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FEATURES OF *Lonicera caerulea* L. REPRODUCTIVE BIOLOGY

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Abstract

Blue-berried honeysuckle (*Lonicera caerulea* L. s. l.) of the Honeysuckle family (*Caprifoliaceae*) is a high-quality berry plant which has been actively cultivated in recent years in various countries with temperate climate. Blue-berried honeysuckle is valued for ultraearly fruit ripening, as well as high content of antiscorbutic vitamin and biologically active phenolic compounds with antioxdidant, immunomodulating, antibacterial, antiviral, antifungal, antiallergic and other activities widely used in medicine, cosmetic surgery, food industry and agriculture. Variation of reproductive ability of *L. caerulea* cultivars and selections in different conditions of introduction in Russia and abroad prevents realization of potential fruitfulness of industrial plantations. For the purpose of finding out possible causes of decrease in fruit set and weight, morphological full-value of pollen, self-fertilization and interpollination were assessed, self-incompatibility of this species cultivars was studied. Blue-berried honeysuckle cultivars of various ecological-geographical and genetic origin widespread in West Siberia and north-east China were studied, which belong to the subspecies *L. caerulea* subsp. *altaica* (Pall.) Gladkova (syn. *L. altaica* Pall.), *L. caerulea* subsp. *venulosa* (Maxim.) Worosh. (syn. *L. edulis* Turcz. ex Freyn), *L. caerulea* subsp. *kamtschatica* (Sevast.) Gladkova [syn. *L. kamtschatica* (Sevast.) Pojark., *L. caerulea* var. *kamtschatica* (Sevast.) Pojark.]. Self-pollination and interpollination of 8 honeysuckle cultivars (Salyut, Berel', Goluboe vereteno, Zolushka, Tomichka, Parabel'skaya, Pamyati Gidzyuka and Kamchadalka) were studied by data of field research in 1999-2002 on the experimental plot in Novosibirsk. Cytoembryologic research, including that of microsporogenesis products and possible meiosis disturbance of 19 honeysuckle cultivars, was conducted from 1999 to 2014. The results obtained showed a decrease in pollen fertility to 0.8 % connected with anomalies in meiosis. Significant variations in fruit set (0.9-64.0 %), weight and seed quantity were determined by the genetic control of self-incompatibility under self-pollination and in different variants of cross-pollination of blue-berried honeysuckle cultivars. As morphological manifestations of self-incompatibility, anomalies in growth of pollen tubes in style tissues after transpollination of closely related cultivars and autogamy were determined. The main causes of loss cultural plantations productivity of blue honeysuckle may be low pollen fertility in some cultivars *L. caerulea* subsp. *altaica* and partial self-incompatibility with the cross-pollination varieties due to their closely related origin. The cultivars for effective pollination of blue-berried honeysuckle plantations were selected (selection from different families). For varieties that are derived from the parent form Start — Goluboe vereteno, Sinyaya ptica, Lazurnaya, Zolushka, Gerda, Berel' best pollinators may be cultivars derived from the initial form of Del'fin — Tomichka, Parabel'skaya, Pamyati Gidzyuka, Vasyuganskaya, Narymskaya. It is necessary to include additional cultivars of pollinators when planting high-yielding varieties Barhat, Salyut, Berel' or new cultivars produced with their involvement which are characterized by low pollen fertility.

Keywords: *Lonicera caerulea*, pollen sterility, self-fertilization and interpollination cultivars, self-incompatibility, fruit set, seed production, pollen tubes

In recent decades, in temperate climate countries, the culture of blue-berried honeysuckle has been intensively developing (*Lonicera caerulea* L. s. l., *Caprifoliaceae*). The value of this species is due to early ripening, high content of vitamin C [1, 2] and biologically active phenolic compounds [3-5], which thanks to their antioxidant [6-8], immunomodulating [1], antibacterial [8], antiviral [1], antifungal [2], antiallergic and other activities [1] are widely used in medicine

[9], cosmetology, food industry and agriculture. In Russia, significant advances have been achieved in selection of blue honeysuckle. More than 100 varieties of *L. caerulea* have been entered in the State Register of Breeding Achievements Approved for Use.

