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Inheritance of some Leaf Characters in *Salvia němecii* HBÝ

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Dědičnost některých charakteristik listů u *Salvia němecii* HBÝ.

Mezidruhový hybrid *Salvia němecii (S. nutans* × *S. jurišićii)*, popsaný autorem již dříve, je plně plodný. Proto byly na 238 rostlinách F_2 generace sledovány tyto znaky: typ svazků cévních v řapíku, poměr délky řapíku k délce čepele, délkošířkový index čepele listové a členitost čepele, vyjádřená poměrem ideální obrysové plochy listu k jeho skutečné ploše. Všecky tyto charakteristiky srovnány se situací u rodičovských druhů i F_1 hybrida. Bylo zjištěno:

1. Typ II svazků cévních je jednoduše a úplně dominantní nad typem III (štěpný poměr 172 : 66, $\chi^2_{(1)} = 0{\cdot}94$, $P \doteq 0{\cdot}35$).

2. Všechny vnější morfologické znaky jsou založeny polygenně. Štěpení v F_2 je velmi široké a extrémní typy přesahují hodnoty u rodičovských druhů.

3. Typ svazků cévních se dědí nezávisle na vnějších morfologických znacích. Průkazné korelace zde nebyly zjištěny.

4. Vnější morfologické znaky mezi sebou jsou však průkazně korelovány. Zvláště je kladná korelace mezi délkou řapíku a členitostí čepele ($r = 0{\cdot}31$) a záporná korelace mezi členitostí čepele a délkošířkovým poměrem ($r = -0{\cdot}42$). Lze z toho vyvodit, že menší část příslušných polygenních systémů je ve vazbě, tj. lokalisována v tomtéž chromosomu. Většina jich se však dědí vzájemně nezávisle.

Summary

As the species hybrid *Salvia němecii* (= *S. nutans* × *S. jurišićii*) is highly fertile, genetic analysis of the segregating F_2 generation has been carried out. In 238 plants of F_2 the following leaf characters were investigated: type of the vascular bundle course in the petiole, the ratio of the petiole to leaf blade length, the ratio of the length of the leaf blade to the breadth, and the segmentation of the leaves, i.e. ratio between an ideal contour surface and the actual surface of the leaf blade. All these characteristics were compared with those of the original parental species as well as of the F_1 generation. It was found that:

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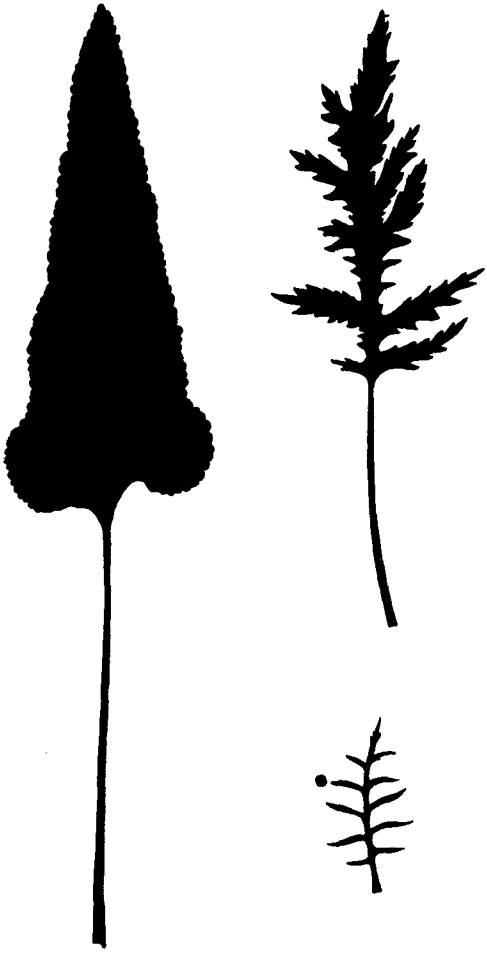


Fig. 1. Leaves of *S. nutans* (left), *S. němecii* (right above) and *S. jurišićii* (right below). Reduced 1 : 3.

1. Type II of vascular bundle course has simple dominance over type III (segregating ratio 172 : 66, $\chi^2_{(1)} = 0{\cdot}94$, $P \doteq 0{\cdot}35$).

