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INTERSPECIFIC HYBRIDIZATION IN LAVANDIN (*Lavandula* × *intermedia* Emeric ex Loisel.) BREEDING FOR ESSENTIAL OIL QUALITY

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Abstract

Lavandin cultivars (*Lavandula* × *intermedia* Emeric ex Loisel.) are sterile interspecies hybrids *Lavandula angustifolia* Mill. × *L. latifolia* Medic. They are of great interest for the essential oil industry. Lavandin cultivars express 1.5-2-fold higher yields of raw biomass and essential oil production, as well as 4-fold higher essential oil yield per area unit as compared to the used lavender cultivars. World production of lavandin essential oil is 1200 thousand tons, and lavender oil production is only 200 thousand tons. However, the quality of lavandin essential oil is lower compared to lavender one because of camphor, 1,8-cineole and borneol significant amounts. Besides, it is impossible to use lavandin cultivars in further breeding works, as they are sterile. The main trend in lavandin breeding is to improve the essential oil quality by reducing unwanted components to a minimum. In order to create lavandin hybrids characterized by high essential oil quality we had first synthesized tetraploid forms of *L. angustifolia* and *L. latifolia* and then crossed these forms with each other. As the result, their sterility was overcome and amphidiploid hybrids were obtained. Those hybrids were further used to create new highly effective cultivars. Crossing between amphidiploid hybrid № 48 and lavender cultivars (Belyanka, Record, Prima) let us to select cross combinations and create lavandin cultivars with minimum amount of camphor, borneol and 1,8-cineol. It was revealed that obtained plants often demonstrated intermediate when compared to their parental forms. Thus, initial forms with high content of linalool and linalyl acetate and lower content of unwanted compounds should be used in breeding works. In cross combinations Amphidiploid 48 × Belyanka, Lavandin hybrids with high content of linalool (up to 68.8 %) were derived. Some hybrids had the content of borneol (up to 0.5 %), camphor (1.9 %) and 1,8-cineole (1.8 %) similar to that of parental forms. In cross combination Amphidiploid 48 × Prima hybrids were obtained with high content of linalool (up to 57.9 %) and linalyl acetate (up to 32.8 %) and low content of camphor (0.2 %), borneol (1.6 %) and 1,8-cineole (up to 0.9 %). The results of our investigations demonstrated that it is possible to create Lavandin hybrids with borneol amount lower than in the original forms. Camphor and 1,8-cineole content depression was not beyond the intermediate type of inheritance. We suppose that the extremely low content of 1,8-cineole and camphor in the lavender chemotypes selected for breeding corresponds to their lower biological limit of these metabolites. Hybrid plants (*L.* × *intermedia*) can only approximate these characteristics of *L. angustifolia*. Lavandin hybrids with the best essential oil composition have been obtained by crossings between the most closely related, from a biological point of view, chemotypes with dominant alleles of linalool and linalyl acetate and recessive alleles of camphor and 1,8-cineole in *L. angustifolia*, which is possible under creating Lavandin hybrids with two genomes of *L. angustifolia* and one genome of *L. latifolia*.

Keywords: allotriploid, Lavandin, *Lavandula* × *intermedia* Emeric ex Loisel., hybrid, essential oil composition

Selection of lavandin (*Lavandula* × *intermedia* Emeric ex Loisel.), which is promising for essential oil production, is associated with the production of interspecific hybrids F_1 at a diploid level using crossing of true lavender (*L. angustifolia* Mill.) with spike lavender (*L. latifolia* Medic.). The resulting hybrids are characterized by heterosis in terms of essential oil content and yield [1-3], which explains the interest in them. However, the quality of lavandin essential oil is lower than that of lavender essential oil due to the presence of components that have a negative effect on it, i.e. cineole, borneol, camphor, inherited from spike lavender. The studies on a more detailed characterization of the composition of interspecific hybrids essential oil are known [8, 9].