A unique collection of blue-berried honeysuckle has been formed at the University of Saskatchewan (Canada), including 32 varieties of Russian selection, 50 species from nurseries and scientific institutions in North America and Russia, and original wild-type material collected during expedition scientific tours in Japan (Hokaido Island), Canada, the USA. Based on this collection, a group of outstanding varieties was created in Canada, including those suitable for mechanized harvest [10]. Marketable gardens of blue-berried honeysuckle (*L. caerulea* subsp. *emphyllocalyx*) have been established in Japan on Hokkaido since 1970 [11]. At present, internal production of honeysuckle in Japan is about 200 t/year (85 ha), the biology of this subspecies is being actively investigated [12]. Successful introduction of blue-berried honeysuckle is being implemented in the USA [13]. Numerous studies are underway in European countries, such as Poland [14-17], Czech Republic, Slovakia [9, 18], Romania [19], Estonia [20], Lithuania [21]. Significant progress has been made in the industrial cultivation of berries and their processing in China [22, 23]. For establishing industrial plantations of blue-berried honeysuckle in Heilongjiang Province, mainly Russian varieties are used, as well as seedlings of wild plant forms, such as *L. boczkarnikowae* Plekh. (syn. *L. regelyana* Boczkarn.), growing in the northeast of China [22], and *L. caerulea* subsp. *venulosa* (Maxim.) Worosh. (syn. *L. edulis* Turcz.ex Freyn.) from the natural populations of the Lesser Khingan mountain range.

Despite the interest of researchers to *L. caerulea*, there are almost no investigations on reproductive biology of this species. Lack of knowledge about the peculiarities of the biology of pollination and fertilization leads to grave mistakes in the implementation of programs for the wide introduction of a new culture into production. Our survey of nurseries in Heilongjiang Province, conducted in 2014, showed that only one variety of Russian selection breeds on an industrial scale, i.e. Berel', which was isolated based on a set of economically valuable signs in the collection plantations of several farms in the northeast of China. The analysis of data on the productivity of *L. caerulea* in Heilongjiang Province, as well as at various points of introduction in Russia [23, 24] revealed a wide range of variability in the reproductive capacity of varieties and selected forms of blue-berried honeysuckle.

The study of biological features of the productivity development in the *L. caerulea* varieties was conducted in 1994-2004 in the Central Siberian Botanical Garden of SB RAS (CSB, Novosibirsk, Russia). The findings have been partially published [25, 26], but the number of professionals dealing with blue-berried honeysuckle in Russia and abroad continues to increase. Therefore, consideration of the evidence on the biology of pollination of *L. caerulea*, obtained earlier and supplemented in recent years, remains relevant.

We were the first to establish that the reasons for the decline in productivity of the blue-berried honeysuckle cultivated crops are partial incompatibility in the cross pollination of varieties caused by their closely related origin and the low quality of pollen in some hybrids of *L. caerulea* subsp. *altaica*.

The aim of the present work was to identify possible reasons for the decrease in the potential productivity of blue-berried honeysuckle and choose the varieties for joint cultivation, and to achieve it, we evaluated male gametophyte fertility, self-sterility, interpollination, fruit weight and seed growing potential, and also investigated the incompatibility in the *Lonicera caerulea* L. varieties of various geographical and genetic origin.

Techniques. Studies were conducted in the Central Siberian Botanical Garden of SB RAS, in the forest-steppe zone of the south of Western Siberia, in a continental climate with a moderate supply of heat and moisture. We studied varieties and selected forms of blue-berried honeysuckle of different ecogeographical and genetic origin.

