AN ANALYSIS OF THE MORPHOLOGY AND INHERITANCE OF SINGLE VERSUS DOUBLE FLOWERS IN THE GARDEN BALSAM

by

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INTRODUCTION

Morphology Of Double Flowers In General

Many studies on both the morphology and manner of inheritance of single and double flowers have been published. Concerning the morphology, the more important types are here reviewed and summarized.

According to Saunders (1913), double flowers occur as a result of the following:

1. Petalody, which consists of a petaloid modification of floral parts (for the most part stamens) not usually petal-like, as exemplified in Aquilegia (columbine).
2. Augmentation in number of petals resulting from the increase in the total number of parts present. This occurs in Lobelia erinus (lobelia) which has a single calyx and a multiple corolla.
3. Isolation of organs which are ordinarily united.
4. Prolification (proliferation) consisting of the formation of buds within the flower, as seen in Matthiola (stocks).
5. Dissection of petals and the formation of outgrowths.

Saunders, states that classes 1 and 2 occur more frequently than do the other classes and that combinations of 1 and 2 appear to occur more frequently than either alone. In agreement with Saunders, Lettellier (1930) states that doubling consists in multiplication and transformation of certain parts of the flower, usually in multiplication of the petals. In the main, Gerome (1923) agrees with the above writers. He states that doubles in the families

Rosaceae, Ranunculaceae, Papaveraceae, and Malvaceae result from the transformation of stamens into petals, while doubles in the families Cruciferaceae and Carophyllaceae are due to repetition of petals. He mentions the following special cases.

Doubles caused by the growth of a corolla tube within the corolla tube, an example of which is Datura (jimson weed). This would appear to be a case of Saunders' class 2, with tubular corolla.

Doubles resulting from the transformation of stamens into petals within the corolla tube, such as is found in Petunia and Azalea. Apparently this is similarly an example of Saunders' class 1, with tubular corolla.

Double appearance caused by a calyx colored like the corolla, examples of which are found in Primeveres, Campanulas and Rhododendrons. Such cases come under Saunders' definition of case 1, departing, however, from the more usual condition in that the additional corolla-like parts are derived from the calyx rather than the stamens.

Doubles caused by proliferations, development of axillary bracts, and the like, such as are found in the Composites. This group may, in part, fit in Saunders' class 4, while the remainder appears to constitute a distinct type.

Eyster and Burpee (1936) find that in Tropaeolum majus (nasturtium) doubling results almost entirely from the proliferation of the three lower, stalked petals. From their description this case would apparently fit into Saunders' class 5.

It is well known the doubles are frequently sterile. According to Saunders (1911), there are three types or grades of sterility in double flowers.

1. In the extreme type, the stamens and carpels become so petaloid that, as a rule, neither pollen nor ovules are produced, as in Arabis (rock cress) and Cardamine (bitter cress). Such plants are commonly propogated by vegetative methods.
2. In the second class, either stamens or pistil become modified and sexually functionless. The carpels of the double Petunia are sexually functionless, but good pollen is produced in large quantities. In Dianthus (pinks), on the other hand, the double flowers may be destitute of pollen while the female organs remain normal. Carnation and Sweet William are also examples of this condition.
3. In the remaining class, doubling occurs without the loss of function in the reproductive organs of either sex, as e.g. in the double form of Cheiranthus (wallflower), Althaea (hollyhock), and many others. In doubles of this class, considerable variation in degree of doubling is often to be found, even among the flowers of an individual plant.

Letellier (1930) also indicates that sterility is often associated with doubleness. Miyake and Imai (1927) report that the degree of petalody in Pharbitis (Japanese morning glory) shows a remarkable grading, in one plant, from a minimum extreme of "false singles" having quite normal stamens to the maximum limit of full double containing no vestige of pollen sacs. Numerous additional examples of sterility might be mentioned. Obviously sterility in double flowers presents a handicap in the genetic analysis of the trait.

Inheritance Of Single Versus Double In Flowering Plants

A summary factorial analysis published by Beatty (1937) has been modified and reproduced as Table I. In the majority of species reported in this table, doubles are simply recessive to singles. In the genera Dianthus (pinks),Godetia (godetia), Pharbitis (morning glory), and Papaver (poppy), species are known in which doubles are dominant to singles. Dominant and recessive doubles are found within the same species in the genera Impatiens (balsams), Nicotiana (tobacco), Nigella (fennel flower), Papaver (poppy), Pharbitis (morning glory), and Tropaeolum (nasturtium). Two pairs of factors appear to be responsible for the inheritance of double versus single in Godetia rubicunda (godetia), Impatiens balsamina (garden balsam), Matthiola (stocks), Nicotiana (tobacco), Petunia, Phlox, and probably in Aquilega vulgaris (columbine). In the last named, according to Letellier (1930), there is a principal factor and a reinforcing modifier. The presence of modifiers of various types have been reported also in Godetia amoena (farewell-to-spring), Matthiola incanna (stocks), Mimulus tigrinoides (monkey flower), Papaver rhoeas (poppy), Papaver somniferum (opium poppy), and Phlox drummondii (phlox).

