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ON DIFFERENT FORMS OF FLOWERS IN THE SAME SPIKE IN *DIGITALIS PURPUREA* L., f. *HEPTANDRA* DE CHAMISSO

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ON DIFFERENT FORMS OF FLOWERS IN THE SAME SPIKE IN *DIGITALIS PURPUREA* L., f. *HEPTANDRA*

DE CHAMISSO

1. INTRODUCTION AND PRESENTATION OF MATERIAL

In a previous article (1) the present paper was announced as 'in preparation' (1, ref. 12). We now present some, still somewhat preliminary observations, chiefly made by the first author when the previous paper was prepared, and thereafter.

The material covers firstly drawings made on a single day on single spikes, of mostly 6 flowers, taken at proper distances, as far as the flowering along the spike allowed. In the drawings and graphs picture and point no. 1 always represents the lower and eldest flower, no. 6 (rarely 5 or 7) the highest and youngest flower.

As indication of the stage of a flower, we have used the numbers 1– 9, as representing the stages 1–9 selected on plate XV in (1).

The occurrence of a shorter or longer subsequent series of these stages in a single spike 'suggests the continuity of the sequence between fairly normal flowers and extreme *heptandra*'s' (1, p. 9).

Apart from reproducing some selected drawings of representative series of flowers on one spike, we have covered a larger amount of material in tables and graphs, indicating the stage between 1 and 9 for each flower in each spike. Series of flowers per spike cover 6 different types, viz., existing of 3 stages or less, of low numbers (type I) or of high numbers (type II) or covering more than 3 stages (type III), all running from 'more *heptandra*' to 'less *heptandra*', i.e. in the direction stages 9 to 1 when going from flower no. 1 to flower no. 6. The types I to III together as described form *Group A*. *Group B* contains the same 3 types, however, runnining from 'less' to 'more' *heptandra*, i.e. from stages 1–9 when going from flower no. 1 to flower no. 6.

The long range of narrow steps between practically normal flowers ('stage 0'), and the strongest staminification of corollar parts comes out very clearly in (1), fig. 25, plates XIII and XIV. That, as said above, a considerable range of variation may exist in a single spike, is of great interest, since it suggests that a single Mendelian factor may bring about the decision 'normal' or '*heptandra*', but that additional influences will have to be considered for the degree of expression this factor actually obtains. It is as yet not clear whether these influences are of a genetic or a physiological nature. One may probably accept that, in a crude way, the genetic pattern of all the flowers along a spike is the same, while two ways of differences in expression seem possible, viz., 1) starting from the chromosomes themselves, via RNA-effects or otherwise, 2) induced by 'place factors', including, e.g., nutritional effects, light effects, age effects of the plant, etc. It remains curious that the development along the spike may be from more to less *heptandra* or the reverse (see above). The relation to the stage of flowering of the entire spike is not yet clear.

2. Discussion of data

We will now proceed to a more detailed discussion of the accompaning plates, graphs and tables.

Table I contains all data used in the graphs of figs. 1 and 2; representative pictures from each series (A I, II, III, B I, II, III) are shown in figs. 3–8. Each of the latter figures shows pictures of 6 flowers from one spike, drawn at one day. As already mentioned, in these figures, picture 1 represents the oldest and lowest flower chosen, picture 6 the youngest and highest one. Along with each picture the st-figure gives the '*heptandra*-stage' the flower is estimated to represent in the range 1–9 of (1), plate XV. In the figures 1 and 2 each point represents a flower. The ordinates indicate the stages 1–9, the abscissae the flowers 1–6. Thus, the course of the curves represents the shift along each spike, of the stage of the flower. The impression of the material used in this paper is that the majority of the spikes represents a shift (in the direction from bottom to top, as far as in flower) from more to less *heptandra* (*group* A, fig. 1) and that in the majority of the spikes the shift is over more than 3 stages (A III). This indicates a considerable flexibility in the expression of the basic genetic pattern. A shift in the reverse direction (group B, fig. 2 less to more *heptandra* from bottom to top) was found less frequently. We have as yet no definite data as to whether the finding of the A- or B-type of succession depends on the flowering stage of the spike, i.e., whether

Table I. Sequence of stages of investigated flowers from bottom to top of single spikes. Arranged according to types (see text). Per spike same day; × : selected for picture
Group A

Spike number	Flower →	1	2	3	4	5	6	(1 = oldest)
Type I (see text)								
1	Stages →	7	7	7	6–7	5	–	
6	Stages →	8	7	6	6	6	6	
15	Stages →	7	7	7	7–6	6	5	× (Fig. 3).
18	Stages →	7	6–7	6	6	6	6	
21	Stages →	6–7	6–7	6	6	6	6	
25	Stages →	9	7	7	7	7	7	
		44.5	41	39	38	36	30	
	Average stage marks	7.4	6.8	6.5	6.3	6.0	6.0	
Type II								
12	Stages →	2–3	3	2–3	2–1	1	1	
14	Stages →	2–3	2	2	1–2	1	1	
17	Stages →	3	2	2	1–2	1	1	
20	Stages →	2	1–2	1	0–1	0–1	0–1	
23	Stages →	2–3	1–2	1–2	1	0–1	0–1	× (Fig. 4).
31	Stages →	3	2	1	1	0–1	0–1	
		15.5	12	10	7	4.5	4.5	
	Average stage marks	2.6	2.0	1.7	1.2	0.75	0.75	