Field trials were conducted in 1999-2002. Pollen fertility, fruit set and weight and seed growing potential were assessed in self- and interpollination in 8 varieties (Salyut, Berel', Goluboe vereteno, Zolushka, Tomichka, Parabel'skaya, Pamyati Gidzyuka and Kamchadalka) of three subspecies with a tetraploid set of chromosomes ($2n$ = 36): *L. caerulea* subsp. *altaica* (Pall.) Gladkova (syn. *L. altaica* Pall.), *L. caerulea* subsp. *venulosa* (Maxim.) Worosh. (syn. *L. edulis* Turcz. ex Freyn), *L. caerulea* subsp. *kamtschatica* (Sevast.) Gladkova [syn. *L. kamtschatica* (Sevast.) Pojark., *L. caerulea* var. *kamtschatica* (Sevast.) Pojark.] [27]. Controls were variants obtained from natural open pollination. All variants of pollination were investigated in three replications on different plants of the same variety, choosing branches of the same age.

Honeysuckle forms compact inflorescences, consisting of two closely arranged flowers (double-flowered), the pollination of which gives one infructescence, that is why gauze coverings were used to isolate not individual flowers, but at least 100 double-flowered plants in each replication (under each gauze cage). The flowers were isolated 3-5 days before the beginning of flowering. Pollination was performed in the mass flowering phase 2-3 times under each gauze cage with an interval of 1-2 days. In the period of full maturation, the number of set fruits, the average weight of one fruit in each pollination option, the number of completed seeds and undeveloped ovules were recorded. The results were reported separately for each gauze cage. Pollen was harvested from colored yellow buds, dried under diffused light, tested for fertility and stored in a desiccator in glass vials until pollination [28].

In 1999-2014, in 19 varieties of blue-berried honeysuckle, pollen fertility was assessed by staining with acetocarmine [29, 30]. The results were recorded using the Primo Star light microscope (Carl Zeiss, Germany). The proportion of normal pollen grains from the total number of studied ones was determined.

The best pollinators were considered the varieties that provided the percentage of set fruit higher than in control, equal or close to it. Varieties that ensured setting of 50-70 % of the fruit as compared to control were allocated to a group of admissible pollinators. Varieties for which the setting of fruit was below 50 % vs. control were attributed to poor pollinators [28].

Observations of the growth of pollen tubes in pestle tissues in each pollination option were carried out by standard methods [32]. Pistil styles were recorded 6, 12, 24, 36 hours after pollination. The preparations of germinating honeysuckle pollen tubes were stained with fluorochrome (aniline blue). The preparations were analyzed using a ML-2B fluorescent microscope with the MFN-10 camera adapter (LOMO, Russia).

Mean (X) and standard error of the mean (S_x) were calculated using mathematical statistics [31] and the Microsoft Excel software package.

Results. Data on variety studied in the paper is presented in Table 1.

The success of fertilization largely depends on the viability of the pollen grains. The analysis of pollen fertility (1999-2014) showed its high morphological adequacy in varieties of the Kamchatka and Primorsky Krai origin. When stained with acetocarmine, pollen fertility in the *L. caerulea* subsp. *kamtschatica* samples averaged 96.2±1.5 % with a coefficient of variation (Cv) of 4.1 %. For the *L. caerulea* subsp. *venulosa* samples, fertility of pollen grains was 91.2±3.4 %, although there were more pronounced fluctuations by years

(Cv = 9.2 %).

1. The geographical and genetic origin of the *Lonicera caerulea* L. varieties used in the study

Name	Origin	Taxon
Goluboe vereteno Sinyaya ptitsa Zolushka Lazurnaya	Seedlings from open pollination of the selected form Start from the Kamchatskaya population	*L. caerulea* subsp. *kamtschatica* $2n = 36$
Gerda	A seedling from pollination of the Sinyaya ptitsa variety with a mix of pollen from a seedling of the wild blue-berried honeysuckle from the Kamchatskaya population	
Kamchadalka	A seedling from open pollination of the selected form from the Kamchatskaya population	
Salyut Galochka Sirius Barkhat	Seedlings of wild honeysuckle from the Rudnyi Altai (Eastern Kazakhstan, Leninogorsk district)	*L. caerulea* subsp. *Altaica* $2n = 36$
Ognenny opal Selena	Seedlings from open pollination of the selected form of honeysuckle from the Rudnyi Altai	
Berel'	A seedling from pollination of the selected form № 12-19 (Sirius) from the Rudnyi Altai with a mixture of pollen taken from the Goluboe vereteno, Sinyaya ptitsa and Lazurnaya varieties	*L. caerulea* subsp. *altaica* × *L. caerulea* subsp. *Kamtschatica* $2n = 36$
Bakcharskaya	A seedling from open pollination of the selected form № 15-63 from Primorsky Krai	*L. caerulea subsp. Venulosa* $2n = 36$
Tomichka Pamyati Gidzyuka Narymskaya Vasyuganskaya Parabel'skaya	Seedlings from open pollination of the selected form № 68-2 (Del'fin) of a seedling of wild honeysuckle from the Dalnegorsky district of Primorsky Krai	

