# THE PURPLE ALLELIC SERIES IN *COLEUS*

By DAVID C. RIFE
*Institute of Genetics, Ohio State University*

(With Plate 11)

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*Coleus blumei* is characterized by wide variations in leaf colour, many of which are simply inherited. A pair of alleles affecting the distribution of anthocyanin in the leaves was first identified by Boye & Rife (1938). The dominant allele ($P$) resulted in uniform distribution of anthocyanin throughout the leaf, while the homozygous recessive condition ($pp$) appeared to restrict the anthocyanin to the epidermal tissues on the upper side of the leaf, surrounded by a margin free from anthocyanin. This phenotype was referred to as pattern.

Boye (1941*a*) later discovered allele ($p^G$) in the same series which produces solid green leaves, also apparently dominant to pattern. Solid purple and solid green show no dominance to each other, the heterozygote ($Pp^G$) being of a different phenotype, known as grey. Boye (1941*b*) also reported a fourth allele ($p^s$) which resulted in solid green in the homozygote but lacked dominance to pattern, the heterozygote showing several small brown spots in the central portion of the upper leaf surface.

Rife (1945) observed a plant whose leaves were characterized by an uneven distribution of anthocyanin in the epidermal tissue. Breeding tests showed that this phenotype resulted from an allele ($P^L$), which also appeared to be dominant to pattern, but which blended with $p^G$ to form an uneven grey ($P^Lp^G$).

Another variation apparently due to another allele ($p^{-m}$), which resulted in semi-pattern, but which was completely recessive to the purples ($P$ and $P^L$) and pattern ($p$), was reported by Rife & Duber (1946).

## ADDITIONAL ALLELES

Four more alleles have subsequently been discovered and are herewith discussed. They are known as raspberry, chocolate, transient and recessive green.

### (1) *Raspberry*

A plant characterized by dark purple leaves with deep black spots was purchased from a commercial greenhouse. It also differed from plants of even and uneven purple phenotype in possessing much darker blue flower petals, and in having purple spots on the stems. The plant was crossed with a homozygous dominant ($p^Gp^G$) green plant, and all of the progeny were of a new phenotype, a peculiar uneven blend of purple and green which we shall designate as 'lilac'. When selfed, lilac produced 17 green, 45 lilac and 15 raspberry. Lilac was also crossed with pattern, and produced 11 green and 10 raspberry offspring. These observations strongly suggest that the gene responsible for the raspberry phenotype ($P^R$) is still another allele in the purple series.

### (2) *Chocolate*

A commercial variety, characterized by solid chocolate-brown leaves and stems, was obtained for investigation. When selfed, offspring occurred in the ratio of approximately 3 chocolate to 1 pattern (74 chocolate, 19 pattern). Chocolate was also crossed with a purple ($PP$), producing offspring characterized by brown stems, as contrasted with the greenish stems of typical purple-leaved plants. It was assumed that they carried the gene for chocolate as well as purple ($P$). Tests were made to determine the relationships of the genes responsible for purple and chocolate. Selfing resulted in 28 offspring, all of which were purple or brown. A cross with a patterned plant produced 40 purple or chocolate and no pattern or green. These results indicate still another allele ($P^c$) as being responsible for the chocolate phenotype (Finck, 1951).

### (3) *Transient*

A commercial variety, known as Beckwith Gem, is characterized by patterned leaves, differing from other patterned clones in having more brown on the stems. When selfed, the resulting seeds produced both purple and patterned seedlings. At first it was assumed that an error had been made, as all previous observations had shown pattern to be completely recessive to purple. The purple appeared to be identical with that resulting from $P$.

