Euphytica 29 (1980) 807–812

CHIMERICAL STRUCTURE AND CAROTENOID INHERITANCE IN *CHRYSANTHEMUM MORIFOLIUM* (RAMAT.)

F. A. LANGTON

Glasshouse Crops Research Institute, Worthing Road,
Littlehampton, W. Sussex. BN16 3PU, UK

Received 6 February 1980

INDEX WORDS

Chrysanthemum morifolium (RAMAT.), chrysanthemum, carotenoid pigmentation, inheritance, chimerical structure, polyploidy.

SUMMARY

Progeny analysis showed that yellow-flowered chrysanthemum sports with carotenoid only in L1 are indistinguishable from their white progenitors in breeding behaviour; those with carotenoid in L2 breed quite differently. Chimerical structure has, therefore, to be considered when analysing flower colour inheritance data. Segregations were consistent with the action of the single dominant gene I. Such simply inherited characters may be useful in studies to distinguish between the several alternative patterns of inheritance which can be suggested in the species.

INTRODUCTION

Chrysanthemum morifolium (RAMAT.) [*Dendranthema morifolium* (RAMAT.) TZVELEV]., the florists' chrysanthemum, is an outbreeding polyploid with a variable somatic chromosome number. It is usually considered to be a hexaploid, $2n = 6x = 54$ (DOWRICK, 1953), but the precise pattern of inheritance in the species is not clear. Genetic studies are made difficult by the paucity of simply inherited qualitative characters so far identified.

A character that does appear to be qualitatively inherited is carotenoid pigmentation in corolla cells of the ray florets. Carotenoids give a yellow colouration in the absence of anthocyanins and a red-bronze colouration in their presence (KAWASE & TSUKAMOTO, 1974). A simple genetic control is suggested by the frequent and distinct somatic flower colour mutations, white to yellow and pink to bronze, which occur in vegetatively propagated stocks. A single gene was postulated by MIYAKE & IMAI (1935); the dominant allele gave white and pink cultivars and the recessive gave yellow and bronze cultivars. STEWART & DERMEN (1970) have speculated that such a gene might act as a suppressor of carotenoid formation. Genetic evidence for a single gene (I) has, however, only recently been presented (REIMANN-PHILIPP & JORDAN, 1978). In spite of such apparently simple inheritance, there are segregation data which cannot easily be explained (e.g. CULBERT, 1957).

The great majority of yellow-flowered cultivars grown all-year-round in Britain are sports which originated by somatic mutation and are presumed to be periclinal chimeras. Since chrysanthemum corolla tissue is derived from two apical layers, L1 and

L2, and because male and female gametes are thought to be derived only from L2 (STEWART & DERMEN, 1970), it can be expected that some phenotypically yellow cultivars will behave genetically as their white progenitors whilst others will not. The study reported here was undertaken to confirm the single gene basis for carotenoid inheritance and to compare the breeding behaviour of some yellow sports and their white progenitors.

METHODS

The periclinal structure (L1 and L2) of corolla tissue of parental cultivars was determined by microscopic examination of sections cut with a freezing microtome. The distribution of yellow chromoplasts could readily be observed. The presence of carotenoid pigment in progeny was scored by direct observation of ray florets at anthesis.

The maximum likelihood statistic was used to calculate χ^2 values, though the choice of appropriate test ratios presented problems. Table 1 gives phenotypic test ratios for

Table 1. Monogenic control of carotenoid occurrence: test ratios for three types of inheritance.

Cross	Inheritance types					
	hexasomic				tetrasomic	
	diploid-like (selective pairing)		random chromosome pairing		random chromosome pairing	
	− : +		− : +		− : +	
Nulliplex × Nulliplex	0	∝	0	∝	0	∝
Simplex × Nulliplex	1	1	1	1	1	1
Simplex × Simplex	3	1	3	1	3	1
Duplex × Nulliplex	3	1*	4	1	5	1
Duplex × Simplex	7	1*	9	1	11	1
Duplex × Duplex	15	1*	24	1	35	1

− = carotenoid absent; + carotenoid present.
*Ratio assumes non-pairing dominant alleles in the duplex parent (I_1 and I_2): otherwise all progeny would lack carotenoid.

monogenic segregation in crosses between nulliplex, simplex and duplex parents for the gene I assuming three different patterns of inheritance. Diploid-like inheritance has been suggested by WATANABE (1977) as a consequence of his and DOWRICK's (1953) findings that bivalent formation is the norm and that multivalents are rare. Random chromosome assortment is a second possibility; non-homologous pairing has been invoked to explain high bivalent frequencies in a pentaploid species hybrid (WATANABE, 1977). A third possibility, suggested by REIMANN-PHILIPP & JORDAN (1978) and used to fit their data for gene I, is tetrasomic segregation.