TABLE I. A FACTORIAL ANALYSIS OF FLOWER DOUBLING IN VARIOUS SPECIES OF PLANTS. (MODIFIED FROM BEATTY, 1937)

Name of Species	Doubleness		Factor pairs		Modifiers	Investigators
	Dom.	Rec.	1	2		
Althaea ficifolia		X	X			Saunders,1917
Althaea rosea		X	X			Saunders,1917
Aquilegia vulgaris	X		X	?		Letellier,1930
Begonia		X				Bateson and Sutton,1919
Cardamine pratensis		X				Blaringhem,1922
*Cheiranthus cheiri		X	X			Gairdner,1936
Chelidonium majus		X	X			Sax,1918;Dahlgren,1918
Delphinium orientale		X	X			Beckman,1928
Dianthus barbatus		X	X			Saunders,1917;Lilienfeldowna,1922
Dianthus caryophyllus	X		X			Saunders,1917;Batcheler 1912
Dianthus sinensis	X		X			Letellier,1930
Eschscholtzia californica		X	X			Beatty,1936
Fragaria vesca		X	X			Richardson,1918
Godetia amoena	X		X		2	Rasmuson,1921
Godetia rubicunda	X			X	1	Letellier,1930
Godetia whitneyi		X				Rasmuson,1921
Impatiens balsamina		X	X			Davis,1932;Kanna,1926
Impatiens balsamina	X			X		Davis,1932
Matthiola incana		X		X		Saunders,1911
Matthiola incana		X	X			Philp and Huskins,1931
Matthiola incana		X	X		1	Goldschmidt,1913; Winge,1931
Matthiola incana		X		X	2	Muller,1918
Matthiola incana		X	X		2	Waddington,1929
Meconopsis cambrica	X		X			Saunders,1917
Mimulus tigrinoides	X		X		2	Brozek,1926

TABLE I. (Continued) A FACTORIAL ANALYSIS OF FLOWER DOUBLING IN VARIOUS SPECIES OF PLANTS. (MODIFIED FROM BEATTY, 1937)

Name of Species	Doubleness		Factor pairs		Modifiers	Investigators
	Dom.	Rec.	1	2		
Nicotiana (special types)						
calycanthemy........	X		X			White,1916
calycina............		X	X			Setchell et al.,1922
catacorolla.........		X	X			Lodewijks,1911
Klebs-types.........		X	X			Klebs,1916
Klebs-types.........		X		X		Kelaney,1925
Nigella damascena....		X	X			Toxopeus,1927
Nigella damascena....	X					Toxopeus,1927
Oenothera...........		X	X			Shull,1925
Papaver rhoeas.......		X			X	Philp,1934
Papaver somniferum..		X	X		X	Kajanus,1919;Miyake and Imai,1927
Papaver somniferum..	X		X			Kajanus,1919;Miyake and Imai,1927
Pelargonium zonale..		X				Ballard,1918
Petunia violacea....		X	X			Saunders,1910,1916
Petunia violacea....	X			X		Ubisch,1923
Pharbitis nil........		X	X			Miyake and Imai,1927
Pharbitis purpurea..	X		X			Baker,1917;Imai,1927
Phlox drummondii....	X			X	X	Kelly,1929
Portulaca grandiflora..............	X		X			Yasui,1920
Primula sinensis....		X	X			Gregory,1911
Rhododendron indicum		X	X			Miyazawa,1922
Silene pendula.......		X	X			Letellier,1930
Specularia...........		X	X			Letellier,1930
Tagetes erectus (special types)....		X	X			Punnett,1923
Tropaeolum majus.... (super-double)	X		X			Eyster and Burpee,1936
Tropaeolum majus.... (double)		X	X			Eyster and Burpee,1936

*Not included by Beatty; see bibliography.

The Experimental Work

Experimental work on the garden balsam has been carried on for a number of years by Dr. Donald W. Davis of the College of William and Mary and his associates. The inheritance of various traits has been studied. Numerous crosses have been made and their F_2 progenies have been grown in comparatively large numbers. As a result, an extensive set of records has been accumulated and preserved. The writer has participated in the experimental work for three summers, giving special attention to the problems of singles versus doubles. The data reported in this paper have been secured from the records resulting from this cooperative enterprise, and the writer is deeply indebted to Dr. Davis and his associates for their help in making this paper possible.

