

INHERITANCE IN TOMATOES¹

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Received February 6, 1925

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INTRODUCTION

In connection with my experimental work on size inheritance in the tomato (*Lycopersicum esculentum*) I have accumulated considerable genetic data on fruit characteristics and stature of plant. As these observations have an important bearing on the linkage situation in this species, it seems advisable to report them, especially since critical data have not yet been published. Because the tomato is so well adapted for a study of size inheritance it becomes imperative that the heredity of the simpler qualitative characters of this plant be thoroughly understood before the more complex problems of quantitative inheritance are attacked.

The varieties of tomatoes that I chose for work with size possessed qualitative characters, which may be described as follows:

Flesh color: Red (*R*) dominant over yellow (*r*). Gene *R* governs the formation of red needle-shaped crystals occurring within the cells of the mature fruit, while *r* produces the yellow granular color bodies. DUGGAR (1913) has named the red pigment produced by *R*, lycopersicin, replacing

¹ Paper No. 5, Department of Genetics, IOWA STATE COLLEGE, Ames, Iowa. Mr. W. A. CARVER, graduate student in genetics, assisted in making the pollinations and in recording field notes.

the term lycopin previously used by SCHUNCK (1903) and WILLSTÄTTER and ESCHER (1910).

Skin color: Yellow (*Y*) dominant over colorless (*y*). Gene *Y* produces a distinct, yellow pigment suffused throughout the cell walls of the epidermis of the fruit, whereas its allelomorph, *y*, produces a transparent or colorless condition in these epidermal walls.

Skin structure: Smooth (*P*) dominant over "peach" (*p*). Gene *P* is responsible for the ordinary smooth, shiny texture of the epidermis of the fruit. Such fruits also lack an appreciable amount of pubescence. Gene *p* gives a distinct pubescence on the mature fruit. The general structure of the epidermis is also changed so as to give a dull appearance to the fruit. The effect of these genes is perhaps analogous to the situation found in the nectarine and peach-tree fruits.

Stature: Tall (*D*) dominant over dwarf (*d*). In addition to the greater length of plant, the *D* factor produces a less-wrinkled type of leaf than does the *d* factor. The foliage of a dwarf plant is distinctly rugose and is much darker green in color than is the standard type.

The inheritance of each of the four pairs of characters may be explained on a single-factor basis. They are relatively easy of classification. The dominance in each case is practically complete. Notes have been taken on other characteristics, such as foliage color (dark and light green) and type of leaf, but the classification was found rather uncertain, and for this reason these characters have not been included.

Commercial varieties of tomatoes inbred one year were used as the source of material. The following is a list of such varieties together with their abbreviations and genetic formulae with respect to the four characteristics noted above:

<i>Variety</i>	<i>Constitution</i>
Red Cherry (RC)	<i>RR YY PP DD</i>
Bonny Best (BB)	<i>RR YY PP DD</i>
New Globe (NG)	<i>RR yy PP DD</i>
Ponderosa (P)	<i>RR yy PP DD</i>
Yellow Cherry (YC)	<i>rr YY PP DD</i>
Yellow Plum (YPl)	<i>rr YY PP DD</i>
Yellow Peach (YP)	<i>rr yy pp DD</i>
Red Peach (RP)	<i>RR yy pp DD</i>
Golden Beauty (GB)	<i>rr yy PP DD</i>
Dwarf Giant (DG)	<i>RR YY PP dd</i>

These varieties have been crossed, with the necessary precautions against contamination, in various combinations, and the F_1 , F_2 , F_3 and backcross generations grown both in the field and in the greenhouse.

Earlier investigations have shown that three of the four pairs of genetic factors controlling the above characteristics may be interpreted as involving a simple, monohybrid situation (CRAIG 1907; GILBERT 1912; HALSTED 1905; HEDRICK and BOOTH 1907). Apparently but little critical data have been published concerning the inheritance of the "peach" type of fruit (PRICE and DRINKARD 1908), but this character I find to be a simple recessive to the smooth or non-pubescent type, characteristic of most of the commercial varieties.

As far as I have been able to ascertain, the linkage relations of these factors have not been investigated to any extent. JONES (1917) has listed a few cases of linked inheritance in the tomato, from data reported by other investigators, but in these linkages one of the characters involved has been of a quantitative nature, the mode of heredity of which is still unknown.

