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ON THE INHERITANCE OF THE FLOWERING TIME IN PEAS AND RICE.

By

Yuzo Hoshino, *Nōgakushi*.

INTRODUCTION.

The multiple-factor hypothesis, which was proposed by Nilsson-Ehle (1908) for the interpretation of the inheritance of quantitative and physiological characters and carried further by Lang (1911), seems to be gaining a steady acceptance in the scientific world. The investigators who have accepted the above hypothesis support their views by the facts that the F_1 is intermediate between parents; that the F_2 shows a wider variation than the F_1 , mostly varying within a combined range of the parents, but some producing transgressive variation; while in the F_3 , some vary like the F_2 , others, in several grades of variation ranges. The majority of the investigators, however, do not explain the exact number and nature of the factors which may concern the heredity of the characters.

So far as the author knows, there are only two works which touch on the latter subject. The one is Tschermak's (1911) and the other is Punnet and Bailey's (1914). Tschermak proposed, for the interpretation of his experimental results on the inheritance of the flowering time in peas, two alleromorphic pairs; Punnet and Bailey, for the interpretation of their experiments on the inheritance of weight in poultry, four alleromorphic pairs. If we examine their work carefully, however, we can not readily accept their interpretations. We shall not enter here into a minute discussion of the subject, but let us simply make the following remarks. In the work of Tscherm-

mak, the grouping of the individuals in the F_2 into three classes (early, intermediate and late), on the numerical ratios of which Tschermak layed great stress, seems to be quite arbitrary, and the materials of the F_3 and F_4 raisings are insufficient for the affirmation of the proposed interpretation. In regard to the work of Punnet and Bailey, the experimental material seems to us too scanty to prove their assumption positively.

Thus, so long as the number and nature of the factors are not definitely explained, we should have still to hold with Shull (1914), that "for the present, the hypothesis that plural Mendelian genes adequately account for the inheritance of complex quantitative and physiological character, is valuable only to the extent that it is made a working hypothesis."

The author has continued the present experiments since 1907. In the experiments with peas, he has raised the F_2 and the F_3 three times and the F_4 twice, and, besides, he has paid special attention to the inheritance of the flowering time of pure lines in the population of parent varieties. The total number of individuals which he has raised up to the present is over 30,000. As the results of this large raising, the author feels quite confident that the present work will cast a clearer light than has hitherto been shed upon the multiple-factor hypothesis, which will be applicable to the inheritance of such a physiological character as flowering time.

While the author was conducting experiments on the inheritance of flowering time, he noticed the presence of some correlation between the flowering time and flower colour in peas, and found that this correlation might be interpreted by the assumption of gametic coupling.

The author wishes to make grateful acknowledgement for the faithful assistance of the following gentlemen;—Messrs. G. Shimada and W. Oga-wa, his former assistants, and Mr. Y. Shima, his present assistant.

Sapporo, April, 1915.

I. EXPERIMENTS WITH PEAS.

Experimental Methods.

The Experiments were carried on in the College Vegetable Garden from 1907 to 1911, and in the nursery ground of the College Orchard from 1912 to 1914. As peas do not flourish under continuous cropping, care was taken to change the raising place every year, selecting even and homogeneous plots.

The method of raising the offsprings was as follows. At first, we selected a certain number of F_1 plants, and took 30 seeds from each of these selected plants and sowed them according to their origin on different rows. Thus we got a certain number of F_2 families, each of which consisted of 30 individuals. In raising the F_3 progenies, we selected certain F_2 families (rows), and took 30 seeds from every plant of these selected families, sowing them on different rows according to their different origins, just as in the case of the F_2 raising. F_4 raisings were also made according to the same principles.

Thus our method was to raise 30 individuals in one family and to record their flowering time, but, in reality, there were some seeds which failed to sprout, and some individuals which, on account of retarding of flowering time caused by some injuries, such as breaking of stem, insect injury etc., had to be discarded later from records. And moreover, there occurred some few individuals which flowered normally but did not produce a sufficient number of seeds for raising 30 offsprings. Such were the causes of the insufficient number of the individuals in one family that we noticed everywhere throughout the experiments. We did not raise the progenies of those plants which produced too small a number of seeds.

The rows, on which the individual plants were grown 6 inches apart, were 15 feet long and 2 feet apart. When the plants had grown about 10 inches, we gave to every plant a bamboo cane for support, binding the stem to it lightly. Afterwards we repeated this binding two or three times to

prevent entanglement with the adjoining plants. We recorded as the flowering time of every plant, the time when the standard of its first flower opened.

Preliminary Experiments with Peas.

