INHERITANCE OF BROWN AND GREEN MATURE FRUIT COLOR IN PEPPERS

PAUL G. SMITH
University of California, Davis

THE chocolate brown color of the ripe fruit in pepper, *Capsicum annuum** occurs commonly in Mexico and quite probably in all parts of the American tropics where this species is cultivated, according to Bukasov[3] and Bravo.[2] Several people familiar with peppers have reported its frequent cultivation in Mexico, and the author has seen small fields of it grown by Mexicans in Southern Colifornia. Little mention of it, however, appears in the literature.

Atkins and Sherrard[1] in 1915 attempted unsuccessfully to determine the naturé of the brown color, which they apparently believed to be a single pigment. Recently Smith[7] reported that brown was apparently inherited as a simple recessive to red. Further, on the basis of pigment extractions and analyses made by Dr. F. P. Zscheile, it was noted that the brown color was apparently due to the presence of undecomposed chlorophyll in combination with the normal red pigments of ripe fruit. The results described below are a continuation of the study mentioned above.

Genetics and Nature of Brown Fruit Color

Initial crosses were made between normal red and brown fruited types (both obtained from Mexico), and backcrosses with the F_1 were made to each parent. The results (Table I) show the brown color to be inherited as a simple recessive to red.

The brown fruited Ac. 401 was then crossed with Oshkosh, a variety having an orange-yellow ripe fruit color which is inherited as a simple recessive to red. If a recessive gene for retention of chlorophyll were present, as believed, it would be possible to obtain, through recombination, a form having a green ripe fruit color. This combination would be genetic proof of the pigment analysis, as well as a fruit color hitherto unknown in ripe pepper fruit.

The results of this cross (Table II) gave a good 9:3:3:1 ratio, indicating that the genes for chlorophyll breakdown or retention at fruit maturity are inherited independently of the genes *R*-*r* for red and yellow fruit color.

Assigning the symbol *Cl* for the normal decomposition of chlorophyll at maturity and *cl* for the retention of chlorophyll, the genotypes for the four ripe fruit colors would be:

Red $= R\ Cl$
Brown $= R\ cl$
Yellow $= r\ Cl$
Green $= r\ cl$

The intensities of color in both the brown and green may be modified by other genes. In the brown fruited forms, a range from a reddish brown to deep chocolate brown has been observed, resulting from varying intensities of either contributory pigment. Although no genetic analysis has ever been attempted, the red pigment differs in intensity between varieties.

Odland and Porter[6] have shown that the intensity of green in the immature state is governed by two sets of genes G_1g_1 - G_2g_2, which produce three levels of green and one level of sulphury white.

In addition to these three levels of green, the green ripe fruit has the *r* gene governing yellow, the shade ranging from golden to orange. The cross reported above involved the variety Oshkosh, which at Davis, California, develops a definite orange yellow color when

*The use of the binominal *C. annuum* rather than *C. frutescens* is based on data, to be published soon, of the author and Charles B. Heiser, Jr.

ripe. When immature the fruit is medium green in color, while that of the brown parent, Ac. 401, is a deep green. In the eleven plants with green ripe fruit, the ripe color varied from another unattractive yellowish green to a fairly clear deep green with a somewhat olive tint. An even clearer deep green may possibly be secured by crossing varieties with deep green immature color and with a clear yellow mature color. That the yellow pigments are present but masked by chlorophyll has been frequently observed in sun-exposed fruits. On the exposed side, the chlorophyll often bleaches out, revealing the yellow pigments while the unexposed portion of the fruit remains green.

The mode of action of the *cl* gene is not known. It is quite possible, however, that the *Cl* gene controls the development of an enzyme necessary for the decomposition of chlorophyll at fruit ripening, but in the presence of the homozygous recessive *cl* gene this enzyme is not produced.

For practical breeding purposes, the double recessive green may have some value when incorporated into certain varieties of salad peppers. Not infrequently the development of red pigments in the ripening fruit renders the salad type peppers unmarketable.

Linkage Studies

In the relatively small amount of genetic investigation on the species, only one instance of linkage has been reported. Despande[4] found linkage between flower color and pigmentation on the stems.

The crosses used permitted observations on possible linkage between the *Cl-cl* genes and the genes for fruit position and pungency. Since Odland[5] found no linkage between any of the latter genes, these were not calculated.

Pungency and Fruit Color

That pungency is inherited as a single dominant gene has been shown by a number of investigators. The relatively poor 9:3:3:1 ratio observed here was due to a deficiency in the non-pungent class. Since the organoleptic method of pungency determination was used, some error is understandable when a total of 233 fruits had to be tasted. However, no linkage was evident.

Fruit Position and Color

A fair 9:3:3:1 ratio was obtained, indicating no evident linkage. The low *P* value is probably due to the deficiency of erect fruited plants rather than to any possible linkage.

TABLE I. Inheritance of ripe fruit color in crosses between red fruited (Ac. 406) and brown fruited (Ac. 401) varieties.

Cross	Generation	Red	Brown	Calculated Ratio	*P* Value
Red × Brown	F_1	19	0	—	—
Red × Brown	F_2	270	99	3:1	0.30-0.50
Red × Brown F_1 × Brown	BC	18	19	1:1	0.80-0.90
Red × Brown F_1 × Red	BC	41	—	—	—

TABLE II. Ripe fruit colors resulting from the cross of the yellow fruited variety, Oshkosh, and the brown fruited variety, Ac. 401.

