SEED COLOUR POLYMORPHISM IN THYSANOTUS TUBEROSUS R. BR.*

By N. H. BRITTAN[†]

Thysanotus tuberosus is a liliaceous perennial herbaceous plant with a distribution extending from south-east South Australia through Victoria and New South Wales to Queensland and reaching the northern limit of its range at two localities in the Territory of Papua and New Guinea. A collecting expedition in 1959–60 in connection with the author's revisional and experimental taxonomic work on the genus resulted in the collection of herbarium specimens and live plants from a series of localities as far north as southern Queensland. It was found that morphologically variant plants occurred. For example, collection 59/66 from Noosa Heads, Qld., possessed shorter thicker leaves which were curved and deflexed compared with the erect leaves normally found in the species and also had an inflorescence reduced in height. Other collections, e.g. 59/52 from near Caloundra, Qld., had smaller flowers and also differed in size and arrangement of stamens and style. The distribution of the collecting sites of the plants used in the investigation is shown in Figure 1.

The live plants were transferred to Perth where they were grown in an insectproof glasshouse and controlled cross- and self-pollinations were carried out with the object of obtaining hybrid and selfed progeny for chromosomal and genetical studies. The morphology of the anthers is such that only a terminal pore is produced at anthesis and dissection was necessary to extract the pollen. The pollen was transferred to the stigmas by means of a needle. This procedure had also to be followed for self-pollination since, in the absence of manipulation and insect vectors, no seed was set.

It was found that a high proportion of selfed flowers produced capsules. Cross pollination was also reasonably successful except in those cases where the pollen parent was a morphological variant with a shorter style and smaller stamens. These latter short-style plants were fully fertile when selfed. Seed produced as a result of these pollinations, whether self or cross, was typical of the species—uniformly black in colour with a shiny testa having a regular hexagonal pattern and with a yellow aril, an outgrowth from the funicle (Fig. 2).

Self-pollination of the plants grown from the seed resulting from interpopulation crosses was then carried out and the capsules collected from such selfings were found to have varying numbers of atypical seeds. The atypical seeds were dull-surfaced and pale brown in colour instead of being shiny black (Fig. 2). The development

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† Department of Botany, University of Western Australia, Nedlands, W.A. 6009.

of the aril appeared to be unaffected. Preliminary anatomical investigation (Brittan, unpublished data) of the atypical seeds shows disorganization of the outer cell walls of the testa and a lack of pigment development in the tissue. The brown colour is therefore due to the endosperm becoming visible through the now colourless testa.

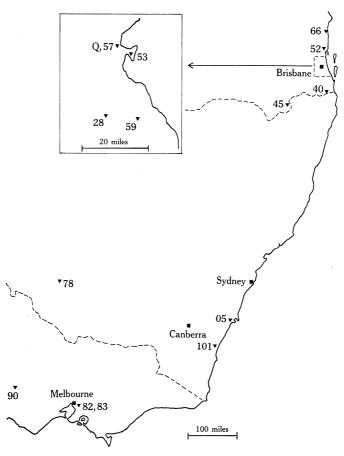


Fig. 1.—Distribution map of the localities from which the experimental plants were collected.

Additional interpopulation crosses were carried out in later seasons in order to widen the range of hybrids available for study. Self-pollination of the hybrids resulted in the data here presented. The results from 1968 (cited because they are the most comprehensive) are given in Table 1. Inspection of these results suggests that three groups can be distinguished, based on the proportion of hybrid plants from a particular parental combination which produces brown and black seeds on selfing compared with those which produce only black. The first group is one in which all plants produce both black and brown seeds, as for example the first three entries; the second group, which contains the largest number of entries, is one in which both types of plant occur. The actual proportion of the two types of plants—brown+black-

seeded and black-seeded only—varies, for example, from the F_1 of the cross 40×28 where 13 "black+brown" occur and 2 "black only" through the cross 57×28 (three plants of each type) to the hybrid 28×59 where only 1 black+brown compared to 8 black only plants occur. The third group, included because they involve, as parents, plants which occur elsewhere in the table—in fact two of the four entries are reciprocal hybrids of parental combinations in group 2—is characterized by the absence of plants producing black+brown plants in the progeny.

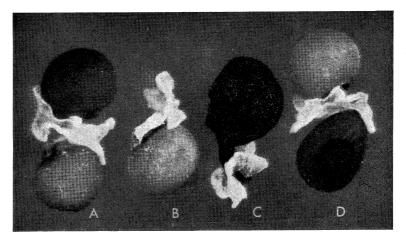


Fig. 2.—Seeds from a capsule resulting from self-pollination of a 28×40 hybrid plant. The pairs of seeds are in the position relative to one another in which they occurred in the capsule. A (upper), dark brown with (upper left) a black segment; A (lower), B, and D (upper), typical light-brown seeds; C, typical black seed; D (lower), dark-brown seed with elliptical black segment. $\times 6$.

Comparisons of the fertilities on selfing of pairs of F_1 plants which produce either brown+black or black only seeds, but which are derived from the same original parental combination, shows the existence of varying situations. For example, the crosses 66×53 (Table 1, lines 4 and 5) and 28×66 (Table 1, lines 16 and 17) show similar values for percentage fertility. In the case of cross 40×59 (Table 1, lines 6 and 7) there is a marked difference—for black+brown plants there is a fertility of $50 \cdot 8\%$ whereas black only plants give a value of $85 \cdot 7\%$. In those cases where a difference in percentage fertility is observed there does not appear to be a correlation between fertility and the occurrence of segregation for seed colour. The reciprocal crosses 40×28 and 28×40 (Table 1, lines 9–12) provide an example. In the former the fertility of the black only seed-producing plants is greater ($81 \cdot 8\%$), whereas in the latter it is the black+brown seed-producing plants which are the more fertile ($68 \cdot 8\%$).