GENETIC RELATIONS

Stature and skin structure,—Dd Pp factors

Complete linkage exists between the *Dd* (tallness *versus* dwarfness) and the *Pp* (smooth *versus* peach skin) pairs of factors. This I observed clearly in the F_2 generation of the cross Dwarf Giant (*dd PP*) \times Yellow Peach (*DD pp*). Seed from the F_1 generation, which was tall in stature and bore smooth or non-pubescent fruit, gave in the F_2 the following distribution among a total of 209 plants: 101 tall smooth : 56 tall peach : 52 dwarf smooth : 0 dwarf peach. No double-recessive plants (*dd pp*) appeared. A few of the dwarf F_2 plants were tested in the F_3 generation and all bred true to the smooth type of fruit as well as to dwarfness, indicating that the dwarf-peach combination does not appear at all.²

Such data obviously are characteristic of complete linkage. The approximation to the 2 : 1 : 1 ratio typical of such a situation is extremely

² In one later F_3 progeny from an open-pollinated dwarf smooth F_2 plant, two distinct peach (pubescent) dwarfs appeared among five plants. On the complete-linkage hypothesis these could scarcely have occurred by pollen contamination, since the mother plants were presumably homozygous *dP.dP*. The only obvious explanation is that of mutation from *dP.dP* to *dP.dp* in the F_2 plant, whereby the peach type would appear in F_3 as a recessive segregate. That such mutations of pubescence occur is not uncommon, especially in the case of the nectarine and the peach-tree fruits. I have also observed in the tomato that in F_2 and F_3 generations involving the smooth and peach types, considerable variation in the degree of pubescence occurs. In some cases I have seen in the same fruit-cluster of an F_2 or F_3 peach type, a relatively smooth fruit at maturity. Some of these variations are now being investigated.

The quadruple recessive type, *rryyppdd*, which I have just developed from the plants noted above, has been crossed with the tetrahybrid condition, *RrYyPpDd*, and should give some critical data on the *P-D* linkage.

close, the deviations from the calculated proportion of 105 : 52 : 52 being only 4 : 4 : 0, respectively.

An interesting verification of the complete-linkage theory was afforded by some F_3 seedling progeny tests. Ten F_3 progenies from tall-peach type F_2 plants all bred true for the tall character. Of ten F_3 progenies grown from tall-smooth type F_2 plants, none bred true for tallness, all segregated for dwarfs. In other words, one can predict which of the F_3 progenies, arising from the dominant tall F_2 plants, will breed true for tallness by the type of skin structure of the mother plants. The F_3 progenies from dwarf-smooth F_2 plants, ten in number, all bred true for dwarfness. These facts are in full accord with the expectation if D and P are considered as being completely linked in inheritance.

This situation is perhaps known in the commercial world, since there are no dwarf varieties recorded with "peach" skin. GROTH (1910) noted this phenomenon in the days before genetic linkages were understood.

In any case of complete linkage it becomes of interest to speculate whether the situation really is one in which two different pairs of genetic factors are actually correlated in inheritance because they are borne on the same chromosome, or whether there is fundamentally only one pair of factors with a third allelomorph concerned. On the basis of complete linkage, the following three genotypes only are expected in the F_2 generation:

- 1 $Dp . Dp$,—tall peach
- 2 $Dp . dP$,—tall smooth
- 1 $dP . dP$,—dwarf smooth

This situation accounts for the experimental facts very well.

If we could conceive of some physiological correlation between factors for stature and those for structure of skin, we might assume that multiple allelomorphs were concerned. That there may be some apparent relation here is not altogether inconceivable if we think in general terms. The "peach" factor is one that permits the epidermal hairs to persist on the fruit until mature. At least this is its most obvious effect, although the actual structure and appearance of the epidermis are also modified. In "smooth" fruits the epidermal hairs are apparently formed but drop or fail to develop in the earlier stages of fruit growth. It is conceivable that this same effect of "persistence" might be related to the tendency of the plant to persist in growing until it eventually develops into the tall type of plant. However, the fact that we have true-breeding varieties that normally are tall and *smooth-fruited* would seem to invalidate this physiological-correlation hypothesis. Also, there appears to be no obvious

reason for any physiological incompatibility between dwarfness and the peach type of fruit.