The main task in lavandin selection (along with an increase in the total yield of essential oil from 1 hectare) is a decrease in the amount of undesirable components in raw materials [10-12]. However, there is no theoretical justification for the selection of parental pairs, which makes it difficult to purposefully obtain hybrids with given properties. In our opinion, the creation of hybrid genotypes by means of distant hybridization involving the induced polyploid forms is a promising approach. This requires a preliminary study of patterns of traits inheritance in such combinations of crossing.

This report, for the first time, suggests a theoretical approach to the selection of parental pairs for lavandin crossing in the selection for improving the composition of essential oil. The results of obtaining induced amphidiploid forms of *L.* × *intermedia* and hybrid progeny based on them are presented and the patterns of target traits inheritance are analyzed.

The purpose of this study was to select parental forms, to develop a scheme for lavandin crossing when breeding for quality and to compare the manifestations of target traits in the hybrid genotypes and their parents.

Techniques. The following varieties were the initial parental forms of true lavender: Belyanka, of a linalool type with a total content of linalool and linalyl acetate about 80% and a predominance of linalool (up to 67%); Prima of a linalyl acetate-linalool type with a total content of these components about 80% and a predominance of linalyl acetate (up to 50%); Rekord with an approximately equal content of linalool and linalyl acetate, which in total are 70% of the essential oil. These lavender varieties are characterized by a relatively low content of camphor (not more than 1.9%), borneol (no more than 3.5%) and cineole (no more than 0.3%). Amphidiploid No. 48 was obtained by colchicination of sterile lavandin F_1 and refers to the linalool type with high linalool content (up to 62.5%), and a medium content of linalyl acetate (up to 12.9%), camphor (10.6%), cineole (3.4%) and borneol (5.8%).

The following combinations of crossing were used in the studies: Amphidiploid No. 48 × Belyanka, Amphidiploid No. 48 × Rekord, Amphidiploid No. 48 × Prima (Amphidiploid No. 48 was the female parent). Hybrids and the initial forms were grown under the same conditions on the collection sites of the Nikitsky Botanical Garden (Crimea). The paper presents average data for 2015-2017.

Cytological analysis of hybrids was carried out according to Z.P. Pausheva [18] using a Jenamed microscope (Carl Zeiss Jena GmbH, Germany, magnification ×900).

Mass fraction of essential oil was determined by 1-hour hydrodistillation according to Ginsberg (State Pharmacopoeia of the USSR. M., 1987) in fresh raw materials. The experiments were arranged in 3 replications. The composition of the essential oil was detected using a gas chromatograph 6890N (Agilent Technology, Inc., USA) with a mass spectrometric detector 5973N. The HP-1 column is 30 m long and the inner diameter is 0.25 mm. The thermostat temperature was programmed from 50 to 250 °C with a change rate of 4 °C/min.

The injector temperature was 250 °C, the carrier gas was helium, and the flow rate was 1 cm^3/min. The temperature of the transition line from the gas chromatograph to the detector was 230 °C, with the temperature of the ion source 200 °C. Electron ionization was carried out at 70 eV at m/z from 29 to 450 [19]. The essential oil components were identified by comparison with the library data of mass spectra NIST 05 (http://nistmassspeclibrary.com/) and WILEY2007 (http://www.sisweb.com/software/ms/wiley.htm) (total about 500000 mass spectra).

The software STATISTICA v.6.0 (StatSoft, Inc., USA) was used for statistical processing. Mean (*M*) and standard errors of means (±SEM) were calculated. The significance of differences between the variants was evaluated by the arithmetic mean and variation coefficient at $p < 0.05$.

Results. The initial parental forms have different chemotypes. The crossing of Amphidiploid No. 48 with the true lavender diploid resulted in the hybrid genotypes that have a somatic number of chromosomes $2n = 72$, include two genomes of *L. angustifolia* (AA) and one genome of *L. latifolia* (L), are allotriploids with the genomic composition AA-L. Their formation can be represented as follows (Fig. 1).