Table I (continued); × : selected for picture
GROUP A

Spike number	Flower no. →	1	2	3	4	5	6	7	
Type III (see text)									
2	Stages →	9	7	6–7	6	5	5		
3	Stages →	6	6	3–2	3–2	3–2	2		
4	Stages →	9	9	7	6–5	5	3		× (Fig. 5).
5	Stages →	6	6	–	3–2	–	1		
7	Stages →	5	5–3	3–2	2–1	2–1	1–0		
16	Stages →	9	7	7	5	2–3	2		
19	Stages →	5	2–3	2	2	1	1		
22	Stages →	5	3	2–3	2	2	2		
24	Stages →	6	5	2–3	2	2–3	2–3		
27	Stages →	7	7	7	6	6	2–3	2–3	
28	Stages →	6	6	6	6	2–3	2		
29	Stages →	6	6	6	3	1–2	0–1		
		79	69	52	44	32	24		
	Average stage marks	6.6	5.75	4.7	3.7	2.9	2.0		
	Total stage marks								
	(A, I)	44.5	41	39	38	36	30		
	(A, II)	15.5	12	10	7	4.5	4.5		
	(A, III)	79	69	52	44	32	24		
		139	122	101	89	72.5	58.5		
	(A, I, II, III) *Overall averages*	5.9	5.1	4.4	3.7	3.1	2.4		

most flowers to be used are in the lower or in the upper part of the spike.

Table I contains the data for the different series of 6 flowers that were originally drawn (these series are referred to as 'sheets' furtheron, cf figs 3–8). The sheets are marked with a number and arranged in the groups A and B, each divided in types I to III as explained earlier. For each sheet, the successive figures 1–6 have received a grading according to (1), plate XV (see above). Counting the stage numbers as arithmatic figures, averages have been obtained for each type of graphs which have been indicated by + signs in figs. 1 and 2. These averages reinforce the conclusion that a smooth segregation occurs in flower types along a spike. The factors determining or reinforcing this segregation are still wholly unexplored; they may well affect the number of stages occurring in a single spike. It did appear superfluous to reproduce all sheets of pictures of spikes explored. Those selected for reproduction are marked by × in table I.

The preceding results induced us to analize some cards present in our stock in which (mostly 6) flowers were picked from a spike and arranged in the order less to more *heptandra*, and photographed. The photographs were the basis for the analysis. The data are collected in table II (pag. 12). The arrangement being from less to more *heptandra* on each card, this order sometimes corresponds with

Table I (continued); × : selected for picture
GROUP B (see text)

Spike number	Flower →	1	2	3	4	5	6	
	Type I							
10	Stages →	6	6	6	7	7	8–9	× (Fig. 6)
	Type II							
8	Stages →	2–3	2–3	2–3	2–3	3	–	
11	Stages →	2–3	3–5	3	4–5	5	5	× (Fig. 7)
26	Stages →	1–2	1	1	1	2–3	–	
		6.5	7.5	6.5	8.0	10.5	(5)	
	Average stage marks	2.2	2.5	2.2	2.7	3.5	(5)	
	Type III							
9	Stages →	2–3	6	6	6	6	7	
13	Stages →	2	2–3	5–6	5–6	6	7	× (Fig. 8)
30	Stages →	1	–	2–3	3	–	6–7	
		5.5	8.5	14	14.5	12	20.5	
	Average stage marks	1.8	4.3	4.7	4.8	6.0	6.8	
	Total stage marks							
	(B, I)	6	6	6	7	7	8–9	
	(B, II)	6.5	7.5	6.5	8.0	10.5	(–)	
	(B, III)	5.5	8.5	14	14.5	12.0	20.5	
		18.0	22.0	26.5	29.5	29.5	34	
	(:) (B, I, II, III)	7	6	7	7	6	5	
	Overall averages	2.6	3.7	3.8	4.2	4.9	6.8	

from old to young flowers, and in most cases from young to old flowers. This has been indicated by arrows in the table.

Like in the data discussed earlier in this paper, there is a clear shift in the degree of *heptandra* characters along the spikes, as indicated by the average figures. The data of table II have been represented graphically in figure 9 which clearly shows the trend discussed. Two cards with flower photographs have been represented as examples (figs. 10 and 11); they are indicated by × in table II. After what has been said above, we believe that these data do not require further discussion.

Additional remarks. 1). The sequence of flowers in the spike has not been changed in the photographs. However, in contrast to what has been presented in table I and figures 1 and 2, the arrangement has been from less to more *heptandra*, which may correspond either to from old to young or (mostly) from young to old flowers. In some cases the age sequence of the flowers on the cards could no more be determined with certainty (indicated by? in table II).

