Euphytica 24 (1975) 467–470

A DOMINANT GENE FOR YELLOW FRUIT IN THE RASPBERRY

D. L. JENNINGS and ELEANOR CARMICHAEL

Scottish Horticultural Research Institute, Dundee, United Kingdom

Received 23 August 1974

SUMMARY

A gene for yellow fruit, designated *Y*, segregated in progenies obtained by crossing *R. phoenicolasius* with the red raspberry and backcrossing to the raspberry. Another gene, designated *Ys*, suppressed its expression in *R. phoenicolasius* itself and in the F_1. Gene *Y* was dominant to alleles for red fruit in the red raspberry; it was epistatic to gene *T* and its expression was not influenced by genes which intensify the expression of this gene. It had no visible effect on the anthocyanin content of vegetative parts and its effect on the fruit was due to reduction in the content of all the anthocyanins and not to supression of any particular one.

INTRODUCTION

The intensity of fruit colour in red raspberries is largely determined by their content of anthocyanins. Gene *T* is the most important known gene influencing anthocyanin production both in fruit and vegetative parts, its recessive allele *t* giving either yellow fruits and non-pigmented growth or, in the presence of gene P, red-tinged spines and apricot fruits (CRANE & LAWRENCE, 1931). MACHA (1966) found colours ranging from yellow to red in material derived by crossing a yellow-fruited form of the red raspberry (*Rubus idaeus/strigosus*) with a yellow-fruited form of the black raspberry (*R. occidentalis*), apparently because segregation occurred for genes which intensified anthcyanin production when gene *T* was absent. BRITTON et al., (1959) showed that the colour of purple or black fruits was due to genes which intensified anthocyanin production in the presence of gene *T*, though it was not certain whether these included a major gene (*Bl*) as well as minor ones. These workers also pointed to the advantages that would occur if the heterosis of hybrids between red and black raspberries could be obtained without their undesirable purple fruit colour. They investigated whether the colour-intensifying genes from the black raspberry would produce red instead of purple-fruited hybrids if combined with the allele *t* instead of *T*, but concluded that these intensifying genes produce no effect in the absense of *T*, because the fruits obtained were either yellow or orange. A different gene for yellow fruit has been discovered during breeding work with *R. phoenicolasius*; this paper reports upon its inheritance and upon its expression in hybrids of red and black raspberries.

METHODS

Anthocyanin determinations were done as follows, using methods described by BLUNDSTONE & CREAN (1966): the anthocyanins were extracted with methanol acidified with 1% acetic acid, separated by passing the extract through a column of polyvinyl pyrrolidone and estimated quantitatively by spectrophotometry. They were then identified by chromatography, using cellulose thin layers to compare the extracts with known reference anthocyanins, the solvents employed being either a 15:3:82 v/v mixture of acetic acid: hydrochloric acid: water or a 3:97 v/v mixture of hydrochloric acid and water.

Because fruits of the hybrids between *R. phoenicolasius* and the raspberry were semi-sterile, parthenocarpic fruits were induced by treating open flowers with 0.5% agar containing 500 p.p.m. gibberellic acid.

RESULTS

Segregation. No yellow-fruited segregates occurred when *R. phoenicolasius* was selfed or crossed with raspberry cultivars, but segregation occurred in the first backcross of the hybrids to the raspberry (Table 1). It was therefore postulated that a dominant suppressor gene, designated *Ys*, was present in *R. phoenicolasius* and prevented the

Table 1. Segregation for yellow fruit in progenies of *R. phoenicolasius*.

