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Inheritance of fruit colour and of shoot's pigmentation in the case of interspecific raspberry hybrids

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Summary: In our research, fruit colour and the shoot's red pigmentation were evaluated in the hybrids of *Rubus idaeus* and *Rubus parvifolius* crossings. Y and Ys genes beside the T genes determine the fruit colour of interspecific hybrids, which is characteristic for raspberry. For the explanation of the significantly higher results of segregation then expected at the yellow fruit colour hybrids, we have supposed the presence of a second yellow gene (Y_2). In the yellow colour, a lot of different shade colours can be identified from light yellow to the apricot colour. In the regulation of the production of yellow and red colour, several other genes can participate also. Identification of these genes would require more additional research. The C gene determines the shoot colour of raspberry and in the case of wild raspberries we have revealed the role of a dominant Pr gene. The Y and Pr genes are descended linked. The value of crossing over is approximately 15%. The anthocyanin production inhibitory effect of the Y gene extends only for fruit. At the shoots of yellow fruit plants, strong anthocyanin production was observed.

Key words: *Rubus idaeus* L., *Rubus parvifolius* L., interspecific hybrids, fruit colour, cane colour, inheritance

Introduction

One of the promising opportunities in raspberry breeding for producing new varieties is the use of East-Asian raspberry-relative species. In our research institute, we have successfully crossed the European raspberry with several *Rubus* species from the *Idaeobatus* sub-genus. In this paper, we present some characteristics of these hybrids of *R. parvifolius* and the cultivated raspberry (*R. idaeus*). During the long breeding time at the research station we have experienced that in the results of the crossing of red fruit species and red fruit raspberries and the backcrossing of hybrids there is a high rate of yellow fruit seedlings. In these yellow fruit seedling group, the cane has generally purple colour and among them there is significantly higher number of disease resistant plants than in the red fruit hybrids, which has brown cane colour. For the sake of more effective selection work in the future, we have made an attempt to analyse the data of the existing population to clear up the inheritance characteristics of these features.

In the cultivated raspberry, the anthocyanin production both in the fruit and in the vegetative parts of the plant (leaf, cane, spines) is dependent from the dominant T allele. In the absence of T allele, for the t allele homozygote plants, the fruit has yellow colour and there is no red colour appearing on shoots (*Crane & Lawrence,* 1931). Activity of T gene is blocked by a recessive inhibitor gene (i). The Tii plants were examined by *Keep* (1984) to have orange fruit colour but differently from the tt genotype of yellow fruit hybrids, the anthocyanin production here is not blocked on the shoots.

In the case of some *Rubus* species, the yellow fruit colour is determined by a dominant gene. The yellow fruit colour of hybrids originating from the crossing of *R phoenicolasius* Maxim. and *R. idaeus* L. is determined by the Y gene, which is epistatic to the T gene.

In the red fruit *R. phoenicolasius* parent, the activity of the Y gene is blocked by a suppressor (Ys) gene, so in this way a normal amount anthocyanin is produced. In the backcrossed hybrids, the yellow fruit plants appeared because of segregation of the Ys gene (*Jennings & Carmichael,* 1975; *Jennings & Carmichael,* 1980).

In this paper, we have summarized all the data regarding fruit and shoot colour of *R. parvifolius* x *R. idaeus* hybrids.

As we found during the research, there are only a few papers in the literature about anthocyanin pigmentation of raspberry's shoots. *Crane & Lawrence* (1931) stated that the red colour of raspberry shoots is determined by a C gene. The above-mentioned gene works only in the presence of a T gene. The different degree in the pigmentation is probably the result of the mutual effect of genes.

Material and method

With the crossing of the *R. parvifolius* and the cultivated raspberry we have produced fertile hybrids. We have tried to unify the vitality and resistance of wild raspberry and the fruit quality of the cultivated one with several backcrossings. For the recurrent parent we always choose the cultivated raspberry. In order to avoid the simplification of genetic variability, we have produced generations with the inter-crossing of hybrids.

