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Genetic Analysis of Colour Mutants in *Salvia splendens*

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Ad memoriam Professoris Dr. K. Hrubý dedicatum

Abstract — In *Salvia splendens*, 4 genes have been identified which participate in the type of inflorescence pigmentation: the gene for the presence or absence of anthocyanin (Pp), the gene for the chemical quality of anthocyanin (differing in the degree of hydroxylation of the aglycone B'-ring; Vv), and genes modifying in various ways the intensity of pigmentation Int int and Ll.

The presence of two unusual complex anthocyanins has been stated, and genotypes of five original and three newlygained coloured forms of *Salvia splendens* have been determined.

Introduction

The original red form of the ornamental species *Salvia splendens* possesses intensively bright red-coloured inflorescence (bracts, comparatively large calyces, corollae, and the upper parts of the stem). This species, however, occurs also in spontaneous mutant forms of other colours or other intensities of inflorescence pigmentation. The flower pigments are represented, here, by anthocyanins.

On the whole, there are three main types of anthocyanins occurring in *Salvia splendens*: the red salvianin, which is a derivative of pelargonidin (newly, according to Karrer, 1958 it is very likely a 3,5-diglucoside of pelargonidin esterified by one molecule of 4-hydroxy-cinnamic acid, probably in the position 7, and by two molecules of malonic acid-monomethylester in glucose residues; in spite of this in our material mono- and diglucosides of the remaining analogical structure are considered to be found); and further, structurally analogical, probably not yet named, derivatives of cyanidin and delphinidin (Hendrychová-Tomková, in print). Besides different chemical qualities of anthocyanins also variations are occurring, here, concerning the intensity of colouring and the anatomical distribution of the pigment: a ful, normal—or weak intensity, on one hand or uniform, e.g. normal—or not uniform distribution of pigment, on the other hand (further designated as "limited localization").

The mutual crossing of five differently coloured forms, and a genetic analysis of three filial generations made it possible to determine the heritable bases of inflorescence colour in the studied species. Chemical analysis of anthocyanins carried out simultaneously contributed to approximate definitions of function in some of the ascertained genes.

Material and methods

A brief description of the original coloured forms of *Salvia splendens*:

F. *rubra*: Intensively and uniformly distributed red-tinted inflorescence contains mostly red salvianin with a week addition of the purple derivative of cyanidine. The pigment is present in the cells of epidermis including the papillae and trichomes tinted to the same degree while the inner epidermis of organs is of almost the same intensive red as the outer one.

F. *violacea*: The violet inflorescence is intensively and uniformly pigmented. It contains mostly violet and purple derivatives of delphinidin and cyanidin, red salvianin in small amount only. The distribution of pigment as in f. *rubra*; f. *violacea* is of somewhat lower and more subtile growth.

F. *rosea*: The inflorescence is rose-tinted; the total content of anthocyanins is much lower than in f. *rubra* but of almost the same composition. The anatomic pigment distribution is uniform and identical with the above forms. This forms is of a taller and slimmer growth (lateral branches and leaves form a more acute angle) with a tendency to a rank growth as compared with the f. *rubra*; the leaves are of a lighter green.

F. *carnea*: the inflorescence is of a finer salmon-red which is caused partly by a total weaker intensity of pigmentation against the f. *rubra*, partly and chiefly, by a limited localization of pigment: the margins of both corolla lips, and the whole of middle tip of the lower lip are only lightly tinted being almost white. At the same time only the outer corolla epidermis is distinctly pigmented, the inner one is also almost white; the inner epidermis of the calyx is less tinted than the outer one. The finer, lighter red shade of this form is also caused by a much weaker trichome pigmentation against the epidermis (in the calyx they are almost white). The chemical quality of pigment in the f. *carnea* corresponds with the f. *rubra*.

In the *f. carnea* there is, besides that a frequent occurrence of flower abnormities: the enlarged and crooked connective with a sterile branch bearing a stunted anther. Also the rudimentary staminodia are fairly often enlarged and terminated with an anther. These abnormities are usually acompanied with the fissure of corolla upper lip.