Significant variability in pollen fertility (0.8 to 98.6 %, Cv = 67.2 %) was observed in the varieties of the Altaic origin and a hybrid obtained with their participation (Berel'). A large number of defective pollen grains were found during the investigation of pollen in the Galochka, Sirius, Barkhat, Salyut and Berel' varieties. A high quality of pollen, which did not depend on growing conditions, was typical for the Ognenny Opal (91.6 to 97.5 %) and Selena (87.3-96.6 %) varieties. The Berel', Salyut, Sirius, Galochka and Barkhat varieties also had very poor pollen productivity, i.e. a low number of microspores was formed. In the samples of the Sirius and Barkhat variety, most of the anthers did not contain microspores. Both on ready-to-open and fully opened flowers, most of the anthers were green and sluggish.

In our additional studies [33], these samples showed numerous abnormalities at different stages of meiosis, which could lead to low fertility of the pollen grains. Reduced fertility of pollen grains was also observed in hybrids obtained with the participation of these varieties [34]. Among the hybrids in which the Berel' and Salyut varieties were used as female parents, samples were found with a high-fertile (up to 97 %) and low-fertile (down to 2-37 %) pollen. At the same time in hybrid families, where the low-fertile variety acted as a paternal form, all seedlings showed high fertility of pollen. This indicates a probable inheritance of the sterility of the pollen grains along the maternal line and the need for mandatory quality control of pollen in selection work, as well as when choosing pollinators for joint cultivation in the blue-berried honeysuckle farm-scale plantations.

Many researchers devoted their investigations to self-incompatibility in blue-berried honeysuckle [35-37]. It has been established that the samples of this species belong to self-sterile plants, and when they are forced to self-pollination within the clone, the fruits are not set at all, and instead fruits with uncompleted seeds with low germination or small seedless fruits are set. Self-incompatibility in the representatives of *L. caerulea* is manifested by stopping the growth of pollen tubes in the lower half of the pistil style [38]. Taking into account the results given in other papers [39, 40], we may suggest a gametophytic type of incompatibility reaction in *L. caerulea*. Self-incompatibility directly affects the productivity, because it serves as the basis for genetic control of sexual reproduction of plants [41, 42]. Single-variety plantings, as well as unfavorable weather conditions during flowering and fruit ripening, which hamper interpollination by insects, are responsible for almost complete infertility. In this regard, it is necessary to study specifically the degree of self-sterility and, for introduction, select forms with the greatest manifestation of self-fertility in the genotype for further consolidation of this trait in the offspring by methods of selection.

The samples of *L. saerulea* we studied appeared to be virtually self-fertile. After forced self-pollination of flowers, the formation of 0.9 to 10.5 % of fruits was observed (Table 2). The Kamchadalka, Goluboe vereteno, Parabel'skaya and Pamyati Gidzyuka varieties were characterized by the highest degree of self-fertility; in certain years, during self-pollination, the set of fruit in these cultivars was 20.0, 15.9, 15.6 and 15.2 %, respectively [43]. The Salyut and Berel' varieties, obtained based on the samples from Altai, as well as the Zolushka variety of the Kamchatka origin, had a low degree of self-fertility. In most varieties, the formation of a small number of fruits after self-pollination was observed. During the period from flowering to ripening, they slightly increased in size, reaching $^1/_3$-$^1/_2$ of the weight of fruits obtained from interpollination. With the onset of the mass ripening, the fruits acquired a typical moderately blue color. The analysis of seed productivity showed that they were seedless to a greater degree (Table 3). The set seeds failed to germinate and produce plants.

