

The Production of Female-sterile Flowers by Hermaphrodite Plants of *Fuchsia procumbens*

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[Read by title and abstract before the Otago Branch on November 19, 1957, received by
Editor, December 3, 1957]

Abstract

Fuchsia procumbens flowers annually in late summer. The brief flowering season begins and ends with the production of a proportion of imperfect flowers—some fall without opening, others open normally but have defective styles and stigmas. Continuous long-day treatment extends the flowering season and increases the number of flowers produced throughout, but this is supposed not to be directly a day-length effect on flower initiation but on vegetative growth. Neither bud abscission nor female sterility could be shown to be simple day-length effects, but both appear to be induced primarily by low temperatures, in conjunction perhaps, with long days in the case of abscission, and short days in the case of style abortion.

INTRODUCTION

KIRK (1893) originally described *Fuchsia procumbens*, R. Cunn as heterostylic, considering that the three forms of flower, long, mid- and short-styled, are equivalent to the three forms in the classical case of tristily, *Lythrum salicaria*. Godley (1955) has shown, however, that this is quite erroneous, for the long and short-styled forms are not only self-incompatible, but actually male and female sterile, respectively. This means that in fact, the species is not tristylic but trioecious, the mid-styled form being hermaphrodite. Actually Godley shows that there are, in all, five types of plant; for there are also two forms each of both the female and male kinds.

The plant cultivated in gardens is, of course, the mid-styled or hermaphrodite form. Cheeseman (1914) mentions that it produces fruit in "comparative abundance" and from Godley's analysis of the species, it is obvious that this form alone can be capable of fruiting in isolation. Cheeseman's qualification "comparative", implies that even here, self fertility is not very high, so it may be partially self-incompatible. On the other hand, Godley has mentioned (1955) that a proportion of the flowers produced by the hermaphrodite form also are short-styled and female sterile. This also helps, then, to account for some of the flowers not setting. Figure 1 shows that female sterility is due to abortion of the upper part of the style including the stigma. The ovary and ovules appear to be normal.

On bringing these male flowers to the notice of the author, Godley remarked that their production by hermaphrodite plants is seasonal, and suggested that an investigation of environmental effects on the flowering of this species might be rewarding.

EXPERIMENTAL

Two hermaphrodite plants have been established some years in the botany garden at Otago Museum. In 1951, branches from each were potted up in the greenhouse to make a pair of clones. Very few, as a matter of fact, became established but it was possible to select four plants of reasonably equal size from each clone. Two were allotted to "long-day" treatment and two to "short".—

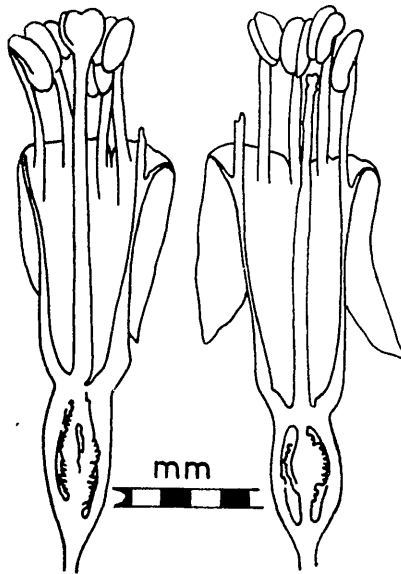


PLATE 1—Hermaphrodite (left) and male flowers of *Luchsa procumbens* from a hermaphrodite plant

The plants were kept on trolleys which stood from 8 a.m. to 4 p.m. in the open greenhouse. At 4, the short-day trolleys were moved into the dark, into a light-proof room adjoining the greenhouse. The long-day trolleys remained in the greenhouse and were there illuminated until 10.30 p.m. by electric light about 45 f.c. at plant height. The greenhouse and darkroom were frost-protected by a thermostat set at 10°C and air was circulated between the two by fans in order to equalise temperature.

Day-length treatment was begun on 25 October, 1951 and at this time, the plants were in leaf but none visibly budded.

As flowers appeared they were pickled in 70% alcohol, either on the day they opened or, if abscised, as soon as they fell off. Subsequently the diameters of the stigmas were measured with a micrometer eyepiece and a note made of whether the style was longer or less than or equalled the stamens.