F. *carnea* is of a typical low and subtile growth, the leaves being dark-green, bare and horizontal.

F. *alba*:[1]) possesses no anthocyanin in any organ (while in other forms the pigment is present even in the stem in the form of cyanidin derivative); it is of a medium, fragile growth, the inflorescence being subject to necrosis when submitted to direct sunshine, or bad weather.

The inflorescences of all the above-described forms were analyzed for anthocyanin contents by means of paper chromatography using the usual analytical methods (acid and alkalic hydrolysis). There was made a separation of the anthocyanin extracts of various colour forms of the species, then the identification of aglycones and the sugar component, and further also the estimation of the presence of the 4-hydroxy-cinnamic and malonic acids. The first purpose of these analyses was a relative qualitative comparison of the chemical composition of the anthocyanins found. According to the intentions of this paper the differences in the aglycones are the most important.

The individual forms were mutually crossed in all possible combinations, the progenies being individually followed from the first to the third filial generation. The results of the reciprocal crossings were all of the same character, therefore, the numerical data of both directions are given summarily for each combination.

The results of the factor analysis are given in this paper, the more detailed results of the qualitative and quantitative gene effects taking part in the inflorescence pigmentation of *Salvia splendens* will be published later, together with a more detailed description of the analytical methods (HENDRYCHOVÁ-TOMKOVÁ' l. c.).

Phenotypes and segregation ratios

First filial generation: The violet colour is incompletely dominant, namely, almost dominant (i.e. somewhat more reddish or, lighter violet colour shade) in all crosses of the f. *violacea* (× f. *alba*, × f. *rosea*, × f. *carnea*, × f. *rubra*); the red is dominant in crosses: f. *rubra* × f. *carnea*, × f. *rosea*, × f. *alba*. The crosses f. *rosea* × f. *carnea*, f. *rosea* × f. *alba* and f. *carnea* × f. *alba* give

[1]) The names of these coloured forms by HRUBÝ (1961).

a complementary effect, normal deeply red colouring of the inflorescence of hybrid plants. Both directions of all crosses give identical results.

Segregation in the second filial generation:

Monohybrid:

1. f. *violacea* × f. *rubra*:
F_1 reddish violet,
F_2 violet 380, red 117 plants,
namely, the segregation ratio 3 : 1 ($\chi^2 = 0{,}564$; P = 0,50).

The frequency of violet homozygous and reddish-violet heterozygous plants are further and always counted together because of a difficult distinguishing of both phenotypes so that the incomplete dominance is not taken into account. Only in this case, for illustration, we introduce segregation ratios in distinguishing both shades, namely in comparison with the segregation ratio of 1 : 2 : 1.

Dark violet 128, reddish violet 250, red −117; ($\chi^2 = 0{,}538$; P = 0,80).

2. f *rubra* × f. *alba*:
F_1 red,
F_2: red 152, white 53,
the segregation ratio 3 : 1 ($\chi^2 = 0{,}0796$; P = 0,80).

3. f. *rubra* × f. *rosea*:
F_1 red,
F_2: red 176, rose 60,
segreagtion ratio 3 : 1 ($\chi^2 = 0{,}0225$; P = 0,90).

4. f *rubra* × f. *carnea*:
F_1 red,
F_2: red 186, salmon red 64,
the segregation ratio 3 : 1 ($\chi^2 = 0{,}048$; P = 0,80).

Dihybrid segregations:

5. f. *violacea* × f. *rosea*:
F_1 reddish violet,
F_2: violet 243, light violet 76, red 70, rose 32,
the segregation ratio 9 : 3 : 3 : 1 ($\chi^2 = 2{,}6557$; P = 0,50).

6. f *violacea* × f. *carnea*:
F_1 reddish violet,
F_2: purple 122, light violet 35, red 47, salmon red 19,
the segregation ratio 9 : 3 : 3 : 1 ($\chi^2 = 3{,}685$; P = 0,30).

Dihybrid with interaction; without the change of segregation rations:

7. f *carnea* × f. *rosea*:
F_1 red,
F_2: red 261, salmon red 85, pink 85, light pink 34,
the segregation ratio 9 : 3 : 3 : 1 ($\chi^2 = 0{,}9495$: P = 0,80).

