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INVESTIGATIONS OF THE INHERITANCE OF FLOWER VARIEGATION IN *MIRABILIS JALAPA* L. 1. GENERAL INTRODUCTION AND 2. INHERITANCE OF COLOUR IN UNIFORMLY COLOURED FLOWERS

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SUMMARY

Mirabilis jalapa plants are very showy through an abundance of reddish, yellowish, white and variegated flowers. The last phenomenon has fascinated various research workers. The authors have studied the inheritance and performed supporting investigations.

In this paper a general introduction is given and the colour inheritance of uniformly coloured flowers discussed.

PART 1. GENERAL INTRODUCTION

For several centuries plants with variegated flowers of *Mirabilis jalapa* L., the four-o'clock-flower, marvel-of-Peru, have been described (GERARD, 1597). Even before the rediscovery of Mendel's laws the inheritance of this phenomenon – an irregular pattern of differently coloured sectors, flakes and spots – had attracted the attention of researchers.

M. jalapa has its origin in Peru. In the 16th century it was introduced in Europe, where it is grown as an ornamental. The species was perhaps introduced at an earlier date in Africa, where it is occasionally cultivated as a fetish plant (DALZIEL, 1937). In countries where no winterkilling occurs it may become a pestweed, as plants, seeds and tubers are killed only by low temperatures.

The genus *Mirabilis* belongs to the Nyctaginaceae. It is characteristic of the family that flowers open in the evening (nyctagineus, four o'clock), bloom all night (nacht-schone, belle-de-nuit) and close for good in the morning. The following evening new flowers open. Owing to the abundance, the elegant colours and the fragrance of the flowers this plant is an excellent ornamental.

Botanically the 'flower' is a calyx, whereas the 'calyx' is an involucre of bracts (HUTCHINSON, 1969). In this paper and the following ones the term flower is adhered to instead of calyx.

Self-pollination is common (CRUDER, 1973), but as many fouraging insects visit the flowers geitonogamy and – if several plants grow together – allogamy are possible as well. The plant is easy to propagate by seed (the fruit contains one seed) and, if needed, by cuttings and tubers.

Several colour forms have been described: white, hues of red and yellow; further,

bicoloured variegates of white/red, white/yellow or yellow/red and a tricoloured variegate of white/yellow/red. The various hues of yellow and red give rise to many colour types.

The growth habit of the plant ranges from large to compact, bushy, types.

The leaves are generally green, but plants with pale green or variegated leaves are also found (CORRENS, 1909, 1910). The reddish colour is not confined only to the flower. Other parts as the lower surface of the cotyledon, the hypocotyl, the first leaves and the stems of the branches may be reddish too.

The somatic chromosome number is high, viz. $2n = 58$ (VAN KESTER et al., 1975), which suggests that the plant is a polyploid.

M. jalapa has been used as an experimental species since KÖLREUTER in the 18th century crossed it with *M. longiflora* L. and *M. dichotoma* (FOCKE, 1881; CORRENS, 1902). LINNAEUS, GAERTNER (FOCKE, 1881), NAUDIN (1865) and others made similar crosses. However, NAUDIN's pictures of an F_1, *M. longiflora* × *jalapa*, show flowers of *M. jalapa*, which was also pointed out by CORRENS (1902).

Various authors have discussed the inheritance of flower variegation, but none of them except CORRENS (1905, 1910) gives a satisfactory explanation. This is why we undertook to investigate this subject. The results are given in the following parts.

MATERIAL AND METHODS

Dr. M. D. DIJT, Haarlem, the Netherlands, sent five seed samples in 1970. He had obtained this material from seeds collected in the Botanical Garden of Budapest, Hungary in 1948. The five samples received were from red, yellow and white plants, and white/red and yellow/red variegated plants. The plants produced corresponded with the description, which suggested that they where true-to-seed. From each lot one individual was selected as parent for our further investigations: plant 1) yellow/red variegated; plant 2) white/red variegated; plant 3) yellow; plant 4) white; plant 5) red.

In the autumn of 1970 the plants were transferred to an insect-proof greenhouse and used as crossing parents. I_1's, F_1's and F_2's were grown either in the greenhouse or in the field depending on the season and on the space available in the greenhouse. Emasculation took place early in the afternoon about one hour before the flowers opened. After the flowers had opened, the stigmas were dusted with pollen.