Amphidiploid — $2n = 96$, AALL (metaphase I) — 24_{II} *L. angustifolia* + 24_{II} *L. latifolia* × Diploid — $2n = 48$, AA — 24_{II} *L. angustifolia*

Gametes AL ($n = 48$)   Gametes A ($n = 24$)

$2n = 72$, AAL

Fig. 1. Combination of crossing the amphidiploid (lavandin) with diploids of lavender *Lavandula* sp. used in hybridization for lavandin breeding.

A cytological study of F_1 hybrids showed that they are all germ-free and have a chromosome number $2n = 72$, that is, balanced 24-chromosome gametes of the true lavender and 48-chromosome Amphidiploid No. 48 participated in their formation. The study confirmed the hybrid nature of the plants obtained from crossing and showed that they are allotriploids. Thus, the studied hybrids (total 96 genotypes) do not differ in the number of chromosomes, which excludes the influence of the specified factor on the content and composition of the essential oil.

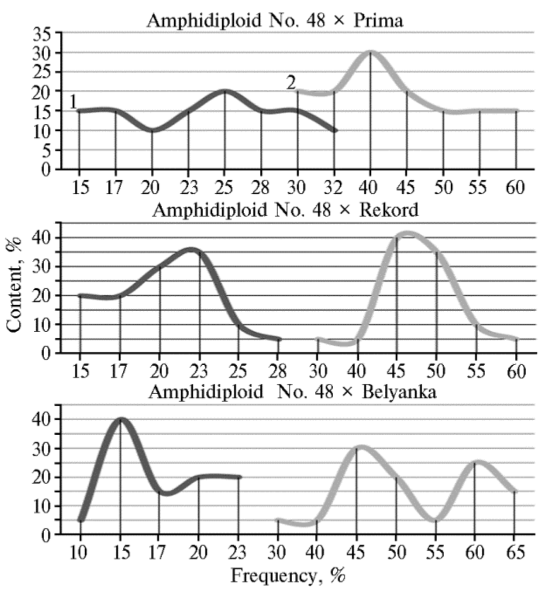

Fig. 2. Distribution of interspecies hybrids F_1 of lavender (*Lavandula angustifolia* + *L. latifolia*) × *L. angustifolia* according to the content of linalyl acetate (1) **and linalool** (2) **in different combinations of crossing.**

A significant increase in the variation of the essential oil content was observed in hybrids of all variants of crossing [13, 20]. Most of the hybrids inherited this trait for an intermediate type, with the mean values of the sample close to the high oleic forms, regardless of the type of crossing. The deviation of hybrids towards high oleic forms was observed when using the Rekord as a paternal component. Thus, the content of the essential oil is inherited towards the forms with a large manifestation of this trait with a certain influence of the paternal form [20].

When analyzing the patterns of variability and inheritance of the essential oil composition (Figs. 2-4), only its main components, linalool and linalyl acetate (see Fig. 2), as well as compounds that reduce its quality, i.e. cineole, camphor, and borneol (see Fig. 3), were considered.

When crossing Amphidiploid No. 48 and the true lavender varieties Rekord and Prima used as pollinators, the accumulation of linalool in hybrids is approximately the same. The content of linalyl acetate in all hybrids is characterized by an intermediate type of inheritance, and the average indicators are shifting toward the maternal form.