Dihybrid segregation with interaction and modified segregation ratio:

8. f. *alba* × f. *rosea*:
F_1 red,
F_2: red 264, rose 86, white 140,
the segregation ratio 9 : 3 : 4 (recessive epistasis), ($\chi^2 = 3{,}365$; P = 0,2).

9. f *alba* × f. *carnea*:
F_1 red
F_2: red 158, salmon red 57, white 61,
the segregation ratio 9 : 3 : 4 (recessive epistasis), ($\chi^2 = 1{,}5086$; P = 0,50).

Dihybrid segregation with interaction and linkage:

10. f *violacea* × f. *alba*:
F_1 reddish violet,
F_2: violet 191, red 2, white 66,
(i. e., after a correction: violet 191, red 2, white 2 + 64; explanation below, in the folloving chapter).

The segregation ratio of three classes given by a recessive epistasis is modified by a linkage of two genes for the anthocyanin synthesis of 1,5% recombination rate.

Deduction of genotypes from the data of F_1 and F_2

1. The dominant violet and recessive red phenotypes are alternative manifestations of one gene designated as Vv. This gene controls the chemical quality of anthocyanin concerning the degree of hydroxylation of the B-circle (V—delphinidin and cyanidin, the violet phenotype; v—pelargonidin, the red phenotype; further, see pag. 224). The monofactorial segregation was proved in cross no 1; V is incompletely dominant over v, the heterozygote Vv possesses a somewhat redder shade of violet than the homozygous Vv.

F. *violacea* in this gene is of a VV constitution, f. *rubra* vv.

2. The difference in the intensity of pigmentation is also monofactorial as follows from the no 3. crossing f. *rubra* × f. *rosea*; f. *rubra* possesses normal, deep pigmentation (dominant, Int), f. *rosea* possesses a weak pigmentation (recessive, int), with the same quality of pigment.

Hence, f. *rubra* is of the vv Int Int genotype, f. *rosea* being of the vv int int genotype.

The independent assortment of genes Vv and Int int follows from the cross of forms differring also in quality of pigment (f. *violacea* × f. *rosea*, see no 5).

The genotype of the f. *violacea* is VV Int Int.

In F_2 of this cross, besides intensively violet phenotypes (the original f. *violacea* VV Int Int and somewhat more reddish or lighter violet dihybrids and monohybrids in the first or second gene), and rose phenotypes (the second parent vv int int), appear also phenotypes which are a combination of colour and intensity: light violet (type "rosea"; of the expected genotypes VV int int, and the slightly distinguishable Vv int int) and a deep red one (vv Int Int and vv Int int).

3. The limited localization of pigment typical for f. *carnea* is, again, simply recessive against the normal, uniform distribution of pigment of f. *rubra* (see cross no 4). The corresponding gene was designated as Ll.

Thence, f. *rubra* is vv LL, f. *carnea* vv ll.

The independent assortment of genes Vv and Ll follows from dihybrid cross of parents different in colour and pigment localization (f. *violacea* × f. *carnea*, see no 6).

The genotype of f. *violacea* is VV LL.

In F_2 occur, again, besides the parental types, recombinations of colour and pigment localization: phenotypes light violet (of the "carnea"type; bluish light-violet of an expected genotype VV ll and reddish light-violet of an expected genotype Vv ll), and red (genotypes vv LL and vv Ll).

The phenotype with a decreased colour intensity as well as the phenotype with limited pigment localization may appear independently of colour, the genes Vv and Int int on one hand, and Vv and Ll on the other hand combining independently.

4. In the cross f. *carnea* × f. *rosea* (no 7; forms, which differ in the way of decrease in full colour) a complementary effect is gained in F_1 a deeply red pigmentation. That proves on the first, that, the constitution of f. *carnea* is Int Int ll, and f. *rosea* int int LL, and on the second, that for the realization of the phenotype of the original form of *Salvia splendens* (f. *rubra*), at least one dominant allele of each modifying gene Int and L, is necessary. The existence of LL and Int Int in f. *rubra* is proved, of course, by both corresponding monohybrid crosses: f. *rubra* × f. *rosea* (cross no 3), and f. *rubra* × f. *carnea* (cross no 4).