The symbol system that was used for marking the origin of combinations is explained via an example. In that, F_1 BC_3 is the third backcrossing of the seedling deriving from the first hybrids (F_1) while F_3 BC_2 is the second backcrossing of selected seedlings of the F_3 generation. The genetic rules of colour's succession can be deduced by tracing back the rate of the backcrossed generations.

In the course of evaluating the various hybrid populations, several features of seedlings were registered. Among other characteristics, we have recorded fruit and shoot colour of seedlings. The seedlings were classified into two groups: for the red fruit and for the yellow fruit plants. Both of the apricot and orange colour fruit seedlings were considered as yellow fruit plants. The probability of the supposed segregating rates were checked by a χ^2 test.

Results

Fruit colour

In the F_1 hybrids of the red colour *R. parvifolius* and the red fruit raspberry (*R. idaeus*) we have found only seedlings with red fruit colour. Besides the red colour plants, different yellow shades (light yellow, orange, apricot colour) seedlings appeared in the breaking generations and in the seedlings of the backcrossed generations of raspberries. The gene or genes determining the yellow colour can only be derived from wild species because for the crossings we have only used homozygote raspberries of red colour (cvs. 'Malling Promise', 'Malling Exploit', Canby, F. 103.).

At the evaluation of the segregation rates coming from different combinations we have used the existing literature data. According to that, the yellow fruit colour in the hybrids of the Asian *R. phoenicolasius* and a dominant Y gene determines the European raspberry but a suppressor Ys gene can prohibit the appearance.

The succession was described at the species of *R. phoenicolasius* has similarity with the succession observed at *R. parvifolius*. The only difference is that the yellow fruit hybrids in the segregating generations has higher rates then was previously expected. According to the hypothesis based on the presence of the Y and the Ys genes, the maximum rate of yellow fruit cannot be higher than 50% in the seedlings which were back-crossed with red colour homozygote raspberries. On the other hand, in more combinations the yellow fruit seedling rate was substantially higher. From these combinations such a group can be formed where the rate of yellow and red fruit is 3:1.

The difference between the succession rate was described in the literature for *R. phoenicolasius* and the experienced segregating rate of *R. parvifolius* can be easily explained if we suppose that there is another dominant gene next to the Y gene responsible for yellow fruit colour. According to the available data, we cannot decide that this gene is different from the known Y gene or the same. For the future we have marked conditionally this gene Y_2 differing from Y gene.

The segregating rate was calculated according to the two yellow genes (Y and Y_2) hypothesis by eliminating the difference between the one Y gene calculated theory and the actually experienced data (*Table 1*). With the help of the two yellow genes, it is easy to explain the majority of yellow fruit hybrids in the population.

In order to save the favourable features deriving from the wild species, we have chosen hybrids for backcrossing according to their resistance. Since in the yellow fruit group there was the more resistant suppressor Ys gene, which was missing from these plants, since it has been eliminated step by step during the selection. For avoiding the loss of other favourable recessive genetic characteristics and for maintaining the genetic variability, we have produced breaking generations by crossings of backcrossed generations among themselves.

As a result of the above-mentioned research, we have succeeded to produce red fruit raspberries hybrids where the habitat is differing from wild species but contain the resistance of those plants. The ongoing research is focusing on the improvement of the growing value of the hybrids.

The red discolouration of the seedlings

Characteristically to the different raspberry species, there is an anthocyanin forming on the shoots of the plants. The pink or the light red colour always appears first on the sunny side of the plants then later at the end of the summer the whole shoot becomes red or pink. The dark red or purple shoots are extremely characteristic to those hybrids where one the *R. occidentalis* is among the ancestors. The hybrids of the European red raspberry (*R. idaeus*) and the American black raspberry (*R. occidentalis*) were named after the colour of the shoots as purple raspberry.

During the interspecies crossing, we have used the species *R. parvifolius* of which the shoots have also purple or dark red colour. The F_1 hybrids are derived from the crossing of the mentioned species and cultivated raspberry to inherit the colour of the wild species. In the backcrossed raspberry hybrids, the canes with dark anthocyanin colour can easily separate from the green or red coloured canes of raspberry. The rate of the wild raspberry colour canes in the F_2 generation is 3:1, while the rate in the backcrossed generation is 1:1 (*Table 2*). So, it is supposed that the genes deriving from the wild species cause the dark purple colour of the canes.

