CANNA CROSSES I

BY

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At present it seems to be taken as a matter of fact that after crossing two types that differ in a number of factors larger than the haploid number of chromosomes no independent Mendelian segregation 1) will take place in the second generation for all factors concerned. But I know that in 1913 when I crossed a variety of *Canna glauca* by one of *C. indica*, fewer genetici were convinced.

The choice of these two types which should differ in more than eight or nine factors (eight or nine should be the haploid number of chromosomes 2)) was a satisfactory one, and with respect to the question perhaps even too good as the difference is probably twenty factors or more as may be suggested by the following description.

Discriminative characteristics.

Organ	Canna indica	Canna glauca
stem	*tall* 3) about 2 M. stalks keeping close together	short, about 1 M. stalks spread by creeping rhizome (pl.VIII)
leaves	short, longest about 40 c.M., average 33,9 c.M.	*long*, longest about 54 c.M., average 47,8 c.M.

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1) I hope Mr. E. Lehmann (Zur Terminilogie und Begriffsbildung in der Vererbungslehre, Ztschr. f. ind. A. u. V. XXII, S. 236, 1920) will excuse this pleonasm. Mr. Lehmann is quite right, but video meliora proboque deteriora sequor.

2) Koernicke (1903) and Strasburger (1904) found 8 chromosomes, Honing (1915) diploid 16, but after Kuwada the number should be 9, diploid 18. See: Tischler, G. Allgemeine Pflanzenkaryologie, S. 587, 1922. Belling (Proc. Nat. Acad. of Sciences, vol. 7, p. 197, 1921): „Most of the Cannas examined were diploid, showing nine dyads before the first division in the pollen-mother-cells, and these in most plants separated into 9 + 9." — In pollen mother cells I also found 9 + 9 chromosomes.

3) See text p. 4.

Organ	Canna indica	Canna glauca
	broad, largest about 16 c.M., average 14,6	narrow, largest about 12 c.M., average 11,4
	with *broad red margin*	entirely green
	shiny	*dull* on account of a layer of wax
bracts	long, ± 30—45 m.M.	short, ± 15—25 m.M.
staminodes	two, the middle one failing	*three*
	deep scarlet	pale yellow with some pink spots
	short, average 59 m.M.	*long,* average 87 m.M.
	narrow, average 10,8 m.M.	*broad,* average 16,2 m.M.
	nearly rectangular to each other	all three almost in one plane
	spoonform	top recurved 1) (fig. 1)
	stiff, rather thick	noticeably thinner (fig. 2)
style	short, top of anther as high as the stigma or even a trifle higher; selfpollination thereby very easy	long, top of anther 5—6 m.M. under the stigma; selfpollination very improbable (fig. 3)
	broad	narrow
ovary	red	green
fruit	opens by drying of carpels	*keeps closed*
seeds	small, weight of 300 seeds 43,08 gr., volume of same in cylinderglass 57 c.M.^{3}	*big,* weight of 300 seeds 82,89 gr., volume in the same glass 106 c.M.^{3}
	round	*oblong*
	black 2)	mottled black and brown

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1) If doubtful best visible on the „first" staminode (st$_1$ in fig. 827, p. 621 Strasburger, Lehrbuch der Botanik für Hochschulen, 14 Aufl.).

2) See text p. 4.

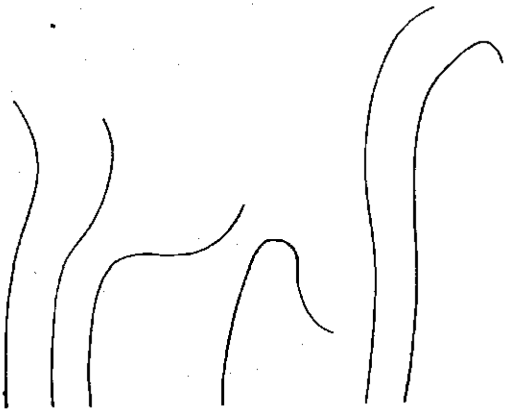

Fig. 1. Spoon form of staminodes of *C. indica* in 4 subsequent stages and recurvate staminode top of *C. glauca*.

The *C. glauca* used for the cross J 4—2 was a second generation plant after repeated selfpollination and similar to the specimens grown from seeds received from Java and to the F_1, other F_2 plants, F_3 and F_4. It has the long and lanceolate leaves of *C. glauca γ rubro-lutea* [1]), much attenuated at the base and the glaucous hue, but not the slender reddish margin, the leaves being entirely green. The flowers have 3 staminodes of a yellow paler than that of the *rubro-lutea*, more like those of *C. glauca β rufa* [2]) but still paler and in stead of having narrow red stripes along the veins it has only some minute pale pink spots along the middle. The latter characteristic is variable, in some flowers it seems to be absent, but never in all flowers of the same plant, i. e. the opposite phenomenon of that mentioned by Miss MARRYAT [3]) concerning one of her *Mirabilis* crosses. In the labellum and the filament of the anther the pink colour is always distinctly visible. Thereby it differs from *C. glauca* as it is described (very incompletely) bij MÜHLE [4]).

The *C. indica* R 13—4—3 belonged to the type with broad leaf base and broad red leaf margin [5]) of which R 13 had been a segregating hybrid but R 13—4 a constant „red" type in all its 252 descendants of four generations.

After many failures one fruit with two seeds was obtained

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1) CURTIS's Botanical magazine vol. 62, no. 3437.

2) CURTIS's Botanical magazine vol. 49, no. 2302.

3) MARRYAT, D. C. E., Hybridisation experiments with Mirabilis Jalapa. Reports to the evolution committee V, p, 34, 1909.

4) MÜHLE, ARPAD. Das Geschlecht der Canna, 1909.

5) HONING, J. A. Kreuzungsversuche mit Canna-Varietäten, Rec. d. tr. bot. néerlandais XII, 1915, p. 5.

from the cross *glauca* × *indica*. One seed was deaf and the reciprocal cross never succeeded so that the entire F_1 consisted of a single individual. It is tall, has a creeping rhizome (but less so than *C. glauca*), long rather broad leaves with a red margin and a covering of wax, somewhat orange-tinted red flowers with 3 long, broad staminodes with at least partly recurvate tops, a style intermediate in form and position of stigma and anther, red ovaries and big oblong black seeds. The dominant characters are printed in italics. When the indication of dominance fails, the type of heredity is more or less the Zea-type.

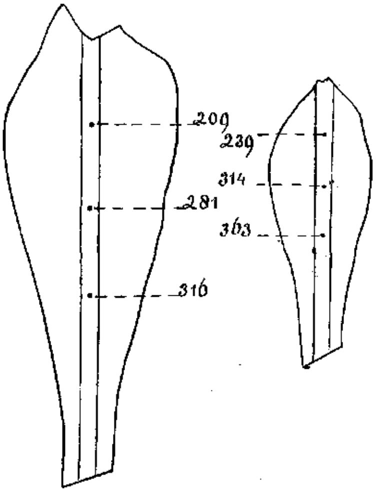

Fig. 2. Staminodes of *C. glauca*, large and thin, and of *C. indica*, small and thick. The figures indicate the thickness in microns, averages from 50 measurements each.

Very peculiar is the phenomenon that the dark colour of the seed coat of the F_1 that, in the tropics, covered almost absolutely the brown and black mottling, was less developed in Europe, so that the speckledness was visible and dominance could scarcely be spoken of.

Fig. 3. Broad style of *C. indica* with pollen immediately in contact with the stigma, and narrow style of *C. glauca* with pollen half a centimeter beneath the stigma. Nat. size.

For tallness of *indica* and shortness of *glauca* the behaviour in Europe was changed even more. In contravention of the rule in Sumatra, the *indica* at Wageningen both in 1921 and 1922 was considerably shorter and *glauca* much longer to such a degree that they had interchanged for tallness and shortness.

And as the F_1 remained tall one could say that both types had interchanged for dominance and recessiveness.

There has been raised at Medan a F_2 of 1168 seedlings of which 867 after artificial selfpollination and 301 after free pollination at a time when no other *Cannas* grew in the neighbourhood. Not a single specimen of these 301 was a phaenotype that did not occur also among the other 867 sisterplants. A large number of the 1168 seedlings died before flowering so that the ratios found for many characters may not be exactly the real ones. The deviations from the numbers that could be expected in case of an independent Mendelian segregation, however, are sometimes so considerable that these numbers cannot possibly be reduced to Mendelian ratios, sometimes even on the assumption (for the rest very improbable) that all the dead individuals should have belonged to the type or types of which there was a shortage.

But apart from the deviations the ratios for the same characters are different at different times, notwithstanding the fact that all seeds are gathered from the single F_1 individual. Hereof many instances will be given in the following pages.

Leaf length and breadth.

As the leaf of *C. indica* is short and broad (on an average 34 c.M. length and 14,6 c.M. breadth) and that of *glauca* much longer and noticeably narrower (on an average almost 48 c.M. long and 11,4 broad) one might expect that it should be very easy to distinguish different types among the F_2. So far as the extremes short-broad and long-narrow are concerned, this expectation proves to come true. But for the rest it is impossible to count the numbers of plants with long, intermediate or short leaves. Although very many leaves have been measured and noticed for each plant separately, I have not been able to state for a certainty how many phaenotypes for leaf length and breadth may be present, neither by measuring all the leaves nor by using only the longest leaf of each stem.

The leaf length of F_1 (mean 44,38 c.M.) is almost that of the parent with long leaves, *glauca* (47,76 c.M.), the breadth (mean 14,039 c.M.) almost that of the broad leaved *indica* (14,593); „long" is nearly completely dominant to „short" and „broad" completely dominant to „narrow".

Taking all leaves of the first sowing of F_2 as a whole the mean leaf length (38,135 c.M.) is more like that of *indica* (33,946) than that of *glauca* (47,764) and the mean breadth (11,493) is the same as that of the narrow leaved *glauca* (11,429). The amplitude of variation however is much wider, the limits surpass in

TABLE I. LEAF LENGTH OF CANNA INDICA, C. GLAUCA, F_1 AND F_2.

Length in c.M.	C. indica	C. glauca	F_1	Second generation					
				first sowing [1])			third sowing [2])		
				with red margin	green	total	with red margin	green	total
7–9			1						
10–12	5		1	10	10	20			
13–15	9		3	47	52	99			
16–18	11	4	3	70	91	161			
19–21	8	6	6	98	115	213			
22–24	15	2	3	105	130	235	1		1
25–27	21	4	12	132	158	290	1		1
28–30	28	12	4	154	192	346	2	1	3
31–33	30	12	6	185	230	415	3	2	5
34–36	41	14	12	270	254	524	2	11	13
37–39	**53**	9	14	**297**	**261**	**558**	4	17	21
40–42	46	17	13	270	213	483	6	19	25
43–45	26	29	16	243	201	444	19	20	39
46–48	17	21	17	253	174	427	9	33	42
49–51	3	38	**26**	202	118	320	19	47	66
52–54		**50**	**27**	157	97	254	28	**49**	**77**
55–57		45	13	129	63	192	37	39	**76**
58–60		24	14	81	43	124	**41**	35	**76**
61–63		12	4	32	21	53	31	24	55
64–66		9	6	35	19	54	36	16	52
67–69		1	4	10	4	14	**42**	6	48
70–72				4	3	7	14	1	15
73–75				1	—	1	9		9
76–78					1	1	5		5
79–81							1		1
Number of leaves	313	309	205	2785	2450	5235	310	320	630
Mean	33,946	47,764	44,380	39,584	36,488	38,135	58,394	51,719	55,003
Standard deviation	8,7536	10,8048	12,7888	11,8003	11,413	11,7202	9,8995	8,2429	9,6886
Limits of variation in c.M.	11–50	17–69	9–69	12–73	11–78	11–78	22–80	28–71	22–80

1) All uninjured leaves have been measured.

2) The longest leaf of 10 stems per plant have been measured.

one or in both directions those of *indica* and *glauca* together (table I and II).

Without doubt there exist new combinations of factors for length and breadth in leaves much longer than those of *glauca* that are absolutely but not relatively broader than those of *indica*. Also there appeared a type with leaves shorter than those of *indica* and narrower than those of *glauca*. This and especially the fact that a Mendelian analysis seems to be out of the question reminds us for example of the crosses of Egyptian cotton of COOK 1), MARSHALL 2) and KEARNEY and WELLS 3), and to the *Dianthus* crosses of WICHLER 4).

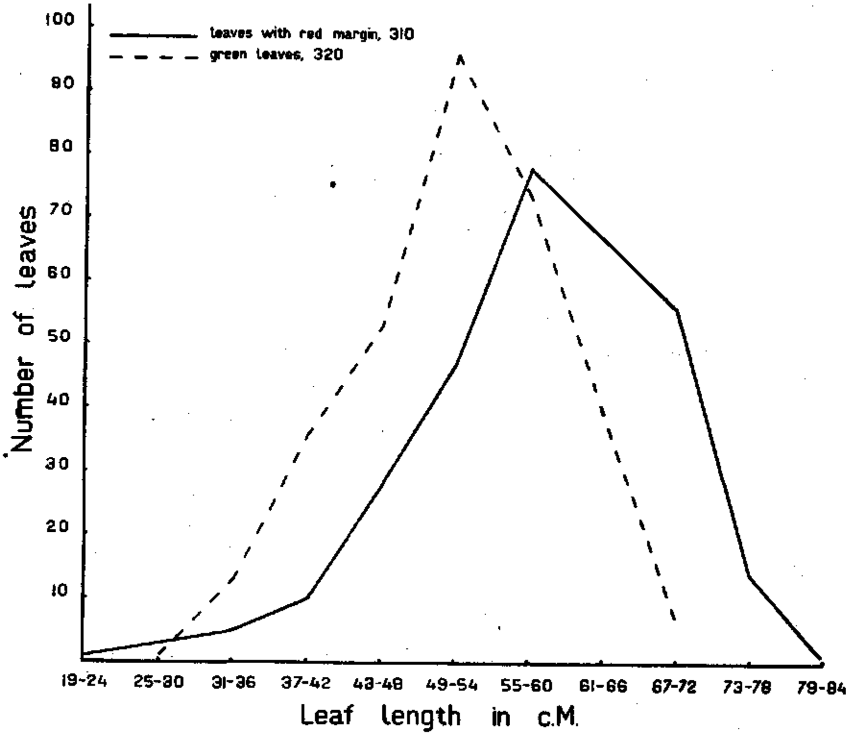

Fig. 4. Difference in leaf length in F_2 between red edged and green leaves.

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1) COOK, O. F. Suppressed and intensified characters in cotton hybrids. U. S. Dep. of Agric. Bur. of plant ind. Bull. 147, 1909.

2) MARSHALL, G. Perjugate cotton hybrids. The journ. of hered. VI, p. 57, 1915.

3) KEARNEY, Th. H. and W. G. WELLS. A study of hybrids in Egyptian cotton, The Am. Nat. LII, p. 497, 1918.

4) WICHLER, G. Untersuchungen über den Bastard Dianthus Armeria × Dianthus deltoides nebst Bemerkungen über einige andere Artkreuzungen der Gattung Dianthus. Ztschr. f. ind. A. u. V. X, S. 177, 1913.

TABLE II. LEAF BREADTH OF C. INDICA, C. GLAUCA, F_1 AND F_2.

Breadth in c.M.	C. indica	C. glauca	F_1	Second generation					
				first sowing [1]			third sowing [2]		
				with red margin	green	total	with red margin	green	total
2,5–3				2	6	8			
3,5–4		4		11	33	44			
4,5–5		5	2	35	73	108			
5,5–6	3	4	3	88	112	200		1	1
6,5–7	7	9	3	121	129	250		1	1
7,5–8	6	9	4	175	239	414		4	4
8,5–9	11	23	4	237	**292**	**529**	2	15	17
9,5–10	13	37	7	**273**	252	**525**	1	19	20
10,5–11	13	46	11	252	250	502	6	29	35
11,5–12	18	**55**	18	**294**	217	511	10	31	41
12,5–13	28	51	23	257	214	471	12	**48**	**60**
13,5–14	32	20	25	254	212	466	**28**	30	58
14,5–15	34	22	**32**	204	150	354	22	27	49
15,5–16	**39**	17	24	160	116	276	17	26	43
16,5–17	**40**	8	25	127	74	201	16	19	35
17,5–18	21		6	117	38	155	24	**26**	**50**
18,5–19	23		11	86	27	113	29	16	45
19,5–20	20		2	51	10	61	**33**	8	41
20,5–21	4		4	24	2	26	31	13	44
21,5–22	1		1	10		10	30	3	33
22,5–23				4		4	17	–	17
23,5–24				–		–	17	2	19
24,5–25				1		1	6	2	8
25,5–26							6		6
26,5–27							3		3
Number of leaves	313	310	205	2783	2446	5229	310	320	630
Mean	14,593	11,429	14,039	12,134	10,812	11,493	18,374	14,159	16,233
Standard deviation	3,4103	2,6350	3,1969	3,7170	3,4116	3,6377	3,8569	3,5206	4,2492
Limits of variation	5,5–21,5	3,5–17	4,5–21,5	2,5–24,5	2,5–21	2,5–24,5	8,5–26,5	6–25	6–26,5

1) All uninjured leaves have been measured.
2) The longest leaf of 10 stems per plant has been measured.