The genotype of f. *rubra* is thus vv Int Int LL.

Both genes, Int Int and LL mutually assort at random as manifested in the F_2 generation of the cross of f. *carnea* × f. *rosea* (cross no 7). There appeared plants of a new light-rose phenotype (in a corresponding frequency) which may be explained as combination including, in homozygous state, recessive alleles of both genes: int int ll; the corresponding dominant combinations, however, cannot be distinguished as phenotypes from the red phenotype of dihybrids repeating F_1.

5. Deriving the white-form genotype (f. *alba*): The difference white—red is monofactorial, the coloured form being dominant (cross no 2). Complementary effect (red inflorescence) in F_1 when crossing the f. *alba* with both forms of recessive tinting modification (f. *alba* × f. *rosea*, cross no 8, and f. *alba* × f. *carnea*, cross no 9) indicated that f. *alba* is homozygous dominant in both modifying genes, Int and L.

F. *alba* is thus --Int Int LL.

The difference f. *alba*—f. *rosea* and, analogically also f. *alba*—f. *carnea* is, however, difactorial (cross no 8 and no 9); if the crossing of f. *rubra* × f. *alba* gives monofactorial segregation the first question is whether it is not an allelic absence of pigment for violet and red. Dihybrid segregation in the combination of f. *violacea* × f. *alba* (cross no 10), however, indicated the existence of a further gene, Pp, conditioning the very synthesis of anthocyanins; the segregation of the red phenotype in this crossing may be, namely, explained only by a recombination provided f. *alba* itself being a bearer of a faculty to form red pigment, namely the gene vv; it is however, without pigment owing to the homozygous recessive state in the basic gene, pp; in f. *violacea* then both genes are homozygous dominat (PP VV); by recombination, a red phenotype is thus formed (Pv), together with a white phenotype (pV, found indeed by further crossings, as will be later published).

The presence of vv in the original f. *alba* is proved also by an increased synthesis of red salvianin in reddish violet hybrids of f. *violacea* × f. *alba*, the same as in the incompletely dominance of the heterozygous f. *violacea* × f. *rubra*—both compared with the homozygous f. *violacea*—ascertained in a preliminary colorimetric determination.

Thence, the outgoing genotype follows, f. *alba*: pp vv Int Int LL; all forms with pigmented inflorescence possess genotypes PP--.

There exists a relation of recessive epistasis between the genes pp and Vv as may be judged from what has already been said; that follows, especially, from the results of the crossing: f. *alba* × f. *rosea* (cross no 8; pp vv Int Int × PP vv int int) where the empirical segregation ratio of the phenotype categories indicates a good agreement with the theoretical assumption 9 red: 3 rose : 4 white typical for the recessive epistasis; quite analogical is the situation in the combination of f. *alba* × f. *carnea* (cross pp vv LL × PP vv ll) with the following segregation categories: red, salmon-red and white. Thence follows the independent assortment of the genes PP and Int Int, and PP and LL the relation of Pp to Vv remaining yet unknown.

The "basic" gene Pp, however is linked with the gene for the chemical quality of anthocyanin Vv. This is evident from a combination where the two-factor difference between the parents relates just to these two genes, namely when crossing f. *violacea* × f. *alba* (PV . PV × pv . pv). In F_2 there is a considerable disproportion in the frequency-ratio of phenotype classes against

the presumption for a recessive epistasis. There was a three class empirical segregation ratio for the cross-over value calculation provided (assumed the reciprocal recombination products were of the same frequency): 191 violet: 2 red : 66 white was made up to: 191 violet (phenotype PV) : 2 red (phenotype Pv) : 2 white (phenotype pV) : 64 white (phenotype pv).

The approximate cross-over value between the configurations PV and pv is 1,5% of recombinations.