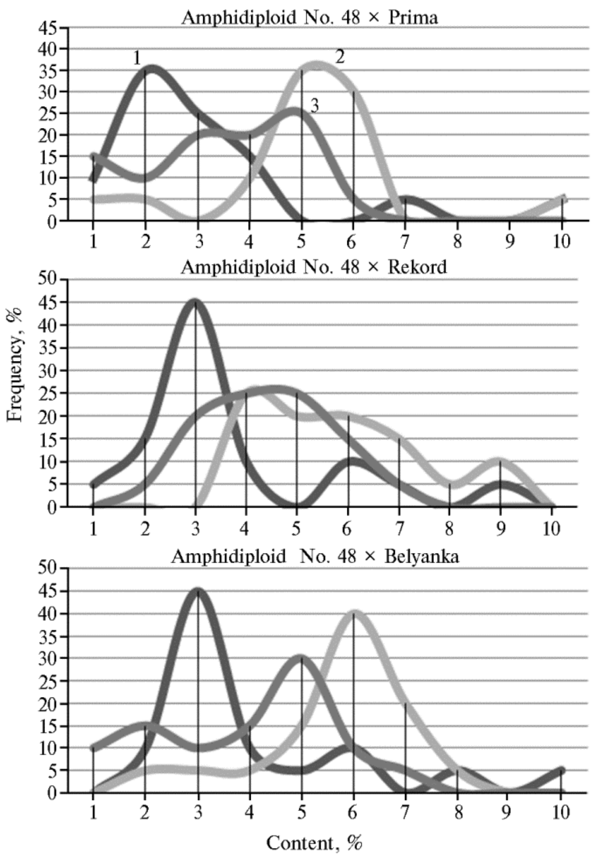

Fig. 3. Distribution of interspecific hybrids F_1 of lavender (*Lavandula angustifolia* + *L. latifolia*) × *L. angustifolia* according to the content of terpenes 1,8-cineole (1), **camphor** (2) **and borneol** (3) **in different combinations of crossings.**

Inheritance of undesirable components was characterized by a more pronounced intermediate type. It was shown that only in a small number of plants, the content of borneol, cineole, and camphor is lower than in parental forms, but the depression is very small, 3%. These plants were identified in a crossing combination with the use of true lavender of the Belyanka variety as a paternal form (Table 1).

In general, the inheritance of the considered components in the used variants of crossing is predominantly intermediate, with a deviation towards the maternal line and a heterotic effect on the content of linalool in it.

1. Variation in the main components of essential oil in interspecific hybrids F_1 of lavender ♀(*Lavandula angustifolia* + *L. latifolia*) × ♂*L. angustifolia* obtained with Belyanka, as compared to the parents (*M*±SEM, *n* = 32, Nikitsky Botanical Garden, 2015-2017)

Component	Content, %	♂ Belyanka	♀ Amphidiploid No. 48	F_1
Linalool	Average	63.7±1.7	60.3±2.1	54.6±1.8
	Limits of variation	60.1-64.3	57.5-62.5	51.5-68.8
	Cv, %	4.5±0.5	6.8±0.9	15.1±1.4
Linalyl acetate	Average	13.9±0.7	9.4±0.9	10.4±0.8
	Limits of variation	9.8-15.4	7.5-12.9	9.7-16.2
	Cv, %	11.5±0.8	6.7±0.5	22.8±2.9
Cineole	Average	2.7±0.2	3.4±0.3	3.6±0.5
	Limits of variation	2.1-2.9	3.1-5.2	1.8-9.6
	Cv, %	2.2±0.1	6.5±0.4	57.2±4.9
Borneol	Average	1.8±0.3	5.8±0.3	3.6±0.4
	Limits of variation	1.6-2.1	4.7-7.2	0.5-6.8
	Cv, %	6.5±0.4	9.2±0.3	49.1±5.6

Continued Table 1

Camphor	Average	2.1±0.1	10.6±0.9	5.3±0.3
	Limits of variation	1.6-2.3	9.8-12.0	1.9-7.2
	Cv, %	7.5±0.2	8.7±0.8	26.8±2.1

N o t e. Cv — coefficient of variation at $p < 0.05$.

The crossing of the used chemotypes did not result in hybrids with high-quality essential oil. Only in the hybrid progeny of Amphidiploid No. 48 × Prima the content of linalyl acetate in a number of plants slightly exceeded the main commercial lavender variety Rekord (standard) (Table 2). When the Rekord, Prima and Belyanka were used as the paternal forms, a wide variation in the content of linalool (36.7-68.8%) was observed in hybrid plants.