The fruit colour of this strong anthocyanin colour cane plant is generally yellow. Consequently, the Y gene deriving from wild species is against of T gene responsible for epistatic pigment production and inhibits the anthocyanin production on the fruit but not on the shoots.

We have proposed the Pr (purple) code for the gene, which is responsible for more intensive pigmentation in the shoots of the wild species besides C gene raspberry.

According to the analysis of the backcrossed generations, we have experienced that the yellow colour deriving from the

Table 1 Backcrossing of red and yellow fruit interspecific hybrids with homozygote (TT) cultivars for red fruits

Family	Ancestry	Parents	Seedlings: red fruit	Seedlings: yellow fruit	Expected segregation	X^2	p
Red fruit hybrid (yy y_2y_2 ysys) x raspberry (TT)							
6706	F_3BC_3	6611/61 x F. 103	13	–	1 : –	0.00	–
6703	F^3BC_3	6621/28 x F. 103	10	–	1 : –	0.00	–
6713	F_3BC_3	6609/8 x M. Exploit	13	–	1 : –	0.00	–
6702	F_3BC_3	6622/80 x M. Exploit	6	–	1 : –	0.00	–
Yellow fruit hybrid (Yy y_2y ysys or yy Y_2y_2 ysys) x raspberry (TT)							
6711	F_3BC_3	6621/5 x M. Exploit	27	33	1 : 1	1.10	0.20
6712	F_3BC_3	6624/12 x Meeker	11	18	1 : 1	1.68	0.20
6716	F_3BC_3	6611/31 x M. Exploit	11	11	1 : 1	0.00	0.99
6759	F_3BC_3	6621/17 x M. Exploit	16	16	1 : 1	0.00	0.99
6718	F_3BC_3	6608/20 x M. Exploit	10	15	1 : 1	1.56	0.20
6701	F_3BC_3	6607/19 x M. Exploit	5	5	1 : 1	0.00	0.99
		Σ	***80***	***98***	***1 : 1***	***1.82***	***0.20***
Yellow fruit hybrid (Yy Y_2y_2 ysys) x raspberry (TT)							
6707	F3BC3	6621/10 x M. Exploit	2	7	1 : 3	0.02	0.90
6709	F3BC3	6626/3 x F. 103	1	9	1 : 3	1.20	0.20
6714	F3BC3	6611/1 x M. Exploit	1	11	1 : 3	1.70	0.20
6756	F3BC3	6624/14 x M. Exploit	4	10	1 : 3	0.09	0.00
		Σ	***8***	***37***	***1 : 3***	***1.28***	***0.20***

Table 2 Inheritance of shoot colour in the case of *R. parvifolius* x *R. idaeus* hybrids

Family		Ancestry	Parents	Shoot colour of parents	Segregation of seedlings: B	Segregation of seedlings: P/z	Proposed code for parent's genotype	Expected segregation	x^2
1.	6184	F_1	R. parvifolius x R. idaeus	B x P/z	15	0	PrPr x prpr	–	0.00
2.	6607	F_1BC_2	F. 103 x 6478/10	P/z x B	5	4	Prpr x prp	1:1	0.10
3.	6609	F_3BC_2	6546/3 x F. 103	B x P/z	4	4	Prpr x prp	1:1	0.00
4.	6611	F_3BC_2	6546/4 x Schöneman	B x P/z	14	13	Prpr x prp	1:1	0.02
5.	6759	F_3BC_3	6021/12 x M. Exploit	B x P/z	12	15	Prpr x prp	1:1	0.32
		Σ_{2-5}		***B x P/z***	***35***	***36***	***Prpr x prp***	***1:1***	***0.00***

B = purple
P/z = green with red washing in

Table 3 Correlation between the fruit colour and the shoot colour in the backcrossed combinations