2. All morphological characteristics of the leaves behave as though governed by polygenic systems. The segregation in F_2 is always very wide and the extreme segregants exceed the values present in both parental species.

3. The type of vascular bundle course in the petiole is inherited independently of the morphological signs of the leaves. There is practically no correlation between vascular bundle type and any of the morphological ratio indices.

4. Between the morphological characters, on the other hand, there are significant correlations, especially between the length of the petiole and segmentation of the leaf ($r = 0{\cdot}31$), and between the segmentation and the length-breadth ratio ($r = -0{\cdot}42$). Therefore, some of the polygenes concerned may be linked together, i.e. localized in the same chromosome, but most of them are transferred independently.

Introduction

Salvia němecii is an interspecific hybrid from the section *Plethiosphace* between the Pontic species *S. nutans* L. and the Macedonian endemic species *S. jurišićii* Koš. This hybrid is remarkable for the fact that it has been repeatedly obtained several times since 1931, when it first appeared. In all instances, though parental plants of different origin were used, the hybrids were quite identical. The results of reciprocal crosses have also been quite the same. *S. němecii* has already been thoroughly described (Hrubý, 1933, 1935); its cytological investigation has also been published (Hrubý, 1948). Owing to nearly normal meiosis, it is relatively highly fertile, thus offering the possibility of further genetic analysis of different characters. It appears to be intermediate between the parental species, which is a characteristic of interspecific hybrids in general.

In the present paper attention will be paid to leaf characters, namely to some morphological and anatomical signs and to their mutual relations. As shown in fig. 1, the leaves of *S. němecii* look intermediate in general, as well as in total size, in length of the petiole and especially in their segmentation. The general appearance of the leaves cannot, however, be estimated as a single

character, but the inheritance of individual component characters should be followed separately. An extremely wide segregation in the F_2 generation, which in extreme cases exceeds the parental forms, does not point to a simple hereditary basis, but indicates a more complicated one of a polygenic type.

Fig. 2. Types of vascular bundle course in the petiole: type II at left, type III at right.

Besides external morphological signs, the course of the vascular bundles in the leaf petiole is very typical for different species of the genus *Salvia*. On a cross-section the petiole is usually semicircular, with two lateral edges and a variably shallow ridge between them on the upper side. Big strips of collenchyma always run in the edges, followed by chlorenchyma underneath. The body of the petiole is filled with parenchymatic tissue in which the vascular bundles are situated. In all species belonging to all sections,one vascular bundle runs immediately at the side of each lateral collenchyma strip. Between these bundles and the main conducting system in the centre of the petiole there may lie one or two small bundles. This depends on the massiveness of the petiole. In all the structures just mentioned there are no substantial or characteristic differences between species from different subgenera and sections. Very characteristic are, on the other hand, the vascular bundles in the centre of the petiole, and their arrangement. One or more vascular bundles may run along here. They are oriented by their bast parts to the lower side of the petiole and by the woody part towards the upper ridge. According to the number and arrangement of these vascular bundles, four general types with several subtypes may be distinguished. These types are characteristic for subgenera, sections and even species of the genus *Salvia*, as already stated earlier (HRUBÝ, 1955).

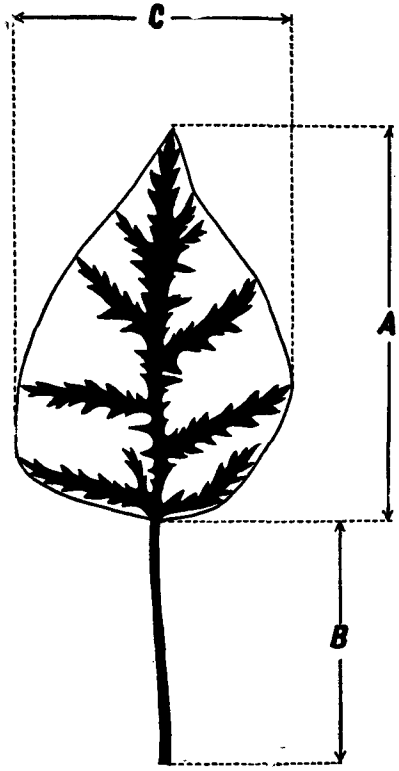


Fig. 3. Schematic drawing showing the methods of getting ratio indices of the morphological signs of the leaves.