2. Variation in the main components of oil in interspecific hybrids F_1 of lavender ♀(*Lavandula angustifolia* + *L. latifolia*) × ♂*L. angustifolia* with Rekord (standard) variety, as compared to parents (*M*±SEM, *n* = 32, Nikitsky Botanical Garden, 2015-2017)

Component	Content, %	♂ Rekord	♀ Amphidiploid No. 48	F_1
Linalool	Average	40.5±0.4	60.3±2.1	46.3±1.1
	Limits of variation	39.0-42.0	57.5-62.5	39.8-58.2
	Cv, %	8.2±0.7	6.8±0.9	10.4±0.8
Linalyl acetate	Average	32.2±0.2	9.4±0.9	19.7±0.7
	Limits of variation	30.0-34.0	7.5-12.9	15.3-28.6
	Cv, %	5.5±0.3	6.7±0.5	15.8±1.1
Cineole	Average	0.2±0.1	3.4±0.3	3.1±0.4
	Limits of variation	0.1-0.4	3.1-5.2	0.9-8.1
	Cv, %	2.5±0.1	6.5±0.4	60.8±5.8
Borneol	Average	3.5±0.2	5.8±0.3	3.9±0.3
	Limits of variation	2.0-4.0	4.7-7.2	1.7-6.8
	Cv, %	2.4±0.2	9.2±0.3	34.0±3.5
Camphor	Average	1.4±0.1	10.6±0.9	6.4±0.4
	Limits of variation	0.4-1.9	9.8-12.0	4.1-10.1
	Cv, %	4.1±0.2	8.7±0.8	20.7±2.1

N o t e. Cv — coefficient of variation at $p < 0.05$..

The same pattern of inheritance with intermediate values of the indicator was found in hybrids by accumulation of 1,8-cineole and camphor. In all crossings, the proportion of plants with a lower camphor content than in the standard was 60%. According to the amount of borneol, the depression was observed in 9% of hybrid progeny. Thus, the influence of the maternal form characteristics on the nature of essential oil composition inheritance is observed in all combinations of chemotypes.

Hybridization of linalool-linalyl acetate and linalool-camphor chemotypes (Table 3) made it possible to obtain hybrids in which the content of linalool is higher, the content of linalyl acetate is approximately equal, and the content of borneol is lower compared to those of commercial lavender variety Rekord. At the same time, the amount of 1,8-cineole in the resulting hybrids (the range of variation is 0.9-9.7%) is significantly higher than that in the standard variety Rekord (0.01-0.04%).

3. Variation in the main components of oil in interspecific hybrids F_1 of lavender ♀(*Lavandula angustifolia* + *L. latifolia*) × ♂*L. angustifolia* with Prima variety, as compared to parents (*M*±SEM, *n* = 32, Nikitsky Botanical Garden, 2015-2017)

Component	Content, %	♂ Prima	♀ Amphidiploid No. 48	F_1
Linalool	Average	32.8±0.4	60.3±2.1	46.8±1.6
	Limits of variation	31.0-33.0	57.5-62.5	36.7-57.9
	Cv, %	3.8±0.2	6.8±0.9	14.8±1.3
Linalyl acetate	Average	46.6±0.3	9.4±0.9	23.4±1.2
	Limits of variation	44.1-50.4	7.5-12.9	15.5-32.8
	Cv, %	9.8±0.5	6.7±0.5	22.3±1.9
Cineole	Average	0.3±0.1	3.4±0.3	2.7±0.5
	Limits of variation	0.2-0.4	3.1-5.2	0.9-9.7
	Cv, %	2.8±0.2	6.5±0.4	81.8±8.9

Continued Table 3

Borneol	Average	0.8±0.2	5.8±0.3	2.9±0.4
	Limits of variation	0.2-1.3	4.7-7.2	1.6-5.4
	Cv, %	3.4±0.4	9.2±0.3	55.6±7.1
Camphor	Average	0.4±0.9	10.6±0.9	5.2±0.4
	Limits of variation	0.1-0.9	9.8-12.0	0.2-6.8
	Cv, %	5.1±0.4	8.7±0.8	30.4±3.6

Примечание. *Cv* — коэффициент вариации при P < 0,05.