RESULTS

The observations cover one summer and part of the next. Unfortunately the experiments had then to be discontinued. In the first season flowering in the greenhouse began at the beginning of December, was at its height in February and continued sporadically until the end of April. The original pair of plants out of doors had a much briefer season. A few buds appeared towards the end of December but all abscised (and were rejected on that account). Good flowers were collected only from the beginning of February to the end of March.

TABLE 1—Incidence of Flowering, Abscission and Short Styles as in the Summer of 1951-2.

Week of 1951	In Long Days			In Short Days			Outdoors		
	Total Flowers	% Abscission	% Short Styles	Flowers Total	% Abscission	% Short Styles	Total* Flowers	% Abscission	% Short Styles
Dec 3	2	100	100						
Dec 10	3	--	--	1	(100)	--			
Dec 17	5	--	20	--					
Dec 21	3	--	--	4	25	--			
Dec 31	6	17	--	1	(100)	(100)			
Jan 7	1	--	--	--					
Jan 14	11	--	--	--					
Jan 21	27	--	--	2	--	--			
Jan 28	11	--	7	7	--	--	**		
Feb 4	19	--	--	13	--	8	9	--	67
Feb 11	3	--	--	1	--	--	17	--	71
Feb 18	29	--	3	1	--	--	14	--	50
Feb 25	16	--	6				5	--	20
Mar 3	21	--	24				10	--	90
Mar 10	14	--	7				7	14	86
Mar 17	9	--	11				10	--	70
Mar 24	4	--	75				4	--	50
Mar 31	10	--	--				2	50	100
Apr 7	8	--	--						
Apr 14	6	--	--						
Apr 21	9	--	11						
Apr 28	6	--	33						
May 5	7	--	57						

* Not to be compared with other treatments as only 2 plants and those large

** Two abscised flowers produced before this date not examined

After a winter in the greenhouse, flowering began much earlier, at the end of September, the second season. A very high proportion of these early flowers in the greenhouse abscised however, and good flowers were not being produced in abundance until a month or so later. Flowering in the greenhouse was still at its height when observations had to be given up in mid-December. Flowering out of doors also, was rather earlier the second season, so that some had been collected there too before the experiments were given up.

Tables 1 and 2 show that in neither day-length was flowering completely suppressed, but a pronounced effect of day-length on the flowering of *Fuchsia procumbens* is, nevertheless, apparent and in two ways: long days increased the number of flowers produced at any one time and, also, considerably prolonged the flowering season. On the other hand, in both seasons, flowering began at approximately the same time in either day-length.

It should be noted, however, that flowering in both seasons was very irregular: the tables show that it ceased completely at times in short days, and examination of the records for the individual plants, shows it stopped and started at times in long days as well. The figures of total weekly flower production, indeed, demonstrate this by their fluctuations.

It is also clear in the tables, that neither day-length completely controlled either bud abscission or the production of short-styled flowers. In the first season it is true that very few flowers abscised anyway and relatively few had short styles either

TABLE II.—Incidence of Flowering, Abscission and Short Styles in the Summer of 1952-3

Week of: 1951	Long Days			Short Days			Outdoors		
	Total Flowers	% Abscission	% Short Styles	Total Flowers	% Abscission	% Short Styles	Total* Flowers	% Abscission	% Short Styles
Sep 21	32	100	19	14	86	57			
Sep 29	93	87	42	16	63	75			
Oct 6	92	80	45	31	35	68			
Oct 13	43	67	63	26	15	73			
Oct 20	14	43	64	14	7	79			
Oct. 27	10	60	50	7	—	14			
Nov 3	13	46	54	1	—	(100)			
Nov 10	8	13	50	1	—	(100)			
Nov 17	9	11	44	—					
Nov 24	15	7	33	—					
Dec 1	9	—	78	—			3	33	67
Dec 8	39	—	41	4	—	75	23	4	4
Dec 15	40	—	25	1	—	(100)	10	10	10
Etc				— (Uncompleted) —					

* Not to be compared with other treatments

(in the greenhouse), but in the second season, by which time all the plants had grown and there were more flowers to compare, it would appear that abscission was rather greater in long days—and certainly continued for longer—whereas the production of short-styled flowers was, if anything, the other way.