MAJOR AND MINOR RESEARCH SUBJECTS

Major subject of the research was the inheritance of flower variegation (SPITTERS et al., 1975). The minor subjects were: colour genetics of uniformly coloured flowers (present paper, part 2), chromosome number, distribution of pigment and chromatography (VAN KESTER et al., 1975), colour genetics of cotyledon and hypocotyl (VOSSELMAN et al., 1975). Detailed information is available in ENGELS et al. (1973).

PART 2. INHERITANCE OF UNIFORMLY COLOURED FLOWERS

INTRODUCTION

It is assumed that research into the genetic system of uniformly coloured flowers forms a basis for the study of the genetic system of flower variegation. The reason is that the phenomenon can only express itself when genes for production of pigment are present.

As early as 1902 CORRENS published his work on the genetics of flower colour in *Mirabilis jalapa* L. As was done later by MARRYAT (1909), KIERNAN & WHITE (1926) and SHOWALTER (1934), he showed that a dominant allele Y conditions the production of yellow pigment or pigments, whereas the dominant allele R effects red pigment or pigments in the presence of Y (for types of pigment see VAN KESTER et al., 1975). The genotype yyRR therefore results in white flowers. This type is called 'dominant white', while yyrr (also white flowers) is described as 'recessive white'. Y and R have dosage effects. The more Y or R the more pigments are respectively produced, resulting in different hues of yellow and red and mixtures of these pigments (Table 1).

Table 1. The genotype-phenotype relationship of the colour of the flower based on KIERNAN & WHITE (1926).

	YY	Yy	yy
RR	crimson	magenta	white
R^PR^P	deep crimson	rhodamine purple	rose pink
Rr	orange red	magenta rose	white
R^Pr	scarlet red	rose red	light pink
rr	yellow	pale yellow	white

KIERNAN & WHITE (1926) showed the existence of a third allele R^P. This allele may have a slight pleiotropic action as in the absence of Y red pigments still appear. In the presence of Y the production of these pigments is greatly enhanced.

SHOWALTER (1934) found the allele R^{P^1}. In the presence of Y the red flower colour becomes darker.

MATERIAL AND METHODS

In part 1 the origin of the material was described. For the present experiment the true breeding plant 3 (yellow), plant 4 (white) and plant 5 (red) were used. A crossing programme was carried out (see Table 2) and I_1's, I_2's, F_1's and F_2's were studied for colour.

An attempt was made to classify the plants according to their homozygous or heterozygous genotype, but the many hues observed made such difficult to realize. Therefore, all reddish plants were grouped together as red and all yellowish as yellow.

Table 2. The colour of F_1 plants and the colours and their numbers of F_2 plants of three crosses.

Cross	Results
Plant 4 × Plant 3	F_1: red (variegated) F_2: 30 (red) + 9 (yellow) + 13 {8 (white/red) + 2 (white/yellow) + 3 (white)} $0.950 < P(\chi^2_{9:3:4} = 0.08) < 0.975$
Plant 5 × Plant 3	F_1: red F_2: 38 (red) + 12 (yellow) $0.750 < P(\chi^2_{3:1} = 0.03) < 0.900$
Plant 5 × Plant 4	F_1: red (variegated) F_2: 38 (red) + 10 {7(white/red) + 3 (white)} $0.500 < P(\chi^2_{3:1} = 0.33 < 0.750$

RESULTS AND DISCUSSION

The true breeding character of the parental plants was shown by their I_1's and I_2's. From Table 1 we may conclude that plant 3 (yellow) has the genotype YYrr. Plant 4 may be either yyRR or yyrr. As the F_1 of the cross plant 3 × plant 4 is reddish (Table 2), plant 4 must carry R and therefore have the genotype yyRR (dominant white).

The genotype of plant 5 may be either YYRR or YYR^pR^p. When R^p is present, no white flowers may be observed in the F_2 of plant 5 × plant 4. Also, the variegated flowers may show no white. In our experiments plants with white or white/red variegated flowers were noticed. From this we may conclude that the genotype of plant 5 is YYRR.

The segregation ratios of the F_2's of plant 4 × plant 3 and plant 5 × plant 3 (Table 2) support the above conclusions. The white/red and white/yellow variegated plants have the basic genotype yyRR for white, as was shown by CORRENS (1905, 1910) and later researchers (see SPITTERS et al., 1975).

The presence of F_1 and F_2 plants with variegated flowers in the crosses plant 4 × plant 3 and plant 5 × plant 4 suggests that there are factors, or that there is a factor for flower variegation in the uniformly coloured parental plants. See further SPITTERS et al. (1975).

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