Statement of Problem

Preliminary conclusions were reported by Davis (1932). It has been the writer's purpose to attempt to analyze the quantitative data that have been collected to date and to draw genetic conclusions based on the available evidence.

DATA AND INTERPRETATIONS

Description Of Flower Types Of Garden Balsam

The following description is largely by Dr. Davis.

Typical single flower. The flowers are borne singly or in small groups in the leaf axils. There are three sepals and five petals arranged in a bilaterally symmetrical manner. The uppermost petal is known as the standard. It has a characteristic form with the midrib and the pointed apex, where these are exposed in the bud, tending to develop chlorophyll. On each side of the standard are two petals having their adjacent edges united for about the proximate one-third of their length. These petals constitute the wings. The sepal on the side of the flower opposite the standard is more or less colored, is broad and petal-like, and bears near it base a spur. The two lateral sepals are usually minute and green. They lie opposite the junction of the two lateral petals; exceptionally, these two sepals are large, colored, and spur bearing. The stamens are five in number, their anthers being united into a ring which closely invests the distal end of the pistil. The ovary is oval and bears five sessile stigmas. The stigmas are completely covered by the anthers until the stage of maturity of the pollen when they protrude through the ring of anthers and expose their stigmatic surfaces.

Double. The parts described above in single flowers appear in doubles with various modifications. The number of cycles of petals may be increased from one to two, rarely to three, four, five or more. Distinctions recognizable among the petals of singles, i.e., the standard with its peculiar form and its tendency toward development of chlorophyll in the portion exposed in the bud, and fusion of the petals constituting the wings, are seen also in the outermost cycle of doubles; but the inner cycles of petals typically show no fusions or other bilateral tendency. Doubles may have wholly normal stamens and pistil and show simply an increase in the number of cycles of petals, an increase in degree quite characteristic of the particular strain. The number of cycles of stamens may also be increased to two or more. In such cases the pollen sacs are usually abnormal and may bear no normal pollen. This condition usually has associated with it a smaller or greater degree of petaloid modification of the stamens.

Growers of balsams have favored full doubles and have doubtlessly directed persistent, painstaking efforts toward establishing strains that would breed true to the double type. Nevertheless many supposedly pure stocks of doubles, supplied by seedsmen, have yielded singles in our plots. These singles may have appeared in consequence of imperfect elimination of recessive factors from the strains or to new mutations in them.

The normal doubles, i.e., those that result solely from multiplication of whorls of petals, are fully fertile. Doubles caused by petaloid modifications of stamens and carpels show a corresponding reduction in the amount of seed produced. Full petaloid doubles produce exceedingly few seed.

<u>Petaloid modification of stamens</u>. In certain strains one or

more of the stamens may bear petal-like enlargements. All of the stamens may be highly petaloid and the pollen sacs vestigial or wholly lacking. There may be found all gradations from a normal stamen to a petal normal in size and showing no indication of pollen sacs. The pistil also may be involved in the tendency to develop petal-like parts, especially when the stamens are extremely petaloid. The pistil may be simply split open on one side exposing the ovules or it may be divided into a number of sections bearing more or less numerous ovules and without any obvious stigmatic surfaces. It is clear that these parts are derived from the gynoecium though there may be no clear indication of the boundary between this cycle and the androecium. In cases of more than one cycle of stamens, all of them may be petaloid, or the outer ones may be petaloid and those of the inner cycle nearly normal. In extreme doubles there are many cycles of petal-like parts, five to each cycle, and no recognizable distinction of androecium or gynoecium except perhaps for a few naked ovules on the innermost parts. There is, then, no satisfactory indication as to whether certain parts are derived from a petal cycle or from androecium or gynoecium. Strains may be found showing almost any degree and combinations of the modifications described yet each maintaining a high degree of constancy to its particular type.

Flowers with only one cycle of normal petals but with petaloid stamens or other abnormalities have been designated as petaloid singles, but there is some indication that these are genotypically doubles.

<u>Aberrant flowers</u>. On certain plants the lowest flowers show a very large number of cycles of petals even when upper flowers of the same plants are normal singles or show only two or three cycles of petals. Again, there is not uncommonly found one terminal flower with very numerous cycles of petals, often associated with great reduction of pigment of the flower and a tendence toward the development of chlorophyll in the petals. These unusual types in both positions show also, very commonly, an increase in the number of spurs and a highly peloric condition generally. These unusual types of flowers at the bottom and at the tip of the main stem are quite uncommon in the intermediate portion and are practically never found throughout the plant. The tendency to form aberrant flowers of these two types is found among both single and double strains, more often in certain strains than in others, and perhaps more frequently in certain seasons. They are disregarded in classifying plants as doubles.