Materials Used.

When the author returned to Sapporo after four years' absence for studies abroad and took charge of the Department of Horticulture of the College, he found in the Department the stock seeds of over twenty varieties of peas which had been harvested in the previous year in the College Vegetable Garden. The dates of the flowering for all of these varieties had been recorded every year, and he could select two varieties which had a difference of about two weeks in their flowering times. A brief description of these two varieties follows.

1. Early variety; Dwarf, white-flowered, tough-podded, white-seeded; cultivated over ten years under the name of "Improved Dwarf" in our vegetable garden. We shall denote this variety as "**I. P.**"
2. Late variety; Pole, red-flowered, soft-podded, gray-seeded; cultivated longer than the former in the garden under the name of "French Large Podded". Afterwards, we identified this variety as "Pois sans parchemin jéant, à très large cosse", according to the description in Vilmorin-Andrieux' "Plantes potagères". We shall designate this variety by the abbreviation "**G. P.**".

In the early part of May, 1907, we sowed twenty seeds of **G. P.**; and when the plantlets had grown up 2 or 3 inches high, we thinned them to ten plants. After the sowing of the **G. P.** seeds, we sowed the **I. P.** seed three times at intervals of ten days. When both varieties came to flower, artificial crossing was practised between them, care being taken to record the pollen parents. When the ripened seeds were harvested, there were 54 seeds of ♀ **G. P.** × ♂ **I. P.** and 23 seeds of ♀ **I. P.** × ♂ **G. P.**

TABLE 1.—Frequency distribution of number of days from sowing to flowering in F_1 of crosses between *G. P.* and *I. P.* (1908)

Designation	Class centers																																	
	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	
<i>G. P.</i>																						2	6	3	6	4	2	5	10	2	5		2	1
<i>I. P.</i>			13	18	8	7	2																											
<i>G. P. × I. P.</i>																2	6	7	14	7	2	6	2		3		1	1						
<i>I. P. × G. P.</i>															1	2		4	2	4	5	2		1	1									

TABLE 2.—Frequency distribution in F_2 of crosses between *G. P.* and *I. P.* (1909)

No.	Designation	Class Centers																																						
		44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80		
	<i>I. P.</i>	14	5	3																																				
	<i>I. P.</i>	1	9	6	3	1																																		
	<i>I. P.</i>	8	8	4	1																																			
	<i>I. P.</i>	10	4	5	1																																			
	<i>G. P.</i>																2	4	2	1		1	2	2	4		1	1												
	<i>G. P.</i>																1	2	3	2	1	2	1	2	4	3	3	1	1											
	<i>G. P.</i>																2	1	1	2	1	1	1	2	3	2	2	2												
1	<i>II</i> × <i>I</i> 3.1	2	1	2	1			1					1		1		1	3				1	1	1	1	1														
2	<i>II</i> × <i>I</i> 3.3				2	1				1.2		1				1	1	1	1	3			2																	
3	<i>II</i> × <i>I</i> 3.4		1	1	3			1				1				2				1	2		2	2	1															
4	<i>II</i> × <i>I</i> 3.5		2		1	1		1				1				1				3			2	2																
5	<i>II</i> × <i>I</i> 3.6			2	1	1					1			4		1				2		2	1	1																
6	<i>16</i> × <i>II</i> 1			1	1	1				1			3		3		1	1	2	1	1	1	1																	
7	<i>16</i> × <i>II</i> 2			1	1	1			1			2			1	1	2	1	3		2	1																		
8	<i>16</i> × <i>II</i> 3	1			1						2			3	1	3	1	2	1	1	1	2	1																	
9	<i>16</i> × <i>II</i> 4		1	3				1	1				1		1	4	1			1	1	1																		
10	<i>16</i> × <i>II</i> 5							3	1	1			1	1	1		1	1	2	2	1	2	1																	
11	<i>V</i> × <i>17</i> 1								3	1	1				1	1		2	4																					
12	<i>V</i> × <i>17</i> 2		2	1						1	1	1			1	1	2		4																					
13	<i>V</i> × <i>17</i> 3	1			1	1		1	1	1					4	1			3		1																			
14	<i>V</i> × <i>17</i> 4		1			2		1	1	1					1	2		4	2	2		2																		
15	<i>20</i> × <i>V</i> 1	1				1	1		1			1	3	1	4	1		1	1		1																			
16	<i>20</i> × <i>V</i> 2				3			1							1	2	2		4			1	1	2	1															
17	<i>20</i> × <i>V</i> 3		1						1				5			3		5					1																	
18	<i>20</i> × <i>V</i> 4			1	2	1			2				2		3		1		2	2	1		1																	
19	<i>20</i> × <i>V</i> 5				2	1		1				1		1	1	1	1	4		1	2		1		3															
		4: 4	7: 0	11: 4	16: 2	5: 3	4: 0	6: 5	6: 12	2: 7	0: 7	1: 4	1: 23	0: 8	8: 36	1: 12	1: 15	2: 42	0: 10	1: 14	1: 22	0: 13	0: 17	0: 19	1: 5	0: 1	1: 0	0: 3	0: 6							0: 1				
		64 + 48 = 112 (Early flowering group)																12 + 247 = 259 (Late flowering group)																						