For abscission, on the other hand, the outstanding feature of the tables is the seasonal trend, the percentage of abscission tailing off from the beginning of the flowering period onwards.

DISCUSSION

1 Flower initiation

It has been shown that the flowering of *Fuchsia procumbens* is reduced by day-lengths of 8 hours but not completely suppressed. It is possible, of course, that it could be suppressed by even shorter day-lengths but even if this were to prove to be so, the partial control by 8-hour days is a curious one. In most cases of partial control of flowering by an unsuitable day-length flowering is delayed whether the number of flowers is reduced or not. Here, the effect is complementary: flowering is reduced but hardly delayed if at all. Another unusual feature of the apparent day-length effect is that the treatment which produced most flowering caused the period of flowering to be extended. This is contrary to the usual rule that earliness of flowering is followed by early senescence, and so a shortened flowering season.

Fuchsia procumbens is, of course, a perennial and it is true that most photo-periodic investigations have been of annual plants. Of most perennials tested (e.g. Garner, 1937; Whyte, 1946) it may be said, however, that where a straight photo-periodic control of flowering has been established, the features of control are not dissimilar from those in annuals. In many perennials on the other hand, day-length seems to play a secondary part in producing seasonal flowering. In what is perhaps the most intensively investigated example, the horticultural chrysanthemum, Schwabe (1950, 1951) has shown that although flowering is favoured by short days, the familiar autumn seasonal blooming is mainly due to the fact that the basal shoots on which the next year's bloom is produced, require a winter for reversionalisation. A vernalisation requirement, and its loss in new growth, might perhaps be postulated to explain the seasonal flowering of *Fuchsia* in continuous long days.

but some evidence against it is, as a matter of fact, available. In the second season some experiments had been begun with *Fuchsia* plants, both seedlings and cuttings, grown in frames at still higher minimum temperatures; with thermostats set at 15 and 25°C respectively. Some of these plants, both seedlings and cuttings, came into flower, and quite abundantly, at both temperatures before the investigation was closed down.

Of recent years interest has quickened in day-length effects in perennial plants, on vegetative growth, rather than on flowering; especially for the particular case of dormancy and bud-break in deciduous trees. These are, as a matter of fact, not unrelated to their seasonal flowering, for in most of them flowers and foliage come out together with bud-break and at a time remote from that of their initiation, which occurs during dormancy or even before. The usual sequence is that dormancy follows spontaneously on leaf senescence, but that bud-break is induced by low temperatures, or by day-length, or a combination of the two (Olmsted, 1951; Wareing, 1956). Now *Fuchsia procumbens* is deciduous, and out of doors the leafy season includes, but is not much longer than, the flowering season. It was observed in the greenhouse in short days, on the other hand, that at irregular intervals loss of leaves occurred for short periods during the summer season itself and, moreover, that the bursts of flowering came each time with renewal of growth.

This rather suggests then an induction of dormancy by short days (perhaps in combination with falling temperatures in the case of winter dormancy) controlling both leaf and flower growth. It would be necessary to suppose that the leaves alone perceive day-length, so that growth could begin again spontaneously even in continuous short days, once the leaves fall.

2 *Flower abscission.*

It can be seen in Table II that if buds which abscised are eliminated from the comparison of flower production in long and short days, the superiority of long days largely disappears. In the data of Table I on the other hand, abscission is hardly evident at all except out of doors. Even in the second season, the percentage of abscised flowers had fallen to zero in the greenhouse by the time the experiment was concluded, though at that time a few buds were being abscised from the plants out of doors. This suggests two possibilities: either that when flowering begins the first buds to be initiated are defective, or, that some environmental factor causing abscission is operative at the beginning of each flowering season.

It will be remembered that flowering began in the greenhouse over two months earlier in the second season than the first. It then seems likely, that the difference in the incidence of abscission in the two seasons, may well have been an environment effect. As the day-lengths were fixed in both seasons, some other factor than day-length must be considered responsible. The occurrence of abscission out of doors after it had ceased in the greenhouse the second season strongly suggests that the responsible factor may have been temperature. Indeed it so happens that the flowering season began the first season just about the time, early December, that abscission ceased in the second season in the greenhouse; and it may then be guessed that low temperatures are the cause of abscission and that by mid-summer they were no longer operative in the greenhouse but still effective out of doors.