In the section *Plethiosphace* the basic types II and III occur (see fig. 2). The parental species of our hybrid differ in the type of their petiolar vascular bundle course. In *S. nutans* there is type III, whereas *S. jurišićii* is characterized by type II. In the hybrid *S. němecii*, type II was always found, thus showing a preponderance over type III. In the present paper the question

will be dealt with of whether this is due to a simple dominance or to a more complicated inheritance of this anatomical character. Further mutual relations between this sign and single external morphological characters of the leaves will be investigated, as well as correlations between these morphological signs themselves.

Material and Methods

The total number of investigated plants of the F_2 generation was n = 238. At least one characteristic leaf was taken from each plant. A cross-section through the petiole was made in the fresh state, this section being precisely in the middle of the petiole. The type of vascular bundle course was determined on this section. Afterwards each leaf was put into a parchment envelope of appropriate size, on which the type was noted and the number of the respective plant. After pressing and drying, the contours of the leaves were carefully drawn. In each leaf three characteristics were evaluated separately: 1. The length of the petiole, 2. the shape of the general contour, 3. the segmentation of the leaf blade.

As leaves of individual plants differ considerably in size, it is necessary to compare relative values of the ratio indices. These indices were calculated in the following manner (see fig. 3). The length of the petiole is characterized by the ratio of the length of the leaf blade (A) to the length of the petiole (B), thus $i_1 = \frac{A}{B}$. Since the petioles were halved for determining the anatomical structure, the length of petiole measured on the actual drawing should be multiplied by two. The contour shape of the leaf was expressed by the length/breadth ratio of the ideal leaf blade, $i_2 = \frac{A}{C}$.

Most difficult to express exactly is the degree of segmentation of the leaf. Comparable values may be offered again by a ratio index of the ideal surface of a complete, entire leaf of the given size and shape to the actual surface of this leaf. Therefore, in each drawing of the leaf its ideal entire contour was also drawn. Then, by means of a planimeter, the area limited by this line was measured and this value divided by the area of the actual leaf (which is black on fig. 3). The respective index is therefore obtained $i_3 = \frac{\text{White area}}{\text{Black area}}$. (The white area includes the black one, of course.) When several leaves were measured from the same plant, the mean value of individual indices was calculated. Each of the 238 plants was therefore characterized by three indices and the type of vascular bundle course. In the same way the respective indices of both parental species and the F_1 hybrid were obtained.

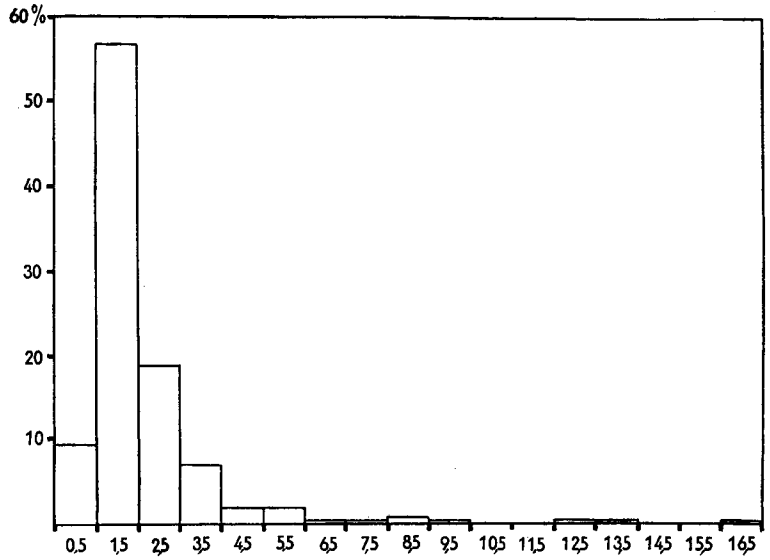
First, each of the characteristic values was judged separately. The arithmetic mean, with standard error, was calculated and the extent of variability estimated by means of the coefficient of variation. The diagrams are in the form of percentage histograms, the values of indices being grouped in whole units. Further, correlations between the type of vascular bundle course and single morphological indices were calculated, as well as mutual correlations between these indices.

