

# NOTES AND COMMENTS

## VARIEGATED MUTANT PLASTID CHIMERAS OF POTATOES

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### 1. INTRODUCTION

THERE is now a considerable literature on the chimerical structure of somatic mutants of potatoes. Most studies have been based on mutants with altered tuber anthocyanin pigmentation or altered habit or leaf-form. For studies of this kind plastid mutants have obvious advantages in that the mutant is expressed in any potentially green tissue. Several plastid mutants have been recorded in the literature (*e.g.* Dorst, 1924; Salaman, 1926, 1931; McIntosh, 1945; Whitehead *et al.*, 1953; Heiken, 1958; Klopfer, 1965) but none has been accorded detailed study. This note records the results of an investigation of three plastid-differential chimeras (Tilney-Bassett, 1963) with the object of determining the relationships of the inner meristem layers and of the mode of transmission of the defect. The usual convention of referring to the meristem layers as  $L_1$ ,  $L_2$  and  $L_3$  from the outside (epidermis) inwards is adopted. Mutant tissue is conventionally described as "white" even though it generally has a yellow tinge.

### 2. OBSERVATIONS

#### (i) *Vegetative propagation*

The three mutants studied were tetraploid ( $2n = 48$ ) South American cultivated forms, members of *Solanum tuberosum* Group Andigena. They were noticed in large seedling populations grown annually at the John Innes Institute during the years 1963-65 (Simmonds, 1966). All were obviously mericlinal at the start and plants were propagated initially by cuttings taken from variegated branches; green shoots were taken as controls.

All the mutants showed signs, sometimes very clear, sometimes sporadic, of an *albomarginata* pattern in the leaflets, suggesting that they were of type  $L_1$  green,  $L_2$  white or mosaic,  $L_3$  green (mesochimeras). That  $L_1$  was constantly green was easily shown by the presence of starch-bearing chloroplasts in stomatal guard cells. Distinctness of  $L_1$  from underlying tissues was suggested by the absence of marginal green patterns and of green flecking on white in *albomarginata*-type leaves. Control plants derived from normal branches and all their descendants, whether propagated by tubers or by stem cuttings, were green (table 1). Among the vegetative progeny of variegated stocks no stable *albomarginata* types were encountered: variegated plants yielded a mixture of stable green, unstable variegated (the most numerous) and lethal white descendants. The pattern of change from variegated towards green or white may be illustrated by two sets of observations of proportions of white tissue in successive leaves (tenths, visually estimated,

from base towards apex in each case). Thus two sister stems of a plant of 64/74 gave:

stem (1): 4, 3, 4, 4, 3, 6, 10, 9, 9, 10, 10 thereafter white  
 stem (2): 1, 1, 4, 1, 2, 2, 3, 0, 1, 0, 0 thereafter green

and a stem of 64/176 that branched at the fifth node gave:

1\*, 8\*, 1, 1  $\left\{ \begin{array}{l} 2, 1^*, 8^*, 1, 2, 2, 1, 1^*, 10, 7, 8, 9, 10, 10 \\ \text{thereafter white} \\ 2, 1, 1, 1, 1, 0, 1, 0, 1, 0, 0 \text{ thereafter green} \end{array} \right.$

The several conspicuous differences between successive leaves (\*) obviously reflected an underlying mericlinal pattern which was apparent also in individual leaves as a tendency towards one-sided distribution of colour.

TABLE 1

*Vegetative propagation of three variegated potato mutants*

Number	Generations	Green controls	Variegated stocks propagated			
			By tubers from		By cuttings from	
			<i>g</i> plants	<i>v</i> plants	<i>g</i> tips	<i>v</i> tips
63/74†	6	20 <i>g</i>	12 <i>g</i>	6 <i>g</i> +15 <i>v</i> +1 <i>w</i>	2 <i>g</i>	11 <i>v</i>
64/176*	5	15 <i>g</i>	6 <i>g</i>	3 <i>g</i> +18 <i>v</i> +4 <i>w</i>	3 <i>g</i>	8 <i>v</i> +3 <i>w</i>
65/160†	4	9 <i>g</i>	2 <i>g</i>	7 <i>g</i> +13 <i>v</i> +12 <i>w</i>	4 <i>g</i>	3 <i>v</i>

*g* = green, *v* = variegated, *w* = white.

\* *Albomarginata* patterns strong and frequent. White tissues of this stock tended to become green on prolonged exposure to light but not green enough to obscure any variegation.

† *Albomarginata* patterns weak and/or sporadic.