Further observation revealed that the purple colour did not develop in the cotyledons, but first appeared in the second leaves, whereas purple develops in the cotyledons of both even and uneven purple phenotypes. More remarkable still, as the plant grew larger, the solid purple no longer developed, the leaves showing the typical pattern instead. As they approached maturity, some of the plants were rather severely pruned. In the new growth, solid purple again appeared in the leaves. I shall henceforth refer to this type of purple phenotype as *transient.*

A Beckwith Gem plant when selfed produced 24 transient purple and 8 patterned offspring with green stems. When a plant heterozygous for even and transient purple ($Pp^T$) was crossed with a patterned plant, there resulted 17 transient purple and 15 even purple offspring. When selfed the heterozygous plant produced 187 offspring, all purple or transient. Subsequent crosses between transient purple and grey ($Pp^G$) revealed that plants carrying both even and transient purple, or those carrying both dominant green and transient purple, produce only two types of offspring in backcrosses, indicating that transient purple ($P^T$) is also an allele in the purple series. Plants heterozygous for transient purple and dominant green ($P^Tp^G$) have solid green leaves with red edges and reddish stems.

### (4) *Recessive green*

A clone of patterned plants was obtained from Purdue University. Some of these were selfed, and produced a total of 90 patterned to 25 solid green progeny. One of the solid green progeny was crossed with a grey ($Pp^G$) and produced approximately equal numbers of purple and solid green offspring. These observations suggest another allele in the purple series which is designated as $p^g$. It appears to be recessive to $P$, $P^L$, $P^R$, $P^C$ and $p$. Its relation to $p^{-m}$ still remains to be determined.

### ALLELES OR PSEUDOALLELES?

It is frequently difficult to distinguish between allelism and pseudoallelism. Recombinations due to crossing-over constitute perhaps the most valid evidence for pseudoallelism or very close linkage, as opposed to true allelism. But even here the possibility of mutation rather than crossing-over cannot be ruled out, especially where the recombinations occur very rarely.

Table 1. *Phenotypic effects of the purple alleles*

| Gene | Symbol | Cotyledons | Leaves | Stem | Genic interrelations |
|---|---|---|---|---|---|
| Even purple | $P$ | Mostly purple, green at base | Solid, even purple | Green, slight amount of brown | Brown stems dominant to both spotted and green, spotted dominant to green |
| Uneven purple | $P^L$ | Mostly purple, green at base | Uneven purple ($P^LP$, solid purple darker than $PP$) | Green, slight amount of brown | |
| Raspberry | $P^R$ | Mostly purple, green at base | Even purple with irregular black splotches | Spotted | Even purple on leaves masks chocolate. Uneven purple or raspberry heterozygous for chocolate show overlying purple and underlying chocolate |
| Chocolate | $P^c$ | Green | Solid brown | Solid brown | |
| Transient | $P^T$ | Green | Solid purple, early leaves. Green with brown near petiole | Brownish green | |
| Dominant green | $P^G$ | Green | Solid green $P^Lp^G$, $Pp^G$, grey; $P^Rp^G$, lilac; $P^Tp^G$, green, red edges | Solid green | Purple cotyledons dominant to green |
| Incompletely dominant green | $p^s$ | Green | Solid green $Pp^s$, uneven brown | Solid green | |
| Recessive green | $p^g$ | Green | Solid green $Pp^g$, purple | Solid green | |
| Pattern | $p$ | Green | Pattern recessive to $P$, $P^L$, $P^R$, $P^c$, $P^G$, $P^T$, solid green; $p^sp$, spotted | Solid green | |
| Semi-pattern | $p^{-m}$ | Green | Semi-pattern | Purplish | |

Positive evidence for true allelism is usually even more difficult to obtain. There are certain situations where such evidence may be provided, however. The following observations in *Coleus* appear to provide evidence of this sort. An even purple plant heterozygous for recessive green ($Pp^g$) was observed to have a branch characterized by even purple leaves. When selfed, seeds produced on different portions of the plant, whether characterized by even or uneven purple leaves, grew into even purple and green seedlings in the ratio of approximately 3 purple to 1 green. No plants showed uneven purple leaves. Presumably the uneven purple colour in the leaves of the one branch resulted from a somatic mutation, $P \rightarrow P^L$. This same type of variegation has been observed on at least two other occasions, on one of which the mutant area was restricted to a portion of one leaf (Pl. 11, fig. 3). The reverse mutation, $P^L \rightarrow P$, has not as yet been observed. Pl. 11, fig. 4, shows another variegated plant, where even purple apparently mutated to chocolate ($P \rightarrow P^c$). These observations suggest that $P$, $P^L$, and $P^c$ are true alleles.