The leaves with red margin are on an average longer than the green ones, the difference of the means being 3,096 c.M. When only the longest leaf of each stem was counted of the plants of the third sowing, the „red" leaves were 6,675 c.M. longer than the entirely green ones (table I and fig. 4).

With respect to the leaf breadth it is quite the same thing, the „reds" are in the first sowing 1,322 c.M. broader than the „greens". In the third the difference in breadth between the longest leaves is on an average even 4,215 c.M. (table II, fig. 5).

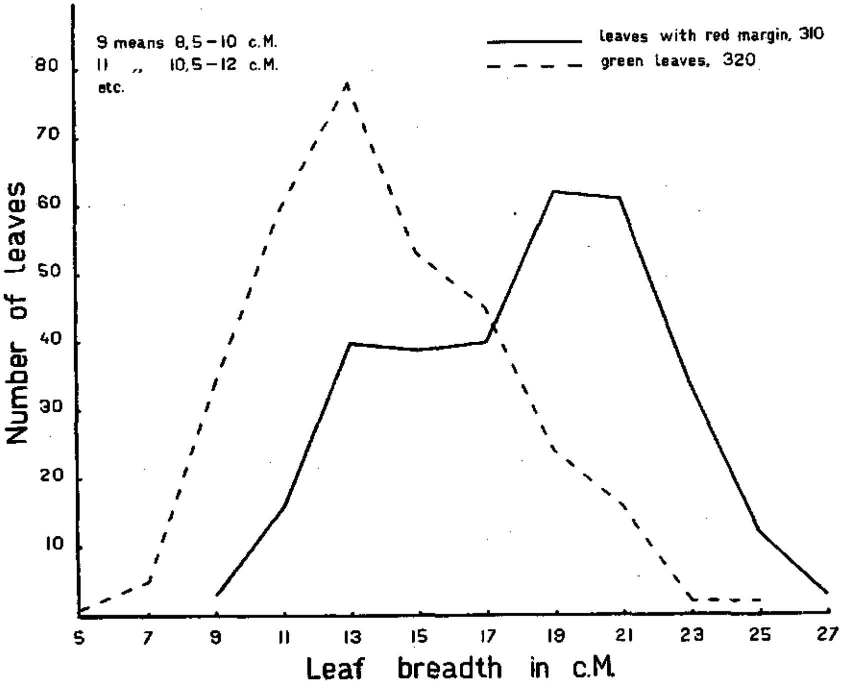

Fig. 5. Difference in leaf breadth in F_2 between leaves with red margin and green ones.

It is obvious that the difference in leaf breadth is relatively greater than that in length so that as a rule the form of the leaves with red edges is broader than that of the green leaves. In the first sowing the curve of the breadth percent of the reds does not differ very much from that of the greens when all leaves are used, namely 0,98 % more. Taking the longest leaf and the one above and that beneath it of ten stems per plant, i. e. 30 leaves per plant, of the same sowing, the difference increases to 2,22 % and in the third sowing, using only the longest leaf of each stem, to 4,09 % (table III and IV). This agrees with the somewhat more robust appearance of the „red" plants,

TABLE III. LEAF BREADTH EXPRESSED IN PERCENTAGE OF THE LENGTH. (F_2 FIRST SOWING, ALL LEAVES MEASURED).

Breadth percent	C. inaica	C. glauca	F_1	Second generation			
				with red margin	green	total	‰
9–10							
11–12				1		1	
13–14				14	1	15	3
15–16		2		33	7	40	8
17–18		15		76	27	103	20
19–20		34		78	67	145	28
21–22		48		87	121	208	40
23–24		**60**		163	192	355	68
25–26		**62**	12	181	257	438	84
27–28		44	32	267	320	587	112
29–30		23	37	**331**	**342**	**678**	**129**
31–32		11	**42**	**333**	300	633	121
33–34	2	–	17	293	240	533	102
35–36	4	1	17	256	186	442	85
37–38	19	–	18	207	161	368	70
39–40	43	2	9	155	98	253	48
41–42	**72**	–	10	111	57	168	32
43–44	68	1	8	69	38	107	20
45–46	47		1	48	15	63	12
47–48	30		1	32	10	42	8
49–50	12		1	20	4	24	5
51–52	2			5	1	6	1
53–54	6			12	1	13	2
55–56	3			4	1	5	1
57–58	1						
59–60	2						
61–62	–						
63–64	1						
Number of leaves	312	303	205	2776	2446	5222	999
Mean	42,99	23,93	31,63	30,65	29,63	30,17	

which is possibly only the expression of a beneficial action of the anthocyanin and does not necessarily indicate a coupling of factors for leaf breadth and red margin. The „green" variety of *indica* is also a little smaller in size than the type with red edges.

TABLE IV. LEAF BREADTH EXPRESSED IN PERCENTAGE OF THE LENGTH.

Breadth percent	First sowing. The three longest leaves per stem, ten stems per plant			Third sowing. The longest leaf per stem, ten stems per plant		
	with red margin	green	total	with red margin	green	total
13–15	8	2	10		2	2
16–18	21	13	34		13	13
19–21	28	58	86	4	30	34
22–24	60	97	157	23	43	66
25–27	98	123	221	22	**77**	99
28–30	**186**	**145**	**331**	59	65	124
31–33	**188**	120	308	**96**	46	**142**
34–36	122	50	172	71	25	96
37–39	87	48	135	31	16	47
40–42	41	21	62	4	3	7
43–45	20	8	28			
46–48	10	3	13			
49–51	1	1	2			
52–54		–	–			
55–57		1	1			
Number of leaves	870	690	1560	310	320	630
Mean	31,13	28,91	30,15	31,47	27,38	29,39

In both series of F_2 plants, the „reds" and the „greens", one can choose some specimens with continually increasing breadth percent (fig. 6). The broadest individuals and also the narrowest are „red". (table V and VI). But in this way, too, it is impossible to discriminate well distinct types, a common phenomenon with quantitative differences as MENDEL 1) already has observed. Possibly the difficulty may be still greater when the factors partly would act on size in general, i. e. on length and breadth together, partly on length only and on breadth only.

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1) MENDEL, G. Versuche über Pflanzenhybriden, p. 7, 1865.

Using CASTLE's [1]) formula for the number of factors $\frac{\sigma F_1 - \sigma F_2}{\text{mean A} - \text{mean B}} \times 100$ I find in CASTLE's table II that the difference in leaf length between *C. indica* and *C. glauca* should be one of 21 factors. With the improved method of estimating according to WRIGHT $n = \frac{D^2}{8(\sigma_2^2 - \sigma_1^2)}$ only one factor should be involved (at least if it is allowed to use any formula when $\sigma_2^2 - \sigma_1^2$ is negative).

The F_1 standard deviation for leaf length is greater than that of the F_2, one might say notwithstanding the F_1 is one individual. But one must say just because it is one individual only. The irregularity is caused to a large extent by the fact that the lowest and the highest of the usually 5—8 leaves on a stem are always much shorter and more variable than the others, especially in the types with large leaves. By adding series as: 37 43 52 48 42 22 and 24 40 48 50 55 48 22 and 13 41 52 56 52 35 and 25

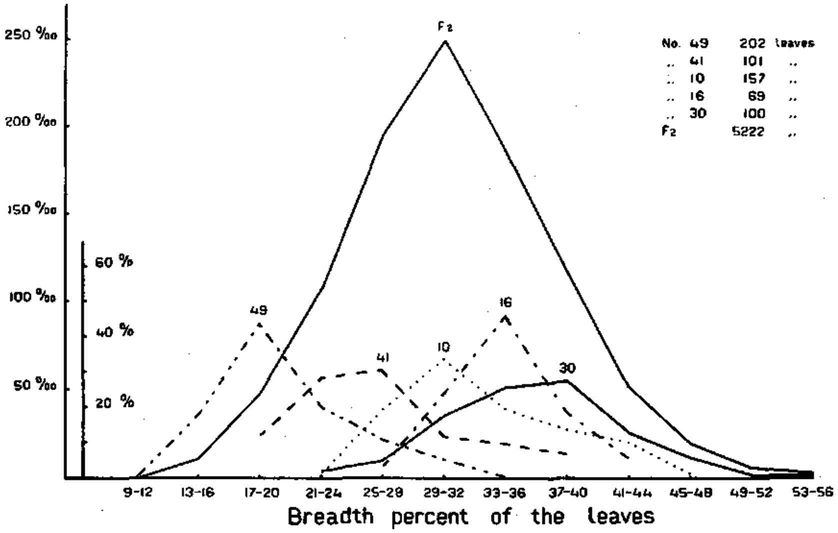

Fig. 6. Breadth percent of leaves of 5 F_2 plants with increasing relative breadth. The number of leaves of every group of percentages is expressed in % of the total number of leaves per plant, for the whole F_2 in ‰ and not sketched on the same scale with the former.

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[1]) CASTLE, W. E. On a method of estimating the number of genetic factors concerned in cases of blending inheritance. Science N. S. Vol. LIV, p. 93 and 223, 1921.

48 59 61 40 etc., all series of F_2 no. 22 or 15 45 53 52 35 and 22 37 48 49 35 19 and 36 45 54 49 40 15 and 47 58 59 45 17 etc., all series of F_2 no. 49, one does not get a regular curve. The curve of most F_2 plants separate is quite as irregular as that of the F_1, for instance of

F_2/no. 22 it is 1 0 1 6 7 3 5 4 4 14 13 19 23 26 16 8 2 1
F_2/no. 18 it is 2 4 4 1 3 1 4 7 5 8 10 22 18 21 16 8 3 1

TABLE V. LEAF BREADTH EXPRESSED IN PERCENTAGE OF THE LENGTH OF DIFFERENT F_2 PLANTS WITH RED LEAF MARGIN.

Breadth percent	No. 49	No. 6	No. 41	No. 44	No. 37	No. 18	No. 13	No. 21	No. 7	No. 30
11–12	1									
13–14	11	3								
15–16	26	12								
17–18	**54**	26	3	1						
19–20	35	**31**	9	9	1					
21–22	21	21	7	23	2	1	5			
23–24	20	14	**22**	**28**	3	1	13	4		2
25–26	16	13	18	**28**	12	8	22	6		1
27–28	6	6	13	23	**14**	25	24	9	3	4
29–30	10	3	7	21	12	**33**	27	22	6	9
31–32	1	3	5	20	11	25	**36**	23	12	9
33–34	–	2	3	14	7	18	20	**26**	12	13
35–36	1		7	9	5	10	15	11	**24**	13
37–38			3	8	4	4	11	13	8	**16**
39–40			4	1	4	8	7	11	7	12
41–42					3	5	5	12	6	8
43–44					1	5	3	3	1	5
45–46					1		3	1	3	5
47–48							3	1	–	1
49–50								2	1	1
51–52									—	—
53–54									1	1
55–56									3	
Number of leaves per plant	202	134	101	185	80	143	194	144	87	100

But for the whole F_2 the curve is regular, the extreme minus variates of the large-leaved plants, dispersed over a wide amplitude, are covered by types as F_2/no. 9 with series as 20 26 33 34 29 17 and 19 30 32 29 21 or F_2/no. 16 with 19 23 22 17 and 16 20 26 23 16. The curves of these types are far more regular:

F_2/no. 9: 4 5 9 12 23 10 12 7 8 3
F_2/no. 16: 1 4 12 20 16 11 4 1

For these small-leaved plants there does not exist the considerable difference between the lowest and highest leaves on one side and all other leaves on the other side, as is the case not only with the F_1 and large-leaved F_2 specimens, but also with the parents *indica* and *glauca* themselves (table I).

TABLE VI. LEAF BREADTH EXPRESSED IN PERCENTAGE OF THE LENGTH OF DIFFERENT F_2 PLANTS WITH GREEN LEAVES.

Breadth percent	No. 56	No. 9	No. 40	No. 45	No. 20	No. 48	No. 61	No. 10	No. 3	No. 16
13–14		1								
15–16	1	7								
17–18	7	12	5	1			1			
19–20	**17**	21	6	21	2		—			
21–22	11	**23**	**25**	21	9		2		1	
23–24	6	9	20	29	14	4	15	2	11	
25–26		6	16	**34**	16	9	18	10	12	1
27–28		6	17	19	**18**	**21**	25	21	21	2
29–30		4	8	14	16	19	**27**	**29**	27	8
31–32		2	9	20	6	12	21	24	**30**	9
33–34		1	5	15	4	10	13	18	19	15
35–36		1	3	5	—	**20**	11	13	18	**17**
37–38			6	3	3	4	9	14	9	11
39–40			1			8	10	8	4	2
41–42						8	4	10	2	3
43–44						4		6		1
45–46						2		2		
47–48						1				
49–50						1				
Number of leaves per plant	42	93	121	182	88	123	156	157	154	69

Consequently: measuring all leaves of all F_2 individuals and adding the figures in one curve is an erroneous proceeding.

At any rate the tables I—VI prove the relatively small value of the statistical methods for genetical analyses.

Anthocyanin in the leaves.

a. The red leaf margin.

It was shown in a previous paper that the difference between the variety of *Canna indica* with a red leaf margin and that with entirely green leaves is one of three hereditary factors, then called **A**, **B** and **C**. The numbers of red and green plants agreed in some cases as well with the ratio 27 : 37 as may be desired, viz. 95 red as against 127 green (theory 93,7 : 128,3) and another time 83 red as against 112 green (theory 82,3 : 112,7). One of the three factors, **C**, could manifest itself separately by a very small red margin only to be seen at close view, theoretically in 21 out of every 37 specimens without broad red edges. In fact it did appear in 30 out of 51 „green" plants (theory 28,9).

TABLE VII. SEGREGATION OF F_2 INTO INDIVIDUALS WITH AND WITHOUT A RED LEAF MARGIN.

Sowing	Sown	Number of seeds	Number of seedlings	With red margin	Green	Theoretically by segregation according to 9 : 7
1	Sept. '14	200	158	83	75	127, 1 : 98, 9 actually 126 : 100
2	July '15	92	68	43	25	
3	Aug. '15	223	202	101	101	
4	Sept. '15	75	60	30	30	
5	Dec. '15	260	233	132	101	131,1 : 101,9
6	March '16	267	232	129	103	130,5 : 101,5
7	May '16	263	215	107	108	
	Total Medan	1380	1168	625	543	
8	Jan. '22[1] Wageningen	263	92	61	31	

[1] The low number of seedlings — and probably also the 2 : 1 ratio — is caused by *Rhizoctonia*.

After crossing the red-edged *Canna indica* by *C. glauca* in stead of its own green variety, segregation according to three independent characters did not occur in one of the eight batches in which the F_2 was sown (table VII). Twice the ratio 9 : 7 was observed with very slight deviations (no.'s 5 and 6) and when the two first sowings are taken together the deviation from 9 : 7 is also small. But in three batches (no.'s 3, 4 and 7) the ratio 1 : 1 is unmistakable. Thus the offspring of a single individual has segregated according to different ratios. There was some suggestion of periodicity in so far as the seeds obtained after pollination and ripening in a dry period segregate according to 1 : 1 and those won during the rainy season according to 9 : 7. For the back cross of F_1 and *glauca* this supposition did not obtain much evidence.

Perhaps RENNER [1]) may be right in his suggestion that this variability could be caused by differences in velocity of growth of the different types of pollen as is the case with *Oenothera* [2]). But then the constancy of the irregularity is still incomprehensible.

The mean error for segregation according to 9 : 7 for $n = 1168$ is 0,2322 per 16. In reality the deviation is 0,4383 per 16 (625 : 543 = 8,5617 : 7,4383). Assuming that the segregations 101: 101, 30 : 30 and 107 : 108, together 238 : 239, are accidental variations of the 9 : 7 ratio, 0,3634 per 16 would be calculated

TABLE VIII. SEGREGATION OF THE F_3 AND F_4 FOR THE CHARACTER OF RED LEAF MARGIN.