Results and Discussion

1. Type of vascular bundle course. In *S. němecii* type II occurs. In F_2 172 plants had type II, and 66 plants type III. The empiric ratio 172 : 66 compared with the theoretical one on a 3 : 1 supposition gives the value of $\chi^2_{(1)} = 0{\cdot}94$, to which corresponds the probability $P \doteq 0{\cdot}35$. From this it follows that the difference between type II and III is based monofactorially,

with a complete dominance of type II. This is an interesting instance of simple Mendelian inheritance in an anatomical character.

2. Length of petiole. The parental species *S. nutans* has leaves with very long petioles, the ratio index $i_1 = 1{\cdot}28 \pm 3 \,.\, 0{\cdot}11$. The variation spread is relatively small, the coefficient of variation being $v = 16{\cdot}40$. The second parental species *S. jurišićii* has, on the contrary, the basal leaves shortly petiolate, the axial leaves very shortly petiolate to completely sessile. Though

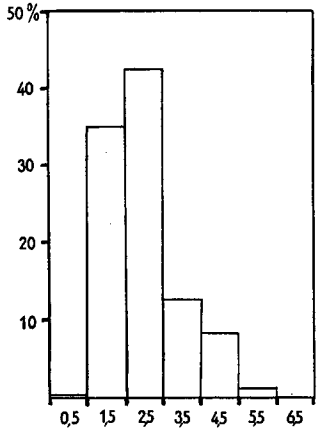


Diagr. 1. A histogram showing segregation of values of petiole length index in F_2 plants.

only the lowest leaves were taken for getting the index, this species displays a much wider—approximately twice—degree of variability, $v = 36{\cdot}30$, the index itself $i_1 = 7{\cdot}11 \pm 3 \,.\, 1{\cdot}15$. Their hybrid, *S. němecii*, does not show intermediarity in this sign, but a considerable preponderance of the character of the species *S. nutans* occurs. The leaves have quite long petioles, though not to such a degree as in the parental species *S. nutans* itself. The value of the index is here $i_1 = 1{\cdot}75 \pm 3 \,.\, 0{\cdot}14$. At the same time the spread of variability remains relatively small, $v = 19{\cdot}45$, only a little larger than in *S. nutans*.

In the F_2 generation a very wide segregation takes place, and the extreme values in both directions exceed the index values of the parental generation. The lowest value of the index has been found to be 0·64, or a leaf with petiole nearly twice as long as the blade, whereas the second extreme value was 16·76 which characterizes a nearly sessile leaf. The coefficient of variation also corresponds to this amplitude, reaching an extraordinary high value $v = 87{\cdot}15$. But the mean value of the index $i_1 = 2{\cdot}18 \pm 3 \,.\, 0{\cdot}12$ does not differ much from the average of the preceding generation, and the modal

value is actually in accordance with it (see diagr. 1), as the variation class of the mean value 1·5 is frequented by 57·2 per cent. The value of this index in the F_1 generation lies in the same class. It may therefore be assumed that the ratio of the petiole length to the leaf blade length is probably inherited, but governed by a large number of units of polygenic character, with a certain preponderance of those inducing a longer petiole. The parental species themselves do not represent the extreme combinations of these multiple factors.



Diagr. 2. A histogram showing segregation of values of length/ /breadth index in F_2 plants.

3. Shape of leaf contour. This character is evaluated by means of the length to breadth index. In the first parental species *S. nutans* the leaves are narrow and long ovate, as expressed by $i_2 = 2{\cdot}16 \pm 3 \,.\, 0{\cdot}17$. The variation amplitude is again relatively small, $v = 16{\cdot}22$. *S. jurišićii* has the leaf contour broadly ovate to cordate, $i_2 = 1{\cdot}63 \pm 3 \,.\, 0{\cdot}15$ and the spread of variation is here a little larger, $v = 20{\cdot}24$. The hybrid *S. němecii* conforms in leaf contour almost completely to its parent *S. jurišićii*: $i_2 = 1{\cdot}62 \pm 3 \,.\, 0{\cdot}07$ and displays in this character considerable uniformity, the variation coefficient value being smaller than in both parental species, $v = 11{\cdot}27$.