Black-faced type indicates number of white-flowered individuals.
* indicates number of dwarf individuals.

TABLE 3.—Frequency distribution in F_3 of crosses between *G. P.* and *I. P.* (1910)

No.	Designation	Parent	Class Centers																									Means of Constants											
			Class	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69		70	71	72	73	74	75					
	<i>I. P.</i>			1	5	17	24	4	6	1	1																												49.88
	<i>G. P.</i>																					2	20	31	18	4	6	2	1								67.55		
1	<i>V</i> × <i>17</i> 2.12	46			1	8	18	3																													49.77		
2	<i>V</i> × <i>17</i> 2.17	46			5	8	11	1	1																												49.56		
3	<i>II</i> × <i>I</i> 3.1.6	45			1	3	17	3	3																												50.15		
4	<i>V</i> × <i>17</i> 1.2	45				5.4	9.2	2																													49.61		
5	<i>16</i> × <i>II</i> 2.14	47				2	4	10	4	5		2																									51.52		
6	<i>16</i> × <i>II</i> 2.20	47				3.1	3.3	3	6.1	4	1																										51.16		
7	<i>16</i> × <i>II</i> 1.3	47				3	8	3	8	3	3																										51.00		
8	<i>16</i> × <i>II</i> 1.17	48				1	10	2	7	5	3																										51.50		
9	<i>II</i> × <i>I</i> 3.1.21	47			1		6	6	8	5	5																										51.35		
10	<i>V</i> × <i>17</i> 2.4	47				8	4	5	2	2																											51.05		
11	<i>II</i> × <i>I</i> 3.1.6	46				1	7	11	2	3																											51.96		
12	<i>16</i> × <i>II</i> 1.20	48				1	2	10.3	4	4	5.2																										51.93		
13	<i>II</i> × <i>I</i> 3.3.2	49				3	2	3	5	3	11																										52.33		
14	<i>16</i> × <i>II</i> 2.22	49						1	9	6	3	1																									53.70		
15	<i>20</i> × <i>V</i> 1.1	49			2	1	4	2	6	4	4	4																									av. 51.19		
16	<i>20</i> × <i>V</i> 2.19	48			1	1		1	6	6	1	1	4	5	2																								
17	<i>II</i> × <i>I</i> 3.3.7	48						1	5	6	2	1	3	1	2	3																							
18	<i>II</i> × <i>I</i> 3.1.19	47						4	4	3	1	1	1	2	5	5																							
19	<i>II</i> × <i>I</i> 3.3.19	48						1	5	6	2	1	3	1	3	3																							
20	<i>20</i> × <i>V</i> 2.7	48						2	1	7	2	1	5	5	4	1																							
21	<i>16</i> × <i>II</i> 1.2	63			1		2	1.3	2		1	1	1			1	1</																						

F₁ Raising in 1908.

On May 8, we sowed all of the cross seeds harvested in the previous year, together with some seeds from the parent plants which were used in the crossing as the seed parents or the pollen parents. With a few exceptions, the seeds sprouted very evenly, and the young plants grew in excellent condition.

During the summer vacation of that year, the author had to take a trip to Manchuria, and at the time when the **I. P.** plants had just begun to flower, he left Sapporo, entrusting all observations to his assistant. On his return to Sapporo in the middle of September, he found all had been harvested in rather miserable condition, and heard that in August a formidable storm had raged in Northern Japan, and many of our plants were badly injured and many of the ripened pods were shaken off. And to our great regret, owing to the misunderstanding of the assistant, all the pods of every parent variety were sacked together without any distinction of the origin.

But, from the records taken, we got the frequency distribution of the number of days from sowing to flowering of the **F₁** offsprings and that of the parent varieties, as shown in Table 1.

From Table 1, we see that the flowering time of the **F₁** is not just intermediate between those of the parent varieties, but inclines much towards that of the late parent. In other words, we may say that in the present instance incomplete dominance of lateness occurs. And there is practically no essential difference between reciprocal crosses.