No. of F_2 or F_3 plant	Generation	Number of seeds	Number of seedlings	With red margin	Green	Ratio red : green	Theory
1	F_3	70	48	36	12	3 : 1	36 : 12
6	F_3	67	49	28	21	9 : 7	27,56 : 21,44
7	F_3	33	6	6	–		
7–6	F_4	16	5	5	–		
13	F_3	79	8	6	2	3 : 1	6 : 2
13–2	F_4	3	1	1	–		
14	F_3	21	11	7	4		
18	F_3	101	42	33	9	3 : 1	31,5 : 10,5
21	F_3	22	8	5	3		
28	F_3	5	2	2	–		
30	F_3	116	88	44	44	1 : 1	
35	F_3	9	5	3	2		
37	F_3	84	11	8	3	3 : 1	8,25 : 2,75
37–1	F_4	60	45	33	12	3 : 1	33,75 : 11,25
38	F_3	26	5	5	–		

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1) RENNER, O. Zur Biologie und Morphologie der männlichen Haplonten einiger Önotheren. Ztschr. f. Bot. XI, S. 305, 1919.

2) HERIBERT-NILSSON, N. Zuwachsgeschwindigkeit der Pollenschläuche und gestörte Mendelzahlen bei Oenothera Lamarckiana. Hereditas I, p. 57, 1920.

as mean error for $n = 477$, but actually it is almost three times as large viz. 1,00.

An explanation of a 1 : 1 ratio, if two factors should co-operate, is very easy, assuming the impossibility of the homozygotic dominant form of one of the two factors, e. g. **A**. When all **AA** forms perish there will remain per 16 combinations **2AaBB**, **4AaBb**, **2Aabb** and **4aa**-forms, i. e. 6 with red margin against 6 without. And it would not be so very strange to search for an explanation in this direction as the F_3 also gives an instance of the 1 : 1 ratio (44 with and 44 without the broad red margin). Moreover there were found after selfing some hybrids 107 specimens with red flowers and 53 with yellow ones, i. e. 2 : 1, whereas on account of the back cross by the recessive yellow type a 3 : 1 ratio was to be expected.

But how can we imagine that one and the same plant should be able to produce repeatedly both homozygous and heterozygous children in succession with only heterozygous ones?

As all 15 selfed F_2 plants with broad leaf margin belonged to the first sowing, the constancy of one or two of them in F_3 and F_4 does not allow of any conclusion. Therefore some individuals

TABLE IX. THIRD AND FOURTH GENERATION OF F_2 PLANTS WITHOUT RED LEAF MARGIN.

No. of F_2 or F_3 plant	Generation	Number of seeds	Number of seedlings	With red margin	Green
3	F_3	8	4	—	4
4	F_3	37	4	—	4
5	F_3	36	0	—	–
8	F_3	42	0	—	–
9	F_3	17	11	—	11
10	F_3	49	4	—	4
10–2	F_4	25	21	—	21
10–3	F_4	107	90	—	90
12	F_3	38	2	—	2
16	F_3	8	3	—	3
22	F_3	42	18	—	18
26	F_3	13	0	—	—
36	F_3	81	58	—	58
37–2	F_4	10	9	—	9
39	F_3	10	4	—	4
75	F_3	113	97	—	97
162	F_3	29	15	—	15
Total		665	340	0	340

of a 1 : 1 segregation had to be selfed and for that reason (among others) the growing of second generation plants was undertaken once more. But then *Rhizoctonia* made a 2 : 1 ratio of it and next year I will try anew.

There is yet another particularity. The factor **C** for the very narrow red edge, in the *glauca* cross, is never seen separately neither in the 543 green seedlings of the F_2 nor in nearly 450 specimens of following generations, nor after back crossing green hybrids by *C. glauca* or after crossing the hybrids by each other, some 900 plants. This leads to the assumption that **C** must be (coupled to **A** or **B**) prohibited or absent and in the *glauca* cross unnecessary for the broad leaf margin.

In the cases of segregation according to 1 : 1 there cannot be any question about a mixture formed by splitting according to the two ratios 9 : 7 and 27 : 37, for in that case some of the green seedlings would have shown that they possessed the factor **C** before they became three months old.

For the same reason the assumption of „crossing-over" with the appearance of partial repulsion for the factors **A** and **B** in combination with absolute coupling of **C** with **A** or **B** is excluded as an explanation for the 1 : 1 ratio, for the **Ab** or **aB** individuals, each almost 25 % of the total number, would have shown with **C** the narrow red leaf margin and this phaenotype is absent.

The F_3 and F_4 do not throw any light either upon the 1 : 1 ratio, which occurs again (table VIII), or upon the absence of the demonstration of the factor **C**. But it is clear that the confusion of the Mendelian segregation involving a large number of factors need not have a permanent effect on the offspring: clean cut Mendelian ratios reappear in F_3 and F_4.

The back cross of F_1 by *glauca* had fairly good results so far as the number of seeds and seedlings is concerned, 150 plants from the cross F_1 × *glauca* and 374 from *glauca* × F_1 (table X). It does not matter what plant is pollen- or ovule-plant, the ratio red to green is in both cases the same: 1 red : 2,75 green and 1 red : 2,79 green, notwithstanding the fact that the former cross was much less fruitful. As compared with the 9 : 7 ratio of the F_2 there is a deficit of greens as 1 : 3 could have been expected. In this connection the shortage of reds in the 1 : 1 ratio is the more remarkable.

The back cross of F_1 by *C. indica*, far more difficult than that by *glauca*, yielded 79 seedlings, all with broad red margin.

The red edged F_2 plant no. 37, typical by its red staminodes with yellow margin (plate I fig. 5 and 6) produced in F_3 8 speci-

TABLE X. BACK CROSS OF F_1 BY C. GLAUCA. SEGREGATION INTO PLANTS WITH AND WITHOUT RED LEAF MARGIN.

No.	Cross	Number of seeds	Number of seedlings	With red margin	Green	Ratio
361	$F_1 \times$ J4—2—3	12	10	5	5	1 : 1
365	$F_1 \times$ J4—2—3	54	48	12	36	1 : 3
370	$F_1 \times$ J4—2—3	3	2	1	1	
371	$F_1 \times$ J4—2—3	25	23	8	15	1 : 1,87
375	$F_1 \times$ J4—2—3	76	67	14	53	1 : 3,79
		170	150	40	110	1 : 2,75
363	J4—2—3 $\times F_1$	45	42	17	25	1 : 1,47
366	J4—2—3 $\times F_1$	49	43	11	32	1 : 2,91
368	J4—2—3 $\times F_1$	15	15	2	13	1 : 6,50
369	J4—2—3 $\times F_1$	58	55	17	38	1 : 2,24
372	J4—2—3 $\times F_1$	67	60	11	49	1 : 4,45
374	J4—2—3 $\times F_1$	24	23	7	16	1 : 2,29
376	J4—2—3 $\times F_1$	94	92	22	70	1 : 3,18
		352	330	87	243	1 : 2,79
364	J4—2—1 $\times F_1$	3	3	1	2	1 : 2
367	J4—2—1 $\times F_1$	21	20	3	17	1 : 5,67
373	J4—2—1 $\times F_1$	20	18	5	13	1 : 2,60
377	J4—2—1 $\times F_1$	7	3	–	3	
		51	44	9	35	1 : 3,89
Total		573	524	136	388	1 : 2,85
Theory			524	131	393	1 : 3

mens with red leaf edges and 3 with entirely green leaves (3 : 1, table VIII) and after selfing one of these reds there appeared in F_4 33 reds and 12 greens, again 3 : 1. Quite in keeping with this segregation the back cross F_3 37—1 × *glauca* J4—2—3 produced half the progeny with red edges and half without, viz. 17 reds and 18 greens. This regular behaviour of F_3 37—1 may be ascribed to its far less heterozygotic nature as compared with the F_1, as it is for instance relatively constant for the characters of wax on the leaves (table XIII) and of the both red and yellow staminodes (although not homozygous for the intensity and extension of the red), perhaps for the factors for leaf length and breadth, anyhow less heterozygous than the F_1 for these factors,and probably it is heterozygous at the utmost for one of the factors for staminode length.

b. Red stripes.

Besides in the red leaf margin anthocyanin occurs also in the form of more or less distinct stripes on the leaf surface as a double line along the midrib and on either side of the veins just as with *C. Warszewiczii* [1]). Often both lines pass over the vascular bundle into each other. The breadth and the intensity of colour varies widely even far more than is evident from table XI as especially the groups „very strong'' and „strong'' are not homogeneous at all. There occur specimens with red leaf margin but without stripes, and also such as have a red midrib only, deep or light coloured, and also such as show midrib and sideways stripes in different degrees from hardly perceptible narrow stripes to a dark purplish brown over almost half the leaf surface. The figures of the different groups do not give any indication about the number of factors concerned, so that an analysis will be very difficult. The chance of getting a definitive solution of the problem is not improved by the (often) lower fecundity of many a F_2 plant as compared with the F_1.

The following data are at our disposal:

1. *C. indica* has the midrib coloured, partly also the veins.
2. The F_1 shows the red leaf colour much more distinctly than *indica*.
3. As a rule the F_2 plants with the thickest wax layer are the reddest.
4. With one exception all 450 red edged F_2 plants show anthocyanin along midrib alone (63) or along midrib and nerves both (386).
5. The intensity varies widely in both series.
6. The back cross of F_1 by *indica* produced 19 or 20 specimens without red stripes out of 53 or 54, and all 19 or 20 are (with one exception only) without a wax layer.

From 2 and 3 may be concluded that an intensification factor is brought into by *C. glauca*; from 3 that at least one of the factors for wax is coupled with an intensification factor for red stripes; from 6 that the coupling of the intensification factor with that for wax is a very strong one.

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1) Curtis's Botanical magazine 81, no. 4854.

TABLE XI. RED STRIPES ON THE LEAVES.

F_2, F_3 or cross	Development of anthocyanin along the nervures				along the midrib only			absent	Total
	very strong	strong	weak	very weak	strong	weak	very weak		
F_2, 1st sowing	1	27	4	1	–	–	–	1	34
2d ,,	3	44	18	1	4	9	–	–	79
3d ,,	3	12	4	–	3	2	–	–	24
4th ,,	3	28	22	11	2	3	–	–	69
5th ,,	2	44	16	3	–	3	–	–	68
6th ,,	3	33	42	6	–	17	–	–	101
7th ,,	–	16	36	3	–	18	2	–	75
Total F_2	15	204	142	25	9	52	2	1	450
F_3/7	–	1	3	–	–	–	–	–	4
F_3/13	–	5	1	–	–	–	–	–	6
F_3/14	–	6	–	–	–	–	–	–	6
F_3/18	–	9	10	4	–	1	–	–	24
F_3/21	–	1	2	–	–	–	–	–	3
F_3/28	–	–	–	2	–	–	–	–	2
F_3/30	2	27	5	1	–	–	–	–	35
F_3/35	–	3	–	–	–	–	–	–	3
F_3/37	–	8	–	–	–	–	–	–	8
F_4/37–1	4	2	–	–	–	–	–	–	6
F_3/38	1	3	–	–	–	–	–	–	4
F_1 × R13–4–5–1–13 (nr. 381)	3	10	–	–	–	–	–	5[1]	18
R13–4–5–1–1 × F_1 (nr. 382)	–	4	1	2	–	–	–	6	13
R13–4–5–1–13 × F_1 (nr. 383)	6	7	–	–	–	–	–	8	21

[1] Probably 6 out of 19, but not absolutely certain.

The simplest interpretation should be given by the assumption that the red midrib and nerves are caused by the factors **A**, **B** (and **C**?) of *indica* as also the red margin, but in a much lower degree and rather variable, and that an intensification factor **G** of *glauca* acts homozygously more strongly than heterozygously. The single F_2 specimen without stripes among the 450 could have been a minus variate, phaenotypically well judged but genotypically a „mistake". There remains however the possibility of separate factors for midrib and nerve colouring.

Wax on the leaves.

Whether a thick wax layer is present on the leaves as with *glauca* or whether it is absent as with *indica* can be fairly well determined on the young seedlings. But for the hybrids with thin or very thin wax layer the chance of error is pretty considerable until 1—1½ month after planting out (in the tropics!) and even then there are still some doubtful individuals which are best judged by subsequently formed shoots.

TABLE XII. SEGREGATION OF F_2 INTO INDIVIDUALS WITH AND WITHOUT WAX LAYER.

Sowing	Number of plants with wax; of these			Number of plants without wax; of these			Ratios			
	red	green	total	red	green	total	wax : no wax	r : gr	r : gr; originally	r : gr; without wax
1	29	27	56	6	2	8	7,00	1,21	1,11	3,00
2	24	15	39	11	4	15	2,60	1,84	1,72	2,75
3	75	76	151	22	9	31	4,87	1,14	1,00	2,44
4	22	23	45	2	5	7	6,43	0,86	1,00	0,40
5	104	75	179	10	7	17	10,53	1,39	1,31	1,43
6	92	73	165	14	9	23	7,17	1,29	1,25	1,56
7	72	49	121	17	10	27	4,48	1,51	1,01	1,70
Total	418	338	756	82	46	128	5,91	1,30	1,15	1,78

The number of factors involved seems to be two or perhaps three of polymeric nature. In the F_2 the numbers of plants with and without wax vary widely and the ratios in the various batches show even greater divergence than those of red margined and green leaves (table XII). Clearly there was no independent Mendelian segregation. The latter probably reappeared in 3 cases of F_3 sowings out of 26, but even these 3 are not wholly above suspicion, especially not the 15 : 1 ratio (table XIII). Of F_2/no.75 which promised to give some indications, again a third generation has been raised at Wageningen, and some

F_3 plants were selfed. But *Rhizoctonia* killed most seedlings, 37 only could be planted out from 189 seeds. Therefore F_2/75 and some F_3 plants have been selfed anew in 1922.

TABLE XIII. SEGREGATION IN F_3 AND F_4 FOR THE CHARACTER OF WAX.

F_2 or F_3 plant		Third or fourth generation							
No.	wax layer	Number of		certainty about	Layer of wax				
		seeds	seedlings		thick	thin	very thin	absent	ratio remarks
1	very thin	70	48	44	–	12	23	9	1 : 2 : 1
3	thick	8	4	4	2	2	–	–	
4	„	37	4	3	2	1	–	–	
6	„	67	49	35	33	2	–	–	
7	thin	33	6	4	1	3	–	–	
9	thick	17	11	6	5	1	–	–	
10	„	49	4	3	1	2	–	–	
10–2	± thick	25	21	14	14	–	–	–	
10–3	thick	107	90	68	68	–	–	–	
12	„	38	2	2	–	–	2	–	
13	„	79	8	8	8	–	–	–	
14	„	21	11	8	8	–	–	–	
18	„	101	41	30	26	4	–	–	
21	„	22	8	6	4	2	–	–	
22	thin	42	18	17	–	15	1	1	15 : 1?
28	absent	5	2	2	–	–	–	2	
30	± thick	116	88	71	44	26	1	–	
35	thick	9	5	5	5	–	–	–	
36	„	81	58	48	25	22	–	1	
37	„	84	11	11	11	–	–	–	
37–1	„	60	45	26	26	–	–	–	variable
37–2	„	10	9	8	8	–	–	–	
38	± thick	26	5	4	4	–	–	–	
39	thick	10	4	4	4	–	–	–	
75	„	113	97	76	20	37	4	15	1 : 2 : 1?
162	absent	29	15	14	–	–	–	14	

„Thick” does not always mean the same degree of thickness; most times it indicates a layer of wax less thick than that of C. glauca, but so well developed that it is visible from a distance. The difference between „thin” and „very thin” is sometimes doubtful, likewise „very thin” and „absent”.

There is an appreciable repulsion between the factors for red leaf margin and those for wax layer, consequently at least one of the factors for red leaf margin is localized in the chromosome(s?) of *indica* homologous to that (or those) in which *glauca* contains a factor for wax. With the exception of the fourth sowing the number of red edged plants without wax is always absolutely and relatively larger than that of the greens without wax, on an average 1,78 times as large, whereas the ratio red to green was originally 1,15 : 1 and by the larger mortality of the green individuals it was changed indeed, but not beyond the 1,30 : 1 ratio.

While the ratio wax to no wax varies from 2,60 : 1 to 10,53 : 1, the ratio red: green among the plants without wax varies from 0,40 : 1 to 3,00 : 1 in the different sowings. Under these circumstances one cannot use the figures for an analysis.

The back cross of F_1 by *glauca* yielded in both reciprocal crosses without any exception only plants with wax (524 seedlings) as was to be expected.

TABLE XIV. BACK CROSS OF F_1 BY C. INDICA.
SEGREGATION FOR THE FACTORS FOR WAX LAYER.