Parents	No. of segregates with fruits:		α^2	P
	yellow or orange	Red or purple		
R. phoenicolasius self	0	40		
F_1 of cross with red raspberry. Postulated genotypes of parents: ysys yy × YsYs Yy.				
Expected ratio: all red				
Lloyd George × *R. phoenicolasius*	0	30		
Glen Clova × *R. phoenicolasius*	0	6		
1st backcross to red raspberry. Postulated genotypes of parents: ysys yy × Ysys Yy.				
Expected ratio: 1 yellow: 3 red				
4a24 × D29/19	7	19	0.05	0.80
5858/123 × D29/10	19	36	2.67	0.10
Total	26	55	2.18	0.10
2nd backcross to red raspberry using 1st backcross hybrid with red fruit.				
(a) Postulated genotypes of parents: TT Ysys Yy × TT ysys yy. Expected ratio: 1 yellow: 3 red				
R7/1 × 6093/26	7	11	1.86	0.20
R7/1 × 6010/52	2	12	0.86	0.30
Total	9	23	0.17	0.70
(b) Postulated genotypes of parents: Tt ysys yy × Tt ysys yy. Expected ratio: 7 yellow: 9 red				
R2/6 × 6093/26	12	15	0.005	0.95
2nd and 3rd backcross to red raspberry using backcross hybrids with yellow fruit.				
Postulated genotypes of parents: ysys Yy × ysys yy. Expected ratio: 1 yellow: 1 red				
61106/41 × 654/121	44	11	19.80	<0.01
61106/41 × 6531/42	37	15	9.31	<0.01
R3/4 × 6944/34	24	40	4.00	0.05
R3/4 × 6944/46	18	13	0.81	0.30
Total	123	79	9.58	<0.01
Cross of a yellow-fruited 2nd backcross hybrid with a black raspberry (R. occidentalis)				
Postulated genotypes of parents: ysys yy × ysys Yy. Expected ratio: 1 yellow: 1 purple				
Munger × 6944/34	39	46	0.58	0.50
Munger × 6944/46	21	24	0.20	0.70
Total	60	70	0.77	0.50

expression of a gene for yellow fruit in *R. phoenicolasius* itself and its hybrids with the raspberry. The latter gene was designated gene *Y*, and was revealed in the first backcross generation when segregation for *Ys* occurred for the first time. The occurrence of yellow-fruited segregates in this generation indicated that gene *Y* was epistatic to gene *T*, and dominant to its alleles for red fruit present in the raspberry. Thus the expectation for a backcross of a red-fruited hybrid was that one yellow-fruited segregate having the phenotypic combination *ys Y* would occur for every three red-fruited segregates, which could have the phenotypic combinations *Ys Y*, *Ys y*, or *ys y*. This expectation was realised in four families, and in a fifth family the segregation was complicated by heterozygosity of the two parents for gene *T*, which reduced the proportion of red-fruited segregates, as all progeny of *tt* constitution would have yellow fruits regardless of their status in respect of gene *Y*. The segregation when yellow-fruited hybrids were further backcrossed was attributed entirely to segregation of gene *Y*, as its suppressor gene was absent, but the results for two of the four families of this type departed significantly from the expectation of a 1:1 ratio of yellow to red-fruited progeny. However, the results when two yellow/orange-fruited hybrids were crossed with the black raspberry 'Munger' were in accord with this expectation. The important observation from this cross was that the segregates had either deep purple, or orange/yellow fruits. Only five of the 60 segregates in the orange-yellow category had a colour intensity approaching a pale red. Hence there was no evidence that genes from the black raspberry which intensify the expression of gene *T* to give purple instead of red fruits in hybrids between the red and black raspberry could similarly influence the fruit colour of *Y* phenotypes to give red instead of yellow or orange fruits. The epistatic action of gene *Y* was maintained and the fruit colour of *Y* phenotypes was essentially the same as in crosses with the red raspberry.

In all families the yellow-fruited segregates frequently had highly pigmented vegetative growth. In two families tested in which the fruit colour ranged from pale yellow to deep orange there was no correlation between scores given for the colour intensity of the fruits and scores given for the intensity of red pigments in the vegetative growth. This is further evidence that the expression of gene *Y* was not modified by genes which influence the expression of gene *T*.

The parent 61106/41 was heterozygous for genes *H* (glabrous stems) and L1 (large fruit) as well as for gene *Y*, but tests for linkage between the three loci gave negative results.

Anthocyanin analyses. Anthocyanin analyses showed that *R. phoenicolasius* fruits contained three of the four anthocyanins which NYBOM (1968) associated with the red raspberry, while hybrids between *R. phoenicolasius* and the red raspberry had all four of them (Table 2). *R. phoenicolasius* differed in having a relatively high content of cyanidin-3-rutinoside, which is usually either absent or present in relatively small quantities in the red raspberry. However, five *Y* phenotypes which occurred in the second backcross generation resembled the raspberry 'Glen Clova' in the particular anthocyanins present, and variation in their fruit colours was clearly related to variation in their total anthocyanin content. The results indicated that gene *Y* caused the fruits to be yellow because it caused reduction in the total content of anthocyanin; there was no evidence that it prevented the production of a particular one.