F₂ Raising in 1909.

From the **F₁** plants we selected the following individuals:—

♀ G. P. II × ♂ I. P. 13,—	No. 1	No. 3	No. 4	No. 5	No. 6
♀ I. P. 16 × ♂ G. P. II,—	No. 1	No. 2	No. 3	No. 4	No. 5
♀ G. P. V × ♂ I. P. 17,—	No. 1	No. 2	No. 3	No. 4	
♀ I. P. 20 × ♂ G. P. V,—	No. 1	No. 2	No. 3	No. 4	No. 5

Notice: Hereafter, we shall denote the plants of a late parent by Roman numerals and those of an early parent by arabic figures, and in the crosses, the antecedent will be the seed parent, the subsequent, the pollen parent. For example, II \times 10 will denote the product of the No. 2 plant of the late parent variety crossed with the No. 10 plant of the early parent variety.

We took 20 seeds from each of the selected 19 F_1 individuals and sowed them on May 6, together with 80 seeds (in 4 rows) of each parent varieties. Sprouting took place evenly, during the two days May 14, 15.

The frequency distribution of the number of days from sowing to flowering in the F_2 and parent varieties is shown in Table 2. Reserving the discussion of the results of the present experiments for a later chapter, we shall simply enumerate here the chief facts observed.

1. The variation ranges of the F_2 families extend from the range of the early parent to that of the late parent. But there does not appear any transgressive variation. In the family II \times 13.5, however, there is one individual whose flowering date exceeds the variation range of the late parent; and it was an exceedingly dwarf (12.5 inches) and weak plant. This abnormal retarding of the flowering time might have been caused by insufficient light and nutrition, as it grew amidst the other stouter and larger plants.

2. By summing up the frequencies of each class perpendicularly in the table, we see a class which has a comparatively small number of frequencies situated at about the middle of the variation means of both parent varieties (class 55). As this fact has a great bearing on our experiments throughout, we shall designate this class as the *minimum frequency class*. The individuals which flowered before this class (this class inclusive) shall be considered as belonging to the *early flowering group*, those which flowered after the class, as belonging to the *late flowering group*.

3. In the early flowering group the white-flowered individuals are more numerous than the red-flowered ones, and in the late flowering group the white-flowered individuals are exceedingly few, and indeed fewer than the red-

flowered ones in the early group. This suggests some correlation between the flower color and the flowering time.

4. The ratios of poles to dwarfs is approximately 3 : 1 in total, and when considered in two separate groups, the ratio also holds the same in each. So we may conclude that there is no correlation between the stem character and the flowering period.

5. We do not see any difference between the progenies of reciprocal crosses.

6. The variation range of the progeny of the late variety **G. P.**, is distinctly wider than that of the **I. P.** progeny. We had noticed a similar fact already in the previous year, but did not pay much attention to it. And the frequency distribution of **G. P.** was quite different from that in ordinary fluctuating variation. In the ordinary variation, the mode must lie in about the middle of the range, and towards both sides of the mode the frequencies must decrease gradually, but in this case, the frequencies in the class 64, situated in about the middle of the variation range, are remarkably small, while in the classes 60 and 67, the frequencies are prominently large. Why did such an irregularity in the variation type occur? This might occur by chance in such a case as this, where only 80 individuals were observed, but it can not be denied that there may be some other complicated causes for such an occurrence. For example, if the population of **G. P.** should consist of from more than one pure line, or if the character of the flowering time were not fixed and if hereditary variation should to some extent occur, there would appear such a variation type as mentioned above. Thus, we were quite convinced that unless we raised hybrid progenies together with the progenies of their original parents and the hereditary modes of the parent varieties themselves are elucidated, we could not reach any exact conclusions. But because of careless harvesting of the seeds of the parent plants in the previous year, we were not able to distinguish the origin of the offsprings of the parent varieties in the present year.

Besides, we found that **I. P.** was not an adequate parent variety for the

experiment, because the flowering time of the dwarf plants which appear as the result of segregation may be influenced by the shading and usurpation of the nutrient of larger growing sister plants, and some of those dwarfs would not produce sufficient seeds for further experiments. (One individual class 79 of the family $II \times 13.5$, already referred to, produced only 3 pods and 8 seeds)

From the two above mentioned causes, we determined to take new crosses and to conduct the experiments anew.

F₃ Raising in 1910.

Having determined to continue the experiments with new materials, we made new crosses during February and March of the present year in a forcing house. But as there was some space in the garden available for the experiment, we raised the F₃ for the purpose of using the results of this raising for reference in our new experiments.