In the F_2 generation the segregation again surpasses the values of the parental generation. There were plants with very narrow, nearly lanceolate leaves, having an index value 5·62, whereas the second extreme was represented by leaves nearly reniform, broader than long, their index value being 0·99 Most plants have leaves broader than F_1, 42·4 per cent are characterized by an index within the limits of 2 and 3 (see diagr. 2), therefore the mean value of the index is also $i_2 = 2{\cdot}45 \pm 3 \,.\, 0{\cdot}06$. The variation spread — $v = 39{\cdot}19$ — is approximately twice that of the more variable progenitor, and four times that of the F_1 generation. This result suggests the following explanation. The leaf contour is again inherited in a complex manner, and a group of factors conditioning a greater breadth of the leaf may somehow be linked together. Thus there are higher frequencies of classes having higher indices than would be expected by free distribution and an independent polygenic basis.

4. Segmentation of leaves. In this character the greatest differences occur between the original parental species (see fig. 1). *S. nutans* has leaves nearly entire, only slightly crenate-denticulate, and is quite constant in this character. This is shown also by the very minimal variability, as the coefficient of variation has the value of only $v = 1{\cdot}92$. A comparison of an absolutely entire ideal leaf contour with the actual situation, expressed by the ratio of these two surfaces (ideal : actual), gives the index $i_3 = 1{\cdot}08 \pm 3.0{\cdot}016$. The leaves of the species *S. jurišićii*, on the other hand, are deeply and simply pinnate, the pinnation nearly reaching the central nerve. The linear segments sometimes show traces of further pinnation. The surface index is $i_3 = 3{\cdot}92 \pm$

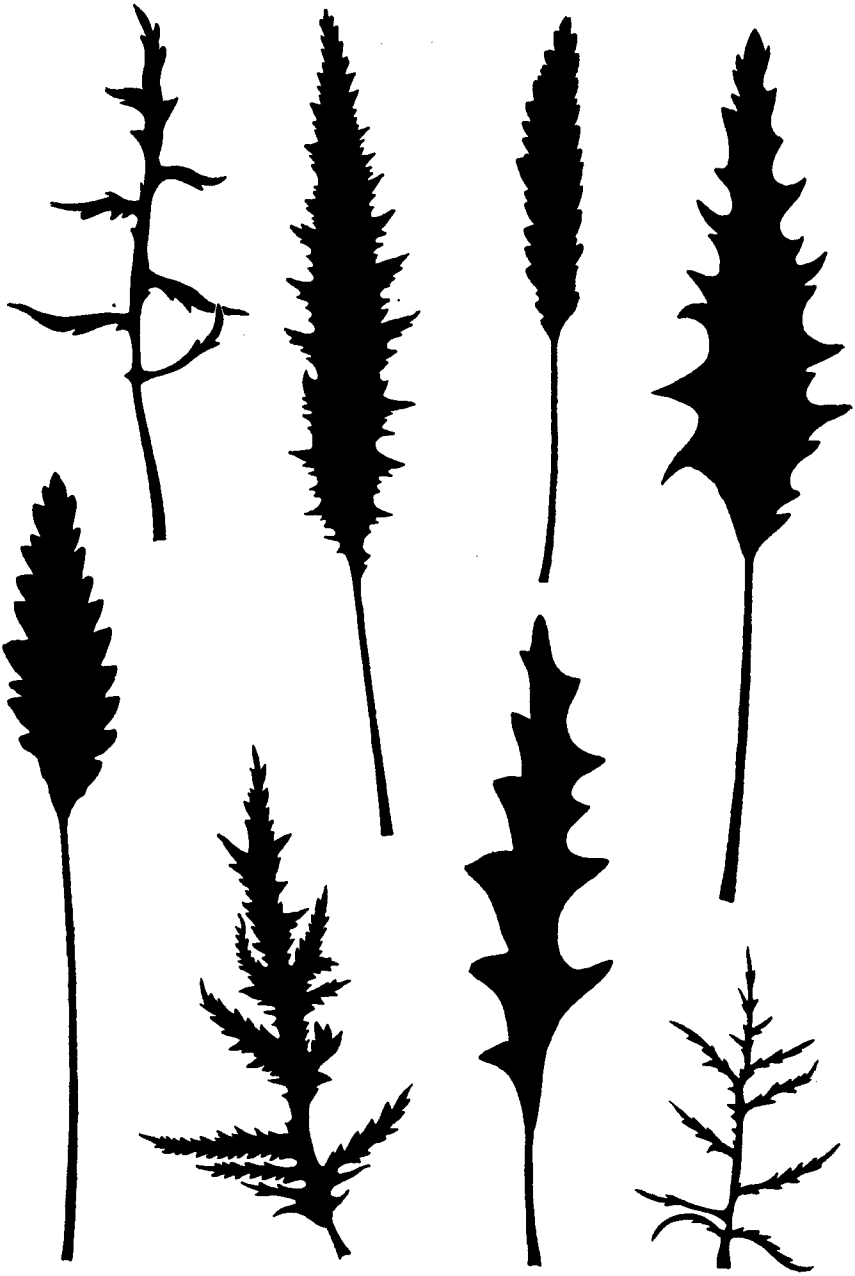
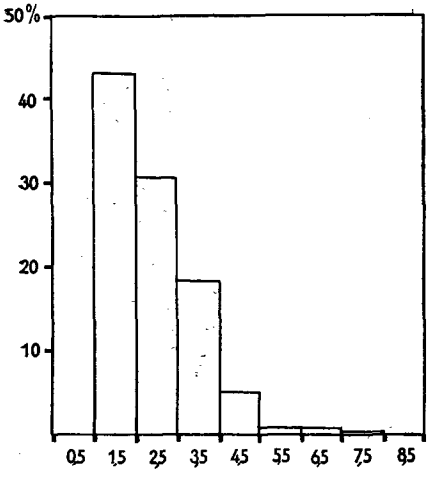