### (ii) *Seed propagation*

Results of crossing variegated stocks reciprocally with unrelated green normal plants are given in table 2. Variegated or white shoots transmit

TABLE 2

*Sexual transmission of defective plastids in potatoes*

Type of cross	Berries	Green	Variegated	White
(1) <i>Variegated stocks listed below as females, crossed by pollen from normal green plants:</i>				
63/74—green tip on green shoot	5	549	0	0
green tip on var. shoot	2	170	0	0
yellow tip on var. shoot	3	1	1	270
64/176—green tip on green shoot	8	944	0	0
green tip on var. shoot	(a) 4	162	0	0
	(b) 3	123	2	4
	(c) 1	1	1	42
var. tip on var. shoot	(a) 2	0	0	100
	(b) 3	3	2	267
65/160—var. tip on var. shoot	3	75	53	39
(2) <i>Normal green plants as females, crossed by pollen from following variegated plants:</i>				
64/176—var. tip on var. shoot	9	821	1	4
65/160—var. tip on var. shoot	9	1047	0	0

defective plastids maternally. The complex, patchy distribution of green and white tissue in  $L_2$  that was evident to inspection, is reflected in irregularities of female transmission: thus green tips sometimes contained islands of white cells (table 2, lines 6 and 7) and white tips, contrariwise, sometimes contained green islands (line 3). Nevertheless, the general maternal pattern is clear enough. Variegated plants as males produced very few non-green progeny; somatic mutation or some very occasional male transmission is implied, but detailed interpretation is impossible. The occurrence of variegated seedlings (especially in 65/160) implies the occurrence of heteroplasmic egg-cells (Burk *et al.*, 1964).

Six variegated seedlings, progeny of variegated females, were grown on and, in the next vegetative generation, reproduced the parental behaviour: three were green, two variegated and one white. One of the variegated plants showed clear signs of a mericlinal  $L_1g$ ,  $L_2g$ ,  $L_3w$  structure, with the characteristic pale green patches along the midribs.

### 3. CONCLUSIONS

All three mutants had a normal green  $L_1$  and were essentially meso-chimeras of constitution  $L_1$  green,  $L_2$  white or variegated,  $L_3$  green. By vegetative propagation they yielded their like together with two different stable phenotypes, namely:  $g-w-w$  and  $g-g-g$ . The former is readily interpreted as the result of displacement at a lateral meristem of a green  $L_3$  by a white  $L_2$ , a process well known in other potato mutants (Howard *et al.*, 1963; Howard, 1959, 1967; Simmonds, 1965). The latter is not so simply interpreted. If  $L_2$  is variegated (*i.e.* mixed green and white) elimination of white by competition or developmental accident within  $L_2$  is sufficient explanation (Burk *et al.*, 1964). If  $L_2$  is white, then layer displacement must be invoked or we must assume that a white  $L_2$  sometimes contains enough green or heteroplasmic cells to regenerate green descendants (as shown here by breeding experiments, para 2 (ii)). In this material (*e.g.* in well expressed *albomarginata* plants of 64/176) segregation of green tissue from an overtly or cryptically variegated  $L_2$  was very probably responsible. That displacement of  $L_2$  by  $L_1$  was the cause is very unlikely, because all the (now rather strong) evidence for potatoes points to permanent differentiation of that layer. Displacement of white  $L_2$  by a green  $L_3$  remains a possibility which unfortunately can not be tested in material (such as this) in which cryptic variegation in  $L_2$  is possible. In other plants, the change from  $g-w-g$  to  $g-g-g$  has usually been interpreted in this way (hard as it is to envisage the process) (Cramer, 1954, review; Dermen, 1960). Cases of inward displacement of  $L_2$  by  $L_1$  are known however (*e.g.* Dermen, 1960) and Tilney-Bassett (1963) argues cogently in favour of this mechanism being more important than has generally been allowed.

### 4. SUMMARY

1. Three plastid mutants of *Andigena* (tetraploid) potatoes were studied. They originated by somatic mutation in layer 2 ( $L_2$ ) and so were essentially mesochimerical.

2. Vegetative propagation showed that all yielded unstable variegated plants together with stable greens and stable whites.

3. The instability was due partly to a mosaic constitution in  $L_2$ , partly to incomplete differentiation between  $L_2$  and  $L_3$  such that the former sometimes displaced the latter.

4. Crossing experiments showed that defective plastids were maternally inherited but with, probably, a very low level of male transmission.

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## GENETIC CONTROL OF RECOMBINATION IN *SCHIZOPHYLLUM COMMUNE*: SEPARATION OF THE CONTROLLED AND CONTROLLING LOCI

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### 1. INTRODUCTION

MATING competence in the basidiomycetous fungus *Schizophyllum commune* is controlled by two unlinked factors, *A*, and *B*, each of which consists of two closely linked loci,  $\alpha$  and  $\beta$ . Frequencies of recombination between the loci of each factor vary widely in crosses of wild-type strains (Raper, Baxter and Ellingboe, 1960; Koltin, Raper and Simchen, 1967). A series of studies has been undertaken to determine the basis for this variation. Stamberg (1968) ruled out structural causes—*e.g.* variations in physical distance between the loci—as the main source of variation in recombination frequencies in both the *A* and *B* factors, and concluded that the variation could best be explained by the presence of two independent gene systems, each of which regulated the frequency of recombination within one of the

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