Each true breeding strain has its characteristic combination of features. Certain strains of singles with one cycle of petals and wholly normal stamens never show any tendency towards petalody. Similarily, certain strains with two cycles of petals show constantly wholly normal stamens and pistils. Still others, with almost equal constancy, show their particular type of modification in stamens, carpels, and petals.

Referring once more to the types of doubling distinguished by Saunders and others, it is clear that certain strains of the garden balsam belong in Saunders' type 1 and others type 2, while still others exhibit simultaneously these two types of doubling.

Double Versus Recessive Single

The data throwing light upon the inheritance of double versus recessive single have been summarized in Table II. Each line in the table represents the progeny of an F_1 double plant self-pollinated. The F_1 doubles from 1a through 4f resulted from four crosses, indicated by the arabic numbers, of homozygous doubles pollinated by recessive singles. The F_1 doubles from 5a through 10g resulted from six crosses of recessive singles pollinated by homozygous doubles.

The F_2 progenies in Table II resulted in fairly good .75:25 (3:1) ratios except in very small progenies and those of 1a, 5b, 6c, and 10g. Ignoring these exceptions, the data indicate that the strains used in the crosses differed in a single pair of genes with double dominant to single. The F_1 individuals were therefore heterozygous for the factors of this pair.

Barring the exceptions noted above, the results found in Table II are explained as follows:

P_1	Recessive Single ss	X	Homozygous Double SS
F_1		Double Ss	
F_2	Double $\underbrace{1SS \quad 2Ss}_{3}$		Single $\underbrace{1ss}_{1}$

TABLE II. DOUBLE VERSUS RECESSIVE SINGLES

F_1 Doubles Self-pollinated	F_2 Progenies: Numbers, Double	Numbers, Single	Proportions, Double	Proportions, Single	O—C	Probable Error
1a	440	216	.67	.33	.08	.0114*
					(.1025)	(.013)
1b	576	174	.7675	.2325	.0175	.0114
2a	119	58	.6725	.3275	.0775	.0219
2b	316	99	.7625	.2375	.0125	.0143
2c	83	16	.8384	.1616	.0884	.0294
#2 Total	518	173	.7496	.2504	.0004	.0111
3a	50	23	.685	.315	.065	.0342
4a	146	60	.71	.29	.04	.0203
4b	185	68	.7325	.2675	.0175	.0183
4c	280	74	.7925	.2075	.0425	.0127
4d	254	76	.7675	.2325	.0175	.0160
4e	173	59	.7475	.2525	.0025	.0191
4f	201	59	.7725	.2275	.0225	.0181
#4 Total	1239	396	.7575	.2425	.0075	.0078
5a	180	75	.7025	.2975	.0475	.0182
5b	165	107	.60625	.39375	.14375	.0177
					(.04375)	(.0203)
6a	9	4				
6b	30	10	.75	.25	.0000	.0462
6c	44	38	.5369	.4631	.2131	.032
					(0256)	(.0369)
7a	195	89	.6875	.3125	.0625	.0173
7b	210	65	.7625	.2375	.0125	.0176
7c	387	156	.7125	.2875	.0375	.0125
7d	325	134	.7075	.2925	.0425	.01364
7e	202	71	.74	.26	.01	.01769
#7 Total	1319	515	.72	.28	.03	.00681
8a	326	96	.7725	.2275	.0225	.0142
8b	252	106	.705	.295	.045	.0154
8c	121	30	.8025	.1975	.0525	.0237
8d	413	158	.7225	.2775	.0275	.0122
#8 Total	1112	390	.74	.26	.01	.0075
9a	288	112	.72	.28	.03	.0146
9b	282	110	.72	.28	.03	.0174
9c	43	13	.7675	.2325	.0175	.0391
9d	164	50	.765	.235	.015	.0199
#9 Total	777	285	.7325	.2675	.0175	.0091
10a	60	22				
10b	20	8				
10c	44	10				
10d	5	0				
10e	25	7				
10f	32	14				
#10 Total(a-f)	166	61	.7313	.2687	.0187	.0194
10g	23	18	.56125	.43875	.18875	.0486
					(.00125)	(.0522)

*The probable errors and O—C inclosed in parentheses are based on a 9:7 ratio, the others are based on a 3:1 ratio.