No.	Cross	Number of seeds	Number of seedlings	Cert. about	Wax layer			
					thick	thin	very thin	absent
380	F_1 × R13–4–5–1–1	7	6	4	2	2	–	–
381	F_1 × R13–4–5–1–13	33	23	19	12	–	1	6
382	R13–4–5–1–1 × F_1	34	23	13	3	3	–	7
383	R13–4–5–1–13 × F_1	29	27	21	11	2	–	8
	Total	103	79	57	28	7	1	21

The back cross with the recessive parent *indica* should reproduce all possible classes of plants heterozygous for the wax factors and the types without wax (table XIV). The figures are too small and too irregular for giving a good idea. Only the nos. 380 and 381 where the pollen was recessive so that no differences in velocity of growth of the pollen tube could cause irregularities, show together a 3 : 1 ratio viz. 17 plants with wax and 6 without. This agrees with the assumption of two polymeric factors, which was also possible on account of the segregation in F_2, F_3 and F_4. The F_1 ovules could be represented by 1 **KL** : 1 **Kl** : 1 **kL** : 1 **kl** in which **K** and **L** both separate and together produce a wax layer.

The numbers 382 and 383 do not affirm this theory. The ratio of 19 plants with wax and 15 without cannot be interpreted in the same way but it does not necessarily contradict the scheme.

Of course differences in velocity of growth of the pollen tubes may have disturbed the ratios.

Comparing the bottom of table XI for red stripes on the leaves and XIV for the wax layer, one is struck by the large number of recessive forms for both sets of factors after back crossing F_1 by *indica* that is dominant for the red stripes and at the same time recessive for the intensification factor and for wax. The 6 specimens of no. 381 without wax are the same as the 6 (probably; certainty for 5!) without red stripes. Of the 7 plants without wax of no 382 5 did not show any red stripes, 2 only to a very low degree. The 8 of no. 383 were quite the same. The back cross proves just as the F_2 the very high degree of coupling between one of the factors for wax and the extension factor for the anthocyanin.

The number of staminodes.

The variety of *C. indica* used, has 2 staminodes as *C. indica β lutea* [1]), *C. Warszewiczii* [2]) and *C. speciosa* [3]). These two are the exterior ones of the species with 3 staminodes. Very seldom, twice out of some thousands of *indica* flowers I have seen the middle staminode developed, noticeably but not very much smaller than the outer ones. More often however a small rudiment is found in the shape of a red filament generally not longer than half a centimeter. *C. glauca* has always 3 staminodes, the F_1 has 3 and the vast majority of the F_2 also have 3.

Two staminodes occurred 9 times out of 672 F_2 plants but flowers with two and three staminodes on one and the same plant were more frequent viz. on 38 plants. The development of the third staminode varies in this group from quite normal to very narrow, 3 to 5 m.M. breadth, and often it is at the same time shorter than the outer ones which may be due to differences in external conditions.

In the first sowing there was one specimen with two and three staminodes among 64 plants, in the sixth there were 10 out of 127, that is five times as many. That the number of plants with the unstable constitution varies rather considerably in the different sowings is clear from table XV.

The ratios of F_2 — setting aside the variation — could be explained by assuming three polymeric factors for more than

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1) CURTIS's Botanical magazine vol. 46, no. 2085.
2) CURTIS's Botanical magazine vol. 81, no. 4854.
3) CURTIS's Botanical magazine vol. 49, no. 2317.

TABLE XV. THE NUMBER OF STAMINODES OF F_2 AND F_3.

F_2 and F_3	Number of staminodes				
	Certainty about	> 3	3	2 and 3	2
F_2, 1st sowing	64	6	56	1	1
2d „	33	4	27	2	–
3d „	140	3	131	6	–
4th „	49	–	44	4	1
5th „	178	8	157	9	4
6th „	127	3	113	10	1
7th „	81	6	67	6	2
Total F_2	672	30	595	38	9
(Theory		31,5	567	63	10,5 ?)
F_3/1	22	6	15	1	–
„ /4	2	2	–	–	–
„ /6	18	1	12	4	1
„ /9	5	–	1	4	–
„ /14	8	–	8	–	–
„ /18	22	2	5	10	5
„ /21	6	1	4	1	–
„ /22	14	2	12	–	–
„ /28	2	1	1	–	–
„ /30	39	9	29	1	–
„ /35	5	2	3	–	–
„ /36	28	3	21	4	–
„ /38	2	–	1	1	–
„ /75	72	2	58	12	–
„ /162	14	1	8	4	1

two staminodes. The unstable group with 2 and 3 could contain the forms heterozygous for one factor only and the plant having frequently or regularly more than 3 staminodes could be homozygous for two factors and at least heterozygous for the third. Comparing the found numbers 30 : 595 : 38 : 9 with the theoretical ones 31,5 : 567 : 63 : 10,5 it does not look so bad. But the results of the back cross of F_1 by *indica* do not encourage us to be very tenacious in this supposition. In stead of finding one eighth part of the number of plants with merely two staminodes (**mno**) and three eighths in unstable condition (**Mno, mNo, mnO**) I found after the cross *indica* × F_1 6 and 16 representatives of these groups against 4 specimens with 3 staminodes; once more there is a shortage of the dominant type. The reciprocal cross with only one type of pollen agreed somewhat better but here also the numbers are too small. Furthermore the single individual with 3 and 4 staminodes suggest that the 30 specimens of that group in the F_2 (table XV) cannot well be regarded as homozygous for two factors and

TABLE XVI. THE NUMBER OF STAMINODES OF BACK CROSSES.

Back cross	Number of staminodes				
	Certainty about	> 3	3	2 – 3	2
F_1 × R13–4–5–1–1	2	–	2	–	–
F_1 × R13–4–5–1–13	17	1	6	7	3
	19	1	8	7	3
R13–4–5–1–1 × F_1	7	–	–	4	3
R13–4–5–1–13 × F_1	19	–	4	12	3
	26	–	4	16	6
F_1 × J4–2–3	128	2	124	2	–
J4–2–3 × F_1	263	7	255	1	–
J4–2–1 × F_1	41	–	41	–	–
J4–2–3 × (J4–2–3 × F_3/10–3)	175	28	145	2	–
(J4–2–3 × F_3/10–3) × J4–2–3 nr. 386	14	–	14	–	–
nr. 387	54	2	52	–	–
nr. 388	3	2	1	–	–
nr. 390	5	1	4	–	–
	76[1])	5	71	0	0
(J4–2–3 × F_3/10–3) × J4–2–1	4	1	3	–	–
(J4–2–3 × F_3/10–3) selfed nr. 391	44	10	30	4	–
nr. 392	40	12	28	–	–
nr. 395	43	12	31	–	–
	127[1])	34	89	4	0

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[1]) It is not quite certain whether the numbers may be added as belonging to the same ratio.

at least heterozygous for the third as the single plant of table XVI should be **MmNnOo.**

The numerousness of the recessive form in the back cross could again be ascribed to differences in velocity of growth of the pollen tubes. But this supposition is only a change of difficulties as it remains incomprehensible why there are no more recessive forms in the F_2. The figures do not give an explanation.

F_2/no. 16 with 2 staminodes in all flowers was, after selfpollination, sterile. After free pollination it yielded in some months 8 seeds of which 3 germinated, but all three seedlings died before blooming. F_2/no. 57 with two and three staminodes was also almost sterile.

That no independent Mendelian segregation occurs but partial coupling of the factors for colour and number of staminodes will be discussed later on.

The length and breadth of staminodes.

The staminode length of *C. indica* differs considerably from that of *C. glauca*, the parental ranges do not overlap (table XVII). In the former species it varied from 45 to 69 m.M. and the average length of 482 flowers was 59,3 m.M. For

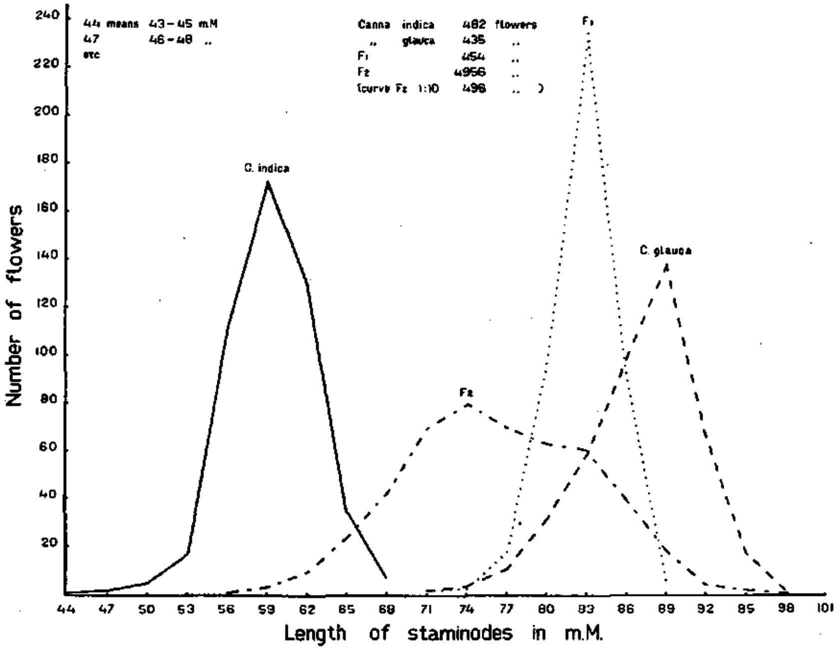

Fig. 7. Staminode length of *C. indica, glauca*, F_1 and F_2.

TABLE XVII. LENGTH OF STAMINODES.

Length in mM.	indica	glauca	F_1	Plants of second generation no.								Second generation				Average length of the back cross of F_1 by	
												sowing			total		
				16	10	3	38	36	22	4	1	1st	3d [1]	4th [2]		glauca	indica
43–45	1																
46–48	2																
49–51	5																
52–54	17																
55–57	112			1								2	2	5	10		1
58–60	**173**			8								10	3	14	35		5
61–63	130			28	1	1	1	1				40	10	29	99		4
64–66	35			71	3	8	4	1	1			110	32	51	240		8
67–69	7			**76**	37	23	13	—	—			219	55	72	428	1	**11**
70–72		2	2	15	**128**	58	53	2	1	1	3	434	72	108	706	7	5
73–75		4	3		58	**61**	**72**	6	3	3	1	**502**	**110**	122	**804**	11	6
76–78		11	18		2	12	11	44	14	13	—	426	94	**132**	709	27	3
79–81		32	97			1		**82**	**52**	37	4	353	79	**132**	636	53	2
82–84		59	**235**			1		18	47	**71**	23	327	67	**132**	612	74	
85–87		100	93					1	7	29	**40**	205	59	94	404	**101**	
88–90		**139**	6								30	108	24	33	189	58	
91–93		68									4	15	7	21	46	43	
94–96		18										1	5	19	26	19	
97–99		2											1	10	11	9	
100–102														1	1	1	
Number of flowers	482	435	454	199	229	165	154	155	125	154	105	2752	620	975	4956	404 plants	45 plants

[1] 10 flowers per plant. [2] 25 flowers per plant.

TABLE XVIII. BREADTH OF STAMINODES.

Breadth in mM.	indica	glauca	F_1	Plants of second generation nr.												Second generation sowing			
				3	12	16	39	38	10	36	14	4	1	25	9	1st	3d[1]	4th[2]	Total
8	9			1	1											2	2		4
9	30			5	4			1								12	3	7	25
10	120			12	7	10		2		1						35	29	27	94
11	**217**			**85**	**28**	76	2	4	1	–						205	33	21	288
12	95			56	25	**92**	16	7	3	3		1	1	2		246	74	54	445
13	7	9		5	3	21	**60**	46	31	2		11	1	1		270	**109**	104	557
14	2	28	3				25	**83**	**122**	56	18	24	4	3	1	549	80	141	853
15		80	20				1	10	64	**79**	**37**	**55**	13	2	–	**577**	**90**	**198**	**962**
16		**149**	190					1	7	14	2	**53**	**47**	3	2	419	73	180	784
17		99	**215**						1		1	10	35	20	7	244	50	95	455
18		45	24						1				4	**24**	**39**	121	36	86	279
19		20												10	25	56	26	39	133
20		4												2	8	11	5	18	41
21														1		1	5	5	18
22																	5		5
23																			1
Number of flowers	480	434	452	164	68	199	104	154	230	155	58	154	105	68	82	2748	620	975	4949

1) 10 flowers per plant. 2) 25 flowers per plant.

C. glauca the figures were 70—97 m.M. with an average of 87,1 from 435 measurements.

The staminodes of the F_1 were 70—89 m.M. long, mean 82,7, i. e. somewhat shorter than those of *glauca*. In comparison with *glauca* the extent of variation is limited which is no doubt explained by the fact that the F_1 consists of a single individual, whereas the flowers of 30 *indica* and 14 *glauca* plants were measured. (In this connection may be remembered the opposite conclusion for leaf length. The flowers however do not show an incomparability of dimensions dependent on their position on the floral axis.)

TABLE XIX. LENGTH OF STAMINODES.

Species or hybrid	Number of flowers	Limits of variation in m.M.	Average	Standard deviation
C. indica	482	45—69	59,297	3,225
C. glauca	435	70—97	87,076	4,383
F_1	454	70—89	82,661	2,438
F_2, sowing 1	2752	57—95	76,346	6,467
F_2, sowing 3	620 1)	57—97	76,732	7,097
F_2, sowing 4	975)	56—100	77,277	8,206
F_2, total	4956	56—100	76,449	7,076

1) 10 flowers per plant. 2) 25 flowers per plant.

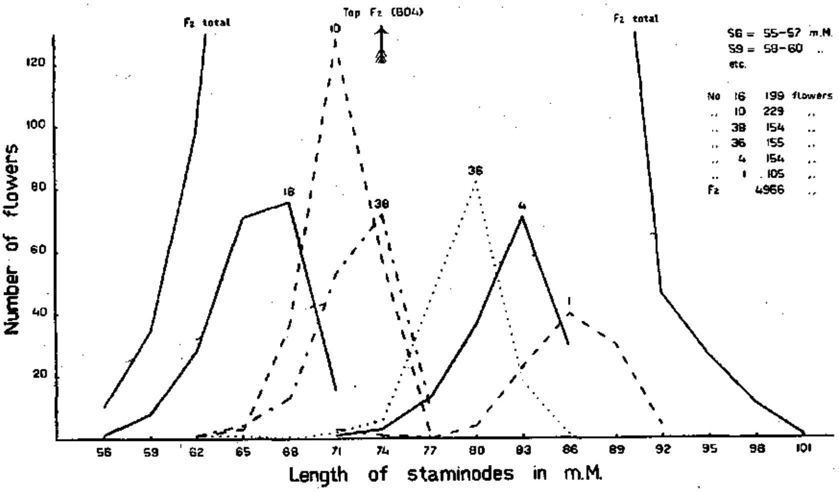

Fig. 8. Curve of staminode length of 6 F_2 plants with the lower end of the curve for F_2 total.

There is not much difference between the 1st, 3d and 4th sowing of the F_2, the averages being 76,3, 76,7 and 77,3 m.M., that is a little more than the midpoint of the parental means 73,2 m.M. The limits of variation are 57—95, 57—97 and 56—100 m.M. Only one specimen of the 4th sowing surpassed *glauca*.

The curve of staminode length of the F_2 as a whole is nearly regular though it shows a small increase where the F_1 has its top (table XVII, fig. 7).

TABLE XX. BREADTH OF STAMINODES.

Species or hybrid	Number of flowers	Limits of variation in m.M.	Average	Standard deviation
C. indica	480	8—14	10,808	0,962
C. glauca	434	13—20	16,235	1,334
F_1	452	14—18	16,524	0,696
F_2, sowing 1	2748	8—21	14,508	2,050
F_2, sowing 3	620 1)	8—22	14,429	2,541
F_2, sowing 4	975 2)	9—21	15,135	2,236
F_2, total	4949	8—23	14,637	2,240

1) 10 flowers per plant. 2) 25 flowers per plant.

In the same way as there could be selected plants with gradually increasing average length and breadth of the leaves, table XVII shows the curves of 8 F_2 plants with different average staminode length compared with those of *C. indica, glauca,* F_1 and F_2 (fig. 8). For staminode breadth table XVIII gives information about *indica, glauca,* F_1, F_2 and 12 separate F_2 plants. Whether all these 8 and 12 specimens are genotypically different is uncertain, even improbable. By the far more regular curves for each separate plant compared with the curves of leaf length, the chance of getting a reliable analysis of the factors for staminode length and breadth is much better.

The colour of the flowers.