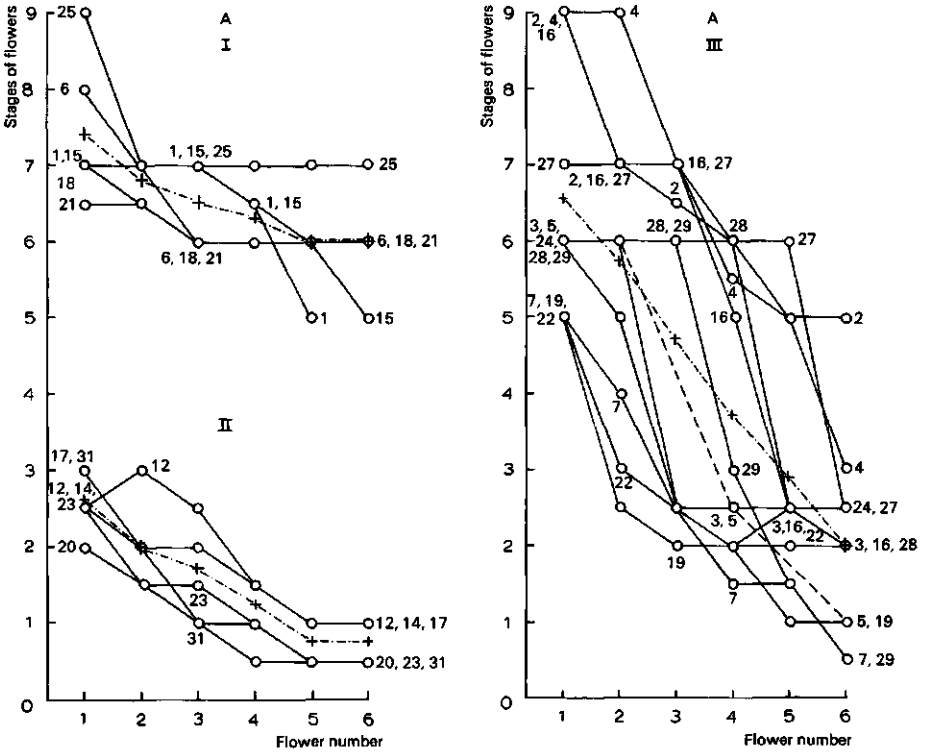


FIG. 1. Sequence of flower stages from bottom to top of single spikes. Data from table I (Group A). Numbering of flower stages according to ref. (1), plate XV.

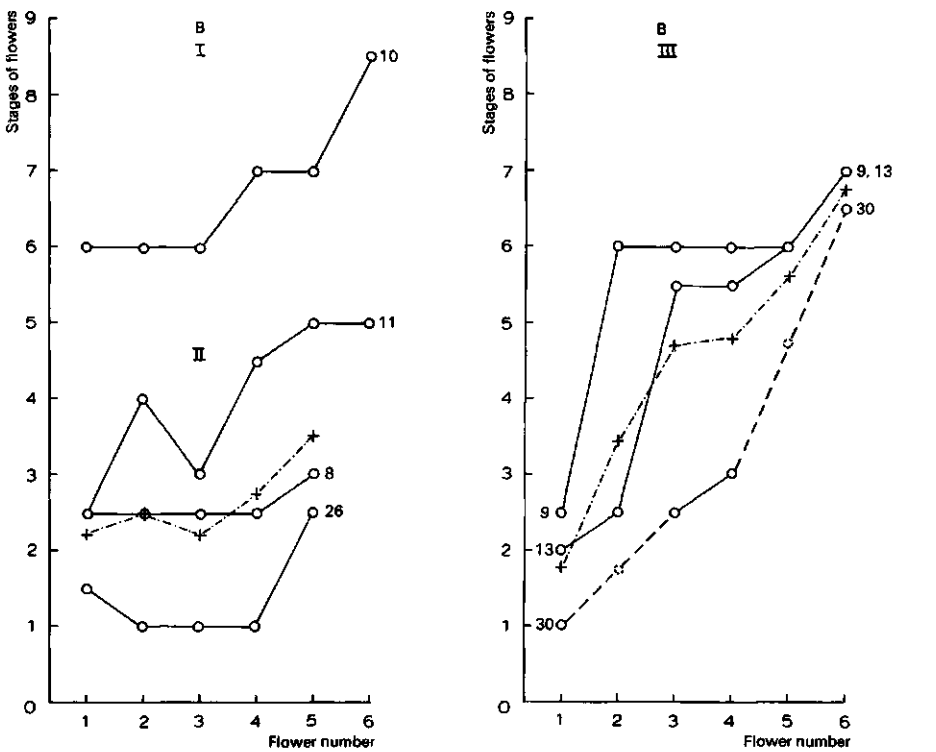


FIG. 2. As fig. 1, but referring to table I, group B.

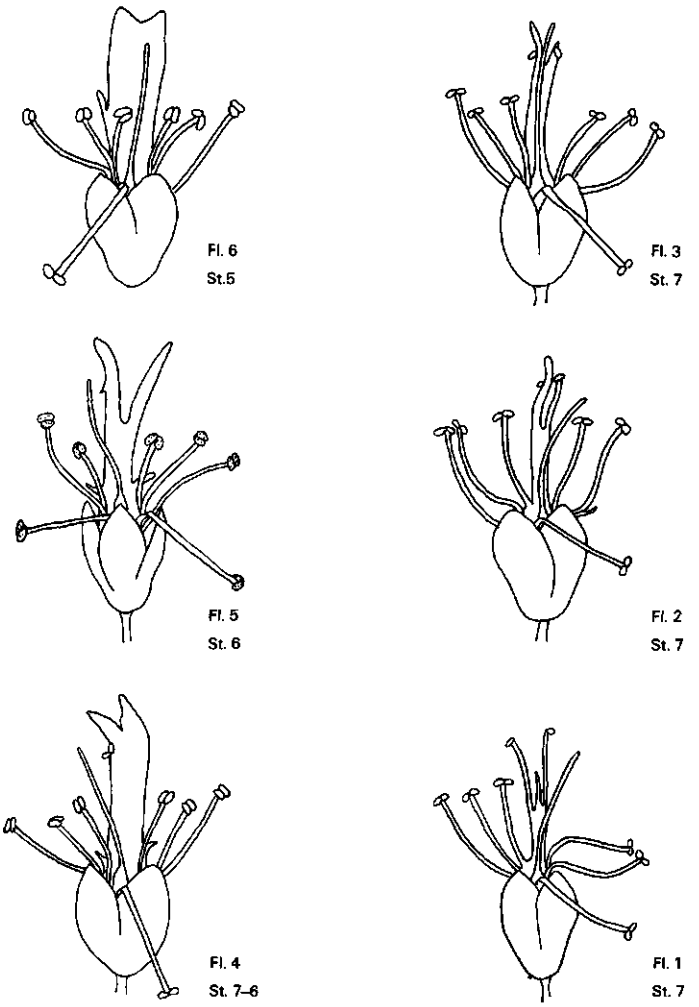
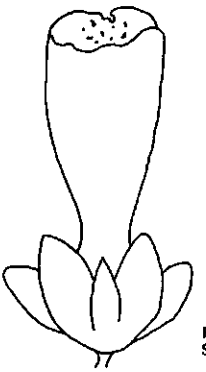
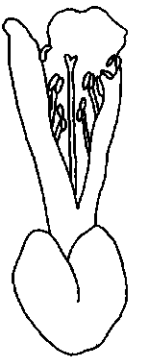
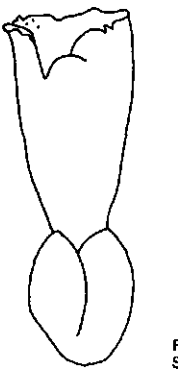
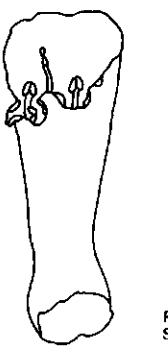


