A parallel situation might exist in the European land snails, *Cepæa nemoralis* and *C. hortensis* (Helicidæ), but comparable estimates of population density are not available. Some of the colour forms in *Cepæa* appear to be cryptic in different habitats, while some do not. The snails are extensively preyed upon and both the mode and intensity of predation may vary in different populations. In their interpretation of polymorphism in *Cepæa*, Cain and Currey (1963) are unable to account satisfactorily for many of the variations in relative frequency of the colour forms. Possibly if measurements of density had been made, evidence of density effects would have been found. I do not mean to imply (either for *L. martensiana* or for *Cepæa*) that population density is the only, or even the most important, factor affecting the polymorphism, but *Cepæa* should be re-examined to see if there are density effects.

## 3. SUMMARY

1. In the African land snail, *Limicolaria martensiana*, polymorphism in shell colour and pattern is greater at high than at low population densities.

2. It is possible that predators build up specific search images of the colour forms and hence at high population densities colours that contrast with each other are at a selective advantage.

3. Cain and Currey (1963), in a study of the European land snails, *Cepæa*, were unable to account satisfactorily for many of the variations in relative frequency of colour and shell-banding patterns. Population density was not measured. It is suggested that polymorphism in *Cepæa* should be re-examined in terms of population density.

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## 4. REFERENCES

CAIN, A. J., AND CURREY, J. D. 1963. Area effects in *Cepæa*. *Phil. Trans. Roy. Soc. London*, *246*, 1-81.

OWEN, D. F. 1963*a*. Similar polymorphisms in an insect and a land snail. *Nature*, *198*, 201-203.

OWEN, D. F. 1963*b*. Polymorphism and population density in the African land snail, *Limicolaria martensiana*. *Science*, *140*, 666.

OWEN, D. F. In press. A population study of an equatorial land snail, *Limicolaria martensiana* (Achatinidæ). *Proc. Zool. Soc. London*.

# CONTROL OF MALVIDIN SYNTHESIS IN THE CULTIVATED POTATOES

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## 1. INTRODUCTION

THE first anthocyanin pigment to be chemically identified in the potatoes was negretein (malvidin 5-glucoside-3-(*p*-coumaroyl-rutinoside)) responsible

for the deep purple colouration of skin and flesh of the tetraploid ($2n = 48$) " salad potato " " Congo " (under the name " Négresse "—Chmielewska, 1936). Malvidin pigments are also known in some wild diploids (John Innes Institute, 1962) but, curiously, have never been found elsewhere among the cultivars, despite deliberate search (Harborne, 1960). The biochemical genetics of pigmentation among the diploid cultivars is now quite well known; in their tubers, red colours are produced mainly by glycosides of pelargonidin and blue-purple mainly by glycosides of petunidin (Dodds and Long, 1955, 1956; Harborne, 1960). The pigment genetics of the tetraploids is less well understood but it is at least clear that they show the same range of chemical phenotypes as the diploids from which they originated. The malvidin pigment of " Congo " remains therefore an outstanding mystery and this note is concerned with a genetic analysis of the situation.

## 2. RESULTS

The general principle adopted was to make dihaploids of " Congo " and analyse the control of malvidin synthesis at the diploid level. " Congo ", however, is infertile and therefore unsuitable as a haploid-producer so crosses were first made by tetraploids in order to obtain a fertile malvidin-producing plant. The results (table 1) suggest that " Congo " is heterozygous for two or three of the basic pigment genes equivalent to *R*, *P* and *I* in the diploids and also for a dominant methylating system that converts petunidin to malvidin. Two malvidin-containing plants (61/202/8 and 62/172/8) were crossed as females by a diploid Phureja clone (C.P.C. 979)

TABLE 1

*Progeny of " Congo "*

| Family | Tubers of progeny | | | | | |
|---|---|---|---|---|---|---|
| | Blue-purple | | | Red | | White |
| | Mv (Pt) | Pt (Pn) | total | Pg (Pn) | total | |
| 4*x*-61/202 Congo × Ulster Magnet (white) | 1* | 1 | 2 | 1 | 1 | 4 |
| 4*x*-62/172 Congo × ZPC 45/2 (white) | 1* | 0 | 3 | 3 | 7 | 3 |
| 4*x*-63/16 Congo × Flourball (red) | 47 | 46 | 93 | 55 | 67 | 115 |
| 2*x*-64/131 62/246/7 × C.P.C. 979 | 40 | 45 | 94 | 20 | 110 | 76 |