RESULTS

Chimerical structure. Sectioning corolla tissue gave the results shown in Table 2. The

Table 2. Carotenoid distribution in corolla tissue of mature ray florets

Cultivar	Origin	Flower colour	Carotenoid distribution	
			L1	L2
Polaris	Seedling	White	–	–
Lemon Polaris	Sport	Pale yellow	+	–
No. 2 Yellow Polaris	Sport	Yellow	–	+
Golden Polaris	Sport	Deep yellow	+	+
Hurricane	Seedling	White	–	–
Yellow Hurricane	Sport	Yellow	+	–
Golden Hurricane	Sport	Deep yellow	+	+
Snowdon	Seedling	White	–	–
Yellow Snowdon	Sport	Yellow	+	–
Bonnie Jean	Seedling	White	–	–
Yellow Bonnie Jean	Sport	Yellow	+	–
Stardust	Seedling	Yellow	±	+
Golden Stardust	Sport	Deep Yellow	+	+
Helen	Seedling	Deep yellow	+	+
White Hope Valley	Seedling	White	–	–

– = absent; + = present; ± = traces.

yellow cultivars, Stardust and Helen, which originated as seedlings, showed chromoplasts in L1 and L2. If it is presumed that Stardust has the same genotype in both layers, its sport, Golden Stardust, could not have resulted from layer rearrangement: it must have originated from a mutation which increases the carotenoid content in the L1. Since the L2 appears to be unchanged, both Stardust and Golden Stardust should behave similarly when used for breeding.

The breeding behaviour of the other seven yellow-flowered sports can also be predicted. Lemon Polaris, Yellow Hurricane, Yellow Snowdon and Yellow Bonnie Jean have carotenoid in the L1 only and should breed as their white progenitors. No. 2 Yellow Polaris which has carotenoid only in L2, and Golden Polaris and Golden Hurricane with carotenoid in L1 and L2 ought to give progenies different from those produced by the original white cultivars.

Hybridisation. Carotenoid segregations in families derived from crossing Polaris or its sports are given in Table 3. The data from reciprocal crosses utilising Snowdon or Yellow Snowdon are shown combined since differences were non-significant. The ratios can be readily explained by assuming segregation of the single gene I. Polaris, Lemon Polaris, Snowdon, Yellow Snowdon and Bonnie Jean are then seen as simplex for the dominant allele, and No. 2 Yellow Polaris, Golden Polaris and Helen as nulliplex. The test ratios 1:1 and 3:1 are appropriate for each of the three suggested modes of inheritance (see Table 1).

The further segregation data in Table 4 suggest that Hurricane, Yellow Hurricane and White Hope Valley are duplex, Yellow Bonnie Jean is simplex, and Golden Hurricane. Stardust and Golden Stardust are nulliplex. These conclusions were reached after fitting test ratios appropriate to each of the inheritance patterns. Discri-

Table 3. Carotenoid segregations in progenies derived from Polaris or its sports.

Cross	Progeny		Test ratio	Probability of a larger value of χ^2
	−	+		
Polaris × Bonnie Jean	55	20	3:1	0.75–0.50
Lemon Polaris × Bonnie Jean	39	20	3:1	0.25–0.10
No. 2 Yellow Polaris × Bonnie Jean	31	34	1:1	0.75–0.50
Golden Polaris × Bonnie Jean	11	13	1:1	0.75–0.50
Polaris × Helen	41	39	1:1	0.90–0.75
Lemon Polaris × Helen	23	28	1:1	0.50–0.25
Golden Polaris × Helen	0	20	0:∞	
Polaris × Snowdon Snowdon × Polaris	58	23	3:1	0.25–0.10
Polaris × Yellow Snowdon Yellow Snowdon × Polaris	47	16	3:1	0.95–0.90

− = carotenoid absent (white or pink-flowered seedlings); + = carotenoid present (yellow or bronze-flowered seedlings).

Table 4. Carotenoid segregations in progeny derived from Hurricane or its sports, and Stardust or sport.

Cross	Progeny		Test ratio	Probability of a larger χ^2 value	Test ratio	Probability of a larger χ^2 value	Test ratio	Probability of a larger χ^2 value
	−	+						
Hurricane × Bonnie Jean	78	15	7:1	0.50–0.25	9:1	0.10–0.05	11:1	0.03–0.01
Hurricane × Yellow Bonnie Jean	69	11	7:1	0.75–0.50	9:1	0.50–0.25	11:1	0.25–0.10
Yellow Hurricane × Bonnie Jean	70	6	7:1	0.25–0.10	9:1	0.75–0.50	11:1	0.90–0.75
Yellow Hurricane × Yellow Bonnie Jean	63	5	7:1	0.25–0.10	9:1	0.50–0.25	11:1	0.90–0.75
Golden Hurricane × Bonnie Jean	29	40	1:1	0.25–0.10				
Golden Hurricane × Yellow Bonnie Jean	35	33	1:1	0.90–0.75				
Stardust × White Hope Valley White Hope Valley × Stardust	110	24	3:1	0.05–0.03	4:1	0.75–0.50	5:1	0.75–0.50
Golden Stardust × White Hope Valley	96	18	3:1	0.03–0.01	4:1	0.25–0.10	5:1	0.90–0.75

− = carotenoid absent (white or pink-flowered seedlings); + = carotenoid present (yellow or bronze-flowered seedlings).

mination between the alternatives is not possible at this stage. However, if diploid inheritance operates, the duplex cultivars must carry non-pairing dominant alleles (I_1 and I_2).