We selected 20 F₂ individuals which flowered within the variation range of the **I. P.** variety, 25 F₂ individuals which flowered within the variation range of **G. P.** variety, 3 **G. P.** individuals which flowered in 67 days, and 3 **I. P.** individuals which flowered in 46 days. We tried to take 30 seeds from each of the selected individuals, but some dwarf individuals did not produce the required number of seeds, as in the case of the parents of the last two families No. 44 and 45 in Table 3.

The sowing of the seeds was done on May 5. After the sowing, dry weather prevailed and sprouting was retarded, but on the 23rd and 24th of that month, plantlets appeared evenly.

The results are shown in Table 3. From this table we see that some of the selected early and late F₂ plants produced offsprings whose variation ranges and types strongly suggest that the parent F₂ plants had become constant (homozygous) in their flowering character (Nos. 1-14 in the early; Nos. 36-45 in the late), and the remaining F₂ plants produced offsprings whose variation types are irregular and suggest that they must be offsprings of

variable (heterozygous) parents (Nos. 15–20 in the early; Nos. 21–35 in the late). The variation ranges and means of the would-be constant families descended from the early or the late F_2 are not in exact coincidence with those of the corresponding parent varieties. For example, the variation means of the families No. 1 to No. 4 are very near to, but those of the families No. 5 to No. 14 are larger than, those of **I. P.**, especially that of No. 14. And in the variation types of the variable families, there is much irregularity and complicity; for example, in the variable families from the selected late F_2 , No. 21 and No. 22 vary with the combined ranges of both parent varieties, while other variable families vary with different narrower widths of range.

Thus we see, as Tschermak (1904) already observed, that among those F_2 plants which flowered within the variation range of the early parent variety, as well as among those which flowered within the variation range of the late parent variety, only one part was constant and the other part showed segregation. As to the interpretation of such complicated phenomena, we shall treat it fully later in the present paper.

Experiments Proper with Peas.

For the reason stated in the preceding pages, we selected a new variety for the early parent in the present experiments. A short description of the variety is as follows:—

Half dwarf, 86.02 cm. high (measured in 1910); white-flowered; tough-podded; flowering time about the same as **I. P.**; cultivated for over 10 years in the College Vegetable Garden under the name “Mans”. We shall denote this variety as “**M. P.**”.

We selected some 50 seeds of both **G. P.** and **M. P.** from the stock seeds harvested in 1909 in the sample section of the Garden, and sowed 32 seeds of **G. P.** on Dec. 2, 1909, in a forcing house. From the 9th to 11th of the same month, all the seeds sprouted, and after the plantlets grew to about 2 inches high, one half of them were thinned out. The first sowing of

the **M. P.** seeds (16 in number) was made on Jan. 11, 1910, and the second on the 25th of the same month. From our experience in the raising of the F_2 of the **G. P.** \times **I. P.** cross in the previous winter, we found the above mentioned intervals in the sowing times of the parent varieties to be suitable for crossing. The thinning of **M. P.** was done in the same manner as in the case of **G. P.**

The dates on which first flowers appeared were as follows:—

G. P.			M. P.		
No.	I	Feb. 19	No.	I	Feb. 21
"	XV	" 19	First Sowing	"	2 " 24
"	II	" 20		"	3 " 24
"	XI	" 20		"	4 " 22
"	III	" 24		"	5 " 24
"	X	" 24		"	6 " 23
"	XVI	" 24		"	7 " 24
"	VII	" 25		"	8 " 24
"	IV	March 7		"	9 March 8
"	XII	" 8		Second Sowing	"
"	XIV	" 10	"		11 " 9
"	VI	" 11	"		12 " 9
"	V	" 12	"		13 " 8
"	XIII	" 14	"		14 " 11
"	VIII	" 18	"		15 " 9
"	IX	" 20	"		16 " 9

Here we see again that the variation range of the early variety is quite narrow, while that of the late variety is remarkably wide.

By crossing two varieties, we got 106 seeds in ♀ **G. P.** \times ♂ **M. P.** and 64 seeds in ♀ **M. P.** \times ♂ **G. P.** The cross seeds reached maturity suitable for sowing in the middle of May. So we sowed these cross products together with some seeds of both parents on May 21.

Before recording the flowering times of the hybrid progenies, we shall first treat here the observations on the inheritance of the flowering time in

the parent varieties.

Inheritance of the Flowering Time in the Progenies of the Parent Varieties.

Raising in 1910.