The staminodes of *C. indica* are deep scarlet (plate I, fig. 1 and 2 is not deep enough), a trifle deeper of tint than scarlet no. 85 shade 4 of OBERTHÜR 1), nearly red no. 26 of KLINCKSIECK and VALETTE 2). Those of *glauca* are pale yellow, sulphur yellow

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1) OBERTHÜR, R. Répertoire de couleurs, Société française des chrysanthémistes, 1905.

2) KLINCKSIECK, P. et TH. VALETTE. Code des couleurs, 1908.

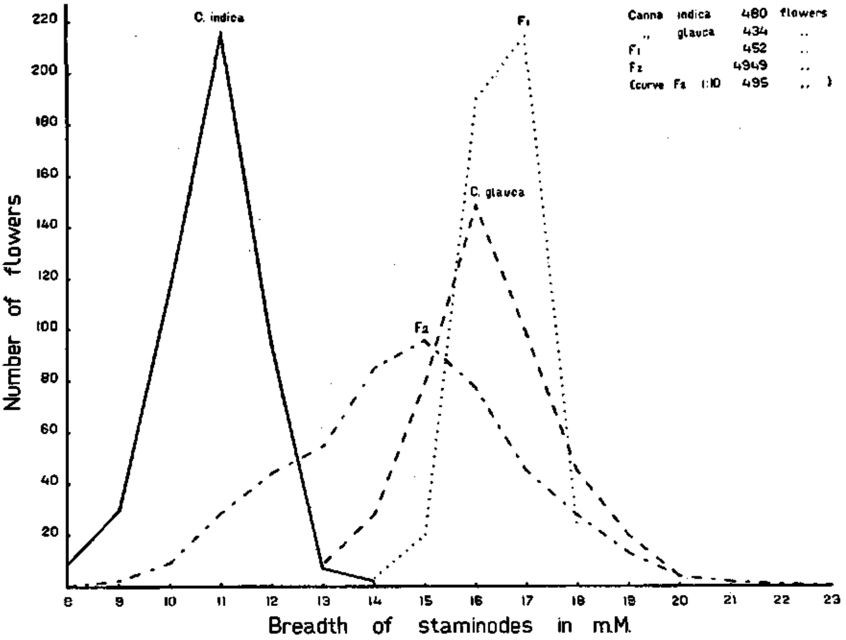

Fig. 9. Staminode breadth of *C. indica, glauca,* F_1 and F_2.

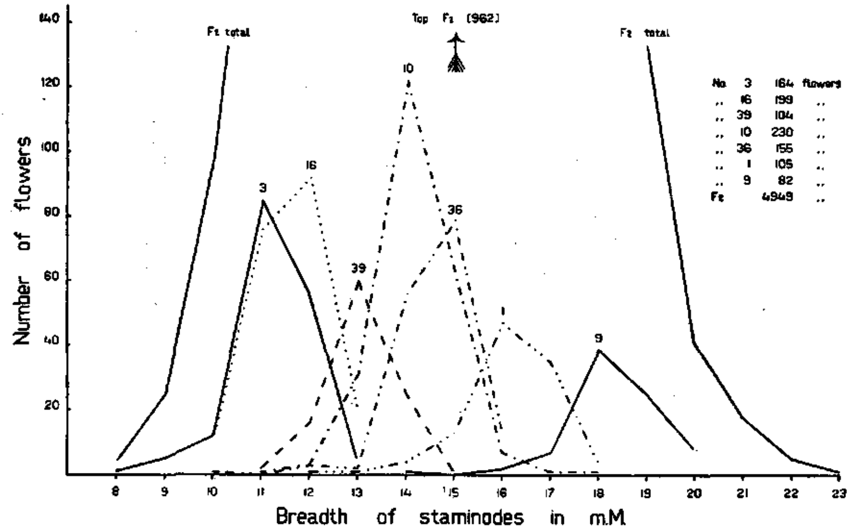

Fig. 10. Curve of staminode breadth of 7 F_2 plants with the lower end of the curve for total F_2.

no. 18—1 of Oberthür or between the nos. 216 and 221 of Klincksieck and Valette, and with some pink spots along the midveins (plate I, 4 and II, 5). These minute pink spots vary widely in number and dimensions from hardly visible for the naked eye to some millimeters. The yellow bleaches in course of the first blooming day.

TABLE XXI. SEGREGATION OF F_2 INTO PLANTS WITH RED AND WITH YELLOW FLOWERS.

Sowing	Number of plants				Ratios	
	total	leaves with red margin flowers	leaves green flowers		*a* : *b* : *c*	red: yellow
		a red	*b* red	*c* yellow		
1	64	34	15	15	2,27 : 1 : 1	3,27 : 1
2	33	22	5	6	3,67 : 0,83 : 1	4,50 : 1
3	140	76	19	45	1,69 : 0,42 : 1	2,11 : 1
4	49	24	10	15	1,60 : 0,67 : 1	2,27 : 1
5	178	108	18	52	2,08 : 0,35 : 1	2,42 : 1
6	127	79	23	25	3,16 : 0,92 : 1	4,08 : 1
7	81	49	18	14	3,50 : 1,29 : 1	4,79 : 1
Total	672	392	108	172	2,28 : 0,63 : 1	2,91 : 1
Theory	672	378	126	168	2,25 : 0,75 : 1	3 : 1

This pale yellow colour is no sap colour but limited to chromoplasts (plate IV*b*). The scarlet colour of *indica* is caused by a bluish red, carmin purple, cellsap turned into brillant deep scarlet by deep yellow chromatophores (plate IV*a*).

The flower of the F_1 is bright fiery red (plate I, 3).

With a view to the intensity of red in the flowers of the F_2 probably six different groups of tints can be distinguished, but partly under the influence of the different types of yellow, eleven shades of red were used for classification and some of these classes probably represent more than one genotype.

Among the yellow flowers there may be distinguished as groups pale yellow, yellow and deep yellow of which the yellow is present in one variable or perhaps in two shades (Oberthür 18—2 and 18—3) and the deep yellow as three shades of yolk yellow (Oberthür 24).

TABLE XXII. BACK CROSS OF F_1 BY C. GLAUCA. SEGREGATION INTO PLANTS WITH RED AND WITH YELLOW FLOWERS.

No.	Cross	Number of plants				Ratios	
		total	leaves with red margin flow. *a* red	leaves green flowers *b* red	leaves green flowers *c* yellow	*a* : *b* : *c*	red : yellow
361	F_1 × J4–2–3	7	4	1	2		2,50 : 1
365	F_1 × J4–2–3	36	8	2	26		0,38 : 1
370	F_1 × J4–2–3	2	1	1	–		
371	F_1 × J4–2–3	21	7	5	9		1,33 : 1
375	F_1 × J4–2–3	62	12	11	39		0,59 : 1
		128	32	20	76	0,42 : 0,26 : 1	0,68 : 1
363	J4–2–3 × F_1	36	15	5	16		1,25 : 1
366	J4–2–3 × F_1	25	8	5	12		1,08 : 1
368	J4–2–3 × F_1	8	2	4	2		3,00 : 1
369	J4–2–3 × F_1	33	11	11	11		2,00 : 1
372	J4–2–3 × F_1	55	9	16	30		0,83 : 1
374	J4–2–3 × F_1	21	6	5	10		0,91 : 1
376	J4–2–3 × F_1	85	21	24	40		1,12 : 1
		263	72	70	121	0,60 : 0,58 : 1	1,18 : 1
364	J4–2–1 × F_1	3	1	–	2		0,50 : 1
367	J4–2–1 × F_1	18	3	5	10		0,80 : 1
373	J4–2–1 × F_1	17	5	3	9		0,89 : 1
377	J4–2–1 × F_1	3	–	1	2		0,50 : 1
		41	9	9	23	0,39 : 0,39 : 1	0,78 : 1
	Total	432	113	99	220	0,51 : 0,45 : 1	0,96 : 1
	Theory	432	108	108	216	0,50 : 0,50 : 1	1 : 1

The only means to get an idea of a factorial analysis consists in beginning with a treatment of the flower colours collectively as groups, in the first place reds and yellows. In the former it is easy to separate at once the plants with entirely green leaves from those with red margin that always have red flowers.

a. The red colours.

The ratios of plants with red and with yellow flowers in the F_2 are given in table XXI. For F_2 in total it does not differ very much from 3 : 1 and among the red flowered plants the ratios of plants with red leaf margin and those without is also nearly 3 : 1, but evidently there is a shortage of plants with green leaves and red flowers.

Neglecting the irregularities of the different sowings, the conclusion should be that one factor should decide whether a plant is to develop red or yellow flowers and that in the group of the red flowered plants those with red leaf margin have again one factor more than those with green leaves. Hence one of the factors for red leaf margin must be at the same time a factor for red flower colour or absolutely coupled with it.

TABLE XXIII. INTENSITY OF THE RED FLOWER COLOUR AFTER BACK CROSSING F_1 BY C. GLAUCA.

Back cross	Total number	Classes of red no.								uncertain.
		8	7	6	5	4	3	2	1	
J4–2–3 × F_1										
with red margin	72	4	**28**	15	11	4	7	1	1	1
with green leaves	69		2	4	**36**	9	9	6	3	
F_1 × J4–2–3										
with red margin	32		**20**	3	3	1	2	1		2
with green leaves	20			4	**12**	1	2	1		
J4–2–1 × F_1										
with red margin	9		**4**	2	–	–	3			
with green leaves	9			1	**5**	–	2	1		
Sum, with red margin	113	4	**52**	20	14	5	12	2	1	3
Sum, with green leaves	98		2	9	**53**	10	13	8	3	
Red margin transposed for the classes 8—3				4	**52**	20	14	5	12	

The back cross of F_1 by *glauca* (table XXII) corroborates with the results of the F_2: one factor for red sap colour that should be at the same time one of the factors for red leaf margin. And here also is a shortage of the type with red flowers and green leaves.

Numbering the shades of red hitherto observed in F_2, F_3, F_4, back crosses, etc., starting from the palest salmon pink as no. 1 and following the different tints to that of *indica* as no. 11, the back cross of F_1 by *glauca* ranges from no. 1 to no. 8 (the F_1 is red no. 7). The most numerous class of the plants with red leaf margin is bright fiery red class no. 7 and that for the plants with green leaves class 5 (table XXIII). The first impression is that the second factor for red leaf margin **B** acts as an intensification factor for the red flower colour **A**, but as there are among the plants with red leaf margin some specimens with shades of pale salmon pink reckoned to the classes 1 and 2, it is probable that a separate factor **E** showing a rather high degree of coupling with **B**, is responsible. This however remains uncertain as the same result may be reached when **B** should act as intensification factor only in the presence of one of the other intensification factors.

Class 5 is exactly the type of flower colour after the cross *glauca* × F_3/10—3 (plate II, 4) of which 232 seedlings have been planted and nearly 200 bloomed, all uniform in flower colour, coral red OBERTHÜR 76—1 or rosy scarlet OBERTHÜR 90—3 on the margin and 76—2 along the midveins (KLINCKSIECK and VALETTE no. 66 in the middle and somewhat paler towards the margin). Next day after opening the colour is less brillant by bleaching of the yellow and looks more like salmon pink OBERTHÜR 126. There was only one exception, a plant with flowers noticeably deeper of tint, coral red 76—2 at the staminode margin (plate II, 3).

In this cross *glauca* was used as ovule plant as it yields considerably more seeds than F_3/10—3 by producing more stalks and often more seeds per fruit.

Of F_3/10—3 a F_4 has been raised of 90 seedlings of which 66 bloomed, all like the parentplant (plate II, 1 and 2). Of *glauca* I got ± 150 specimens flowering and all were similar. As the ± 200 blooming plants of *glauca* × F_3/10—3 were uniform with the exception of one plant with a somewhat deeper tint of red, but without yellow specimens or paler reds, there is a chance that F_3/10—3 was homozygous for flower colour as well as *glauca*.

The back crosses *glauca* × (*glauca* × F_3/10—3) and (*glauca* × F_3/10—3) × *glauca* — (considering F_3/10—3 as a type and not as a descendant of a *glauca*-hybrid we might speak, as DE VRIES does, of iterative and sesquireciprocal crosses) —

yielded a nearly equal number of red and yellow flowered plants, 123 and 132. The surplus of yellows is in cross 384 (table XXIV) where the pollen plant is red.

The type of heredity of the red flower colour of F_3/10—3 (class 9 to 10) is the *Zea*-type (plate II, fig. 1, 2, 4, 5), J4—2—3 × F_3/10—3 belongs to class 5. Back crossing by *glauca* for a second time does not originate once more an intermediate type of reds, but, apart from the yellows, five classes of reds of which the highest with the deepest tints is the most numerous.

TABLE XXIV. SEGREGATION FOR FLOWER COLOUR AFTER BACK CROSSING FOR A SECOND TIME F_3/10–3 BY C. GLAUCA.

No.	Cross	Number of plants	Flower colour red, class nr.						yellow
			5	4	3	2	1	total	
384	J4–2–3 × (J4–2–3 × F_3/10–3, nr. 354–3)	175	57	3	11	6	3	80	95
389	J4–2–1 × (J4–2–3 × F_3/10–3, nr. 354–3)	4	3	–	–	–	–	3	1
386	(J4–2–3 × F_3/10–3, nr. 354–2) × J4–2–3	14	4	2	–	–	–	6	8
387	(J4–2–3 × F_3/10–3, nr. 354–10) × J4–2–3	54	17	6	2	3	–	28	26
388	(J4–2–3 × F_3/10–3, nr. 354–3) × J4–2–3	3	1	–	–	–	1	2	1
390	(J4–2–3 × F_3/10–3, nr. 353–7) × J4–2–3	5	3	1	–	–	–	4	1
	Total	255	85	12	13	9	4	123	132

Probably an explanation could be given by assuming that the hybrid *glauca* × F_3/10—3 contains the factor for red flower colour **A** and an intensification factor **D**. When one wishes to ascribe some significance to the figures of cross 384 in table XXIV, the most numerous of all, it is possible to detect some regularity by adding the classes 5 and 4 (in fact very approaching) and the classes 3, 2 and 1. The ratio 60 : 20 or 3 : 1 for the deeper and paler reds is only possible when the *glauca* J4—2—3 and the hybrid J4—2—3 × F_3/10—3 both are heterozygous for the intensification factor **D**, hence no.384 should be **aaDd** × **AaDd**.... and the result the phaenotypes 3 **AD**, 1 **Ad**, 3 **aD** and 1 **ad**. Of course the constancy of F_3/10—3 after selfing has no importance here and the constancy of J4—2—3 after selfpollination does not necessarily produce difficulties. When the factor **D** has no influence upon the pink spots of *glauca* it does not matter for the constancy of the type whether *glauca* possesses **D** or not, and if the intensity of the spots does depend on **D** and consequently *glauca* must be constantly heterozygous, the case would not be an isolated one; the homozygous form may perish, a phenomenon already known from yellow mice [1]), *Oenothera* [2]) and *Drosophila* [3]).

TABLE XXV. SEGREGATION FOR FLOWER COLOUR OF (J4–2–3 × F_3/10–3) AFTER SELFING.

Nr.	Plant selfed	Number of offspring	Flower colour									
			red, class nr.									yellow
			8	7	6	5	4	3	2	1	total	
391	J4–2–3 × F_3/10–3. nr. 353–7	44		5	8	**13**	5	1			32	12
392	J4–2–3 × F_3/10–3, nr. 354–2	40	2	–	5	**15**	1	2	–	1	26	14
395	J4–2–3 × F_3/10–3, nr. 354–8	44		4	4	**17**	–	2	–	1	28	16
396	J4–2–3 × F_3/10–3, nr. 354–9	8			1	–	–	2	–	1	4	4
397	J4–2–3 × F_3/10–3,nr.354–10	24	1	3	2	**7**	3	–	1		17	7
	Total	160	3	12	20	**52**	9	7	1	3	107	53

Some support is afforded to such an additional hypothesis by the results of selfing J4—2—3 × F_3/10—3. In stead of finding the 3 : 1 ratio expected for red and yellow the ratio is 107 : 53 or 2 : 1 (table XXV). There were 119 seedlings more planted out, children of selfed sisterplants, but they did not bloom when I left Medan. For this 2 : 1 ratio it does not matter whether homozygosis of the factor for red colour **A** or the intensification factor **D** acts killing or of **A** and **D** both separate and together. In the first and second case there remain 8 reds and 4 yellows out of 16 and in the third 6 reds and 3 yellows. What decides in the three possibilities, are the ratios of types of red of different intensities. No. 384 with 3 coral reds: 1 salmon

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1) CASTLE, W. E. and C. C. LITTLE. On a modified mendelian ratio among yellow mice. Science N. S. XXXII, p. 768, 1910.