2. The set of fruit in the blue-berried honeysuckle (*Lonicera caerulea* L.) plants of different varieties depending on the pollinating variety (X±S_x, Novosibirsk, 1999-2002)

Pollinated variety	Pollinating variety 1	2	3	4	5	6	7	8	Control
Berel'	0.9±0.76	39.6±2.89	24.5±5.34	29.6±4.70	36.2±3.21	29.6±5.25	26.7±5.09	44.6±1.82[a]	59.0±1.55
	1.5	67.1	41.5	50.2	61.7	50.5	45.6	75.7[a]	
Goluboe	23.3±4.05	9.3±2.01	28.9±8.26	39.0±3.86	41.0±7.66	39.5±8.46	11.4±3.64	41.6±3.46[a]	52.9±6.47
vereteno	43.9	17.5	49.2	65.7	69	66.5	19.2	70.0[a]	
Zolushka	27.3±14.45	14.0±6.81	3.2±0.71	42.6±1.67[a]	40.2±7.62[a]	32.2±6.02	24.4±5.85	42.6±5.64[a]	54.7±6.80
	49.9	25.6	5.8	77.9[a]	73.5[a]	58.8	44.6	77.8[a]	
Kamcha-	13.4±6.10	23.6±4.65	20.6±3.02	8.1±4.93	29.9±3.49[a]	28.0±5.73[a]	18.6±6.45	16.8±4.33	37.7±7.01
dalka	35.6	62.7	54.6	21.5	79.4[a]	74.4[a]	49.5	53.5	
Pamyati	24.5±6.29	38.0±4.16[a]	27.8±4.41	26.4±7.20	10.5±2.99	20.0±3.73	12.0±3.91	15.8±2.52	51.8±2.49
Gidzyuka	47.3	73.5[a]	53.7	51.1	20.4	38.6	23.2	30.5	
Para-	25.4±3.48	42.1±7.48[a]	45.2±2.62[a]	40.4±4.03[a]	20.6±4.36	8.2±3.26	13.3±3.77	31.3±3.85	54.9±5.46
bel'skaya	46.3	76.7[a]	82.4[a]	73.6[a]	37.6	14.9	24.2	57.1	
Salyut	16.0±6.40	27.2±3.02	30.2±4.28	31.7±3.90	38.4±6.28[a]	27.1±3.83	3.4±1.17	31.1±7.39	53.9±5.84
	29.7	50.4	56	58.7	71.1[a]	50.2	6.3	57.6	
Tomichka	35.1±3.47	53.4±3.23[a]	38.0±8.44	41.1±8.96	38.1±6.53	25.5±6.52	18.3±5.11	6.0±1.33	64.0±6.86
	54.9	83.4[a]	59.3	64.2	59.5	39.9	28.5	9.4	

Note. 1 — Berel', 2 — Goluboe vereteno, 3 — Zolushka, 4 — Kamchadalka, 5 — Pamyati Gidzyuka, 6 — Parabel'skaya, 7 — Salyut, 8 — Tomichka; control — open pollination. Above the line — the average rate of fruit set, %; under the line — vs. control, %; a — the best options of pollination based on the compatibility.

The set of fruits in autogamy and open interpollination varied widely over the years of studies. This is due to the negative impact of unfavorable weather conditions (a prolonged drop in temperature down to 3 C, rain with snow) on fertilization, which was observed during the flowering period in 2001 and 2002. The most stable percentage of useful ovary was seen in the Berel' and Pamyati Gidzyuka varieties.

The investigation of the mutual variability of forms and varieties of *L. cepinella*, carried out earlier in various research institutes in Russia and abroad, showed in most cases the successful repollination of forms belonging to the *Caeruleae* subsection and those having the same set of chromosomes [27, 36, 37, 44]. Crossability between di- and tetraploid honeysuckle species from the *Caeruleae* subsection is feasible, however, the fruit set and yield of full seeds were very low, and the viability of triploid ($2n$ = 27) hybrids was reduced [12, 27]. Consequently, the use of samples with different numbers of chromosomes as pollinators is unacceptable.