Table 2. The anthocyanin contents (mg cyanidin/100 g fruit) of fruits obtained from *R. phoenicolasius*, Glen Clova raspberry and derivatives of the cross *R. phoenicolasius* × raspberry.

Source of fruit	Colour	Cy-3-Gl	Cy-3-Ru	Cy-3-Sop	Cy-3-GlRu	Total
R. phoenicolasius	red	2.49	18.40	0.31	0.0	21.20
R. phoenicolasius[1]	red	1.73	11.99	0.26	0.0	13.98
Glen Clova	red	2.18	0.0	13.20	2.04	17.42
R. phoenicolasius[1] × G. Clova	red	0.52	2.13[2]		3.61	6.26
Segregates from the 2nd backcross to red raspberry						
6944/74	pale yellow	0.01	0.0	trace	0.0	0.01
6944/4	yellow	0.02	0.0	0.01	0.0	0.03
6943/22	apricot	0.10	0.0	0.08	0.0	0.18
6943/95	pale orange	0.72	0.0	0.31	0.0	1.03
6944/45	deep orange	1.16	0.0	3.98	0.72	5.86

Cy-3-Gl = Cyanidin-3-glucoside; Cy-3-Ru = Cyanidin-3-rutinoside; Cy-3-Sop = Cyanidin-3-sophoroside; Cy-3-GlRu = Cyanidin-3-glucosylrutinoside.

[1] Samples from plants fruited in the glasshouse; all other samples from field-grown plants.

[2] Cy-3-Ru and Cy-3-Sop did not separate sufficiently in this hybrid for their accurate quantitative estimation and the data given indicates their combined content.

DISCUSSION

The factors which determine the sythesis of anthocyanins and their distribution within the plant are inevitably complex. It seems likely that gene *T* has a basic role in anthocyanin synthesis, since it affects the production of the pigment in all plant parts, while gene *Y* acts at a later stage and merely limits pigment production in the fruit. It is therefore not surprising that genes which modify the action of gene *T* did not affect that of gene *Y*. Nevertheless, the idea of using major genes which affect fruit colour to modify the undesirable fruit colour of hybrids between red and black raspberries merits further study, as there are probably many major genes in the genus *Rubus* which affect fruit colour. HEDRICK (1925), for example, records yellow or orange fruit colours in *Rubus biflorus*, *R. ellipticus*, *R. louisianus*, *R. palmatus*, *R. spectabilis* and *R. xanthocarpus*; and other genes for yellow fruit may be suppressed as in *R. phoenicolasius*. The requirement is for a gene which acts at a point in anthocyanin synthesis which allows synthesis to proceed, but which modifies the anthocyanin in the fruit to give an optimum colour.

REFERENCES

BLUNDSTONE, H. A. W. & D. E. C. CREAN, 1966. The pigments of red fruits. Bull. Fruit and Vegetable Preservation Research Association, Chipping Campden, UK.

BRITTON, D. M., F. J. LAWRENCE & I. C. HAUT, 1959. The inheritance of apricot fruit-colour in raspberries. Can. J. Genet. Cytol. 1: 89–93.

CRANE, M. B. & W. J. C. LAWRENCE, 1931. Inheritance of sex, colour and hairiness in the raspberry, *Rubus idaeus* L. J. Genet. 24: 243–255.

HEDRICK, U. P., 1925. The small fruits of New York. Rep. N.Y. St. agric. Exp. Stn 33, II: 614 pp.

MACHA, R. L., 1966. Variability studies of fruit colour and other plant characteristics in interspecific crosses of yellow-fruited raspberries. Diss. Abstr. 27: 2952-B.

NYBOM, N., 1968. Cellulose thin layers for anthocyanin analysis, with special reference to the anthocyanins of black raspberries. J. Chromat. 38: 382–387.