The atypical seeds were found to be viable and percentage germination comparable with that found for black seeds is shown by the results in Table 2. There is apparently no physiological difference which markedly affects germination of the brown seeds.

Discussion

The only other occurence of seed polymorphism dependent upon testa colouration which has come to the author's notice is that reported by Cole (1957, 1961) in *Chenopodium album*. Compared with the present investigation there are two differences: (1) the average percentage of brown seeds is much lower $(1 \cdot 26 - 2 \cdot 64 \%)$ although "in certain instances all seeds on a plant may be large and light brown"

CROSSES									
Parents		${f No.}$ of	Fertility	Total	Ratio of Brown to	Proportion of Brown Seeds to			
Ŷ	้จ	Plants	(%)*	Seeds	Black Seeds	Total Seeds (%)			
Q	28	3	$7 \cdot 2$	11	1:0.375	72.7			
Q	78	3	$20 \cdot 5$	9	$1:0\cdot 5$	$66 \cdot 7$			
66	40	3	$43 \cdot 7$	31	1:0.55	$64 \cdot 5$			
66	53	2	$89 \cdot 5$	61	$1:0\cdot79$	$56 \cdot 0$			
		1	$100 \cdot 0$	16		t			
40	59	7	$50 \cdot 8$	155	$1:1\cdot 2$	$46 \cdot 0$			
		2	$85 \cdot 7$	42		Ť			
57	59	1	$11 \cdot 3$	11	$1:1 \cdot 2$	$45 \cdot 5$			
40	28	14	60.5	350	1:1.4	$41 \cdot 0$			
		2	$81 \cdot 8$	23		Ť			
28	40	12	$68 \cdot 8$	379	$1:1 \cdot 6$	$38 \cdot 0$			
		4	$42 \cdot 7$	122	·	†			
78	4 0	1	$27 \cdot 8$	8	1:1.7	$37 \cdot 5$			
		3	$55 \cdot 0$	43		t			
4 0	66	3	$66 \cdot 1$	85	$1:2\cdot 54$	$28 \cdot 2$			
28	66	2	$85 \cdot 7$	125	$1:5\cdot 9$	$14 \cdot 4$			
		7	$94 \cdot 8$	445		Ť			
82	28	1	16.7	9	$1:8 \cdot 0$	$11 \cdot 2$			
		1	$30 \cdot 4$	11		†			
28	59	1	$100 \cdot 0$	22	$1:10 \cdot 0$	$9 \cdot 1$			
		8	$74 \cdot 7$	222		†			
57	28	3	$53 \cdot 4$	208	$1:18 \cdot 0$	$5\cdot 3$			
		3	$33 \cdot 3$	83		ŧ			
28	78	7	$78 \cdot 2$	354		Ť			
59	28	3	$55 \cdot 8$	163		Ť			
40	$\overline{78}$	$\frac{1}{2}$	$48 \cdot 4$	56		t			
Q	40	- 3	$27 \cdot 4$	8		÷			

TABLE	1
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Results obtained from selfing F_1 hybrids resulting from interpopulation crosses

* Successful/total pollinations. † All black seeds.

(Cole 1961); and (2) the production of brown seeds occurs following selfing in plants from natural populations. The evidence from morphology of the seeds in *Chenopodium* (Baar, reported in Williams and Harper 1965) demonstrates a reduction in thickness of the testa in the brown morphs. In *Chenopodium*, in contrast to *Thysanotus*, physiological differences have been detected which result in different responses of the brown seed to chilling and to the effect of ions in solution and in different dormancy characteristics (Williams and Harper 1965). Dissimilar results—evaluated as percentage production of brown seeds on selfing F_1 hybrids from reciprocal crosses—are found in some combinations of parental lines (66×40 , 78×40 , and 28×59 . Table 1). This suggests that the genetic system probably involves interaction between the testa and a cytoplasmic component.

When the original F_1 seed is produced it possesses the normal testa and cytoplasm complements of the female parent and, like the seed resulting from selfing such a plant, is always black. All the seed from a particular selfed F_1 hybrid plant must be uniform in testa and cytoplasmic constitution but will vary in embryo and endosperm genetic constitution. Segregation for testa colour under these circumstances would indicate involvement of the genetic constitution of either or both the embryo and endosperm in the genetic control of the pigment synthetic pathways.

			CONSTITUTI	ON SHOW	/N		
		Black Seeds			Brown Seeds		
Parents							
Ŷ	5	No. Sown	No. Germin- ating	%	No. Sown	No. Germin- ating	%
28	40	64	20	31	35	14	40
4 0	28	164	82	50	51	22	43
40	59	79	26	33	25	5	20
66	40	5	3	60	4	1	25
78	40	36	14	39	6	1	17
66	53	5	4	80	2	2	100

Table 2 germination of brown and black seeds from selfed F_1 hybrids of the

In addition to seeds which are either entirely black or entirely brown small numbers of seeds occur which are predominantly brown but with variable amounts of black (Fig. 2). In comparison with entirely brown seeds it is usually found that the brown areas of such "piebald" seeds are somewhat darker. The occurrence of such piebald seeds suggests that they represent examples of breakdown to a greater or lesser extent of the genetic system.

Further data must be obtained before a firm genetic hypothesis can be formulated.

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