Accordingly, complete linkage of two different factor pairs seems to present the simpler and more reasonable explanation of the inheritance of these characters.

Stature and flesh color,—Dd Rr factors

These factors are inherited independently of each other. The F₂ data of the crosses, Dwarf Giant (*dd RR*) × Yellow Peach (*DD rr*), and Dwarf Giant × Yellow Cherry (*DD rr*), demonstrating this, have been arranged in table 1. There is not sufficient deviation from the 9 : 3 : 3 : 1 ratio in

TABLE 1
F₂ data involving factors *Dd Rr* from the parental combinations *Dr dR*.

CROSSES	TALL RED <i>DR</i>	TALL YELLOW <i>Dr</i>	DWARF RED <i>dR</i>	DWARF YELLOW <i>dr</i>
Dwarf Giant × Yellow Peach	121	36	36	16
Dwarf Giant × Yellow Cherry	48	18	9	2
Total	169	54	45	18
<i>Theoretical</i>	<i>160.9</i>	<i>53.6</i>	<i>53.6</i>	<i>17.9</i>

Deviation from 10 : 6 ratio = 8.25 ± 5.52

these hybrid generations to justify any suspicion of linkage. When the parental classes (*Dr* and *dR*) are grouped against the non-parental classes (187 : 99) the conclusion that *D* and *R* are independently inherited becomes obvious, since the deviation from the 10 : 6 ratio in this case is only about 1.5 times as large as the probable error.

Stature and skin color,—Dd Yy factors

Dwarfness is also inherited independently of skin color. Proof for this is afforded by the F₂ generation of the cross, Dwarf Giant (*dd YY*) × Yellow Peach (*DD yy*). From a total of 209 F₂ plants the following results were obtained:

123 tall yellow-skin (*DY*) : 34 tall colorless-skin (*Dy*) : 37 dwarf yellow-skin (*dY*) : 15 dwarf colorless-skin (*dy*).

The theoretical expectancy on a 9 : 3 : 3 : 1 basis is 118 : 39 : 39 : 13. Obviously, the agreement is so close that factors *D* and *Y* must be independently inherited.

Flesh color and skin color,—Rr Yy factors

These factors are responsible for the actual color of the tomato fruit (HURST 1906). Their four different combinations produce the following well-known colors:

RY, orange red (due to red flesh showing through yellow skin)

Ry, red (the pink or purple of commerce)

rY, dark yellow

ry, pale yellow

I have experienced no real difficulty in classifying mature tomato fruit colors on this basis, despite the fact that occasionally a yellow-fleshed fruit will show a faint red blush at the distal end.

Data from F_2 and backcross generations involving both the "coupling" and "repulsion" phases of linkage are available and have been arranged in tables 2 and 3.

TABLE 2

Fruit color in F_2 generations of various tomato crosses involving flesh and skin colors.

CROSSES	<i>RY</i>	<i>Ry</i>	<i>rY</i>	<i>ry</i>	DEVIATION FROM 10 : 6 RATIO
<i>F₂ of RR YY × rr yy</i>					
Red Cherry × Golden Beauty	34	7	6	3	
Golden Beauty × Red Cherry	50	18	6	4	
Yellow Peach × Bonny Best	51	14	11	3	
Bonny Best × Yellow Peach	41	12	10	6	
Dwarf Giant × Yellow Peach	118	39	42	10	
Total	294	90	75	26	
<i>Expected</i>	273	91	91	30	17.0 ± 7.2
<i>F₂ of RR yy × rr YY</i>					
New Globe × Yellow Cherry	14	8	0	3	
Yellow Cherry × New Globe	39	10	10	1	
Ponderosa × Yellow Plum	31	7	10	4	
Total	84	25	20	8	
<i>Expected</i>	77.0	25.7	25.7	8.6	6.0 ± 3.8

In table 2, which gives the F_2 generations of five different crosses, there is an approximation to a dihybrid distribution with independent inheritance. Where *R* and *Y* were contributed by the same parent, there resulted 294 orange-red : 90 red : 75 yellow : 26 pale yellow, when 273 : 91 : 91 : 30, respectively, were expected. Grouping the parental classes (*RY* and *ry*) against the non-parental (*Ry* and *rY*), there results 320 : 165. This

deviates from the 10 : 6 ratio of independent inheritance by 17 individuals, a deviation which is 2.4 times larger than its probable error, and might suggest linked inheritance. However, the excess of red-fleshed fruits is responsible in some measure for the large deviation.