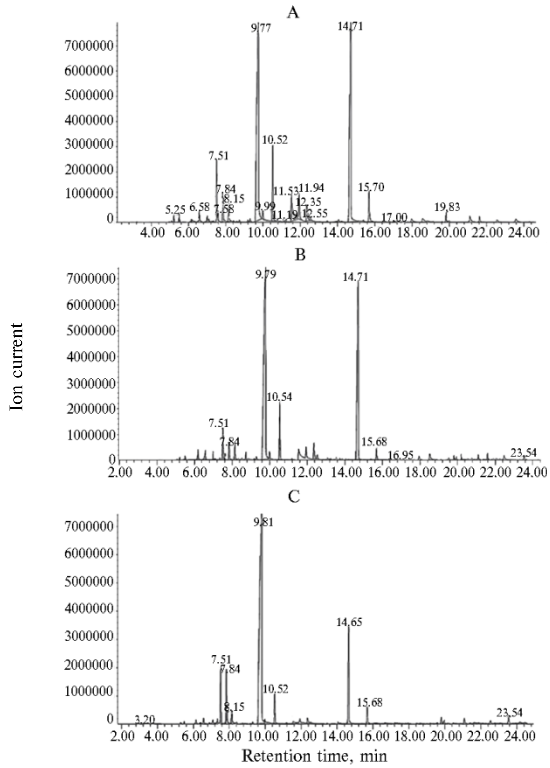

Fig. 4. Essential oils of interspecific hybrids F_1 of lavender (*Lavandula angustifolia* × *L. latifolia*) × *L. angustifolia* in crossing Amphidiploid No. 48 × Prima (A), **Amphidiploid No. 48 × Rekord** (B) **and Amphidiploid No. 48 × Belyanka** (C) (Nikitsky Botanical Garden, 2015-2017). Peaks: 1,8-cineole (7.51), linalool (9.77-9.81), camphor (10.52-10.54), borneol (11.58), linalyl acetate (14.65-14.71) (a gas chromatograph/mass spectrometer 6890N, Agilent Technology, Inc., USA).

Hybrids from crossing with Belyanka, which has approximately the same linalool and linalyl acetate content as the parent plants (Amphidiploid No. 48) of the linalool chemotype, also show inheritance for these traits with a deviation towards the maternal Amphidiploid No. 48).

With respect to undesirable components, depression was observed in most hybrid genotypes in all combinations used. For example, there was a reduced amount of borneol (from 9 to 48%). However, none of the hybrids actually improved the performance of the standard in terms of the content of camphor and 1,8-cineole. At the same time, a rather significant part of progeny in the variant Amphidiploid No. 48 with Belyanka, on the contrary, showed a heterotic effect in these characteristics, especially in the content of 1,8-cineole.

The greater part of hybrids was characterized by a depression of linalool content in all variants of crossing, but some showed a heterotic effect, reaching 127.9-131.0%. When using Belyanka, the yield of plants with a heterotic effect was maximal and amounted to 18% (see Fig. 2). A small heterotic effect was also seen in the content of linalyl acetate, but only in combination Amphidiploid No. 48 × Prima and only in 3% of the hybrids obtained.

It should be noted that the combination Amphidiploid No. 48 × Prima gives a significant yield of hybrid plants with essential oil close to the standard Rekord variety in terms of quality, and 100% of the hybrids resulted from the crossing Amphidiploid No. 48 × Belyanka were better than Rekord variety in the linalool content.

By analyzing the obtained results, it is possible to make the following assumptions on the prospects of lavandin breeding for a certain content and composition of essential oil. The initial forms of true lavender and Amphidiploid No. 48 have a number of genetic features. Chemotypes of true lavender are characterized by the presence of dominant alleles controlling the synthesis of linalool (L) and linalyl acetate (A), recessive alleles controlling the biosynthesis of cineole (c), borneol (b) and camphor (k). In Amphidiploid No. 48, the dominant alleles control the biosynthesis of linalool (L), borneol (B), and camphor (K). The biosynthesis of linalyl acetate is not characteristic of this clone and is controlled by a recessive allele (a).