FIG. 3; spike no. 15.
FIGS. 3–8. Flower arrangement on different spikes, selected as examples from table I, and figs. 1 and 2. Cf. table I, and text.









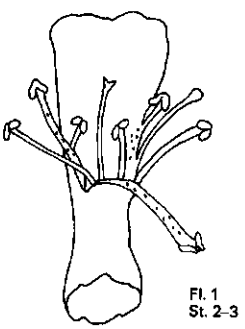


FIG. 4. Spike no. 23; cf. legend fig. 3–8.

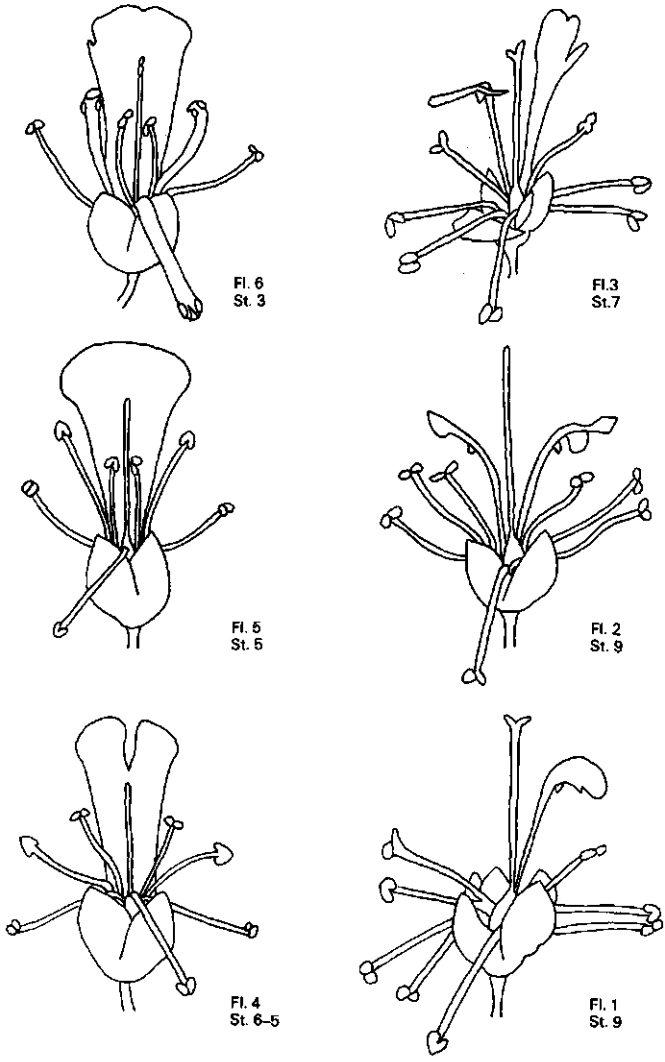


FIG. 5. Spike no. 4; cf. legend fig. 3–8.

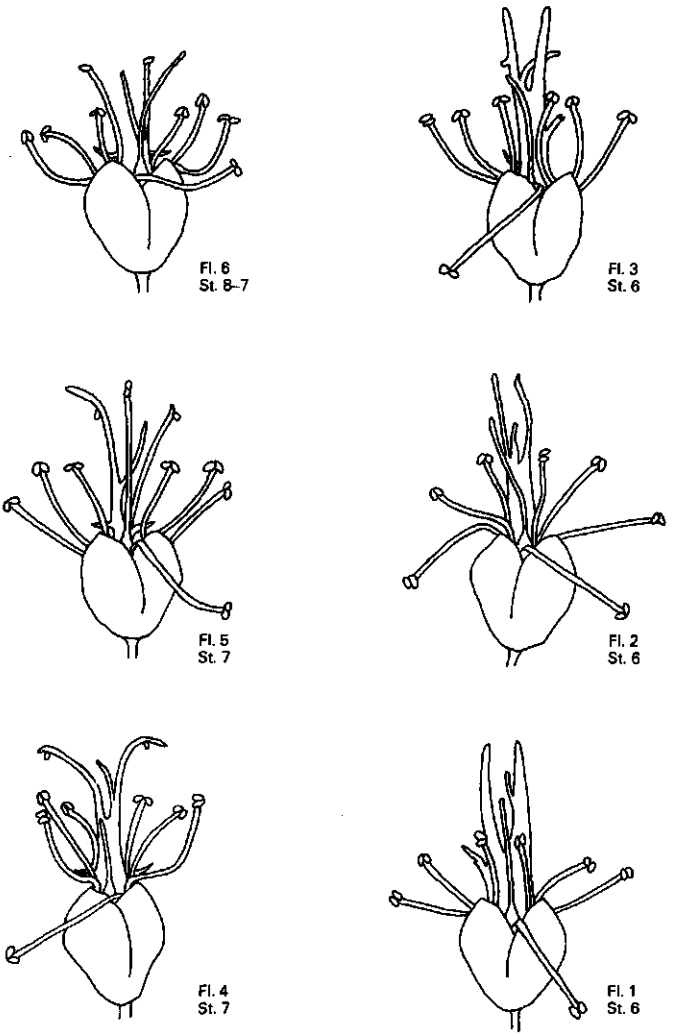


FIG. 6. Spike no. 10; cf. legend fig. 3–8.