Segregation in the third filial generation

In mohohybrid crosses (f. *violacea* × f. *rubra*, f. rubra × f. *alba*, f. *rubra* × f. *rosea* and f. *rubra* × f. *carnea*) a segregating part of progenies indicated ratios analogical to F_2, the monofactorial nature of the difference thus being confirmed: 1. in the presence or absence of pigment, (P—p), 2. in the chemical quality of the pigment (V—v), 3. in the intensity of pigmentation (Int—int), and 4. in the anatomical distribution of the pigment (L—l).

In dihybrid crosses the following phenotypical compositions of the F_3-progenies were found, detecting the respective F_2-parental genotypes:

In crossing f. *violacea* × f. *carnea*:

F_2-parent plant (phenotype):	F_3-progeny (phenotypes):	F_2-parent plant (genotype deduced):
violet	no segregation	VVLL
	— segr. into violet and red	VvLL
	— segr. into violet and light violet	VVLl
	— segr. into violet, red, light violet and salmon red	VvLl
red	no segregation	vvLL
	— segregation into red and salmon red	vvLl
light violet	no segregation	VVll
	— segregation into light violet and salmon red	Vvll
salmon red	no segregation	vvll

A similar situation is in F_3-progenies of crossing f. *violacea* × f. *rosea* where f. *violacea* double dominant VV Int Int and f. *rosea* double recessive vv int int is.

In crossing f. *carnea* × f. *rosea*:

F_2-parent plant (phenotype):	F_3-progeny (phenotypes):	F_2-parent plant (genotype deduced):
red	no segregation	vv Int Int LL
	— segr. into red and rose	vv Int int LL
	— segr. into red and salmon red	vv Int Int Ll
	— segr. into red, rose, salmon red and light rose	vv Int int Ll
rose	no segregation	vv int int LL
	— segr. into rose and light rose	vv int int Ll
salmon red	no segregation	vv Int Int ll
	— segr. into salmon red and light rose	vv Int int ll
light rose	no segregation	vv int int ll

In crossing f. *alba* × f. *carnea*:

F_2-parent plant (phenotype):	F_3-progeny (phenotypes):	F_2-parent plant (genotype deduced):
red	no segregation	PP vv LL
	— segr. into red and white	Pp vv LL
	— segr. into red and salmon red	PP vv Ll
	— segr. into red, white and salmon red	Pp vv Ll
salmon red	no segregation	PP vv ll
	— segr. into salmon red and white	Pp vv ll
white	always white	pp — —

A similar situation arises when combining analogically f. *rosea* (PP vv int int) and f. *alba* (pp vv Int Int).

The segregation of progenies in F_3 generation of the given combinations confirmed thus the presence of assumed genotypes in F_2 generation and thus, the genotypes previously derived. The numerical results of all combinations correspond even in F_3 to previous assumptions, therefore, they are not given, here.

Only the data on the combination f. *violacea* × f. *alba* were tested by means of analyses of the B_1 generation of backcross [f. *alba* × (f. *violacea* × f. *alba*)]. Here, the numerical results are given since they appear somewhat different against F_2; there was the three-class segregational ratio gained in B_1 (99 violet : 3 red : 80 white) provided again for further calculations as: 99 violet (phenotype PV) : 3 red (phenotype Pv) : 3 white (phenotype pV) : 77 white (phenotype pv).

The cross-over value calculated from backcross is approximately 3,5% recombinations between the PV and pv configurations, namely, somewhat higher against the previous data from F_2 (1,5%). This may be explained by two factors being involved: in *Salvia splendens* a certain percentage of autogamy cannot be excluded in artificial crossing(white phenotype) and further, it is fairly probable that the frequency of recombinations is not the same in both sexes, hence the difference in the results between F_2 and B_1. This question is further studied.

Nevertheless, even here, the occurence of the assumed segregation categories is confirmed: in the first place, the dihybrid nature of the difference between the forms f. *violacea* × f. *alba* (and thus also the genotype f. *alba* as pp vv), in the second place, the existence of a close linkage between the genes Pp and Vv.