Fig. 4. Several leaves of F_2 segregating plants. Extreme and extraordinary, unexpected forms Reduced 1 : 2.

$\pm$ 3 . 0·33 and the variation spread is relatively small, the coefficient of variation having a value v = 16·85. *S. němecii* appears quite intermediate in this character. The leaves are broadly and deeply pinnatipartite and considerably uniform, and the coefficient of variation is small, v = 15·52. The surface index itself has an intermediate value $i_3 = 2·29 \pm 3 . 0·14$. This value lies just between the arithmetic (2·50) and geometric (2·10) mean of the values of both parental species.



Diagr. 3. A histogram showing segregation of values of index of leaf segmentation in F_2 plants.

The segregation in F_2 is extremely diverse and even the surface index cannot express its morphological diversity. Here plants may be found with leaves nearly entire, others with leaves lobate, dentate, pinnatifid, pinnatipartite to narrow pinnatisect with fine denticulation. A certain picture of this diversity is presented by fig. 4, where extreme cases are drawn together with some unusual forms. The mean value of the surface index does not differ much from that of *S. němecii* (F_1), being $i_3 = 2·45 \pm 3 . 0·07$, but the amplitude of variability is much greater, the value of the coefficient being v = 43·75. The situation of the original parental species is not surpassed in the direction towards entirety, because the index value here is nearly 1 (i.e. 1·08). In the other direction however, the index value is twice as high, as in one plant an index of 7·27 was found. As demonstrated in diagr. 3, the most frequented class—by 42·8 per cent—is that having the index value within the limits of 1 and 2. The variation curve would be of a half-curve type.

When we take into consideration the results mentioned above, the segmentation of leaves may again be considered as an inherited character, governed by polygenes. The similarity of the mean values in F_1 and F_2 generations, as well as the intermediate character in F_1, point most likely to a free, partly additive, partly multiplicative action of polygenes concerned. One of the original parental species represents, however, the minimal dose of the effective genotype; therefore its value cannot be transgressed and the variation curve of the F_2 generation is a half-curve. But this minimum could also have been reached by the action of inhibiting factors in the heterozygous condition, the segregation of which makes it possible for F_2 to surpass considerably the extreme value in the opposite direction. This possibility is also strengthened by the modal character of the lowest variation class.

A complete survey of all morphological characters of the leaves of both parental species and in F_1 and F_2 generations is presented in Table 1.