From every plant which was used as a parent of the cross in the forcing house, we collected all pods which had been left untouched and contained self-fertilized seeds. As mentioned above, the sowing of those seeds together with the cross products was done on May 21. Besides, we took 100 seeds of **G. P.** and 50 seeds of **M. P.** from the stock seeds of the Vegetable Garden and sowed them at the same time.

After the sowing of the seeds, dry weather continued, and they germinated unevenly. The first sprouting appeared in May 30, and it continued until the middle of June. In this case, we can not take simply the number of days from sprouting to flowering as the representative value of the flowering time, because the late-sprouted individuals have always the tendency to hasten their flowering on account of a comparatively high temperature. In fact, by examining the flowering time of every individual of the **M. P.** variety in whose offspring we should expect a narrow range and ordinary type of the variation, from the results obtained in the raising of the previous winter, we see that the number of days from sprouting to flowering was always smaller in the later-germinated individuals than in the earlier-sprouted ones. So we adapt the following formula for finding a representative value of the flowering time:

$$\frac{\text{Number of days from sowing to flowering} + \text{that from sprouting to flowering.}}{2}$$

2

By calculating the representative values of all **M. P.** individuals by this formula, and arranging them in a frequency distribution table, we obtained the result which is shown in Table 4. (The designation **L** means a family consisting of 50 plants grown from the stock seeds). In the table, we see small ranges and regular types of variation in all families of the **M. P.** offsprings,

as we had expected.

The frequency distribution of representative values calculated by the above mentioned formula in the **G. P.** offsprings, is shown in the same table. (The designation **C** means a family of 100 plants grown from the stock seeds) Here, we see much irregularity of variation. The offsprings of those plants which flowered early in the forcing house (I. XV. XI. XVI.) flowered distinctly earlier than those of the late-flowered plants (XIV. VI. VIII.). In the family **C**, the variation range is quite wide and there are two distinct classes with a larger frequency (class 50 and 55).

Raising in 1911.

From the plants grown in the previous year, we selected the following individuals:—

2	individuals	from	M. P.	I
"	"	"	"	6
"	"	"	"	12
3	"	"	G. P.	I
"	"	"	"	XII
"	"	"	"	VI
"	"	"	"	VIII
20	"	"	"	C

In selecting these individuals from each family, we took care to choose those which flowered on different dates and which made normal growth. We sowed 30 seeds from each selected individual on May 6. After the sowing, extraordinarily dry weather followed, and during the 3 days from the 15th to the 17th of the month, only a partial sprouting occurred, and afterwards the sprouting stopped almost entirely. So, we were obliged to water artificially on the ungerminated parts. From the 26th of the month they were watered every day. As a consequence, sprouting began to take place from the 31st of the month and continued until the 4th of June.

Here, again, we can not use simply the number of days from sowing to flowering as a representative value of the flowering time. The mode of

sprouting in this year was different from that in the previous year. The sprouting then occurred gradually. In this year, however, we can divide all individuals into two groups, one consisting of those which sprouted during the 3 days from the 15th to the 17th of May, and the other, those which sprouted from the 31st of May to the 4th of June. In Table 5, the frequency distribution of the number of days from sowing to flowering in the two groups is shown. The black-faced types indicate the frequencies of the early-sprouted group.

From Table 5, we can affirm the following facts:—

1. The variation types of all families descending from **M. P.** are alike and uniform.
2. Among the families descending from **G. P.** there are two distinctly different types of variation. All families from I, XII and XVI show the early type of variation, and those from VI and VIII the late type of variation. Among the families from **C.**, the first 12 families are of the early type and the remaining 8 families of the late type.
3. In raising the offsprings of one common grand-parent, we took special care to select those parents plant which differed in their flowering times; and in raising those of **C** family, we selected those parents which flowered in different grades within the variation range of the family. But all families descending from a common grand-parent showed the same type of variation; and the variation types of all families from **C** fell into two distinct categories.

From the facts cited above, it can safely be concluded that the character of the flowering time in peas is a fixed and stable one, and that the population of the **G. P.** variety contains two different pure lines. By assuming the presence of two pure lines in the **G. P.** population, we can easily explain the irregularity and wide range of the variation in the **G. P.** offsprings which we have seen in several previous raisings (Tables 1, 2, 3 and 4).

Raisings of **G. P.** Offsprings in 1912 and 1913.

Though we were quite convinced, from the previous experiments, of the stability of the flowering character, we took care, in the raisings of the **G. P.** progenies for the purpose of comparison with the hybrid progenies, to select those parent plants which differed in flowering times. In Table 6, we show the results of the raisings in 1912 and 1913, in which the stability of the flowering character and the existence of two pure lines are clearly shown.

Inheritance of the Flowering Time in Hybrid Progenies.