3. The weight of fruit and number of seeds in blue-berried honeysuckle (*Lonicera caerulea* L.) plants of different varieties depending on the pollinating variety ($X \pm S_x$, Novosibirsk, 1999-2002)

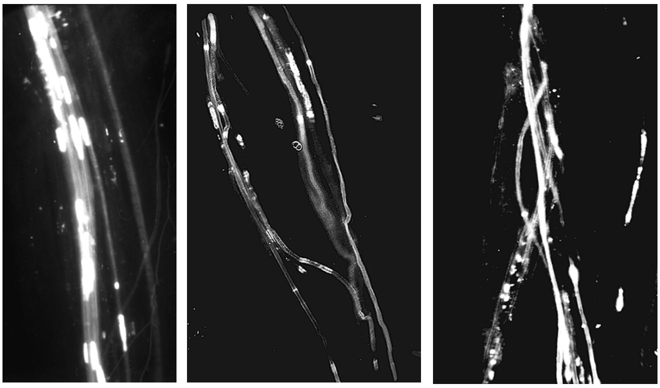
Pollinated variety	Pollinating variety								Control
	1	2	3	4	5	6	7	8	
Berel'	0.35±0.01	0.61±0.01	0.56±0.06	0.60±0.10	0.64±0.03	0.57±0.04	0.45±0.06	0.62±0.03	0.63±0.02
	0	12.0±1.1	7.1±2.4	6.7±3.04	8.0±0.2	7.7±3.3	4.8±0.9	8.9±1.2	10.2±1.6
Goluboe	0.44±0.07	0.37±0.02	0.60±0.10	0.67±0.06	0.73±0.09	0.67±0.03	0.40±0.03	0.73±0.10	0.92±0.03
vereteno	4.1±0.9	1.1±0.2	4.1±3.2	8.7±6.2	14.8±0.1	6.4±2.2	1.4±0.07	17.4±4.3	15.8±1.5
Zolushka	0.50±0.06	0.50±0.01	0.47±0.08	0.70±0.10	0.76±0.19	0.60±0.10	0.43±0.30	0.80±0.03	0.84±0.05
	1.9±0.5	1.8±0.5	0.9±0.05	5.8±2.1	5.9±1.5	5.9±1.6	1.8±0.5	9.9±3.5	9.8±3.1
Kamchadalka	0.44±0.01	0.70±0.10	0.60±0.10	0.24±0.06	0.68±0.14	0.52±0.08	0.43±0.01	0.60±0.03	0.74±0.06
	5.2±3.7	9.5±1.8	4.6±1.2	0.3±0.3	11.9±0.3	7.6±1.5	4.8±2.4	3.3±1.8	9.7±1.6
Pamyati	0.50±0.10	0.72±0.09	0.58±0.09	0.46±0.03	0.25±0.07	0.37±0.06	0.32±0.07	0.43±0.10	0.81±0.05
Gidzyuka	4.7±2.4	13.2±3.7	8.2±3.0	7.3±2.7	1.2±1.1	4.6±2.7	2.4±0.9	3.7±1.2	15.1±0.8
Parabel'skaya	0.54±0.06	0.64±0.08	0.78±0.08	0.63±0.05	0.41±0.04	0.31±0.02	0.30±0.02	0.65±0.08	0.67±0.03
	6.9±2.3	18.3±1.6	15.2±3.7	10.4±2.7	5.4±2.3	1.5±0.6	3.2±1.6	9.4±2.1	13.3±1.6
Salyut	0.36±0.08	0.51±0.07	0.49±0.05	0.55±0.09	0.51±0.09	0.42±0.04	0.30±0.04	0.56±0.10	0.57±0.03
	4.0±2.8	6.0±1.0	5.2±0.3	6.9±2.0	5.1±1.4	3.2±1.4	0.8±0.5	7.6±0.6	6.6±1.1
Tomichka	0.42±0.01	0.53±0.04	0.57±0.09	0.54±0.09	0.46±0.09	0.36±0.09	0.31±0.07	0.21±0.04	0.59±0.01
	8.5±0.6	13.0±2.1	12.3±0.1	7.5±3.6	10.2±4.6	3.7±1.7	6.6±5.0	0.8±0.8	12.9±2.8