*Notes:* Tubers pigmented by glycosides of aglycones as shown; pigment names abbreviated thus (minor components in brackets): Mv malvidin, Pt petunidin, Pg pelargonidin, Pn peonidin. The two plants marked * were parents of dihaploids of which the one in 61/202 yielded the dihaploid 62/246/7.

and, as expected, a minority (three out of 56) of dihaploids appeared in the progeny (Hougas, Peloquin and Ross, 1958; Peloquin and Hougas, 1960): of the three, one was inviable, one an unbalanced plant with $2n = 24+2$, and the third was a vigorous diploid bearing purple-red tubers pigmented by peonanin (Harborne, 1960). This plant (62/246/7, from 61/202/8) was, as often with potato dihaploids, infertile but intensive pollination by C.P.C. 979 yielded a number of berries bearing an average of eight seeds each.

Genetic results are shown in the last line of table 1. The male parent, C.P.C. 979, is a purple petunidin-producing clone of constitution *PpRRAcAcIi* (Dodds and Long, 1955); the segregation of two classes of purples and of reds and whites shows that the dihaploid parent must be *ppR-Ii* and heterozygous for a dominant methylating gene that converts petunidin to malvidin. The data fit these assumptions well for:—

*P* and *I*: 94:110:76 (3:3:2)—$\chi^2[2] = 1{\cdot}90$
*P*: 94:110 (1:1)—$\chi^2[1] = 1{\cdot}25$
*I*: 204:76 (3:1)—$\chi^2[1] = 0{\cdot}69$
Methylating gene: 40:45 (1:1)—$\chi^2[1] = 0{\cdot}26$

## 3. DISCUSSION

Since the gene *Ac* has, as one of its three functions, the methylation of delphinidin to petunidin it is a reasonable guess that the dominant from " Congo " that adds a second methyl group is an allele at the same locus, but several generations of breeding will be needed to test this. On this basis, 62/246/7 would have the constitution *ppR-Ac'—Ii*. It is at least clear that the gene adds another methyl group to petunidin produced under the influence of *P* and is thus hypostatic to *P*.

A remarkably similar situation is provided by *Petunia* (Meyer, 1964) in which the gene *M* is equivalent in action to *P* in potatoes, *F* equivalent to *Ac* and *K* equivalent to the methylating gene from " Congo ". The similarity of action of *F* and *Ac* extends even to the glycosylation-acylation function. In other plants, the evidence for pigment methylation as a unit gene-controlled function is, in general, much less clear (see, for example, review in Harborne, 1962).

## 4. SUMMARY

Among the cultivated potatoes, a tuber pigment based on malvidin is known only in one tetraploid clone (" Congo ", $2n = 48$). A dihaploid ($2n = 2x = 24$) derived from this clone and crossed by a cultivated diploid gave evidence that malvidin biosynthesis by the methylation of petunidin is controlled by a single dominant gene (which may be, but is not certainly, an allele of *Ac*, a locus already known to have a methylating function).

## 5. REFERENCES

CHMIELEWSKA, Z. 1936. Sur les colorants des pommes de terre violette " Negresse ". *Bull. Soc. chim.*, *5*, *3*, 1575-1588.

DODDS, K. S., AND LONG, D. 1955. The inheritance of colour in diploid potatoes. I. Types of anthocyanidins and their genetic loci. *J. Genet.*, *53*, 136-149.

DODDS, K. S., AND LONG, D. H. 1956. The inheritance of colour in diploid potatoes. II. A three factor linkage group. *J. Genet.*, *54*, 27-41.

HARBORNE, J. B. 1960. Plant polyphenols. I. Anthocyanin production in the cultivated potato. *Biochem. J.*, *74*, 262-269.

HARBORNE, J. B. 1962. Chemicogenetic studies of flavonoid pigments. *The Chemistry of Flavonoid Compounds*, ed. Geissmann, 593-617.

HOUGAS, R. W., PELOQUIN, S. J., AND ROSS, R. W. 1958. Haploids of the common potato. *J. Hered.*, *49*, 103-106.

JOHN INNES INSTITUTE. 1962. Potato Genetics Department. *Rep. Innes Inst.*, *52*, 20-29 (1961).

PELOQUIN, S. J., AND HOUGAS, R. W. 1960. Genetic variation among haploids of the common potato. *Amer. Potato J.*, *37*, 289-297.

MEYER, C. 1964. Die Genetik des B-ringes bei *Petunia*-Anthocyanen. *Z. Vererbungsl.*, *95*, 171-183.