The exceptional progenies 5b, 6c, and 10g much more nearly approximate a .5625:.4375 (9:7) ratio than a 3:1 ratio. This would indicate that another pair of factors is operating and that the genes of these two pairs are complementary. These factors may be designated as S', s' and S", s". The possible genotypes in the phenotypic ratio of 9:7 are:

1 S' S' S" S" 2 S' S' S" s" 2 S' s' S" S" 4 S' s' S" s"	9 doubles
1 S' S' s" s" 2 S' s' s" s" 1 s' s' S" S" 2 s' s' S" s" 1 s' s' s" s"	7 singles

In the crosses represented by the numbers 5, 6, and 10 (Table II), the ratios 3:1 and 9:7 occurred in the F_2 progenies. Such results are explained as follows:

P_1	Recessive Single S's's"s"	X	Homozygous Double S'S'S"S"
F_1		Double S'S'S"s", S's'S"s" 1 : 1	

It follows that when a double of the genotypic constitution S'S'S"s" or S's'S"S" is self-pollinated, the ratio of the F_2 progeny will be 3:1. But when a genotype heterozygous for both pairs of factors is self-pollinated, the resulting ratio will be 9:7. The first filial generation above shows that the genotypes

$S'S'S''s''$ and $S's'S''s''$ would be expected to occur in equal numbers, therefore, half of the F_2 ratios in crosses 5, 6, and 10 (Table II) should have been 3:1 and half 9:7. This expectation is realized in crosses 5 and 6, but in cross 10 the 3:1 ratio predominates.

The progeny of 1a does not approximate satisfactorily either a 3:1 or 9:7 ratio. The 3:1 ratios in crosses 1, 2, 3, 4, 7, 8, and 9 (Table II) are explicable on the hypothesis of complementary genes outlined above. The 3:1 ratio would be expected in the F_2 of a cross with $S'S'S''S''$ of either $S'S's''s''$ or $s's'S''S''$.

The evidence, then, indicates that two pairs of factors complementary to each other are responsible for the inheritance of doubles and recessive singles. Table I indicates that two other species exhibit a similar type of inheritance. Two pairs of factors were found to be operating in the inheritance of double versus single in Petunia violacea (petunia) with double dominant to single. Godetia rubicunda (godetia) is similar except that a modifier is also found.

If the above explanation of the inheritance of double versus recessive single is correct, it must be possible to get homozygous single strains which when crossed with each other will give all doubles in the F_1. In spite of some attempts, these strains have not been isolated as yet. It is a rather difficult task, for none of the recessive singles can be distinguished from one another phenotypically. A suitable manner of procedure is as follows:

Choose one or more single strains which when crossed with doubles have given in the F_2 a 3:1 ratio or choose singles that occur in the 3:1 ratio. These will be of the genotype $S'S's''s''$ or $s's'S''S''$. Choose, also, numerous singles from a progeny in which they appear in the ratio of 9 doubles to 7 singles. These should include all of the single genotypes shown on page 18. Make a test cross of each of the singles from the 9:7 progeny with the singles of genotype $S'S's''s''$ or $s's'S''S''$. The test crosses should yield in some cases all singles (4 chances in 7); in some, equal numbers of singles and doubles (2 chances in 7); in other cases, all doubles (1 chance in 7). Of the two singles which, when crossed, give all doubles, one must be of the genotype $S'S's''s''$, the other $s's'S''S''$. Care should, of course, be taken that self-pollinated seed of these should be available for continuing these strains after identification.

Dominant Single Versus Double

The data relevant to the inheritance of dominant single versus double are summarized in Table III. Each line in the table represents the progeny of an F_1 single plant self-pollinated, except in the case of the last two items (20f, 20g) of which explanation is given later. The F_1 singles from 11a through 18a resulted from eight crosses of homozygous dominant singles pollinated by homozygous doubles. The F_1 singles 19a - d resulted from the reciprocal of this cross. F_1 plants 20a-g resulted from a cross of a heterozygous dominant single pollinated by a homozygous double. Two of the resulting doubles were self-pollinated and the results are shown in the last two lines of Table III.

The data in Table IV also bear upon the inheritance of dominant single versus double. A recessive single pollinated by the dominant single gave the F_1 singles 21a-f.

Many of the F_2 progenies in Table III closely approximate a monofactoral ratio of .75:.25 (3:1). Such results evidence the possibility of single versus double being due to a single gene difference in which single is dominant to double. But the occurrence also of the ratios .8125:.1875 (13:3) and .8594:.1406 (55:9) in the F_2 progenies (Table III) indicates the presence of several factor pairs. This is explained on the assumption of a pair of genes of which the dominant produces single, in spite of the factors for double treated in the preceding section, together with genotypes that appear as singles due to recessive single factors. The dominant single may be designated D. This assumption may be somewhat clarified by the list of genotypes and corresponding phenotypes of a 55:9 ratio which follows:

$$\left.\begin{array}{l} DD - - - - \\ Dd - - - - \end{array}\right\} \text{48 Dominant Singles}$$

$$\left.\begin{array}{l} 1\ ddS'S'S''S'' \\ 2\ ddS'S'S''s'' \\ 2\ ddS's'S''S'' \\ 4\ ddS's'S''s'' \end{array}\right\} \text{9 Doubles}$$