2) HERIBERT NILSSON, N. Die Spaltungserscheinungen der Oenothera Lamarckiana, Lunds Univ. Arsskrift N. F. Avd. 2, Bd. 12, S, 27, 1915.

3) MULLER, H. J. An Oenothera like case in Drosophila. Proc. of the nat. Acad. of Sciences 3, p. 619, 1917.

pink should suggest that the intensification factor **D** may be present without injurious effect.

The F_3 after selfing F_2/no. 30 proves however that the factor for red colour **A** also may exist homozygous. The F_3 consisted of 23 plants with red flowers and red leaf margin, 11 with red flowers and green leaves and 9 with yellow flowers, nearly 2 : 1 : 1 and more than three times as many red flowered plants as yellows. If the **AA** forms perished and the **BB** were left alive, the ratio per 16 should be 6 : 2 : 4, i. e. twice as many yellows as reds with green leaves. When however the second red leaf margin factor **B**, if homozygous, kills its bearer, the ratio will be 6 : 3 : 3 or 2 : 1 : 1.

But this factor **B** is absent in the F_3/10—3 back crosses spoken of above, hence either **A** and **D** together are homozygously impossible, or there exists another factor Q lethal if homozygous (and here lethal factor is as usual another expression for something I do not know).

The results of the two least small back crosses reciprocal to no. 384, the nos. 386 and 387, chime fairly well with the scheme. There are 34 reds and 34 yellows, the ratio coral red : salmon pink is 29 : 5 in stead of 25,5 : 8,5 and selfing these two motherplants of the back cross yielded 43 reds : 21 yellows, just 2 : 1.

Apart from the 2 : 1 ratio after selfing (J4—2—3 × F_3/10—3) there is one argument more to consider all reds as heterozygous for at least one of the factors: among the 107 reds not a single one reached the claret (Oberthür 167 shade 3—4, Klincksieck and Valette ± 6) of F_3/10—3, class 9 to 10.

Whether the figures are reliable may be uncertain, but it is a fact that the palest group, class 3—1 of J4—2—3 × F_1 is for the plants with red leaf margin exactly one eighth of the total number, 9 out of 72, and for the plants with green leaves one fourth, 18 out of 69 (table XXIII). The same thing is to be seen for the sum of all plants with red margin when the former series is combined with those of the reciprocal back cross and that by J4—2—1, viz. 15 out of 113, and the sum of the greens 24 out of 98. This indicates a third intensification factor **F**, present in F_1 but also in F_3/10—3, which lacks **B**, eventually also **E**. The deep tint of F_3/10—3 moreover requires more than the factor **D** only.

b. The yellow colours.

Although the brightness of the red colours is influenced by the presence of the yellow ones, the latter are hypostatically covered by the former.

As never a white flowered plant arose,[1] both *glauca* and *indica* will contain the pale yellow that in *indica* is turned into (or covered by?) deep yellow by *two* factors **H** and **I.** This follows from the segregation in the progeny of the deep yellow plant F_2/no. 75 which broke up in F_3 in close approximation to the 9 : 3 : 4 ratio, viz. 38 deep yellow, 14 yellow and 16 pale yellow (expectation 38¼ : 12¾ : 17, table XXXVI).

As for so many characteristics already discussed the figures of F_2 are not in accordance with this assumption. In stead of finding a majority of deep yellows among all non-reds there were 23 only out of 172 or 1 : 6,48; and at the same time the proportion is variable (table XXVI). The shortage of deep yellows among the non-reds is a consequence of the surplus of plants with deep yellow chromatophores among the red flowering ones. I confess that a small part only has been controlled with the microscope, but the reds without the brightness caused by the deep yellow were proportionally rare among the deep reds from the tint of the F_1 to deeper (class 7—11), viz. 24, while in class 6 only one was found. In the lower classes as a rule **H** and **I** are absent. In consequence both factors **H** and **I** are coupled to the intensifiers for red.

TABLE XXVI. DIFFERENT TINTS OF YELLOW IN F_2.

Sowing	deep yellow	yellow	pale yellow	total	deep y. : (y. + pale y.)
1	1	12	2	15	1 : 14
2	2	1	3	6	1 : 2
3	6	19	20	45	1 : 6,5
4	–	7	8	15	
5	8	33	11	52	1 : 5,5
6	4	21	–	25	1 : 5,25
7	2	12	–	14	1 : 6
Total	23	105	44	172	1 : 6,48

The difference between the deep yellows and the others is rather sharp but that between yellow and pale yellow is not so distinctly marked in all cases, probably owing to small differences between plants homozygous and heterozygous for one of the factors **H** and **I**. As most yellow flowered plants are

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[1] MÜHLE, l. c. S. 7: Reinweisse Canna zu erziehen ist bis heute trotz einiger verlockenden Anfängen, noch immer der sehnlichste Wunsch der Züchter geblieben.

not very fertile after self pollination it will take some time to make it clear.

Also the deep yellows are by no means exactly the same. F_3/no. 75 contained among the 38 deep yellows 3 exceedingly deep coloured specimens (theory : 4½), of the same deep shade as appeared for instance partly in the descendants of the red leaf margined plant F_2/no. 1 after selfing.

The results of the back crosses of F_1 by *glauca* are in full agreement with those mentioned above. The factors **H** and **I** demonstrating themselves in F_3/ no. 75 as dominants, appeared together among the yellow flowered offspring of the back cross only 5 times out of 220, all 5 no doubt heterozygous for **H** and **I**, the intensity of the deep yellow being that of F_2/no. 75 (plate III, 1) and certainly not the much deeper shade of the 3 specimens of F_3/75 (plate III, 4) and of those F_3/no. 1 individuals. Distinctly yellow were 81, pale yellow 63, the remaining 71 specimens probably partly yellow, for a large part pale yellow or intermediate. Classification of these plants would not have been possible for me without inducing the feeling of making mistakes.

Among the 53 yellows gained after selfing (J4—2—3 × F_3/ 10—3) individuals, there appeared not a single deep yellow specimen, no more among the 132 yellows of the second back cross of F_3/10—3 by *glauca* (tables XXV and XXIV).

c. **Flaking.**

The staminodes of *C. indica* are plain red, those of *glauca* pale yellow with minute pink spots along the middle veins. Among the F_2 apart from the intensity of the red colours and the size of the spots one may discern four types of flaking:

1. a central red part over half the staminode breadth or more with small spurs along the veins in a somewhat paler red border;
2. a central red colouring in a yellow border (like the *Canna* variety *Königin Charlotte*);
3. red spots along the middle of the yellow staminodes like those of *C. glauca*;
4. red spots spread over the whole breadth of the yellow staminode, especially at the top (like the variety *J. B. van der Schoot*).

1. **The deeper vein colouring** is rather easily distinguishable in the pale red types but more difficultly in the deeper reds, is even not always clearly visible in the F_1. Hence it was not accidental that after back crossing F_1 by *glauca*, which pro-

duces paler red tints, the number of plants with noticeably deeper colour in the middle of the staminodes was proportionally much higher than after selfing the F_1, viz. 161 out of 199 as against 56 out of 500 (tables XXVII and XXVIII). Probably we had better speak of at least 56.

There is in the ratio 161 : 38 in the back cross of F_1 by *glauca* a surplus of dominants and *glauca* and F_1 both should have been heterozygous for the vein colouring factor **J**.

TABLE XXVII. PLANTS WITH RED STAMINODES OF DEEPER SHADE ALONG THE VEINS AFTER BACK CROSSING F_1 AND C. GLAUCA.

Back cross	With red leaf margin			With green leaves		
	number of plants	veins deeper tinged; staminode margin		number of plants	veins deeper tinged; staminode margin	
		red	yellow		red	yellow
F_1 × J4—2—3	32	28	1 1)	20	12	1 2)
J4—2—3 × F_1	72	52	4 3)	70	54	5 4)
J4—2—1 × F_1	9	8	1 5)	9	7	1 6)
Total	113	88	6	99	73	7

1) With narrow yellow margin.
2) With narrow yellow margin.
3) With broad yellow margin 2, with narrow 2.
4) With broad yellow margin 2, with narrow 3.
5) With broad yellow margin.
6) With narrow yellow margin.

About the back cross J4—2—3 × F_3/10—3 I have no figures. The second back cross J4—2—3 × (J4—2—3 × F_3/10—3) or reciprocal proved that all plants chosen as ovule plants (perhaps with the exception of no. 388) were heterozygous for **J**, just like *glauca* (table XXIX). As the number of plants with deeper vein colouring is nearly three quarters of the total number, viz. 95 out of 123, the results of this second back cross should be in accordance with those of the back cross of F_1 if not 5 specimens remained uncertain and even 9 (of which 8 of one no.) were variable, changing the appearance of the flowers on one and the same plant. The latter peculiar phenomenon occurred once more after selfing (J4—2—3 × F_3/10—3) plants. Then

TABLE XXVIII. F_2 PLANTS WITH RED STAMINODES OF DEEPER SHADE ALONG THE VEINS.

Sowing	With red leaf margin			With green leaves		
	number of plants	veins deeper tinged staminode margin		number of plants	veins deeper tinged staminode margin	
		red	yellow		red	yellow
1	34	–	1	15	–	2
2	22	2	–	5	1	–
3	76	4	1	19	–	–
4	24	3	–	10	1	1
5	108	11	1	18	1	1
6	79	9	1 1)	23	5	–
7	49	16	–	18	3	1 1)
Total	392	45	4	108	11	5

1) Yellow margin narrow.

17 were uncertain and 1 variable. The rest however showed the clean cut 3 : 1 ratio (67 : 22). The 5 and 17 uncertain and the 9 and 1 variable specimens make the 14 and 22 plain uncertain also. They might have been extreme variates of the variable group, perhaps the 3 : 1 ratio occurred through the merest

TABLE XXIX. SEGREGATION OF RED FLOWERING PLANTS FOR DEEPER COLOUR ALONG THE STAMINODE VEINS AFTER BACK CROSSING FOR A SECOND TIME F_3/10–3 BY C. GLAUCA.

No.	Cross	Number of plants	deeper tinged along the veins	plain	uncertain	variable
384	J4–2–3 × (J4–2–3 × F_3/10–3, no. 354–3)	80	69	9	2	–
389	J4–2–1 × (J4–2–3 × F_3/10–3, no. 354–3)	3	2	1	–	–
386	(J4–2–3 × F_3/10–3, no. 354–2) × J4–2–3	6	5	1	–	–
387	(J4–2–3 × F_3/10–3, nr. 354–10) × J4–2–3	28	15	2	3	8
388	(J4–2–3 × F_3/10–3, no. 354–3) × J4–2–3	2	2	–	–	–
390	(J4–2–3 × F_3/10–3, no. 353–7) × J4–2–3	4	2	1	–	1
	Total	123	95	14	5	9

chance. Two polymeric factors each of which individually is very unstable in its demonstration, are also possible.

2. **Central red colouring in a yellow border** occurred in F_2 4 times on plants with red leaf margin and 5 times on plants with green leaves (table XXVIII). The back cross of F_1 by *glauca* produced 6 resp. 7 specimens (table XXVII).

A typical yellow bordered specimen with red leaf margin F_2/no. 37 was selfed. The F_3 consisted of 11 plants, 8 with red leaf margin and 3 with green leaves, of which 10 bloomed, all with red middle part and yellow border. There were selfed anew one with red leaf margin and one with green leaves. The former F_3/37—1 produced a F_4 of 45, viz. 33 with red leaf edges and 12 greens, of which 26 flowered. The latter F_3/37—2 yielded a F_4 of 9 of which 8 bloomed like the parentplant. Whereas the green leaved F_3/37—2 bred true in F_4 with rather broad yellow margin, the F_4/37—1 did not do so, the yellow margin varying from very broad to nearly absent, broad in all green leaved specimens and also broad in 13 out of the 18 with red leaf margin and 5 with narrow or very narrow yellow border.

TABLE XXX. SEGREGATION OF RED FLOWERING PLANTS FOR DEEPER VEIN-COLOURING AFTER SELFING (J4–2–3 × F_3/10–3).

No.	Hybrid, selfed	Number of plants	deeper vein colouring	plain	uncertain	variable
391	J4–2–3 × F_3/10–3, no. 353–7	32	19	7	5	1
392	J4–2–3 × F_3/10–3, no. 354–2	26	18	7	1	–
395	J4–4–3 × F_3/10–3, no. 354–8	28	19	4	5	–
396	J4–2–3 × F_3/10–3, no. 354–9	4	2	2	–	–
397	J4–2–3 × F_3/10–3, no.354–10	17	9	2	6	–
	Total	107	67	22	17	1

The back cross of the same F_3/37—1 plant by *glauca* (the latter as ovule plant) produced the same results as regards the variability of breadth of the yellow margin. Of the 17 children with red leaf margin 14 bloomed, of the 18 with green leaves 17, together 31 of which 23, i. e. three quarters, showed a narrow or very narrow yellow margin and 8 a broad one. The colouring of almost the entire staminode must be dominant to the slighter extension of the red colour. However the distribution of both types is not proportional to the almost equal numbers of plants with red leaf margin and those without, as the latter contained 7 out of the 8 specimens of the recessive type, whereas only one of the 14 red leaf margin plants was with broad yellow margin, which indicates coupling of the extension factor **P** with **B**, the second factor for red leaf margin. Of course it is possible to explain the 3 : 1 ratio assuming that *glauca* and F_3/37—1 are both heterozygous for the factor **P**. But the results of selfing F_3/37—1 with 5 specimens with narrow yellow margin out of 26 would contradict the supposition; here again there is a surplus of recessives.

That the same factor **J** is responsible for the central colouring in entirely red and in yellow marginated flowers is not certain, as **J**, in whole coloured red types, partially prohibits the action of an intensification factor and in F_2/37 and its offspring it would suppress in the margin the colour factor **A** itself.

The F_5 perished totally owing to a *Rhizoctonia*pest in my cultures at Wageningen and now I must wait for the results of the back cross by *C. indica* that is supposed to be recessive for **J**. Back crossing by pure yellow was impossible, as in 1922 not a single one of the F_2 or other yellows was pure yellow.

3. **Red spots along the middle of the yellow staminode.** The localisation of the red colours is nearly the same as the region influenced by the factor **J,** but often narrower, and the anthocyanin extension is limited to insular splashes in the yellow. While group 2 is counted as red the groups 3 and 4 are reckoned as yellow for practical purposes. It is however still possible

TABLE XXXI. SPREAD OF RED SPOTS ON YELLOW FLOWERS IN F_2.

Sowing	Extension of the red spots						Total
	spread over whole breadth		confined to the middle of the staminodes				
	number	%	stronger than with glauca	nearly like glauca	weaker than with glauca	absent	
1	–	0	6	6	–1)	3	15
2	–	0	–	6	–1)	–	6
3	–	0	23	16	–1)	6	45
4	1	7,1	3	8	1	1	14
5	2	3,8	15	16	8	11	52
6	6	24,0	4	4	5	6	25
7	8	57,1	2	–	2	2	14
Total	17	9,9	53	56	16	29	171
				72			

1) In the first sowings not distinguished from the preceding column.

that the colour factor **A** with or without one or more of the intensifiers is also present in the groups 3 and 4, manifesting themselves in the different shades of red of the spots, so that another factor than **A** might decide between red and yellow, and that the factor **R** effects the patching only and not the colour.

Among the 171 studied yellow flowering F_2 plant there were 29 specimens without any red in the staminodes. This wholly yellow type is the weak point in the analysis as it occurred more than once that a plant noticed for pure yellow after some weeks or months showed very small red points. Whilst in the three first sowings of F_2 the difference between *glauca* and the specimens with still less development of anthocyanin, i. e. the group „weaker than *glauca*”, was neglected on account of the rather considerable variability of *glauca* itself, later on it was evident that the groups „weaker than *glauca*” and „absent” (table XXXI) could not always be separated correctly. The back cross of F_1 by *glauca* produced nearly half the number of yellows with the *glauca*-like type of patching, 115 out of 220 yellows (table XXXII).

TABLE XXXII. SPREAD OF THE RED SPOTS IN THE YELLOW OFFSPRING OF THE BACK CROSSES OF F_1 BY C. GLAUCA.