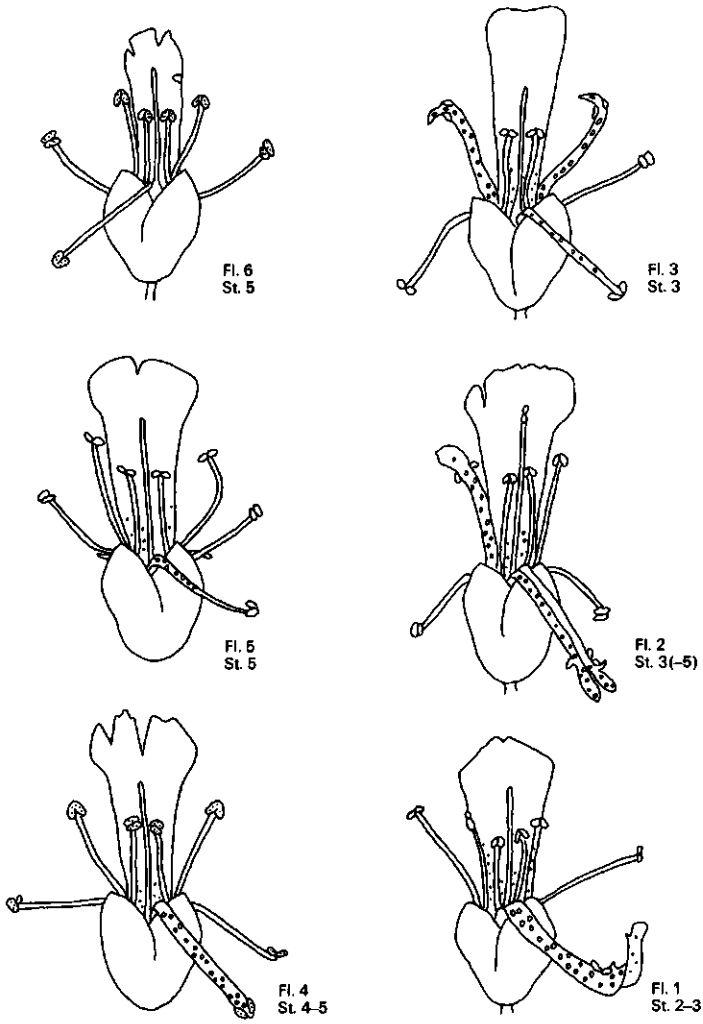


FIG. 7. Spike no. 11; cf. legend fig. 3–8.

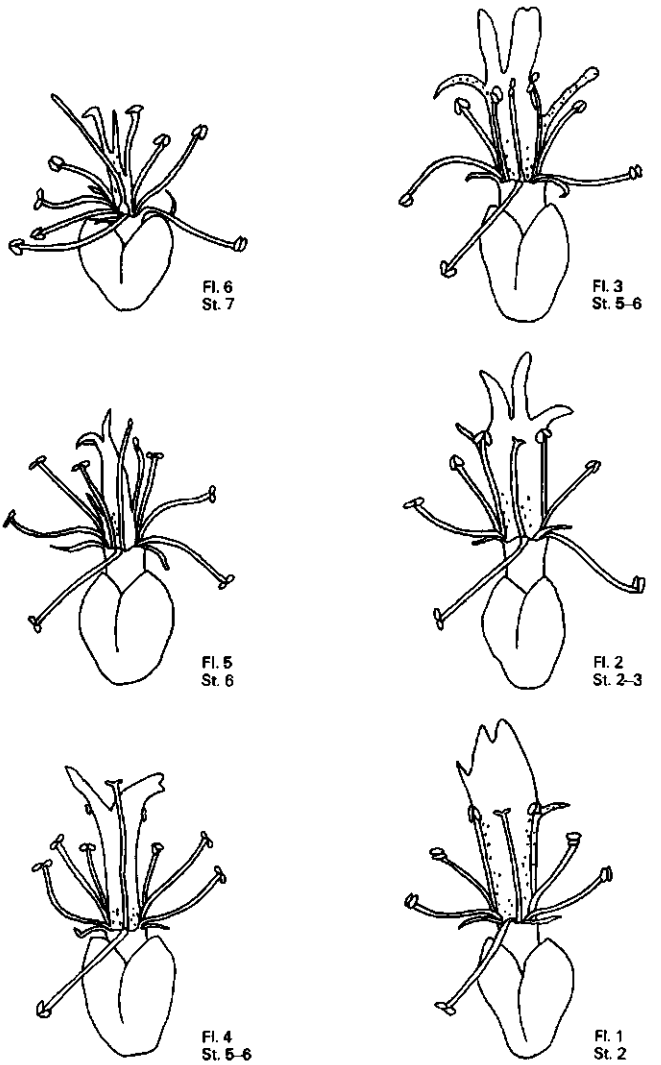


FIG. 8. Spike no. 13; cf. legend fig. 3–8.

Table II. Analysis of flower pictures on cards arranged from less to more *heptandra* types, with indication as to age sequence (→ old to young; ? doubtful). Most flowers picked on June 18, 1971.