Note. 1 — Berel', 2 — Goluboe vereteno, 3 — Zolushka, 4 — Kamchadalka, 5 — Pamyati Gidzyuka, 6 — Parabel'skaya, 7 — Salyut, 8 — Tomichka; control — open pollination. Above the line — the average rate of fruit set, %; under the line — vs. control, %; a — the best options of pollination based on the compatibility.

In our studies, with the artificial interpollination of the *L. caerulae* varieties under investigation, the proportion of the set fruit, their weight and the number of seeds varied greatly, depending on the pollinating variety (see Table 3). Low fruit setting was typical for variants, where Berel' and Salyut were used as pollinating varieties. The poor quality of pollen negatively affected the fertilization. Combinations of pollination, where closely related varieties were used as parental forms, such as Goluboe vereteno × Zolushka, Zolushka × Goluboe vereteno, Pamyati Gidzyuka × Parabel'skaya, Pamyati Gidzyuka × Tomichka, Parabel'skaya × Pamyati Gidzyuka, Tomichka × Parabel'skaya and Berel' × Zolushka, had a relatively low grade of setting (25.6 to 48.6 %) along with a small fruit weight and number of seeds (see Table 2).

This partial compatibility or semi-compatibility in honeysuckle can presumably be due to the gametophytic control of the reaction of incompatibility of pollen and pestle tissues. According to the hypothesis by E.M. East, A.J. Mangelsdorf [45] and molecular studies of recent years [42], the plants of the *S1S2* genotype contain both alleles of incompatibility in the diploid cells of the style, and either the *S1* or *S2* allele in self-pollination of the haploid pollen grains. Both the pollen of *S1* and pollen of *S2* are suppressed in the tissues of the style carrying the same factors. When the plants with gametophyte control of incompatibility within the family are repollinated, which is possible in the abovementioned cases, the crossing of the *S1S2* × *S2S3* heterozygote may occur, resulting in a partial weakening of the incompatibility barrier due to the presence among the pollen grains both those of *S2* that is incompatible with the pistil tissues and those of *S3* that do not cause such a reaction. Depending on how the *S*-alleles of the *S*-locus (locus of incompatibility) were distributed in the offspring, we could observe the intervariety sterility, partial or complete compatibility of the male gametophyte and pistil tissues during the repollination of closely related varieties.

A B C



The growth of pollen tubes in the pistil style in blue-berried honeysuckle (*Lonicera caerulea* L.) plants: A — open pollination (the Zolushka variety, ×365), B — pollination of closely related varieties (Zolushka × Goloboe vereteno, ×277), C - self-pollination (the Tomichka variety, ×295) (the ML-2B microscope, LOMO, Russia, Novosibirsk, 2000).

Observations of the growth of pollen tubes in the pistil tissues showed that in repollination of the varieties having no common genetic origin the growth of pollen tubes (as in open interpollination) was characterized by the mass character and a clear orientation towards the ovules. Straight and brightly fluorescent against the background of the pistil tissues, the pollen tubes grew as a dense bundle closer to the center of the column (Fig., A). Callose plugs were of regular rectangular shape and of the same size and arranged evenly along the entire length of the tube. In variants of crossing closely related varieties, as well as in self-pollination, there was a lack of a clear direction of growth of the pollen tubes to the base of the pistil (see Fig., B). Their bending, twisting and weak luminescence just after passing through the $^1/_2$-$^2/_3$ column were noted. Worm-like or clavate-shaped callose plugs were arranged irregularly and brightly fluoresced on the subtle background (in some cases) of the pollen tubes. The pollen tubes in all the observed variants of autogamy had a fuzzy outline, the callose plugs were numerous and irregularly shaped (see Fig., C), which confirms the findings from the investigations by M.N. Plekhanova [38].