TABLE III. DOMINANT SINGLE VERSUS DOUBLE

F_1 Singles Self-pollinated	F_2 Progenies: Numbers		Proportions		O—C	Probable Error*
	Single	Double	Single	Double		
11a	102	28	.7844	.2156	.0344	.025*
					(.0281)	(.023)
11b	85	22	.7906	.2095	(.0220)	(.0257)
11c	139	55	.7165	.2835	.0335	.021
12a	126	39	.7636	.2364	.0136	.023
12b	44	18	.7097	.2903	.0403	.037
12c	23	4	.85185	.14815		
12d	31	10	.7561	.2439	.0061	.0556
12e	9	3	.75	.25		
#12 Total	233	74	.7590	.2410	.0090	.0166
13a	520	161	.7625	.2375	.0125	.0112
13b	1278	410	.7575	.2425	.0075	.007
13c	478	140	.7725	.2275	.0225	.0117
13d	996	240	.805	.195	(.0075)	(.0077)
13e	919	281	.765	.235	.015	.0084
14a	33	11	.75	.25		
14b	16	5	.7619	.2381	.0119	.0638
#14 Total	49	16	.7538	.2462	.0038	.035
15a (Note 1)	646	172	.7897	.2103	(.0228)	(.0082)
15a (Note 2)	658	160	.8044	.1956	(.0081)	(.0082)
15b (Note 1)	582	160	.7844	.2156	(.0281)	(.0096)
15b (Note 2)	596	146	.8032	.1968	(.0093)	(.0096)
15c (Note 1)	823	277	.7482	.2518	.0018	.0088
15c (Note 2)	838	262	.7618	.2382	.0118	.0088
16a	46	12	.7931	.2069	(.0194)	(.034)
16b	70	18	.7955	.2045	(.0070)	(.028)
#16 Total	116	30	.7945	.2055	(.0080)	(.0217)
17a	77	19	.8021	.1979	(.0104)	(.0268)
18a	80	26	.7541	.2459	.0041	.0284
19a (Note 1)	536	194	.7342	.2658	.0158	.0108
19a (Note 2)	552	178	.7562	.2438	.0062	.0108
19b (Note 1	610	185	.7673	.2329	.0173	.0104
19b (Note 2)	627	168	.7887	.2113	(.0238)	(.0093)
19c (Note 1)	709	241	.7463	.2539	.0037	.0085
19c (Note 2)	739	211	.7779	.2221	.0279	.0085
19d (Note 1)	1205	339	.7804	.2196	.0304	.0074
19d (Note 2)	1272	272	.8238	.1762	(.0113)	(.0067)
20a	20	6	.7692	.2308	.0192	.0573
20b	148	29	.8362	.1638	(.0237)	(.0197)
					[.0232]	[.0177]
20c	174	40	.8131	.1869	(.0006)	(.0179)
20d	181	43	.8080	.1920	(.0045)	(.0176)
20e	153	29	.8407	.1593	[.0187]	[.0178]
20f (Note 3)	14	32	.3043	.6957		
20g (Note 3)	6	24	.2	.8		

*When two probable errors are given, the one underscored is based upon the nearest theoretical proportion. Probable errors and deviations in parentheses are based upon a 13:3 ratio; inclosed in brackets a 55:9 ratio; and all others a 3:1 ratio. No probable errors are given when numbers are too small.

Note 1. Petaloid singles counted as doubles.
Note 2. Petaloid singles counted as singles.
Note 3. F_1 Doubles self-pollinated.

TABLE IV. DOMINANT SINGLE VERSUS DOUBLE

F_1 Singles Self-pollinated	F_2 Progenies: Numbers Single	Numbers Double	Proportions Single	Proportions Double	O—C	Probable Error
21a	13	1				*
21b	272	68	.8	.2	(.0125)	(.0143)
21c	182	40	.8206	.1794	(.0081)	(.0176)
21d	146	27	.8448	.1552	[.0146]	[.0178]
21e	319	60	.8448	.1552	[.0146]	[.012]
21f	738	129	.8509	.1491	[.0085]	[.0079]

*No probable error is given when numbers are too small. Probable errors and deviations inclosed in parentheses are based upon a 13:3 ratio, while those inclosed in brackets are based upon a 55:9 ratio.

1 ddS'S's"s"
2 ddS's's"s"
1 dds's'S"S"   7 Recessive Singles
2 dds's's"S"
1 dds's's"s"

Forty-eight of the above singles are due to the expression of the dominant gene D, while seven are recessive singles caused by the absence of one or both of the essential doubling factors, giving a total of 55 singles : 9 doubles.