5. Correlations. Between the type of vascular bundle course and individual morphological characteristics, the correlation coefficients have always been

Table 1. Mean values of morphological indices and their spread of variation in all three generations

	i_1	v	i_2	v	i_3	v
S. nutans (P_1)	1·28	16·40	2·16	16·22	1·08	1·92
S. jurišićii (P_2)	7·11	36·30	1·63	20·24	3·92	16·85
S. němecii (F_1)	1·75	19·45	1·62	11·27	2·29	15·52
F_2	2·18	87·15	2·45	39·19	2·45	43·75

found to be below the limit of significance. Their values are so minute that no correlation can be conceded between these signs. (Length of petiole/vascular bundle type $r = 0{\cdot}01$, segmentation/vascular bundle type $r = -0{\cdot}06$, only in length-breadth index/vascular bundle type is the coefficient a little larger, $r = -0{\cdot}12 \pm 3 \,.\, 0{\cdot}064$, but this value is not significant either at the $P = 0{\cdot}05$ level.) Thus no linkage relations can be assumed between the gene responsible for the type of the vascular bundle course in the leaf petiole and the polygenic systems governing external morphological characters of the leaves. This gene must be localized in a different chromosome from those polygenic complexes.

On the contrary, if we consider the mutual relations of single ratio indices characterizing external morphological features of the leaves, we always get values of coefficients which are significant or even highly significant. The weakest correlation was found between the length of the petiole and the contour shape of the leaf i_1/i_2, $r = -0{\cdot}15 \pm 3 \,.\, 0{\cdot}064$. This negative correlation, though small, is statistically significant and means that in F_2 plants there is a slight preponderance of leaves which are narrow and have a longer petiole and, on the contrary, a tendency to more sessile leaves, having also a broader blade. Between the length of petiole and the segmentation of leaves i_1/i_3 a highly significant correlation was found, viz. $r = +0{\cdot}31 \pm 3 \,.\, 0{\cdot}061$, which indicates that leaves with longer petioles are less divided, whilst more sessile leaves are more segmented. The strongest, highly significant, negative correlation was determined between the segmentation of the leaf and its length-breadth index i_3/i_2. Here $r = -0{\cdot}42 \pm 3 \,.\, 0{\cdot}059$. That shows that the narrower leaves are more entire, and on the contrary, the broader leaves are more divided.

All these three correlations are markedly expressed in the original parental species. Correlations between partial characteristics suggest a possibility of some linkage between their genotypic bases. Since in all cases there are polygenic systems, it could be formulated in such a way that a certain fraction of the number of polygenes participating in manifestation of a couple of characters may be located in the same chromosome. The greater part, however, are localized in different pairs of chromosomes.

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Наследование некоторых признаков листьев у *Salvia němecii* HBÝ

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Межвидовой гибрид *Salvia němecii* (*S. nutans* × *S. jurišićii*) описанный автором уже раньше, плодоносит совершенно нормально. Поэтому на 238 растениях генерации F_2 были исследованы следующие признаки: тип сосудистых пучков в черешке, отношение длины черешка к длине листовой пластинки, индекс длины и ширины пластинки и степень расчленения листа, выраженная отношением идеальной площади листовой пластинки к его действительной площади. Все эти характеристики сравнивались с положением у родительских видов и F_1 гибрида. Было обнаружено:

1. тип II сосудистых пучков полностью доминирует над типом III (расщепление происходит в отношении 172 : 66, $\chi^2_{(1)} = 0{,}94$, $P \doteq 0{,}35$),

2. все внешние морфологические признаки основаны полигенно. Расщепление в F_2 очень широкое и крайние типы превышают соответствующие величины у родительских видов,

3. тип сосудистых пучков наследуется независимо от внешних морфологических признаков. Доказательные корреляции здесь не были обнаружены,

4. внешние морфологические признаки между собой, однако, коррелируют, что можно доказать на примерах. Особенно положительна корреляция между длиной черешка и расчлененностью листа ($r = 0{,}31$) и отрицательная корреляция между степенью расчлененности листовой пластинки и отношением длины к ширине ($r = -0{,}42$). Из этого можно сказать, что меньшая часть соответствующих полигенных систем взаимосвязана, то есть локализована в той же хромозоме. Большая часть их наследуется без взаимной зависимости.