That day-length modifies the effect of temperature is, however, apparent in the data of Table II, for it is evident that abscission fell to zero some five weeks earlier in short than in long days, and was less in short days in every corresponding week throughout the season. It seems likely that long days may combine with low temperatures to produce abscission out of doors; and as the natural flowering season does not begin until after mid-summer and extends well into the autumn, abscission at the beginning of the season must be mainly due to the day-length; and at the end, to the falling temperatures.

TABLE III—Average Stigma Widths in mm *

Week of	First Season			Week of:	Second Season		
	Long Days	Short Days	Outdoors		Long Days	Short Days	Outdoors
Dec 3	0.97			Sep 21	*	1.26	
Dec 10	2.16	0.90		Sep 29	1.53	1.42	
Dec 17	1.70			Oct 6	1.52	1.39	
Dec. 24	2.04	1.79		Oct 13	1.33	1.35	
Dec 31	1.88	1.31		Oct 20	1.47	1.25	
Jan. 7	2.21			Oct 27	1.75	1.82	
Jan 14	2.15			Nov 3	1.22	1.16	
Jan 21	2.16	1.97		Nov 10	1.33	0.88	
Jan. 28	1.93	1.96		Nov 17	1.50		
Feb 4	1.97	1.76	1.34	Nov 24	1.62		
Feb 11	1.95	1.86	1.36	Dec 1	1.26		1.43
Feb 18	1.89	1.86	1.29	Dec 8	1.57	1.02	1.32
Feb 25	1.82		1.03	Dec 15	1.63	1.02	1.42
Mar 3	1.59		0.82	Etc			
Mar 10	1.70		0.73				
Mar 17	1.74		0.98				
Mar 24	1.16		1.31				
Mar 31	1.94		0.52				
Apr 7	1.99						
Apr 14	2.03						
Apr 21	1.99						
Apr 28	1.73						
May 5	1.45						

* Stigmas of abscised flowers excluded as abscission always before flower fully expanded

3. Short-styled flowers

In Table III, measurements of stigma diameter are shown. Godley (1955) gives sketches of flowers in which the stigma was shrunken but the style as long as in a hermaphrodite flower. Critical examination of short-styled flowers in the present investigation indicates that abortion affects the stigma primarily, and extends down a varying length of the style below, upon occasion. Stigma measurements should therefore provide a more sensitive detection of female sterility than comparison of the style and filament lengths. The data in Table III do not, however, present a very different picture of the incidence of male flowers than Tables I and II.

These experiments were undertaken initially, on the supposition that production of short-styled flowers by hermaphrodite plants is seasonal. There is, however, little confirmation of this in the data collected: the plants grown out of doors, those subject to natural environment, showed indeed a variable incidence of male flowers from week to week, but no recognisable trend as the season advanced. On the other hand, there is an outstanding treatment difference in Table I, which does suggest that female sterility may have an environmental cause: the general difference between the plants outside and those in the greenhouse. Once again this suggests a temperature effect: that female sterility is likely among flowers initiated at relatively low temperatures. In confirmation, attention may be drawn also to the relative abundance of male flowers in the greenhouse the second season compared with the first; that is, in greenhouse temperatures of the spring and early summer compared with late summer. However, if low temperatures are responsible for both bud abscission and style abortion, the effect must be different in each case. To begin with, the two imperfections are not associated in the same flower—the proportion of short-

styled flowers among abscised buds was not materially different at any time from that among flowers which opened normally. Also, if low temperature caused the short-styles out of doors in the first season, why did it not cause an appreciable amount of abscission also? Why also among the long day plants, if the temperature had risen sufficiently by the end of the experiment to prevent abscission, did it not also prevent styles aborting by then?

The relationship between abscission and low temperature on the one hand, and style abortion on the other, is then, obscure. It could be suggested, of course, that style abortion is effected by a much smaller depression of temperature than is bud abscission, but even supposing so, difficulties of interpretation would still remain in the data. It should also be noticed that the effect of long days on abscission is, if anything, contrary to the effect of day-length on style length: for the first six weeks of the flowering period in the second season—i.e., where the incidence is sufficient for a reasonable comparison—male flowers were usually preponderant in the shorter day-length

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