Where *R* and *y* were contributed by the same parent the F_2 distribution was 84 : 25 : 20 : 8, when 77 : 26 : 26 : 9, approximately, were to be expected. This gives 92 non-parental and 45 parental combinations where 86 and 51, respectively, are to be expected. In this case the deviation of 6 is in the wrong direction to indicate any linkage.

TABLE 3

Fruit color in backcross generations of various tomato crosses involving flesh and skin colors.

CROSSES*	<i>RY</i>	<i>Ry</i>	<i>rY</i>	<i>ry</i>	PERCENT CROSSING OVER
Coupling phase (<i>RY</i> × <i>ry</i>)					
F_1 (RC × GB) × YP	21	9	5	9	
F_1 (GB × RC) × YP	9	13	10	8	
YP × F_1 (GB × RC)	13	13	8	6	
F_1 (GB × RC) × GB	9	3	9	9	
GB × F_1 (GB × RC)	11	9	4	6	
F_1 (YP × BB) × YP	9	9	19	13	
YP × F_1 (YP × BB)	9	11	12	18	
F_1 (YP × BB) × GB	7	9	6	6	
F_1 (BB × YP) × YP	12	8	9	11	
YP × F_1 (BB × YP)	12	9	11	8	
Total	112	93	93	94	47.4 ± 1.7
<i>Expected</i>	98	98	98	98	
Repulsion phase (<i>Ry</i> × <i>rY</i>)					
F_1 (NG × YC) × YP	7	14	7	12	
F_1 (NG × YC) × GB	4	5	9	2	
F_1 (YC × NG) × YP	12	14	8	5	
F_1 (YC × NG) × GB	12	5	6	7	
Total	35	38	30	26	47.3 ± 3.0
<i>Expected</i>	32	32	32	32	

* Abbreviations in Roman capital letters are variety names, RC being Red Cherry, etc.

The backcross generations of the same crosses, listed in table 3, offer some indications of a very loose linkage between *R* and *Y*. Both the "coupling" and "repulsion" phases of the situation show this. In one case there is 47.4 ± 1.7 percent and in the other 47.3 ± 3.0 percent crossing over. When, however, these crossover percentages are compared with their

probable errors, the deviations from 50 percent crossing over, characteristic of independent inheritance, fall within the limits of error for inheritance upon an independent basis. To test the actuality of such a loose linkage, much larger numbers are necessary. Undoubtedly, many investigators have such data on hand and it is hoped that they will report them in the near future. In view of the absence of linkage in one of the F_2 generations, however, it is reasonable to suppose that factors R and Y will be found to be inherited independently of each other.

Flesh color and skin structure,— $Rr Pp$ factors

The "peach" type of skin, which is completely linked with stature of plant, is apparently due to the effect of a single recessive gene, and this factor seems to be inherited independently of red and yellow flesh color governed by the Rr factor pair. Data supporting this conclusion are provided by F_2 and backcross generations of the crosses shown in tables 4 and 5.

TABLE 4

F_2 data involving factors $Rr Pp$, the parental combinations being RP and rp .

CROSSES	RED SMOOTH RP	RED PEACH Rp	YELLOW SMOOTH rP	YELLOW PEACH rp
Bonny Best \times Yellow Peach	84	34	24	6
Dwarf Giant \times Yellow Peach	111	46	43	9
Total	195	80	67	15
<i>Expected</i>	<i>201</i>	<i>67</i>	<i>67</i>	<i>22</i>

Deviation from 10 : 6 ratio = 13.0 ± 6.2

TABLE 5

Backcross data involving $Rr Pp$ factors, the parental combinations being RP and rp .

CROSSES	RP	Rp	rP	rp
F_1 (BB \times YP) \times YP	19	19	26	26
YP \times F_1 (BB \times YP)	20	21	26	22
Total	39	40	52	48
<i>Expected</i>	<i>41.75</i>	<i>41.75</i>	<i>41.75</i>	<i>41.75</i>

Crossing-over percentage = 51.4 ± 2.5

In table 4 the F_2 generations derived from the crosses, Bonny Best \times Yellow Peach and Dwarf Giant \times Yellow Peach, both crosses involving RP and rp as parental combinations, approximate fairly closely the

9 : 3 : 3 : 1 ratio of independent inheritance. The parental classes total 210 and the non-parental 147, where 223 and 134, respectively, are to be expected. This shows a deviation of 13, which is only 2.1 times as large as its probable error.