Card no.		Flower number on cards 1	2	3	4	5	6	7	8	old → young ? doubtful
1	Stages →	6	6–7	7	7	7–8	8	9	9	→
2		7–8	8	8	8–9	9	9			?
3		6	6	7	7	7	8–9			←
4		5–6	6	6	6–7	7	8–9	× (Fig. 10)		←
5		6	7	7	9	9	9			←
6		6	6–7	6–7	7	7–8	9			←
7		6–7	6–7	7	7	8	9			←
8		2–3	4	5	6	7	7–8			←
9		5	5–6	5–6	6	6–7	7			?
10		6	7	7	7	7	8			←
11		9	9	9	9	9	9			←
12		0–1	1	1	1–2	2	4–5	× (Fig. 11)		←
13		0	0–1	1	2	2–3	4			?
14		0–1	0–1	1	1	1–2	2			←
15		1	1	4	3–4	4–5	5			←
16		0–1	1	2	3–4	4	5–6			←
17		0–1	0–1	1	2	2–3	5			?
18		0	0–1	1	1	2	2–3			←
19		0	0	1	2	5	4			?
20		2–3	3	3–4	4	4–5	5			←
	Total of stages	71.5	80	90.5	100.5	112.5	130	–	–	
	(:)	20	20	20	20	20	20	–	–	
	Average stage nr.	3.6	4.0	4.5	5.0	5.6	6.5	–	–	
	With exclusion of nrs 2 and 11 Total	55	63	73.5	83	94.5	112	–	–	
	(: 18)	3.1	3.5	4.1	4.6	5.2	6.2	–	–	

× Reproduced in paper.

2). Figure 9 shows that the average is considerably influenced by including the data from cards 2 and 11 which represent only three high values each. The most logical way to include them into the table and the graph appears to be as 1, 3, 5 (or 2, 4, 6) since only 3 flowers were taken out of the flowering part of the spike, because all flowers showed more or less extreme *heptandra* types. Comparison of averages including or excluding cards 2 and 11 shows their influence probably in the most unambiguous way by interpolating figures for the points 2, 4 and 6 which, therefore, has been done.

3. Another approach

A different approach has also been attempted, viz., by picking some flowers from a spike from bottom to top, and repeating this procedure at the same spike after several days, altogether mostly 4 times in a period of 15 days, viz., from 12 to 27 June 1973. Mostly 3 open flowers per spike were collected each time which

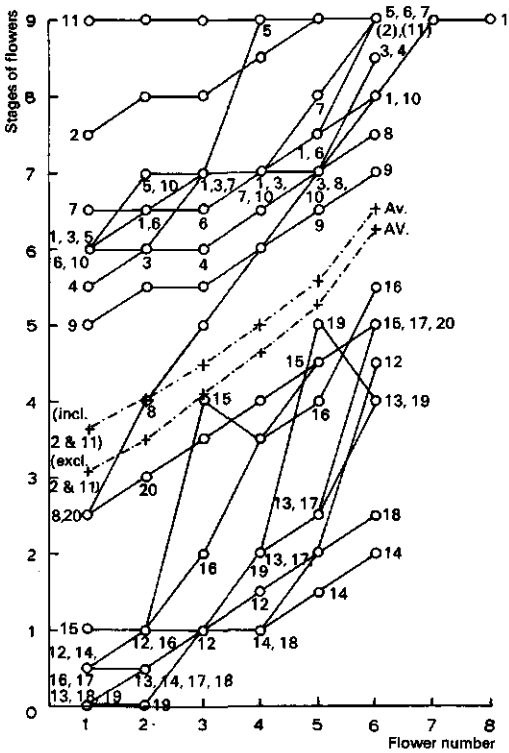


FIG. 9. Graphical representation of the data of table II.

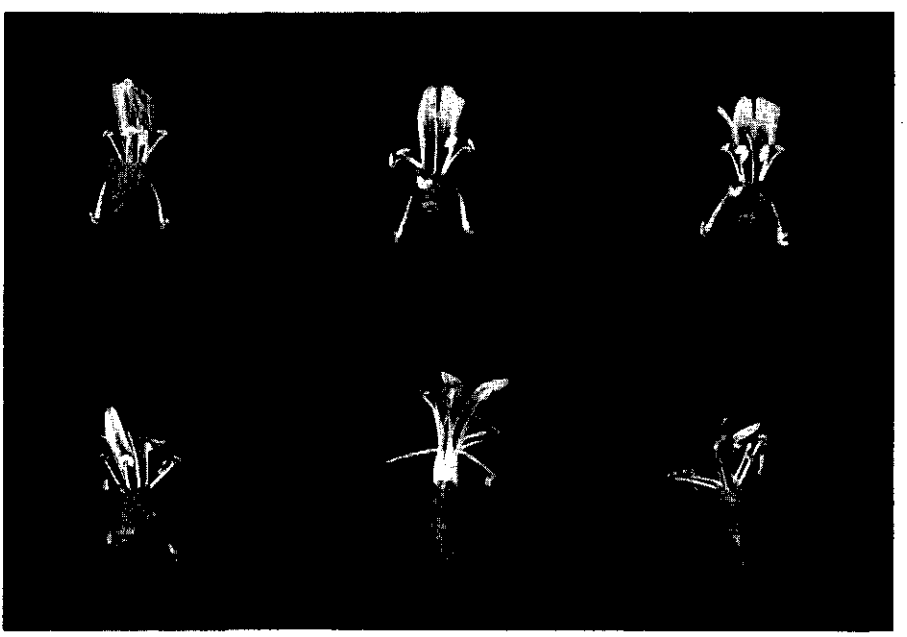


FIG. 10. Card no. 4 as used for data in table II and figure 9.