The results of the crosses represented by the numbers 12, 14, and 18 (Table III) with the exception of 12a are explained as follows:

P_1 Dominant Single X Homozygous Double
DDS'S'S"S" ddS'S'S"S"

F_1 Single
DdS'S'S"S"

F_2 Single : Double
1 DDS'S'S"S" 2 DdS'S'S"S" : 1 ddS'S'S"S"
3 : 1

The results found in 16a and b, and 17a, in which only the ratio of 13:3 is approximated, are explained as follows:

P_1 Dominant Single X Homozygous Double
DDS'S's"s" or DDs's'S"S" ddS'S'S"S"

F_1 Single
Dds'S'S"s" or DdS's'S"S"

F_2 13 Singles : 3 Doubles

The results of the crosses represented by the numbers 11, 13, and 15 (Table III), in which the F_2 progenies gave the ratios 3:1 and 13:3, are explained in the following manner:

Dominant Single X Homozygous Double
DDS'S'S"s" or DDS's'S"S" ddS'S'S"S"

Single {DdS'S'S"S" selfed, yields 3 singles : 1 double
{DdS'S'S"s" selfed, yields 13 singles : 3 doubles

The ratios 3:1 and 13:3 should occur in approximately equal numbers in the F_2 progenies of crosses 11, 13, and 16, and these show six nearer 3:1 and five nearer 13:3.

The F_2 progenies in cross 19 (Table III) were calculated in two different ways, i.e., counting the petaloid singles as doubles and counting them as singles. When they were counted as doubles, the results are explained as follows:

P_1 Homozygous Double X Dominant Single
ddS'S'S"S" DDS'S'S"S"

F_1 Single
DdS'S'S"S"

F_2 Single Double
1 DDS'S'S"S" 2 DdS'S'S"S" 1 ddS'S'S"S"
3 1

The F_2 progenies of 19b and d became better 13:3 ratios than 3:1 when the petaloid singles were counted as singles. The F_2 progenies of cross 16 were calculated in the same manner, but no pronounced changes were made in the ratios. The presence of a petaloid condition in certain strains has given ratios that have been quite puzzling as demonstrated by the results of cross 19. It is recognized that further work is necessary in order to solve the problems involved in the inheritance of petalody. Some phases of this are treated on page 29.

The results found in the F_2 progenies of 20a-g inclusive (Table III) are explained as follows:

Heterozygous Dominant Single X Homozygous Double
DdS's'S"s" ddS'S'S"S"

Single:
- DdS'S'S"S" selfed, yields 3 singles : 1 double
- DdS'S'S"s" / DdS's'S"S" selfed, yield 13 singles : 3 doubles
- DdS's'S"s" selfed, yields 55 singles : 9 doubles

Double:
- ddS'S'S"S" selfed, yields all doubles
- ddS'S'S"s" / ddS's'S"S" selfed, yield 3 doubles : 1 single
- ddS's'S"s" selfed, yields 9 doubles : 7 singles

The expected ratio of the F_1 's above is 1 double : 1 single. The observed numbers are 14 doubles : 18 singles. Five F_1 singles were self-pollinated and the approximate ratios were as follows: one (20a) .75:.25 (3:1); two (20c,d) .8125:.1875 (13:3); and two (20b,e) .8594:.1406 (55:9). Two F_1 doubles (20f,g) were self-pollinated and their progenies approximated a ratio of 3 doubles : 1 single. It is assumed that the remaining theoretical ratios were not obtained because of the relatively small number of F_1 plants self-pollinated.

Finally, the results found in the F_2 progenies of 21a-f inclusive (Table IV)are explained as follows:

Recessive Single X Dominant Single
ddS's's"s" or dds's'S"s" DDS'S'S"S"

- DdS'S'S"s" / DdS's'S"S" selfed, yield 13 singles : 3 doubles
- DdS's'S"s" selfed, yields 55 singles : 9 doubles

The above ratios would be expected in equal numbers and the actual results manifested two (21b,c) that approximated a

13:3 ratio and three (21d,e,f) that approximated a 55:9 ratio.

In conclusion, the evidence supports the assumption that dominant single is due to a single gene difference, designated as D, while double occurs as a result of the operation of two pairs of factors which are complementary to each other and which are expressed phenotypically only in the absence of D.

Change of Petaloid Singles to Doubles

Table V was prepared to throw light on the change of petaloid singles into doubles when dominant single versus double is involved. The numbers in column one of Table V represent seven crosses between dominant single and homozygous double strains. In growing F_2 plants of each cross a few seeds were sown in the greenhouse and transplanted to the field where they were available for repeated description, but the bulk of the F_2 plants from each cross were sown in the field where they were discarded immediately after being described and recorded. Though most of these plants were thus described only once, the dates of descriptions were recorded which makes it possible in various F_2 progenies to compare the portions described at different seasons and at different ages.