F_1 Raising in 1910.

The sowing of the hybrid seeds (106 of **G. P.** \times **M. P.** and 64 of **M. P.** \times **G. P.**; Page 238) was done on the 21st of May. The sprouting of the seeds was so uneven, as to make it necessary to calculate the value of the flowering time of every individual by the formula already mentioned (page 239).

The frequency distribution of the value of the flowering time is as shown in Table 7. From this table, we see the incomplete dominance of lateness in the F_1 , and no difference between the reciprocal crosses.

It was not then known yet that there were two distinct pure lines in **G. P.** population; but as the line of every parent plant was ascertained by the later experiments, we have arranged, in the table, all families into two groups, the early and late lines. By calculating the variation means of both groups separately, we have 47.8 days in the early line group and 49.5 days in the late line group. So the variation mean of the F_1 individuals whose **G. P.** parents belonged to the early pure line, is smaller than that of the F_1 individuals whose **G. P.** parents belonged to the late pure line. This difference of the means in the two groups suggests that the pure line character is inheritable in itself.

As to the morphological characters of the F_1 plants, the color of all of the flowers was red; the height of the stem was not just intermediate, but rather inclined towards, that of **G. P.**, the average height of 100 F_1 plants being 158.8 cm., while that of **G. P.** and **M. P.** was 184.48 cm. and 86.02 cm.

respectively; and the tough-poddedness seemed apparently to dominate over the soft-, but by measurement we could ascertain that the thickness of the scleren-chymatous tissue of the F_1 plant was intermediate, being 81μ , while in **G. P.** and **M. P.** it was 51μ and 100μ respectively ¹⁾.

F_2 Raisings.

In 1911.

From the F_1 plants of the previous year, the following individuals were selected:—

I × 1.2	VIII × 12.1
I × 1.3	THI × 12.4
I × 1.4	VIII × 12.5
4 × XVI.2	12 × VIII.1
4 × XVI.4	13 × VIII.2
4 × XVI.6	

30 seeds from each selected individual were sown on May 6, but, on account of the extraordinary dryness of the weather, uneven sprouting was caused (page 240). In Table 8, group **A** includes the offsprings which had for one of their parents an early pure line individual of **G. P.**, and group **B**, a late pure line individual of the same variety. Each of the groups **A** and **B** is differentiated into two sub-groups, according to the earliness or lateness of the sprouting.

In 1912.

As the sprouting of the F_2 plants in 1911 had been too uneven, we renewed the raising in order to obtain the variation type in the F_2 with normal sprouting. For this purpose, we raised the progenies of the following F_1 plants.

XVI × 3.2	3 × XVI.1
XVI × 3.3	3 × XVI.2
XVI × 3.4	

1) For these measurements the author is indebted to Mr. R. Matsubayashi.

To our regret, no seeds of the F_1 plants which were crosses of the late pure line of **G. P.** had been kept. Sown on May 7, sprouting took place evenly during the three days from the 17th to the 19th of the same month. The frequency distribution of the number of days from sowing to flowering in this raising is as shown in Table 8 **C**.

Chief Results Obtained from the Above Two Raisings of F_1

1. By summing up the frequencies of every class perpendicularly in every group of Table 8 and comparing the sums thus obtained with one another, we find in **A₁**, **B₂** and **C**, the minimum frequency classes (page 234) in the middle between the variation ranges of the parent varieties, 50 in **A₁**, 65 in **B₂** and 53 in **C**. In **A₂** and **B₁** groups, on account of the small number of individuals, it is rather difficult to locate this class, but judging from the position of the class in **A₁** and **B₂**, and comparing actual number of frequencies in every class, we may safely fix this class in **A₂** at 62, and in **B₁** at 52. Thus, we see that the values of the minimum frequency classes of **A₁** and **A₂** are smaller than those of **B₁** and **B₂**. That is to say, the minimum frequency class in the variation of the families descended from the crosses with the early pure line of **G. P.** is situated earlier than that of the families descended from the crosses with the late pure line of **G. P.** This indicates that the pure line character is hereditary. Now, if we examine again Table 2, we may conclude that **G. P. II** and **G. P. V** belonged to the same pure line (probably to the late flowering pure line), because we do not recognize there any difference in the location of the minimum frequency classes among the families of $II \times 13$, $16 \times II$ and $V \times 17$, $20 \times V$.
2. When we divide all individuals of every family into two groups, the early flowering and the late flowering, taking the minimum frequency class as the demarkation line, we see that in the early group the white-flowered individuals are more numerous than the red-flowered ones, and in the late group the number of the white-flowered ones is remarkably small.