The backcross data of the Bonny Best \times Yellow Peach cross appearing in table 5 show conclusively that no linkage is present. In this case the crossover percentage is calculated as 51.4 ± 2.5 percent, indicating independent inheritance between *R* and *P*. Such independent inheritance must follow, of course, since *P* and *D* are completely linked, and *D* and *R* have been shown in a preceding section to be independent.

Skin color and skin structure,—Yy Pp factors

The "peach" characteristic is also transmitted independently of the skin-color factor pair, *Yy*. Here again F_2 and backcross data from the same crosses are available as shown in tables 6 and 7. Both of these distributions are, without doubt, in excellent agreement with the F_2 , 9 : 3 : 3 : 1, and the backcross, 1 : 1 : 1 : 1, ratios. Accordingly, the genes *Y* and *P*

TABLE 6

F₂ data involving Yy Pp factors, the parental combinations being YP and yp.

CROSSES	YELLOW-SKIN SMOOTH <i>YP</i>	YELLOW-SKIN PEACH <i>Yp</i>	COLORLESS- SKIN SMOOTH <i>yP</i>	COLORLESS- SKIN PEACH <i>yp</i>
Bonny Best \times Yellow Peach	85	28	23	12
Dwarf Giant \times Yellow Peach	118	42	36	13
Total	203	70	59	25
<i>Expected</i>	201	67	67	22

Deviation from 10 : 6 ratio = 5.0 ± 6.2

TABLE 7

Backcross data involving Yy Pp factors, the parental combinations being YP and yp.

CROSSES	<i>YP</i>	<i>Yp</i>	<i>yP</i>	<i>yp</i>
F_1 (BB \times YP) \times YP	21	28	24	17
YP \times F_1 (BB \times YP)	23	20	23	23
Total	44	48	47	40
<i>Expected</i>	44.75	44.75	44.75	44.75

Crossing-over percentage = 53.1 ± 2.5

are not linked. This cross is a verification of the independent inheritance between Y and D , a situation which must follow if D and P are completely linked.

TESTS FOR DIFFERENTIAL FERTILIZATION OR POLLEN-TUBE GROWTH

A fairly large series of backcrosses, made reciprocally, afford some information on whether or not there is in the tomato differential fertilization or pollen-tube growth. My data on this point involve the flesh colors,

TABLE 8

Summary of backcross data for comparison of reciprocal backcrosses testing differential fertilization or pollen-tube growth involving the genes Rr , Yy and Pp .

BACKCROSSES	R	r	Y	y	P	p
F₁ as ♀ parent						
(YC × BB) × YC	49	46				
(YC × BB) × YP	25	15				
(GB × RC) × YC	23	37				
(RC × GB) × YP	30	14	26	18		
(GB × RC) × YP	22	18	19	21		
(GB × RC) × GB	12	18	18	12		
(YP × BB) × YP	18	32	28	22	30	20
(BB × YP) × YP	20	20	21	19	15	25
(YP × BB) × GB	16	12	13	15		
(NG × YC) × YP	21	19	14	26		
(YC × NG) × YP	26	13	20	19		
(YC × NG) × GB	17	13	18	12		
(NG × YC) × GB	9	11	13	7		
Total observed	288	268	190	171	45	45
Expected	278	278	180.5	180.5	45	45
Percent observed	51.8	48.2	52.6	47.4	50.0	50.0
F₁ as ♂ parent						
YC × (YC × BB)	38	30				
YC × (GB × RC)	30	30				
YP × (GB × RC)	26	14	21	19		
GB × (GB × RC)	20	10	15	15		
YP × (YP × BB)	20	30	21	29	24	25
YP × (BB × YP)	21	19	23	17	22	18
Total observed	155	133	80	80	46	43
Expected	144	144	80	80	44.5	44.5
Percent observed	53.8	46.2	50.0	50.0	51.7	48.3

R and r , the skin colors, Y and y , and the skin-structure genes, P and p . By comparing the observed results in the backcross progenies when the

F_1 is used as the pistillate parent with results when it is used as a staminate parent, it is possible to detect any excess of one character over another (see table 8).