## Discussion

Breeding results suggest at least ten alleles in the purple series. Three of them result in solid green, phenotypically indistinguishable from each other. When heterozygous for purple or pattern, $p^G$, $p^s$ and $p^g$ each result in different phenotypes. Each of the other seven alleles in the series results in the production of anthocyanin, but varying in distribution and amount, dependent upon genotype. Table 1 lists various phenotypes and genotypes now recognized in the purple series.

There are fifteen genotypic combinations of the five alleles $P$, $P^L$, $P^R$, $P^c$ and $P^T$, all of which have been synthesized in our greenhouse. Some of them are difficult to distinguish phenotypically, but each has been analysed by selfing or backcrossing with the recessive green ($p^g p^g$).

## Summary

1. Ten or more alleles appear to occur in the series known as 'purple'. These affect the amount and distribution of anthocyanin in the plant.

2. The occurrence of chimeras within plants of known genotype indicates that the genes $P$, $P^c$ and $P^L$ are true alleles, rather than pseudoalleles.

## References

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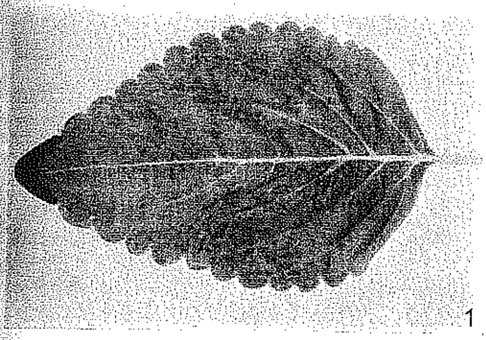
## Explanation of Plate

Fig. 1. Leaf from a plant of 'raspberry' phenotype.

Fig. 2. Progeny of a selfed transient purple, heterozygous for recessive green ($P^Tp$). Note the green cotyledons of the purple segregates, the appearances of pattern on the green segregates. Also note green appearing in the second leaves of one of the large purple segregates.

Fig. 3. Leaf from a plant heterozygous for even purple and recessive green ($Pp$). A large portion of the leaf is of uneven purple phenotype, possibly due to a mutation, $P \rightarrow P^L$.

Fig. 4. A chimera, the darker portion showing the phenotype of even purple, while the lighter portion is chocolate in phenotype.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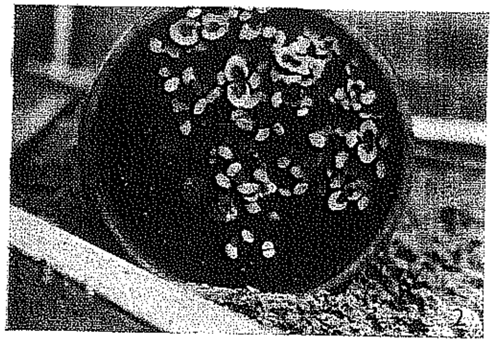
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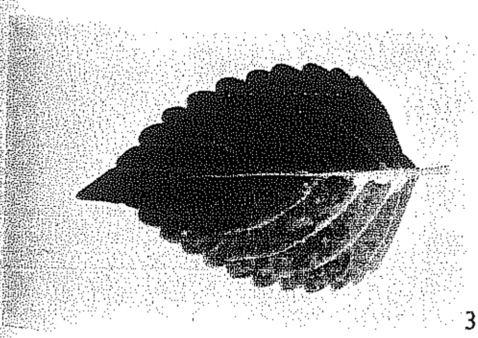
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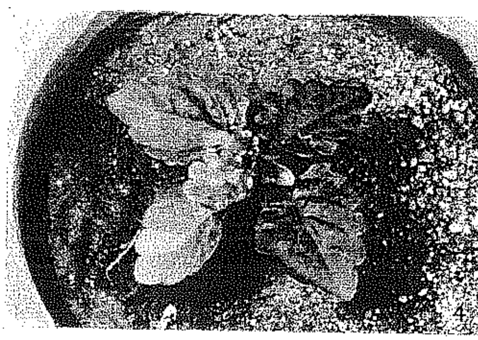
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