In previous studies, it was shown that Amphidiploid No.48 as a donor of the feature of essential oil high yield should be used as a paternal form, since the essential oil content is inherited in the paternal line [13, 20]. At the same time, a high content of linalool and linalyl acetate can be achieved only if chemotypes of true lavender are used as a maternal form. This is especially important with regard to the selection for the content of linalyl acetate, the biosynthesis of which is not characteristic for Amphidiploid No. 48. Thus, the selection of lavandin allows obtaining a simultaneous combination of positive results in terms of both content and composition of essential oil. The foreign literature does not contain data on the evaluation of crossing combinations, and only gives a chemical analysis of the essential oil of lavandin varieties that have been already obtained [21-25]. Comparison of the results of the study on the composition of lavandin essential oil, obtained by us and by foreign researchers, shows that the hybrids we obtained exceed the foreign ones in oil quality [10, 11, 26-28].

The result of selection largely depends on the correct choice of chemotype pairs. In breeding for the content of essential oil, attention should be paid to the fact that the heterotic effect occurs at a certain degree of manifestation of this characteristic in the initial forms. Heterosis on essential oil content is most likely with its content of at least 5% of dry raw material for true lavender and 10% for Amphidiploid No. 48.

Amphidiploid No. 48, as well as the Belyanka variety, has dominant alleles that control linalool biosynthesis. As a consequence, heterosis on this component was observed in all combinations of crossing. The maximum content of linalool is proportional to its quantity in both initial forms, Belyanka and Amphidiploid No. 48. Heterosis on the content of linalyl acetate is rarer and occurs, obviously, only in case of the high content of both linalyl acetate and linalool in the maternal form. It should be noted that the inheritance of the high content of linalyl acetate and linalool cannot be combined, since high values for linalool are achieved when using Amphidiploid No. 48 as a maternal form, and for linalyl acetate when using it as a paternal form. This circumstance can be used in target selection for the content of one of these components.

Earlier, it was reported that the improvement of hybrids in the content of undesirable components 1,8-cineole, borneol and camphor of essential oil is more likely when using Amphidiploid No. 48 as a paternal form [13, 20]. However, only in the case of borneol it is possible to obtain hybrid plants with a depression of its content to a value that is lower than that in the initial forms. Depression in the content of 1,8-cineole and camphor does not exceed the limits of the intermediate type of inheritance. Thus, it can be assumed that the 1,8-cineole and camphor content in the chemotypes of true lavender selected for breeding corresponds to the extremely low amount of these compounds in members of the species. Hybrid plants are only able to be close to these values. When breeding lavandin for the high quality of essential oil, the chemotypes of amphidiploid with a low content of 1,8-cineole and camphor in combination with a high accumulation of linalyl acetate are most appropriate.

Thus, our experiments show that the highest content of essential oil and its best composition result from combinations of Amphidiploid No. 48 with closely related chemotypes of true lavender, bearing the dominant alleles of linalyl acetate and linalool (Prima variety) or the dominant allele of linalool (Belyanka variety). These combinations produce hybrids with the maximum content of linalool and linalyl acetate. In addition, in this case there is the greatest yield of hybrids with heterosis on the desired traits. The study of the combining ability of parental pairs has shown that in order to obtain hybrids with a high quality of essential oil, target interspecific crossings are necessary of Amphidiploid No. 48 with Rekord and Prima varieties of *Lavandula angustifolia*. These result in allotriploids with two genomes of *L. angustifolia* and one genome of *L. latifolia*, in which the mass fraction of essential oil is up to 3.6% of wet weight of the raw material (or 10.25 for absolutely dry weight). The best combination of crossing is Amphidiploid No. 48 × Prima. It allows the creation of allotriploids with a high quality of essential oil containing up to 32.8% of linalyl acetate with a minimum amount of 1,8-cineole (3.7%) and camphor (5.6%). In addition, hybrids with high linalool content (up to 68.8%) for the essential oil industry are obtained in combination Amphidiploid No. 48 × Belyanka. Resultant hybrids with a linalool content up to 68.8% (Amphidiploid No. 48 × Belyanka) and linalyl acetate content up to 32.8% (Amphidiploid No. 48 × Prima) are identified.

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