Cross	Fruit color				Calculated	
	Red	Brown	Yellow	Green	Ratio	*P* Value
Yellow × Brown F_1	10	0	0	0	—	—
Yellow × Brown F_2	132	46	44	11	9:3·3.1	0.50-0.70

TABLE III. Relation of pungency and fruit position to the *Cl-cl* genes in the F_2 of the cross of Oshkosh (non-pungent, upright, yellow fruit) × Ac. 401 (pungent, pendant, brown fruit).

	Segregation for pungency and chlorophyll presence					
	Pungent	Pungent	Non-pungent	Non-pungent	Calculated	
	Red or Yellow	Brown or Green	Red or Yellow	Brown or Green	Ratio	*P* Value
No. observed	147	39	29	15	9:3:3:1	0.5-.10
No. expected	129.4	43.1	43.1	14.4		

	Segregation for fruit position and chlorophyll presence					
	Pendant	Pendant	Erect	Erect	Calculated	
	Red or Yellow	Brown or Green	Red or Yellow	Brown or Green	Ratio	*P* Value
No. observed	137	44	29	10	9:3:3:1	.10-.20
No. expected	123.8	41.2	44.2	13.8		

Summary

The brown color of ripe pepper fruit is a result of the combination of the normal red pigments and undecomposed chlorophyll. The retention of chlorophyll in ripe pepper fruits is inherited as a simple recessive to the normal chlorophyll decomposition, and the symbols *Cl-cl* assigned for the gene pair. Crossing the brown fruited form with a yellow fruited variety, resulted in an F_1 that was red and an F_2 that segregated 9 red : 3 brown : 3 yellow : 1 green. The last color represents a ripe fruit color new for this species.

No evidence of linkage was found between the *Cl-cl* gene pair and the genes for red or yellow ripe fruit color, pungency, or fruit position.

Literature Cited

1. ATKINS, W. R. G., and G. D. SHERRARD. *Sci. Proc. Royal Dublin Soc.* 14:328-335. 1915.
2. BRAVO, H. H. *Anal. Inst. Biol., Univ. Nac. Mexico* 5:303-321. 1934.
3. BUKASOV, S. M. *Bull. Appl. Bot. Genet. and Plant Breeding, Suppl.* 47. pp. 261-273. 1930. (In Russian)
4. DESPANDE, R. B. *Indian Jour. Agr. Sci.* 3:219-300. 1933.
5. ODLAND, M. L. *Minn. Agr. Expt. Sta. Tech. Bul.* 179. 1948.
6. ———— and A. M. PORTER. *Proc. Amer. Soc. Hort. Sci.* 36:647-657. 1938.
7. SMITH, PAUL G. *Science* 107:345-346. 1948.

THE WORLD OF LIFE

IT is refreshing to find a textbook* that carries a central theme from cover to cover —Evolution. Dr. Pauli does not divert from this theme throughout the diverse ramifications of astronomy, chemistry, physics, and biology. However, his idea of evolution, although clearly developed in Part I along astronomical lines, seems to have a restricted application. He states, "This Theory can be expressed with the greatest simplicity: The specialized creatures of today have descended by gradual change from different and usually simpler creatures of the past." Yet he devotes some space to "Cosmic evolution" and chemical and physical changes, although by definition these are excluded. This reviewer would criticize Dr. Palui's repeated assertion "the theory of evolution." He clearly defines evolution and then proceeds to devote over 600 pages to showing that the specialized creatures of today *have been* derived from simpler creatures of the past. It is not a theory but a doctrine.

In Dr. Pauli's excellent book, the orthodox arrangement of most biology texts is reversed in that paleontology preceeds the description of the modern species. This is of course consistent with the theme of evolution which is carried from cover to cover. Throughout the text, anatomy and physiology of the various phyla are only lightly stressed, while a good deal of space is devoted to a large number of individual forms within various groups.

The sequence of material seems much more logical than in many texts. For instance, Dr. Pauli postpones the discussion of the Echinoderms until after the "Highest Invertebrates —the Anthropoda," thus bringing out the fact that: "Leading toward the vertebrates are two other invertebrate groups, some of whose members are strikingly primitive compared to the highly evolved mollusks, crustaceans and insects." The summaries at the close of most of the chapters recapitulate the phase of evolution developed within the chapter, again emphasizing the central theme.

Ecological adaptations are discussed from the conventional point of view of fitness to the environment, such adaptations being brought about by mutations as the underlying cause of evolution. There is no doubt that this is a controversial subject with strong arguments on both sides. This, in spite of the fact that Dr. Pauli says "this statement (of evolution) offers no explanation of how or why such a thing should happen, but merely affirms that it did."

The book is superbly illustrated with photographic material, drawings and diagrams. The format deviates from the conventional and the double column to the page may perhaps be an aid to more rapid reading. Dr. Pauli's language is clear and understandable. It is all in all an admirable text and particularly adapted to a slightly specialized type of course in biology. As a reference book for a senior in biology it is excellent due to the fact that it ties together the entire field of biology into one continuous and coordinated whole.

WILLIAM H. GATES
Louisiana State University

**The World of Life.* WOLFGANG F. PAULI. 653 pp. Houghton Mifflin Co., 1949. $5.00