With respect to the flesh color genes, Rr , it may be seen in table 8 that there is an excess of red-fruited plants in both series of backcrosses. When the F_1 is used as the pollen parent there is 2.0 percent more red fruits than when it is used as the ovule parent. This suggests that the pollen-tubes bearing the R gene are somewhat more effective in fertilization than those carrying the yellow r factor. However, the deviation (11.0 ± 5.7) in this case is only twice as large as the probable error, and accordingly affords no indisputable proof of such differential action.

With none of the other factors is there any significant difference in the two series of backcrosses. The numbers involved are somewhat meager, and reliance could not be placed on them save where unusually large differences existed.

LINKAGE GROUPS IN THE TOMATO

Heretofore, no critical data have been reported on genetic linkage in the tomato. It is true that HEDRICK and BOOTH (1907) suggested a correlation between fruit shape (pyriform) and the Dd factor pair, and JONES (1917) concurs in this idea. As far as I am aware, however, no one has yet proven that fruit shape in tomatoes can be resolved into simple genetic factors. My experience is that the heredity of fruit shape is relatively complex, and has as yet not been analyzed into its component parts. To compute a crossing-over percentage for such a linkage is accordingly somewhat premature.

The same criticism applies to the linkage first reported by PRICE and DRINKARD (1908) and listed by JONES (1917), involving foliage color and number of locules in the fruit. Despite the frequent assertions or implications that locule number is dependent upon a single pair of genes, I venture to suggest that this is not the case. In my work, at least, there are several different factors concerned. Because of the partial dominance of the two-loculed condition and the resulting skew curve in the F_2 generation, there is a temptation to interpret this quantitative data on a single-factor basis. As far as I know no critical F_3 tests have ever been reported to substantiate the claim of a one-factor basis for locule number.

CRANE (1915) reports a similar situation with respect to a correlation involving quantitative characters. He suggests that a linkage exists between general fruit shape (not-pyriform) and certain types of inflorescence.

His data are meager, however, and he does not stress this relation, nor to my knowledge has it been followed up.

In 1924, I reported a case in which the Yy pair of factors was apparently linked with a certain major factor for total size or weight of fruit. Since then I have verified this report with other crosses and have evidence to prove that this is a legitimate genetic linkage and not a physiological correlation. The size factors involved in this linkage are a partially dominant factor for small size that is characteristic of the Cherry type of fruit, contrasted with a factor for large size contributed by the Golden Beauty variety. The Y gene is not necessarily linked with all size factors, but rather with certain ones characteristic of definite, pure varieties. In fact, I have crosses in which the Yy factors are most certainly not linked with size factors brought in by some of the larger-fruited sorts. In some of these crosses the Rr factors show a decided linkage with size factors. Data on these linkages are forthcoming in a later publication.

If we dismiss temporarily these cases of linkage, because at least some of the characters involved are as yet too complex to actually isolate the quantitative gene concerned, we are forced to the conclusion that linkage groups in the tomato are as yet rare. The complete linkage existing between the Dd and Pp factors seems to be a legitimate case.

Accordingly, it is worth recording that the following genetic factors in the tomato form the basis for three different linkage groups:

- Group 1. Dd and Pp
- Group 2. Rr
- Group 3. Yy

All the necessary tests have been made to demonstrate the truth of this situation with the exception of a rare possibility that R and Y are loosely linked. When we consider that the tomato has been reported as possessing twelve pairs of chromosomes it is not surprising, of course, that more linkages have not been discovered.

SUMMARY

1. Complete linkage exists between the Dd pair of genes controlling growth habit (tall *versus* dwarf) and the Pp pair responsible for skin structure (smooth *versus* "peach" type of fruit).
2. Genes Rr involved in flesh color (red *versus* yellow) are inherited independently of both Dd and Pp .
3. The factors Yy controlling skin color are undeniably independent of Dd and Pp and very likely of Rr .

4. These series of interrelations permit the establishment of three provisional linkage groups in the tomato.

5. Backcross data afforded some evidence of a slight differential fertilization or pollen-tube growth involving the genes *R* and *r*.

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