A SERIES OF FIVE MULTIPLE ALLELES¹

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In 1937 Boye and Rife (1) reported a single pair of alleles as being responsible for a solid purple leaf color versus pattern (brown or red area in central portion of upper epidermis of otherwise green leaves). Purple (P) is dominant to pattern (p). The difference between the solid green of the Golden Bedder variety and pattern was likewise shown to be due to a single pair of alleles, solid green being dominant to pattern. In a later investigation Boye (2) found a series of three multiple alleles to be responsible for these three leaf color variations; solid purple (P), solid green (p^G) and pattern (p), as well as for a new phenotype, gray (Pp^G). Boye (3) also found a new allele (p^S) which in the homozygous state results in solid green leaves. It is incompletely dominant to pattern, in the heterozygous condition resulting in a new phenotype, known as spotted. (Numerous small brown or red spots on the upper epidermis of otherwise green leaves.) The various phenotypes and genotypes involving these alleles are shown in Table I.

This paper is concerned with a fifth allele of the same series. A plant which at first was thought to be of genotype PP or Pp, was later observed to differ in certain respects. The leaf color became such an intense purple as to appear black. The entire calyxes were dark purple, and the petals were dark blue. (Plants of genotypes PP and Pp have light blue petals and green calyxes with red bases.) The purple calyx color was maintained, even after the plant reached maturity and was dried out.

A large number of selfed seeds were produced by this plant. The resulting seedlings all appeared to be purple, and because of cramped facilities most of them were discarded. The remaining plants later proved to be of three types, the differences becoming more apparent as they became larger. Some showed the characteristics of plants of genotypes PP and Pp, some developed the black color of the parent, and the others were of a new phenotype, an uneven purple leaf color. Upon flowering, the petals were of a dark purple color, while the calyxes were green with purple at their bases. These observations suggested the likelihood that the parent plant was heterozygous for two kinds of purple, P and a gene responsible for the new phenotype, uneven purple. We shall use the symbol P^L to designate this allele.

Presumably the plants showing uneven purple leaves were homozygous, of genotype P^LP^L. One of them was crossed with a gray plant (P p^G) and produced 9 offspring with black leaves, and 6 with non-uniform, gray leaves. The blacks were assumed to be of genotype P^LP, and the non-uniform grays of genotype

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 P^L p^G . Both the black and the uneven gray plants were crossed with pattern. (Tables II and III.) Offspring of black x pattern (P^LP x pp) occurred in approximately equal numbers of typical purple (P^L) and uneven purple (P^L). Offspring of uneven gray x pattern P^G x pp) likewise occurred in approximately equal numbers of solid green (p^G) and light, uneven purple (P^L). The fact that only two phentypes were produced from each of these back crosses confirms the hypothesis that a new allele (P^L), rather than another pair of factors, is responsible for these variations.

A black plant (P^LP) was crossed with a green one of genotype p^Gp . As shown in Table IV, four kinds of offspring were produced, in approximately equal numbers. The leaves of plants of genotype P^Lp^G differ from those of genotype Pp^G principally in the distribution of anthocyanin, it being much more uneven in plants of genotype P^Lp^G .

When selfed, plants of genotype Pp^G produced offspring in the approximate ratio of 1 uneven purple; 2 uneven gray; 1 green (see Table V). A plant of genotype P^LP was crossed with one of genotype p^Sp^S , but no differences were noted among the offspring. All had brown leaves, like plants of genotype Pp^S .

All plants possessing the gene P^L produce dark blue flowers, and a dark purple color at the base of the calyx. No other alleles in this series produce this effect, except the combination Pp^S . The gene P produces red at the base of the calyx, while the genes p^S , p^G and p produce solid green calyxes. The genes p^S , p^G and p produce light blue petals. In respect to calyx color, red (P) is dominant to solid green $(p^S, p^G$ and p), while purple (P^L) is dominant to both red and solid green. In respect to petal color, dark blue (P^L) is dominant to light blue. The genotypic combinations P^LP and Pp^S produce copigmentation effects.

Table I
Genotypes and phenotypes of the purple allelic series

Genotype	Leaf color	Calyx color	$Petal\ color$
$\mathrm{P^LP^L}$	Uneven purple	Purple at base	Dark blue
$\mathrm{P^LP}$	Black	Solid purple	u u
$\mathrm{P^Lp^S}$	Brown	Purple at base	<i>"</i> "
$P^{L}p^{G}$	Uneven gray	<i>" " "</i>	" "
$P^{L}p$	" purple	<i>" " "</i>	" "
P P	Even purple	Red at base	Light "
$P p^{S}$	Brown	Purple at base	Dark "
P p ^G	Even gray	Red at base	Light blue
$P p p p^{S} p^{G} p^{S} p^{S} p^{G} p^{G}$	Even purple	<i>« « «</i>	u u
$p^{S}p^{G}$	Solid green	Solid green	u u
$p^{S}p^{S}$	u u	<i>"</i>	u u
p^Gp^G	u u	" "	<i>"</i> "
$p^{G}p$	u u	" . "	u u
p ^G p p ^s p	Spotted	" "	u u
p p	Pattern	u u	u u

		Table II			
		$P^{L}P \times pp$			
		Offspring			
	Observed		Calculated		
P ^L p Pp	69		71	df = 1	
		•		$x^2 = 0.112$	
Pp	73		71	p = 0.7 - 0.95	
		Table III			
		$P^{L}p^{G} \times pp$)		
		Offspring			
	Observed	Calculated			
$P^{L}p$	67		69.5	df = 1	
$P^{L}p$				$x^2 = 0.179$	
$P^{G}p$	72		69.5	p = 0.5 - 0.7	
TABLE IV					
	$P^{L}P \times p^{G}p$				
		Offspring			
	Observed	Calculated			
$P^{\mathbf{L}}\mathbf{p^{G}} \ P\mathbf{p^{G}} \ P^{\mathbf{L}}\mathbf{p}$	34			df = 3	
Pp^{G}	35			$x^2 = 0.745$	
	29			p = 0.7 - 0.95	
рр	35		33.2		
		TABLE V			
$P^{L}p^{G}$ selfed					
	Observed			lculated	
$P^{L}P^{L}$ $P^{L}p^{G}$	14		14.5		
$P^{L}p^{G}$	30		29	$x^2 = .054$	
$p^{G}p^{G}$	14		14.5	p = .9599	

SUMMARY

A new allele, which we have designated as PL, has been discovered in the purple series. This gene produces dark blue petals, dark purple at the base of the calyx, and a more uneven distribution of anthocyanin in the leaves than does its allele P.

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