Preliminary consideration of genes function

Gene Pp ("precursor"); for the gene identified as the basic gene for anthocyanin formation the symbol Pp has been elected similarly as in GEISSMAN et al. (1954). Since the analysis for other related aromatic compounds in the plants of pp-genotypes could not be carried out yet no comparison can be made with other "basic" genes for anthocyanin synthesis known in other species causing the absence of pigment in homozygous recessive state. Therefore, the relationship between our P to P or N defined by the above-mentioned author, or to Niv or Inc as introduced by BÖHME and SCHÜTTE (1956), cannot be decided. It means that at present it cannot be said at what stage of bio-

synthesis of anthocyanin pigment in *Salvia splendens* the gene P interferes and thus, at what stage the recessive pp acts as a genetic block.

It has been ascertained, by means of grafting a white phenotype on the pigmented one (pp/PP), similarly as did BÖHME ans SCHÜTTE (l. c.) that the product of the gene P necessary for the synthesis of anthocyanins, is immobile; its absence in the -pp-genotype cannot, therefore, be compensated by diffusion from other tissues; it might be an enzyme acting in but one way, only in a form bound to structures.

The gene Vv (f. *violacea*): the gene thus designated is determining the chemical quality of anthocyanins, distinguished in the degree of hydroxylation in the B-ring of the aglycon. The dominant V determines the prevailing synthesis of anthocyanidin with higher degree of hydroxylation, namely (simultaneously): delphinidin (with hydroxylation in the positions 3′, 4′, and 5′), and cyanidin (with hydroxylation in 3′ and 4′), and only slightly represented pelargonidin (with hydroxylation in 4′). For the present it is not yet possible to compare exactly our gene Vv in *Salvia* to the other genes known for chemical quality of anthocyanidin in its whole action. However, it has, as evident, a relatively wide range of activity according to its anthocyanidin products.

In the meantime, it can only be assumed that in the basic structure of aglycon with OH′-group in the position 4′ in the B-ring only a minimum (in a recessive allele), or a maximum (in a dominant allele) activity manifests itself of the specific oxidase acting in ortho-positions: only exceptionally, in 3′ or 5′ positions in case of a weak activity, which causes the trace formation of cyanidin besides the basic type, pelargonidin, and in 3′ or 5′, and also in 3′ and 5′ simultaneously, in case of a strong activity which causes the formation of delphinidin besides cyanidin, and besides pelargonidin, a remnant of individual unoxydized molecules of the basic structure (the interpretation supported by DVOŘÁK, 1963).

The gene Int int (intensity): this symbol has been used for a gene controlling alternative normal-full, or weak pigmentation both concerning the uniform pigment distribution. It is likely that Int int of *Salvia splendens* corresponds with the gene El el (eluta) of *Antirrhinum* (BÖHME and SCHÜTTE, 1956).

The gene Ll (localization): this gene determines an alternative: normal-uniformly distributed pigmentation, or non-uniformly distributed pigmentation (limited pigment localization); in ll, besides the limited pigment localization also the total pigmentation intensity is somewhat decreased.

Again, it is possible that Ll in *Salvia splendens* corresponds, in a way, with the gene Del del (delila) of *Antirrhinum* (also according to BÖHME and SCHÜTTE, l.c.).

A survey of genotypes and phenotypes

The original form of the species: f. *rubra*-genotype: PP vv Int Int LL,phenotype: red, XIII/181.[2])

The spontaneously mutant forms: f. *violacea* — genotype: PP VV Int Int LL, phenotype: violet, XLV/666—667; a dominant mutation; f. *alba* — genotype: pp vv Int Int LL, phenotype: white; a recessive mutation; f. *rosea* — genotype: PP vv int int LL, phenotype: rose, XIII/188; a recessive mutation; f. *carnea* —

[2]) The phenotypes are tried to be characterized by means of figures of the respective colour shades according to SÉGUY (1936).

genotype: PP vv Int Int ll, phenotype: salmon red, XI/153; a recessive mutation.

Newly combined types: f. *roseoviolacea* — genotype: PP VV int int LL, phenotype: light violet, XLV/664; f. *carneoviolacea* — genotype: PP VV Int Int ll, phenotype: light violet, III/43; f. *carneorosea* — genotype: PP vv int int ll, phenotype: light rose, XIII/189.

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