Back cross	Extension of the red spots				absent?	Total
	over the whole breadth	confined to the middle of the staminode				
		stronger than glauca	nearly like glauca	weaker than glauca		
$F_1 \times J4\text{–}2\text{–}3$	20	–	26	7	23	76
$J4\text{–}2\text{–}3 \times F_1$	26	4	47	15	29	121
$J4\text{–}2\text{–}1 \times F_1$	6	1	13	2	1	23
	52	5	86	24	53	220
			115			
Expectation	55		110		55	220

4. **Red spots spread over the whole surface of the staminode** was for the first time seen in the fourth sowing of F_2. As the 1st and 3d sowing were also used for measuring length and qreadth of staminodes at the same time as the fourth and the

type is strikingly different from *glauca* it could not have been overlooked when it had occurred. Failing in the 66 yellow specimens of the 1st — 3d sowing, it appeared 3 times among the 66 yellows of the 4th—5th sowing, 6 times among the 25 yellows of sowing 6 and even 8 times out of 14 in the 7th sowing. This is indeed one of the most striking cases of variability of segregation.

The back cross F_1 by *glauca* produced the wholly speckled type 52 times out of 220 yellows, that is 23,6 %.

The whole-spotted type seems to be homozygous, as all 15 flowering F_4 plants gained after selfing the whole-spotted F_3/10—2 were spotted over the whole breadth, varying in intensity of the red and considerably in the number of spots (plate VII).

Another selfed specimen, a F_3 of F_2/no. 1 with large fiery red spots on deep yellow was sterile. This plant proved that the factor for patching was hypostatically covered in the red flowered plant F_2/no.1 of the first sowing where the whole-spotted type phaenotypically fails.

The result of the back cross of F_1 by *glauca* (table XXXII) wholly spotted: *glauca*-like: pure yellow as 52 : 115 : 53 or 0,95 : 2,09 : 0,96 leads to the expectation that the whole-spotted type is homozygous and the *glauca*-like type heterozygous for a factor **R** and that *glauca* itself is a constant heterozygote for this factor.

The ratio 2 reds : 1 patched yellow: 1 pure yellow after crossing back (J4—2—3 × F_3/10—3) by *glauca* (tables XXIV and XXXIII) may be brought in accordance with this idea on condition that in (J4—2—3 × F_3/10—3) **R** be almost absolutely coupled with **A**, so that it forms chiefly **AR** and **ar** and occasionally also a few **Ar** and **aR** gametes. Then the result is **AaRR** + **AaRr** + **aaRr** + **aarr** or 2 reds (heterozygous for **A**): 1 *glauca* type: 1 pure yellow, whilst the small amount of wholly spotted yellows **aaRR**, 3 out of 129, should have arisen by meeting of two **aR** gametes, of which that of the hybrid should have been originated by crossing-over.

If that be true, one may expect that in case of selfing (J4—2—3 × F_3/10—3) should produce mainly 1 **AARR** (killed): 2 **AaRr** : 1 **aarr**, i. e. reds and pure yellows only and exceptionally some patched yellows. In fact however, only half of the yellows are pure, 28 out of 53, and the number of **aaRR** is increased, 4 out of 53 in stead of 3 out of 129. Hence the % of crossing-over is much higher (free Mendelian segregation, or 50 % crossing-over would have produced, omitting the **AA** forms, 8 reds : 1

TABLE XXXIII. SPREAD OF THE RED SPOTS IN THE YELLOW FLOWERING PROGENY OF THE BACK CROSS OF F_3/10–3 BY C. GLAUCA.

No.	Second back cross by glauca or selfing (glauca × F_3/10—3)	Extension of the red spots					Total.
		over the whole breadth	confined to the middle of the staminode			absent?	
			stronger than glauca	nearly like glauca	weaker than glauca		
384	J4–2–3 × (J4–2–3 × F_3/10–3, nr. 354–3)	2	3	28	13	47	93
389	J4–2–1 × (J4–2–3 × F_3/10–3, nr. 354–3)	1	–	–	–	–	1
386	(J4–2–3 × F_3/10–3, nr. 354–2) × J4–2–3	–	–	3	1	4	8
387	(J4–2–3 × F_3/10–3, nr.354–10) × J4-2-3	–	–	6	6	13	25
388	(J4–2–3 × F_3/10–3, nr. 354–3) × J4–2–3	–	–	–	–	1	1
390	(J4–2–3 × F_3/10–3, nr. 353–7) × J4–2–3	–	–	–	1	–	1
	Total	3	3	37	21	65	129
391	(J4–2–3 × F_3/10–3, nr. 353–7) selfed	2	–	2	3	5	12
392	(J4–2–3 × F_3/10–3, nr. 354–2) selfed	1	–	3	4	6	14
395	(J4–2–3 × F_3/10–3, nr. 354–8) selfed	1	–	3	4	8	16
396	(J4–2–3 × F_3/10–3, nr. 354–9) selfed	–	1	–	–	3	4
397	(J4–2–3 × F_3/10–3, nr. 354–10) selfed	–	–	–	1	6	7
	Total	4	1	8	12	28	53

wholly spotted : 2 *glauca*-like : 1 pure yellow). The real figures 107 : 4 : 21 : 28 are very nearly approached on assuming a cross-over value of 27,4 % or the gametic ratios 2,65 **AR** : 1 **Ar** : 1 **aR** : 2,65 **ar**, viz. 106,6 : 4 : 21,2 : 28,1, indeed a splendid harmony, too fine to be true. But, although with the crossing-over hypothesis almost every ratio can be „explained", it gives no explanation for the difference in behaviour of (J4—2—3 × F_3/10—3) that in a back cross by *glauca* should have shown less than 3 % cross-overs and in case of selfing about 27 %. A factor in *glauca* which lowers the amount of crossing over?

There has not been made a trial for explanation on a base of dissimilarity of pollen and ovule gametes, as both reciprocal crosses of (J4—2—3 × F_3/10—3) by *glauca* yielded the same results as regards the number of pure yellows in the total yellow flowered offspring (table XXXIII): 47 is as well the half of 93 (no. 384) as 4 is the half of 8 and 13 of 25 (nos. 386 and 387).

It is not certain that all (J4—2—3 × F_3/10—3) specimens will be **Rr** plants as the most fertile ones proved to be.

F_2/no. 1 was rather deep red (class 9) and the red flowered F_3 were at least fiery red as F_1, but most of them deeper. The patches of the deep yellow F_3 specimens were fiery red in stead of pink as in *glauca*. Hence it is clear that the intensifiers for **A** are at the same time intensification factors for **R**.

Coupling of insufficiently known factors.

1. „Coupling" of the factors for the numbers of staminodes and those for colour. Whereas in F_2 the ratio of red flowered plants with red leaf margin: red flowered plants with green leaves: yellow flowered ones is 2,28 : 0,63 : 1 (i. e. the 9 : 3 : 4 ratio with a shortage in the second group of 16 %, the ratio for the same types among the plants with two and two to three staminodes is as 23 : 3 : 21 or 1,10 : 0,14 : 1 (table XXXIV). Relatively the number of plants with 2 staminodes and yellow flower colour is very high. This is the more remarkable as the parent with two staminodes has not yellow but red flowers so that coupling of the factors for red with 3 and for yellow with

TABLE XXXIV. THE PROPORTIONALLY LARGE NUMBER OF PLANTS WITH YELLOW FLOWERS HAVING 2 OR 2—3 STAMINODES.

Sowing	Number of plants				Three to two staminodes			Two staminodes			Ratio red : yellow
	total	leaves with red margin flowers a) red	leaves green flowers b) red	c) yellow	a)	b)	c)	a)	b)	c)	
1	64	34	15	15	1	–	–	–	–	1	1 : 1
2	33	22	5	6	1	–	1	–	–	–	1 : 1
3	140	76	19	45	2	–	4	–	–	–	2 : 4
4	49	24	10	15	1	–	3	–	–	1	1 : 4
5	178	108	18	52	5	1	3	2	–	2	8 : 5
6	127	79	23	25	6	2	2	1	–	–	9 : 2
7	81	49	18	14	3	–	3	1	–	1	4 : 4
	672	392	108	172	19	3	16	4	0	5	26 : 21
		500									

Ratio red : yellow for all flowers 2,91 : 1; and for the plants with 2 and 2–3 staminodes 1,24 : 1.

TABLE XXXV. RELATION BETWEEN LENGTH OF STAMINODES AND COLOUR OF LEAVES AND STAMINODES

Average length in mM.	Second generation			total	F_1 × J 4-2-3			J 4-2-3 × F_1			J 4-2-1 × F_1			Back cross F_1 and C. glauca, totals			
	red margin	leaves green			red margin	leaves green		red margin	leaves green		red margin	leaves green		red margin	leaves green		total
	flowers red	flowers red	flowers yellow		flowers red	flowers red	flowers yellow	flowers red	flowers red	flowers yellow	flowers red	flowers red	flowers yellow	flowers red	flowers red	flowers yellow	
< 62										1						1	1
62–63		1	1	2						–						–	–
64–65		–	–	–						–						–	–
66–67	3	2	6	11						–						–	–
68–69	2	2	1	5						1						1	1
70–71	2	5	–	7				1	3	–				1	3	–	4
72–73	10	**7**	2	**19**			1	–	3	1				–	3	2	5
74–75	**13**	3	3	**19**		2	4	–	–	1			1	–	2	6	8
76–77	12	2	6	**20**	1	1	4	–	3	3		1	–	1	5	7	13
78–79	7	3	4	14	1	2	5	4	8	5		–	1	5	10	11	26
80–81	5	3	6	14	–	2	9	4	**14**	10		2	1	4	**19**	20	43
82–83	5	1	5	11	2	1	8	5	12	15	1	**3**	–	8	16	23	47
84–85	**11**	2	2	**15**	4	**6**	**15**	5	**13**	11	–	1	**7**	9	**20**	33	**62**
86–87	7	2	3	12	**6**	1	10	10	4	**27**	2		4	**18**	5	**41**	**64**
88–89	1	–	2	3	**6**	1	10	6	2	**14**	–		3	12	3	27	42
90–91	1	–	–	1	4		4	10	1	9	**3**		2	**17**	1	15	33
92–93		1	–	1	4		2	**13**	1	4	1		1	**18**	1	7	26
94–95		1	–	1	1		2	4	1	4	1		2	6	1	8	15
96–97			1	1			1	2		4	1			3		5	8
98–99								3		2				3		2	5
100–101								1						1			1
Number of plants	79	35	42	156	29	17	75	68	65	112	9	7	22	106	89	209	404

2 staminodes would not be expected. Difference in velocity of growth of pollen tubes?

2. „Coupling" of **B** with factors for staminode length. As well in F_2 as in the back crosses of F_1 by *glauca*, but most clearly in the back crosses, the red flowered plants with green leaves (**AAbb** or **Aabb**) have on an average shorter staminodes than those with red leaf margin (with **B**) and also shorter than the yellow ones (partly **BB** or **Bb**, partly **bb**). As **B** is a factor present in *indica* and not in *glauca* and long staminodes are a characteristic of *glauca* there should be, just as in the former case, more than 50 % cross-overs (unless the distribution of chromosomes be not a random one in the reduction division).

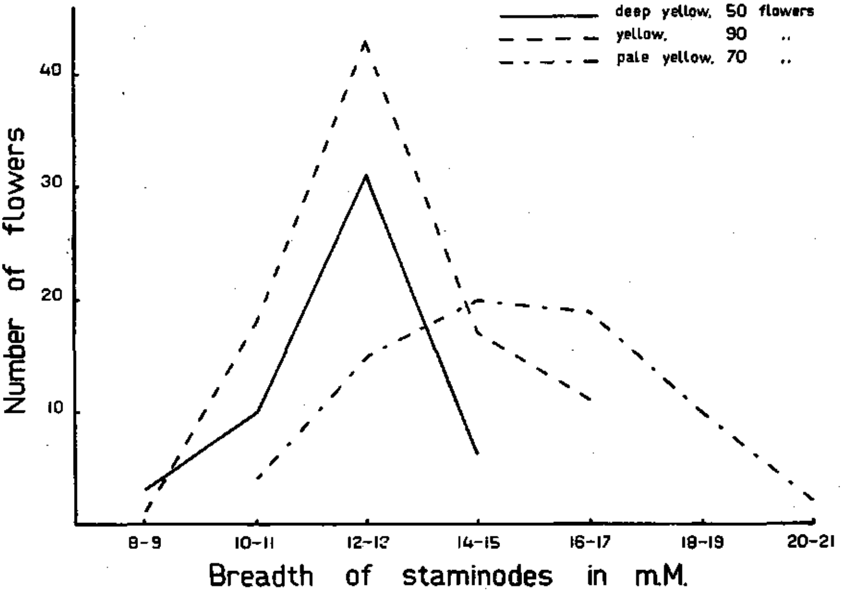


Fig. 11. Deep yellow staminodes are in F_2 as a rule narrower than pale yellow ones.

3. Repulsion of the factors for deep yellow chromatophores and those for staminode breadth. As a rule the deep yellow staminodes are narrower than the pale yellow ones just as the parent with the deep yellow chromatophores *indica* is narrower than the pale yellow *glauca* with broad staminodes. In contrast with the two former sets of characters, there exists here a tendency of keeping together those factors that are inherited from one parent. When however a type is homozygous for staminode breadth as F_2/no.75 seems to be, there is in the follow-

TABLE XXXVI. RELATION BETWEEN BREADTH AND COLOUR OF STAMINODES.

Breadth in mM.	F_2 2d sowing, yellow flowers [1]			$F_3/75$ (F_2/no. 75 was deep yellow) average breadth of plants with flower colour			
	deep y.	yellow	pale y.	deep y.	yellow	pale y.	total
8–9	3	1		4			4
10–11	10	18	4	6	4	3	13
12–13	**31**	**43**	15	**19**	**7**	**9**	**35**
14–15	6	17	**20**	9	1	4	14
16–17		11	**19**		2		2
18–19			10				
20–21			2				
Number of flowers	50	90	70	38	14	16	68 plants
				38,25	12,75	17	expectation

[1] Ten flowers per plant.

ing generation no difference in average breadth between the deep yellow, yellow and pale yellow flowers (table XXXVI and fig. 11).

About the seeds it has already been mentioned that the seed coat of F_1, in the tropics, is more uniformly black than it sometimes is in Holland. The seeds of *glauca* and yellow flowered hybrids, at Medan, were in their speckledness rather variable (often even on one and the same plant) so that I do not trust my figures before I have been able to control them with more homozygous material. And so it is also for form and size of the seeds. No one will make a mistake when selecting *glauca* and *indica* seeds out of a mixture of both, but counting types in a mixture of hybrids seems to me impossible, difficult as it is to judge the seeds of a single plant, which all of them have the same seed coat constitution.

SUMMARY.

1. The F_1 offspring of the cross *Canna glauca* × *indica* segregates for the factors of the red leaf margin, for the layer of wax on the leaves, the number and colour of staminodes in ratios that differ widely in different sowings, in spite of the fact that the F_1 consists of a single individual; so there is variability in segregation of the hybrid.

2. The factor **A** causes red flower colour, **aa** plants have yellow flowers.

B produces together with **A** the broad red leaf margin. The factor **C** necessary in crosses of *C. indica* with its own green leaved variety as third factor for broad red leaf edges (and wherein plants containing **C** but without **A** and **B** both together, showed a very narrow red leaf margin) seems to be absent or totally prohibited in its demonstration in the cross with *glauca*. In some F_2 sowings the inheritance of **A** and **B** proceeds on ordinary Mendelian lines (9 : 7 ratio), in three batches the ratio is 1 : 1. In F_3 the 1 : 1 ratio appeared again, but also 9 : 7 and 3 : 1.

D, **E** and **F** are intensification factors for the red colour factor **A** and also for **R**, the factor for patched staminodes. One of the intensifiers **E** is coupled to a high degree with **B**. From the back cross of F_3/10—3 with *glauca* resulted that the *glauca* used for the back cross J4—2—3 was heterozygous for **D**.

G is an extensification factor for anthocyanin in the leaves. That F_1 has much redder leaves than *indica* depends on the factor **G**, cryptomeric in *glauca* and coupled with a factor for wax.

K and **L** are polymeric factors for the wax layer on the leaves of *glauca*. Judging from the thickness of the wax layer *glauca* should be heterozygous for both factors. The back cross of F_1 by *glauca* however suggests homozygosity of at least one of both.

M, **N** and **O** may be three polymeric factors for the third staminode, which becomes probable from the ratios in F_2, but far from certain on account of the results of the back cross of F_1 with *indica*.

Q is a lethal factor, in (*glauca* × F_3/10—3) absolutely coupled with **A**, killing all **AA** plants in the offspring after selfing that hybrid. Probably it is the same factor that in *glauca* is coupled with **R** and being homozygous kills all **RR** plants.

H and **I** are the factors that constitute together the difference between the deep yellow chromatophores in the staminodes of *indica* and the pale yellow ones in those of *glauca*.

J is a factor for deeper vein colouring present in most red flowered hybrids, almost invisible in the deep reds, clearly visible in the pale ones. Perhaps the central red colouring in a yellow margin is caused by the same factor **J**. *C. glauca* should be **Jj**.