Fruit colour	Shoot colour: Purple – Number	Purple – %	Green / red – Number	Green / red – %	Σ Number
Red	9	16.6	45	83.4	54
Yellow	55	80.9	13	19.1	68
				Total	***122***

Table 4 Recombination rate in the hybrids of the backcrossed generations with raspberry

Combinations	Yellow fruit: Purple shoot YPr	Yellow fruit: Green shoot Ypr (Recombined)	Red fruit: Purple shoot yPr (Recombined)	Red fruit: Green shoot ypr
6607	3	1	1	4
6609	3	1	1	3
6611	10	1	1	9
6759	11	1	3	12
6749	3	1	0	4
Σ	***30***	***5***	***6***	***32***
			15%	

Parents: Ypr x ypr

wild species and the intensive pigmented shoots are linked gentically (*Table 3*).

In the 80 percent of the yellow fruit plants the shoots have purple colour with strong pigmentation. In the red fruit plants, this rate is only 19 percent. The linkage is not absolute (as it can be seen from the tables) because there are yellow fruit plants with poor pigmentation on shoots and there are red fruit plants with strong pigmentation on the shoots. The rate of recombination plants is around 15 percent (*Table 4*). Through the crossing over, there is a possibility for the selection of red fruit and strongly pigmented seedlings.

Discussion

The inheritance of fruit colour in the hybrids of *R. parvifolius* x *R. idaeus* crossings has shown good correspondence to the inheritance circumstances of *R. phoenicolasius* x *R. idaeus* reviewed by *Jennings & Carmichael* (1975). The yellow fruit hybrids in the segregating generations as well as the later dominant type inheritance of the yellow fruit colour correlates to the presence of dominant Y and the suppressor Ys genes. However, in a couple of crossings the actual results of segregating rates are significantly different from the expected results.

The authors experienced higher rate of yellow fruit hybrids than it was early calculated on two occasion from four crossings. The rate of the yellow fruit colour in the backcross generations exceeds the 50 percent. This high rate can be easily interpreted by the introduction of a second yellow colour gene. This second gene was named Y_2.

In the spectrum of yellow colour, a broad diversity of colour variations can be experienced which starts with light yellow and goes through the orange to the red tone of apricot. In the yellow berries, presumably and partly similarly to the yellow flowers, antoxantins form instead of anthocyanin (*Crane & Lawrence,* 1952). Insofar as the inhibition of the anthocyanin forming is not complete, then more or less anthocyanin can form together with yellow antoxantins.

The colour of the fruit that continued from the light yellow to apricot determined the rate of the two-colour material. If the colour material locates in two different cell layers then a red colour can appear on the yellow fruits. We have experienced this phenomenon not only in the hybrids of *R. parvifolius* but in hybrids of *R. phoenicolasius* also.

We have already recognized the correspondence between of the fruit colour and shoot colour in the case hybrids of *R. phoenicolasius* x *R. Idaeus* earlier. In these hybrids, the inhibition of anthocyanin production appeared only in the fruits, while the on the shoots dark-purple pigmentation was observed (*Sági* et al., 1963.; *Porpáczy & Kollányi,* 1993). During the research we proved that in the hybrids of *R. parvifolius* the yellow fruit colour and the purple colour of shoots are inherited linked. The recombined rate of plants appearing in the population is around 15 percent.

The dark pigmentation on the shoots deriving from the wild species strongly differs from the light pink or light red colour of cultivated raspberry that is regulated by the C gene.

We have used the Pr (purple) code for identifying this dark purple gene deriving from wild species.

The more precise recognition of the connection between the yellow fruit colour as well as the dark purple colour of shoots facilitates the effectiveness of the selection for the resistance breeding. According to the results of several years analyses, we have experienced that hybrids with dark shoots have good resistance again cane midge similarly to wild species because the bark of these hybrids is not prone to splitting. The resistance is probably associated with the suitability of the natural splits for oviposition. The only disadvantage is that this favourable feature is accompanied with the unfavourable yellow fruit colour. But the experienced 15 percent crossing over gives good opportunity for the selection of favourable red fruit hybrids, which can be an important step forward in resistance breeding.

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