DISCUSSION

Hybridisation confirmed the breeding predictions made on the basis of periclinal structure. Yellow sports which have carotenoid in the L1 but not in the L2 breed as their white progenitors. This parallels what has been found in many other plant species (e.g.

CLAUSEN & GOODSPEED, 1923) and is a factor which must be borne in mind when planning breeding programmes. The segregations are consistent with the action of the single dominant gene I. It seems though that others genes are able to modify the expression of I as, for example, in Golden Stardust. STICKLAND (1972) has similarly reported quantitative differences in carotenoid concentration between related chrysanthemum sports.

The results may explain the apparently anomalous flower colour data of breeders such as CULBERT (1957). He collated data from very many crosses and found, for example, that about 6% of the progeny from crosses involving yellow, bronze and red chrysanthemums (presumably nulliplex × nulliplex) were white or pink. It may be that the parents included chimeras with the dominant allele I in L2 but not in L1.

Sectioning has shown that the majority of currently grown yellow sports are L1 mutants. To the four which are listed in Table 2 can be added many others such as Yellow Marble and Yellow Arctic. Such sports are agronomically very similar to the cultivars from which they were derived. By contrast this is often not the case with L2 sports; Golden Hurricane for example flowers up to one week later than Hurricane or Yellow Hurricane and has rather different flower characteristics. These observations tend to support the conclusion of DOWRICK & EL BAYOUMI (1966) that changes in chromosome number and chromosome fragmentation are usually responsible for colour changes. The loss of a chromosome carrying I is expected to have little effect other than on colour if it occurs in the L1, but to have larger effects on such characters as flower size and flowering time if it occurs in L2 (STEWART & DERMEN, 1970). The chromosome loss theory is strengthened by the finding in this laboratory that non-chimerical yellow plants grown from the L1 of Yellow Snowdon using the method of ROEST & BOKELMANN (1975) were agronomically very different from either Yellow Snowdon or Snowdon itself.

Carotenoid content of the L2 is a very useful character for studies intended to clarify the inheritance patterns in this cultivated species. An understanding of these patterns coupled with an appreciation of the implications of periclinal structure in relation to flower colour and other agronomic characters should give a greater degree of precision to chrysanthemum breeding programmes.

REFERENCES

CLAUSEN, R. E. & T. H. GOODSPEED, 1923. Inheritance in *Nicotiana tabacum*. III. The occurrence of two natural periclinal chimaeras. Genetics 8: 97–105.

CULBERT, J. R., 1957. Breeding spray type chrysanthemums. In: The Breeder's Handbook, pp. 54–67. National Chrysanthemum Society, Inc. USA.

DOWRICK, G. J., 1953. The chromosomes of *Chrysanthemum*. II: Garden varieties. Heredity 7: 59–72.

DOWRICK, G. J. & A. EL BAYOUMI, 1966, The induction of mutations in chrysanthemum using x- and gamma radiation. Euphytica 15: 204–210.

KAWASE, K. & Y. TSUKAMOTO, 1974. Studies on flower colour in *Chrysanthemum morifolium* RAMAT. II. Absorption spectra of intact flowers. J. Japan Soc. Hort. Sci. 43: 165–173.

MIYAKE, K. & Y IMAI, 1935. A chimerical strain with variegated flowers in *Chrysanthemum sinense*. Z. Indukt. Abstamm. -u VererbLehre 68: 300–302.

REIMANN-PHILIPP, R. & C. JORDAN, 1978. Evidence for tetrasomic segregation of flower-colour characters in hexaploid (?) chrysanthemums. Proceedings of the Eucarpia Meeting on Chrysanthemums, Littlehampton: 61–75.

ROEST, S. & G. S. BOKELMANN, 1975. Vegetative propagation of *Chrysanthemum morifolium* RAM. in vitro. Scientia Hort, 3: 317–330.

STEWART, R. N. & H. DERMEN, 1970. Somatic genetic analysis of the apical layers of chimeral sports in *Chrysanthemum* by experimental production of adventitious shoots. Amer. J. Bot. 57: 1061–1071.

STICKLAND, R. G., 1972. Changes in anthocyanin, carotenoid, chlorophyll, and protein in developing florets of the chrysanthemum. Ann. Bot. 36: 459–469.

WATANABE, K., 1977. The control of diploid-like meiosis in polyploid taxa of *Chrysanthemum* (Compositae). Japan J. Genetics 52: 125–131.