P is an extensification factor for the central colouring. **PP** and **Pp** plants have much narrower yellow staminode margin. In *glauca* **P** should be present heterozygously.

R causes homozygously red patches in yellow flowers spread over the whole breadth of the staminode and heterozygously such spots in the middle of the staminode only. For this factor **R** *glauca* is a constant heterozygote owing to the presence of the lethal factor Q.

3. So far we can judge now (putting not quite certain factors in brackets,

and marked with a point when homo- or heterozygosis is unknown) *C. indica* will be **AABB(CC)DD(EE)FFggHHIIjjkkll(mmnnoo)ppqqrr** and *glauca* **aabb(cc)DdeeffG.hhiiJjKkL.(M.N.O.)PpQqRr.**

4. It is not certain whether the variability of segregation is caused by irregular distribution of the chromosomes whether or not followed by differential fertilization or differential mortality of gametes or differential mortality of zygotes. Shortly I hope to be able to give some cytological information.

5. As a rule the F_3 and F_4 are more regular in their segregation than the F_2; clean cut Mendelian ratios reappear.

6. It has not been possible to work out a factorial analysis for leaf length and breadth, staminode length and breadth, form, size and colour of the seeds.

7. Measuring all leaves of F_1 and separate F_2 specimens and adding the figures for each plant separately, gives curves irregular on the minus side where the limits of variation are extremely wide. For F_2 as a whole this irregularity has vanished and the F_2 standard deviation for leaf length is even smaller than that of the F_1 which is one single individual. The staminode length is far less dependent on the position on the floral axis than the leaf length is dependent on the position on the stem.

I wish to express my thanks to Dr. S. C. J. Jochems for having described some late blooming hybrids with the aid of Oberthür after my departure from Medan, and to Mr. B. J. van Tongeren for the fine pictures of *Canna* flowers after which the plates I, II and III have been made.

EXPLANATION OF PLATES.

Plate I. (± $^3/_5$ nat. size).

Fig. 1–2. *Canna indica* (the shade of red is not deep enough).
„ 3. *C. glauca* × *indica* F_1.
„ 4. *C. glauca.*
„ 5–6. F_4 specimens of the F_2/37 family with red ovary.
„ 8–9. F_4 specimens of the F_2/37 family with green ovary.
„ 8. Abnormal flower with 3 labella.

Plate II. (± $^3/_5$ nat. size).

Fig. 1. F_4/10—3—4.
„ 2. F_3/10—3 not opened flower.
„ 3. J4—2—3 × F_3/10—3, the only specimen with a trifle deeper shade of red.
„ 4. J4—2—3 × F_3/10—3 type (± 200 individuals).
„ 5. *C. glauca.*
„ 6–9. F_3 children of F_2/162, fig. 8 with two staminodes.

Plate III. (± $^3/_5$ nat. size).

Fig. 1. F_2/75.
„ 2–4. F_3 plants of F_2/75, flowers deep yellow.
„ 5–6. F_3 plants of F_2/75, flowers yellow.
„ 7. F_3 plant of F_2/75, flowers pale yellow.

Plate IV.

Fig. 1. Transverse section of staminode of *C. indica*, 350 ×.
„ 2. Transverse section of staminode of *C. glauca*, 350 ×.

Plate V.

Fig. 1. F_3/10—2 on first day.
„ 2. F_3/10—2 on second day, bleached.
„ 3–8. F_4/10–2 specimens.
„ 6. is a young not fully opened flower, fig. 7 an old already bleached one. This peculiar keeping-closed often occurred also on the motherplant F_3/10—2.

Plate VI.

Unripe fruits of *C. indica* (deep red), *C. glauca* × *indica* F_1 (much brighter red) and *C. glauca* (green).

Plate VII.

Ripe fruits of *C. indica* (opens its carpels), *C. glauca* × *indica* F_1 (does not at all or scarcely open its carpels), *C. glauca* (keeps its carpels closed).

Plate VIII.

The creeping power of the rhizom of *C. glauca* demonstrated by the hybrid F_2/nr. 4. The spot where it was originally planted is marked by a gaspipe with a *Canna* leaf in top. Creeping distance two meters and a half in one year and a half.


2
4
6
7
8
9

PLATE 2

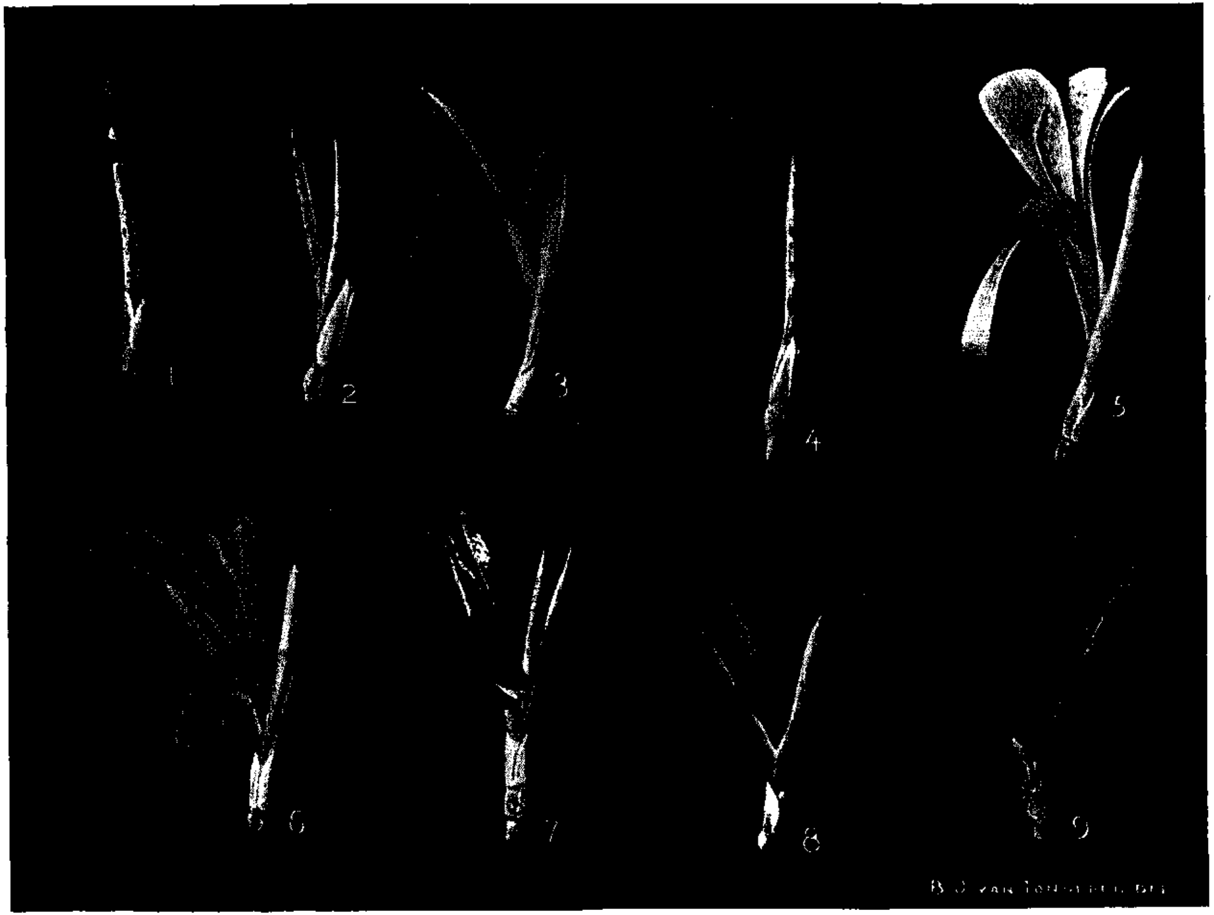
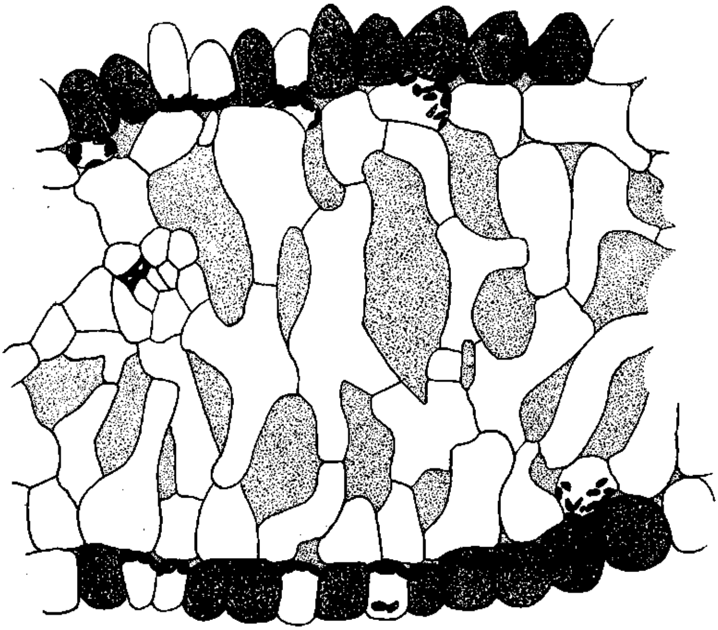


PLATE 3

PLATE 4



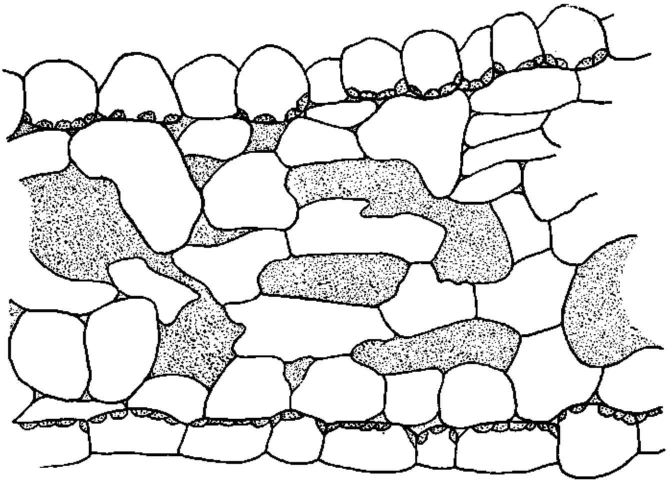


PLATE 5

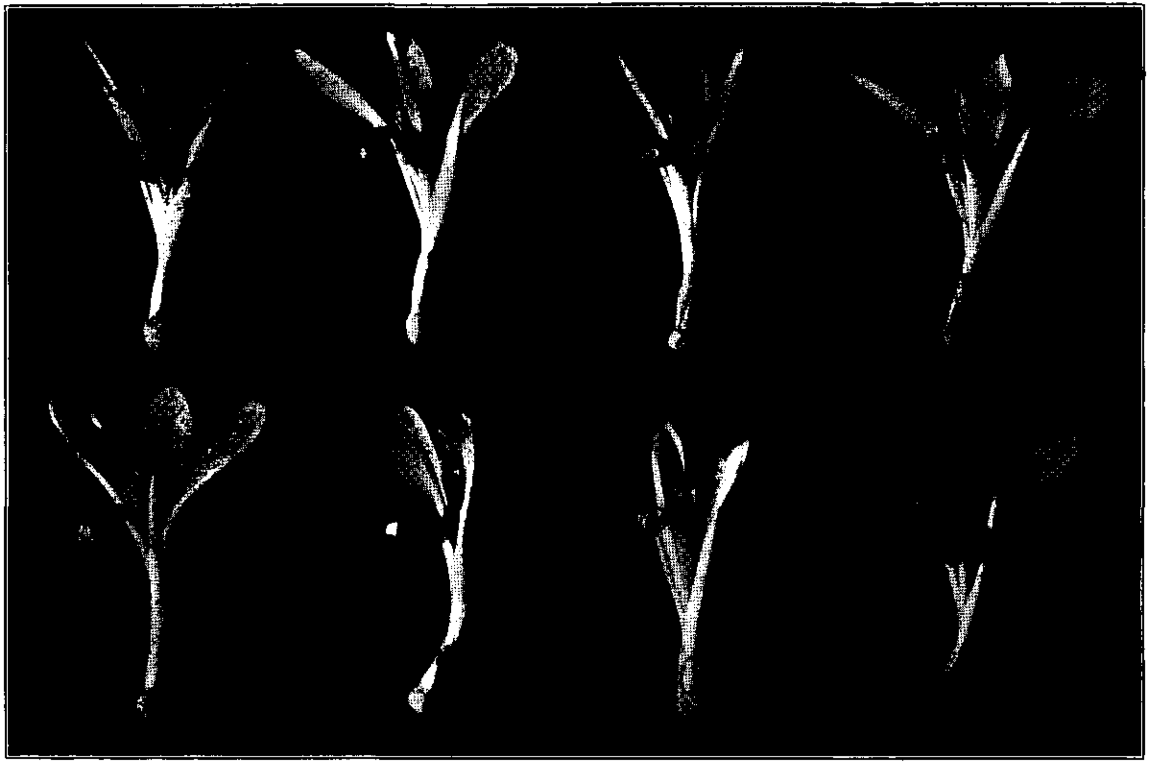


PLATE 7

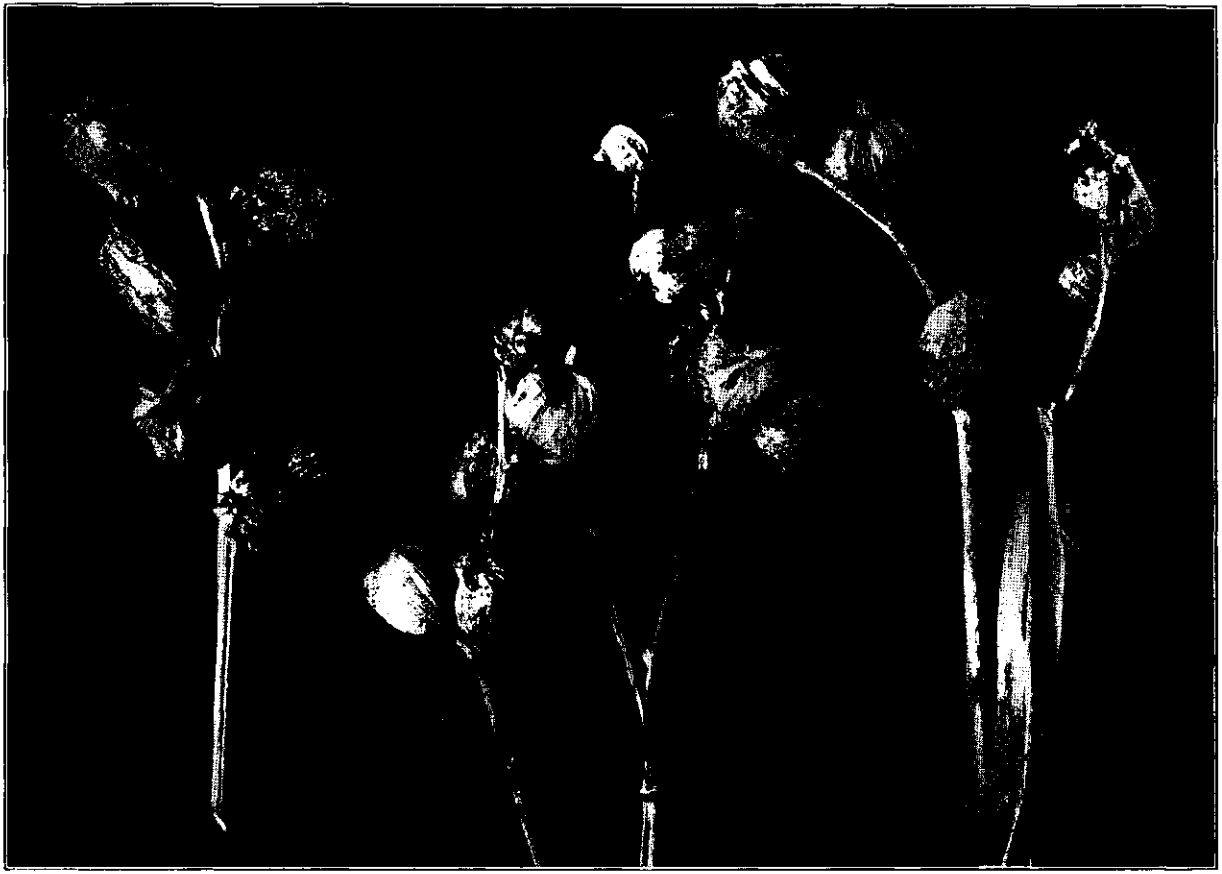


PLATE 8