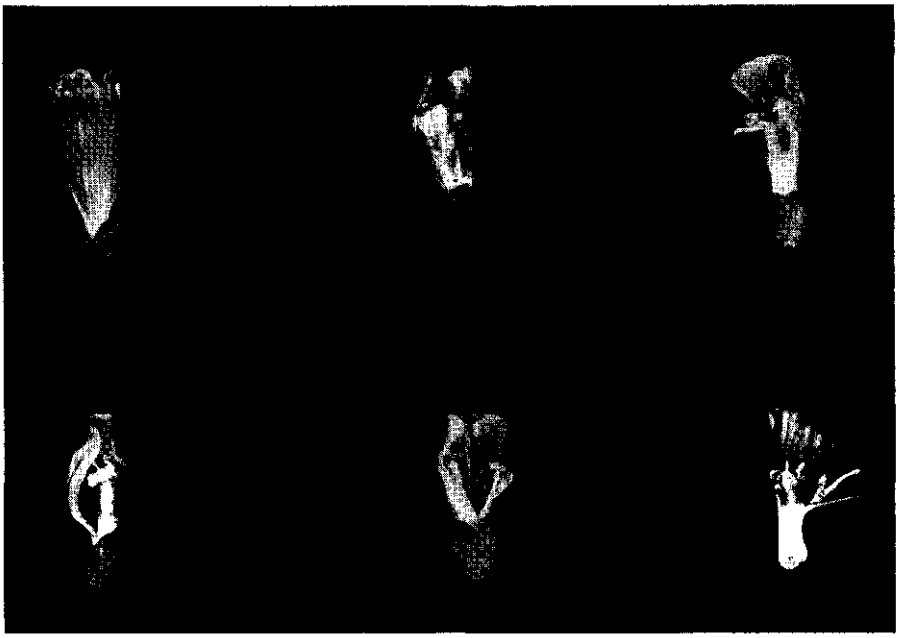


FIG. 11. Card no. 12 as used for data in table II and figure 9.

were photographed in fresh state, and apart of that some further young flowers and buds. Later on the stage of the flowers has been estimated from the photographs. The results are collected in table III, the data considered as arithmatic figures (see above) and averaged; the averages are represented in fig. 12A. From older flowers to younger ones there is a smooth decrease in *heptandra* characteristics, but the average difference is small. Probably this may be expected since in the course of development of a spike flower 2 gradually becomes flower 1, flower 3 flower 2, and the buds renew flower 3, etc. Steeper gradients in *heptandra* type may be produced by selecting series of 3 flowers from specific harvests. Examples have been indicated in table III, represented in fig. 12B, including averages (+), and shown as photographs in figs. 13–19.

In order to evaluate the meaning of these procedures and results, more observations will have to be made. The impression remains that the spikes (arbitrarily) selected for this second way of approach in majority do not show such a wide variety of flower types on each spike as those used in the part of the investiagtion described in the first part of this paper. The relatively short observation period for each spike may be in part responsible herefor.

4. SUMMARY

An attempt has been made to quantitatively grasp differences in the degree of '*heptandra*' in various flowers along the same spike on the same day (sections 1

TABLE III. Stages from older to younger flowers along single spikes at the same date. Observations at several days on the same plants (spikes). × : Selected for pictures.

Plant (spike) no.	Date		Flower numbers (1 = oldest) 1	2	3	4	
1.	12.6.73	Flower stage →	2	5	–		
	18.6.73	Flower stage →	5	5–6	5–6		
	21.6.73	Flower stage →	5–6	5–6	5–6		
	27.6.73	Flower stage →	5–6	5–6	–		
3.	12.6.73	Flower stage →	3	9	–		
	18.6.73	Flower stage →	9	9	6		× (Fig. 10).
	21.6.73	Flower stage →	9	6	9		
	27.6.73	Flower stage →	9	9	9		
4.	12.6.73	Flower stage →	4	9	9		
	18.6.73	Flower stage →	9	6	6–4		× (Fig. 11)
	21.6.73	Flower stage →	9	6–4	7		
	27.6.73	Flower stage →	6	7	6		
5.	12.6.73	Flower stage →	1–2	2	2		
	18.6.73	Flower stage →	1–2	2	1–2		
	21.6.73	Flower stage →	2	1–2	1–2		
	27.6.73	Flower stage →	1–2	1	1		
6.	12.6.73	Flower stage →	3	6	9		
	18.6.73	Flower stage →	9	9	6		× (Fig. 12)
	21.6.73	Flower stage →	6	9	6		
	27.6.73	Flower stage →	6	6–5	5		
7.	12.6.73	Flower stage →	9	7	–		
	18.6.73	Flower stage →	9	7	6		× (Fig. 13)
	21.6.73	Flower stage →	9	6	5		× (Fig. 14)
	27.6.73	Flower stage →	6	5	5		
10.	18.6.73	Flower stage →	6	5	1	2	× (Fig. 15)
	21.6.73	Flower stage →	5	1	2	5	
	27.6.73	Flower stage →	5	5	5	2	
101.	21.6.73	Flower stage →	6	6	6	4	
	27.6.73	Flower stage →	6	6	6		
							(fl. 5)
102.	21.6.73	Flower stage →	9	8	7	7	7 × (Fig. 16)
	27.6.73	Flower stage →	6	7	–	–	
103.	21.6.73	Flower stage →	9	3–4	4	9	
	27.6.73	Flower stage →	9	9	–	–	
Total average stages (flowers 1–3)			210	192	141		
Total average/flower over all dates (: 33) *(:28)			6.4	5.8	*5.0		