4. Potential mutual interpollination of the blue-berried honeysuckle (*Lonicera caerulea* L.) varieties of different ecological and geographical origin based on the experiments conducted in the forest-steppe zone of the south of Western Siberia (Novosibirsk, 1999-2002)

Pollinated varieties	Best pollinators	Acceptable pollinators	Poor pollinators
Berel'	Tomichka	Goluboe vereteno Kamchadalka Parabel'skaya Pamyati Gidzyuka	Salyut Zolushka
Goluboe vereteno	Tomichka	Kamchadalka Pamyati Gidzyuka Parabel'skaya	Berel' Salyut Zolushka
Zolushka	Pamyati Gidzyuka Tomichka Kamchadalka	Parabel'skaya	Berel' Salyut Goluboe vereteno
Kamchadalka	Pamyati Gidzyuka Parabel'skaya	Goluboe vereteno Zolushka Tomichka	Berel' Salyut
Pamyati Gidzyuka	Goluboe vereteno	Zolushka Kamchadalka	Berel' Salyut Parabel'skaya Tomichka
Parabel'skaya	Goluboe vereteno Zolushka Kamchadalka	Tomichka	Berel' Salyut Pamyati Gidzyuka
Salyut	Pamyati Gidzyuka	Goluboe vereteno Zolushka Tomichka Kamchadalka	Berel'
Tomichka	Goluboe vereteno Kamchadalka	Zolushka Pamyati Gidzyuka	Berel' Salyut Parabel'skaya

We divided the varieties into groups (Table 4). The best pollinators were varieties and selected forms that had a remote genetic origin and were characterized by the high pollen fertility. The group of poor pollinators included primarily the varieties with the low-fertile pollen and closely related forms.

Based on the estimations of genetic origin, the Goluboe vereteno, Sinyaya ptitsa, Lazurnaya, Zolushka, Gerda and Berel' varieties were obtained from the Start parent form (*L. caerulea* subsp. *kamtschatica*) [43], while the Tomichka, Parabel'skaya, Pamyati Gidzyuka, Vasyuganskaya and Narymskaya varieties were derivatives of the Del'fin parent form (*L. caerulea* subsp. *venulosa*) [46]. The results of the studies allow suggesting a more high-grade interpollination and realization of potential productivity in the honeysuckle plantings when used in joint plantings of varieties from different selection families.

This rule can also be applicable to newly created varieties. For example, in recent years, the Bakcharsky velikan, Chulymskaya, Gordost' Bakchara, Sil'ginka, Bakcharskaya Jubileinaya and other varieties were created by plant breeders and have become widely spread [46]. As they are of the closely related origin (derived from subsequent generations of the Del'fin form), varieties from another family must be used as pollinators for them.

When establishing the plantations with high-yielding varieties, such as Salyut, Barkhat, Berel' and hybrids with their participation, characterized by poor pollen quality, it is necessary to include additional pollinating varieties.

Thus, pollen fertility in the blue-berried honeysuckle (*Lonicera caerulea* L.) varieties of different ecological and geographical origin varies considerably. Low fertility and very low pollen productivity are characteristic for a part of the representatives of *L. caerulea* subsp. *altaica* from the Rudny Altai. The use of varieties with a high content of sterile pollen as pollinators leads to reduced fruit setting and a decrease in their weight. All studied varieties of *L. saerulea* were self-sterile. Over the years of research, open pollination in the conditions of the forest-steppe zone in the south of Western Siberia ensured on average the setting of 38-64 % of the fruit. When crossing the closely related varieties of blue-berried honeysuckle, > 50 % decrease in the set of fruit, a decrease in fruit weight and seed productivity were found vs. open pollination. In the variants obtained by crossing closely related blue-berried honeysuckle varieties and in autogamy, similar growth anomalies in the pollen tubes in the pistil tissues were observed, which were apparently related to the gametophytic control of self-incompatibility. The varieties were selected to provide a more productive pollination during joint cultivation.

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