260±17.5	14±1.1
Cade 128 (the Netherlands)	0	4	14.5±1.2	g	0-1	9.5±0.8	0.9±0.1	0.65±0.04	80±4.1	w	3.7±0.2	271±12.7	16±1.3
Zolotoi nektar[c] (Russia)	0	5	9.5±0.7	g	0	17.4±1.5	1.4±0.1	0.85±0.05	178±9.5	w	5.5±0.3	284±13.8	34±2.7
Fasol mestnaya ovoshchnaya[c] (Russia)	0	5	11.5±0.8	g	0-1	10.5±0.8	0.8±0.1	0.70±0.03	160±8.7	w	5.3±0.2	207±9.7	22±1.4
Relatively resistant (groups II and III)													
Zinuly (Belarus)	5.6	3	12.2±0.9	g	0	10.5±0.8	1.0±0.1	0.93±0.08	74±4.1	w	3.8±0.2	337±18.3	15±0.9
Bertires (the Netherlands)	0.6	3	9.5±0.7	g	0-1	9.5±0.7	0.8±0.1	0.75±0.06	88±4.7	w	4.1±0.2	285±15.9	15±1.0
Fanacnos (Poland)	2.0	5	10.5±0.8	g	0-1	9.5±0.8	1.0±0.1	0.76±0.05	74±4.5	w	3.9±0.2	275±14.3	13±0.8
Верица (Bulgaria)	9.7	3	10.5±0.9	g	0-1	9.5±0.7	1.1±0.1	0.70±0.04	75±4.3	w	3.9±0.2	319±16.4	19±1.1
Purpiat (Poland)	8.8	2	13.5±1.1	v	0-1	10.5±0.7	1.3±0.1	0.72±0.04	92±5.1	b	3.9±0.2	427±17.2	18±1.0
Kit-№ 79 (China)	6.1	2	17.5±1.3	g	0-1	15.5±0.9	1.3±0.1	0.95±0.07	115±6.7	bl	4.9±0.2	367±15.8	29±2.2

Note. A — BCMV resistance (R, %); B — ripening groups (2 — precocious, 3 — early-ripening, 4 — mid-early ripening, 5 — mid-ripening), C — lower pod attachment height, cm; D — color, E — stringiness, points; F — length, cm; G — width, cm; 3 — thickness, cm; H — yield, g per plant; I — color (dg — dark green, g — green, y — yellow, v — violet фиолетовая, w —white, lb — light brown, b — beige, bl — black); J — number per pod; K — 1000-seed weigh, g; L — yield, g per plant); [c] — climbing bean plants.

provide field resistance to the virus. The resistance stability of a cultivar in different years is influenced by climatic conditions which largely determine the physiological state of the plant, changing expression of *R*-genes responsible for the immune response and appearance of symptoms during infection. Both the dominant gene *I* combination with recessive genes *bc-1²* and *bc-3*, and the recessive combination without dominant gene provide high BCMV resistance. The Cade 128, SP-232, Veritsa, Kit-89, KP-84, Khavskaya universalnaya, Vestochka, and Rant cultivars and breeding samples of resistance stability groups I and (+/+/+ and –/+/+, see Fig. 5, B) are of practical interest for breeding.

When selecting the initial material for target selection, it is important that the samples have not only the necessary genes and high field resistance to the pathogen, but other economically important traits. From this point of view, relatively stable accessions (R < 10% in the epiphytotic years) from groups II and III, which possess a number of valuable characters, in addition to resistant forms from stability group I, are of interest. Among them, 17 accessions have the highest breeding value (Table 5).

Selection of parents for breeding commercial varieties for industrial cultivation are based on following characteristics: early maturity, stable yield, sugar beans, high technological parameters (Izumrudnaya, Khavskaya universalnaya, Oktava, Mulatka as genetic sources); high pod attachment, sugar beans, multiple resistance to diseases (Mulatka, Kit-№ 79, Purpiat, Cade 128); straight long sugar beans (Golden nectar, Mulatka, Ryabushka); suitability for freezing and canning (Octave, Mulatto, Emerald), as well as for some other characteristics

Among the farmers, beans of climbing type are in demand, which allow obtaining fresh young pods during growing season, or varieties of the determinant type but with a long season of pods picked repeatedly yield productions. From this point of view, the samples of interest are Zolotoi nectar, Kit-№ 79, Fasol mestnaya ovoshchnayac, and two varieties bred at FRCVG, Ulyasha and Malume (the latter of climbing type, was submitted for State testing in 2019). The most popular varieties bred at FRCVG are highly resistant to bacterial, fungal and viral diseases [43, 44], including BCMV. These are Mariinka, Svetlyachok, Kreolka, Rant, and Pagoda of groups II and III. In survey of crops of these varieties, severity of BCMV infection over the years averaged 10% at most. Possessing a complex of other economically valuable traits [53], these varieties can also be genetic sources of resistance to BCMV.

Thus, global climate change has intensified the spread of Bean common mosaic virus (BCMV) to the northern regions of the Russian Federation. In the Moscow region, the prevalence of the virus is more influenced by the amount of precipitation, and the lesion index by the air temperature. The BCMV epiphytoties were recorded in 2015, 2016, and 2019. In searching for genetic sources of BCMV resistance, combined estimates of a particular sample must be used. These are disease severity and resistance stability evaluated over several years with different combinations of weather conditions that determine BCMV infectious load. The $\chi 2$ test revealed a significant effect of the *bc-1²* gene on field resistance of bean plants to BCMV. In the local climatic conditions, genotypes *I/bc-1²/bc-3* and *–/bc-1²/bc-3* are of the greatest value as sources of *R*-genes. Seventeen most promising breeding samples of various origins, five varieties (Khavskaya universalnaya, Rant, Zolushka, Mariinka, and Svetlyachok), and two promising cultivars possessing a set of economically valuable traits (SP-232, KP-84, bred at FRCVG) are suggested as genetic sources for breeding asparagus-type beans highly resistant to BCMV.

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