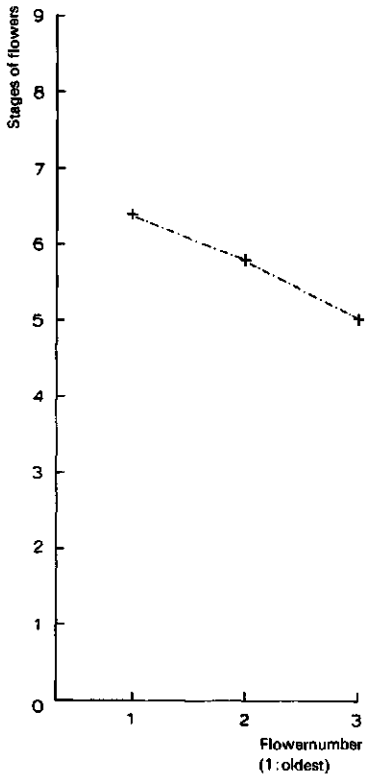


FIG. 12A. Stages from older to younger flowers along single spikes at the same date. Observations at several days on the same plants (spikes). Cf. table III. Average of all estimations for 3 flowers.

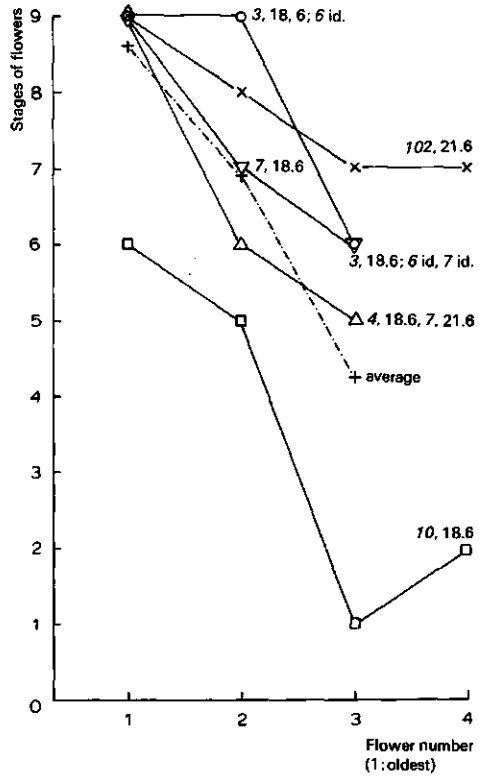


FIG. 12B. Stages from older to younger flowers along single spikes at the same date. Some selected spikes at certain days. Estimations for 3 flowers at each spike.

and 2 of this paper) and in a certain sequence of days (section 3). Smooth segregations between the stages (see text) of successive flowers were found to occur; the gradient may be more or less steep, and, from bottom to top either from more to less '*heptandra*' or vice versa.

5. REFERENCE

1. E. C. WASSINK – Some recent observations on *Digitalis purpurea* L., f. *heptandra* DE CHAMISSO. – *Meded. Landbouwhogesch. Wageningen, Ned.* 72–22 (1972).

FIGS. 13–19. Selected photographs from older to younger flowers along the same spike at the same day. FIG. 13. Plant 3 at 18.6.'73.

FIG. 14. Plant 4 at 18.6.'73, cf also legend figs. 13–19.

FIG. 15. Plant 6 at 18.6.'73, cf. also legend figs. 13–19.

FIG. 16. Plant 7 at 18.6.'73, cf. also legend figs. 13–19.

FIG. 17. Plant 7 at 21.6.'73, cf. also legend figs. 13–19.

FIG. 18. Plant 10 at 18.6.'73, cf. also legend figs. 13–19.

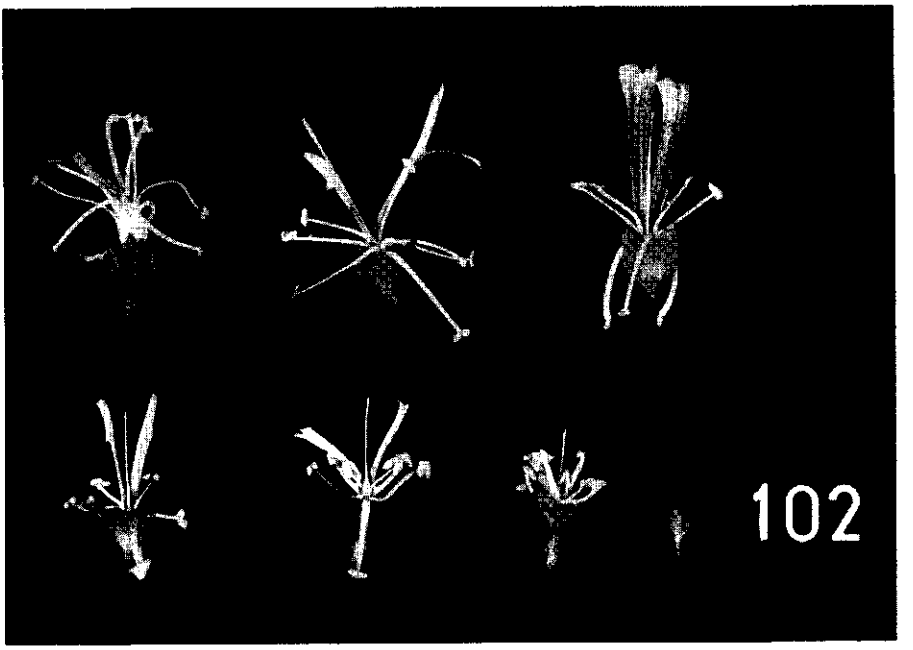


FIG. 19. Plant 102 at 21.6.'73, cf. also legend figs. 13–19.