The progenies of 22a,b,c (Table V) were scored in 1936 at three different periods. The first portion was scored on September 5, the second on September 26, and the final portion on October 13 and 17. The seed had been sown on June 25, 1936. The first of progenies 23a,b,c and 24a was scored before August 21, 1931, while the other portion was scored from that time until

TABLE V. CHANGE OF PETALOID SINGLES TO DOUBLES

F_1 Singles Self-pollinated	F_2 Progenies: Numbers — Single	Numbers — Double	Proportions — Single	Proportions — Double
	*			
22a	42(134)[21]	2(75)[10]	.9545(.6412)[.6774]	.0455(.3588)[.3226]
22b	131(71)[25]	10(51)[33]	.9291(.5819)[.4310]	.0709(.4181)[.5690]
22c	102(24)[33]	1(33)[40]	(.4211)[.4521]	(.5789 [.5479]
23a	95 (72)	24 (26)	.7983 (.7347)	.2017 (.2653)
23b	72 (48)	6 (18)	.9231 (.7273)	.0769 (.2727)
23c	397 (70)	56 (45)	.8764 (.6087)	.1236 (.3913)
24a	295 (21)	48 (8)	.86 (.7241)	.14 (.2759)
25a	494 (68)	71 (11)	.8743 (.8608)	.1257 (.1392)
25b	390 (106)	95 (28)	.8041 (.791)	.1959 (.209)
26a	244 (301)	22 (52)	.9173 (.8527)	.0827 (.1473)
27a	246 (486)	38 (95)	.8662 (.8365)	.1338 (.1635)
28a	173 (146)	21 (20)	.8918 (.8795)	.1082 (.1205)
28b	88 (106)	9 (29)	.9072 (.7852)	.0928 (.2148)

*The first numbers in each space represent F_2 progenies scored early; those inclosed in parentheses represent F_2 progenies scored later; and those in brackets were scored near the end of the flowering season.

close of the flowering season. The seed of F_1 single plants 23a,b,c were sown on May 9,1931, while the seed of 24a were sown on May 16, 1931. Finally, the first of progenies 25a,b, 26a,27a, and 28a,b was scored before August 16, 1933, while the other portion was scored after that date. The seed of the F_1 singles were sown as follows: 25a on April 26; 25b on May 3; 26a on May 20; and 27a, 28a,b on May 26 in 1933.

Except possibly in the cases of 22a and c, the data (Table V) indicate that the plants, when described later, were nearer the maximum production of double flowers than at the earlier dates. Regardless of season, the older the plants the higher were the proportion of doubles.

William M. Anderson, who participated in the balsam breeding, found a similar occurrence in some strains involving the inheritance of double versus recessive single flowers. He investigated some F_2 progenies that, in general, resulted in a 9:7 ratio, but in which several irregularities occurred. Separating the phenotypes into portions based upon time of scoring, it was demonstrated, without exception, that the plants scored later showed a higher proportion of doubles than those scored early. Anderson has also indicated that seasons have nothing to do with the change of petaloid recessive singles to doubles.

The data at hand concerning these strains in which the number of doubles varies so greatly with age of plant, do not permit a satisfactory analysis of the mode of inheritance. The effect of age of plant suggests a possible explanation of some other crosses,not so fully recorded, where ratios were difficult or impossible to interpret. The data presented in Table V are cited as samples of such records not deemed worthy of incorporation here in full, but it is important to recognize the occurrence of such cases not obviously fitting the analysis here given. These strains need to be investigated more extensively and their progenies described at frequent intervals in order to extend, confirm, or refute the present conclusions.

CONCLUSIONS

1. Double flowers in the garden balsam occur most frequently as a result of petalody, or of multiplication in number of petals, or as a result of combinations of both; thus, exemplifying the most frequent type of morphological origin.

2. Doubles in the gardem balsam resulting from petalody are more or less sterile, while the normal doubles are fully fertile.

3. The inheritance of double versus recessive single in the garden balsam involves two pairs of complementary factors, designated as S'-S"-. The recessive ss of either or both of these pairs of genes produces singles.

4. The evidence supports the assumption that dominant single in the garden balsam is due to a single gene difference, designated as Dd, while double results from the expression of two dominant pairs of complementary factors in the absence of D.

5. The evidence indicates that in some strains of the garden balsam, petaloid singles change to doubles as the plants become older, when either dominant single or recessive single is involved. Apparently seasons have nothing to do with this change.

6. There is a need to isolate certain strains of the garden balsam in order to confirm the present conclusions concerning the inheritance of single versus double; particularly to isolate and identify the recessive single strains ddS'S's"s" and dds's'S"S" which when crossed will give all doubles.

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