This fact coincides with what we have seen in Table 2.

3. Keeble and Pellew (1910) from their experiments, concluded that there might be a gametic coupling between stem characters and flowering character. In the present experiments, we could not find the existence of such a correlation. In general, the later the flowering, the thicker the stem and the longer the internode. For example, by exact measurement of the length of the internode of every F_2 individual of the raising in 1912, taking those which appeared to be representative in the length of the internodes in the individual plant, we got the following results:—

Length of internode of M. P. plants	6.0—7.5 cm.
” ” ” ” G. P. plants	9.5—11.0 cm.
” ” ” of F_2 plants in classes 46, 47 & 48.	{ none shorter than 7.5 cm. none longer than 9.5 cm. majority 9.0 cm.
” ” ” of F_2 plants in classes 49, 50 & 51.	{ none shorter than 8.5 cm. majority 9.0 cm.
” ” ” of F_2 plants in the late group	{ none shorter than 9.0 cm. majority 10.5—12. cm.

Thus, the actual results in the present experiments suggested strongly the relation between the stem characters and flowering time to be only a physiological one.

F_3 Raisings.

In 1912.

The sowing was done on May 7, taking 30 seeds from each individual of the following families:—

1×1.4	} Crosses with the early flowering pure line of G. P.
$4 \times XVI.2$	

VIII × 12.1	}	Crosses with the late flowering pure line of G. P.
VIII × 12.4		
12 × VIII.1		
12 × VIII.2		

Sprouting began on the 17th and ended on the 19th of the month. There were a few which sprouted after the 20th, but the flowering dates of such delayed individuals were not recorded. As already mentioned, from this year the experiments were carried on in the nursery ground.

In Tables 9 and 10, Pls. XII—XIV, we show the frequency distribution of the F_3 raisings of the year 1912, arranging all families according to the similarity to their variation types. The white dots indicate the white-flowered individuals and the black dots the red-flowered ones.

In 1913.

In 1913, the F_3 offsprings of the families XVI × 3.2; XVI × 3.3 and 3 × XVI.2 were raised. The seeds were sown on May 9, and sprouting took place during the 3 days from the 21st to the 23rd of the month.

The results of this raising are shown in Table 11, Pls. XV—XVI.

Chief Facts from F_3 Raisings.

In the F_3 raising of 1910 (Table 3) where only the progenies of those F_2 individuals were raised which flowered within the variation ranges of the parent varieties (page 236), we have seen that there were several types of variation of would-be constant (homozygous) and variable (heterozygous). Now in the present F_3 raisings, where the progenies of almost all individuals of each of the selected F_2 families were grown, we see greatly complicated variation types, and can here again distinguish two types of variation, the constant and variable.

At first, we shall treat of the constant families. In Table 9 (Pls. XII and XIII), 19 families, from No. 1 to No. 19, are what might be taken as constant. Judging from the variation modes and means of these constant families, Nos. 1, 2 & 3 seem to be the *early constant* families, having the characteristics

of **M. P.**, and No. 19, *the late constant*, equivalent to **G. P.** Other families are more or less different from those of the parent varieties, but none are transgressive, being all intermediate between the parent varieties. Among these intermediate constants, No. 4 is very near to the early constant, and Nos. 16—18 to the late constant. We shall designate such families as *pseudo-early* and *pseudo-late constants* respectively. Other remaining intermediate constants are to be classified into two groups. Nos. 5—10 are to be grouped together as the *early intermediate constant*, and Nos. 11—15 as the *late intermediate constant*. And it will be seen that the F_2 parent individuals of all families of the former group belonged to the early flowering group and those of the latter group to the late flowering group. (Compare parent classes of these families and minimum frequency classes in Table 7)

In Table 10 (Pl. XIV), Nos. 1 and 2 are considered early constant and No. 3 pseudo-early constant. The 5 families, Nos. 12—16, have the variation types very similar to that of **G. P.**, only 2 of them (No. 12 and No. 13) have a few individuals which flowered a little earlier than **G. P.** and may be designated as the pseudo-late constant. All other intermediate constants are to be classed into two groups just as in the case above mentioned. The 5 families, Nos. 4—8, all descending from the early flowered F_2 plants, are considered as belonging to the early intermediate constant, and the 3 families, Nos. 9—11, descending from the late flowered F_2 plants, as belonging to the late intermediate group. Thus, the mode of distribution of constant families is quite similar in both Table 9 and Table 10, but in the variation types of constant families, there is some difference between them. The variation types of the early constant and the early intermediate constant families in both Tables do not differ much from each other, but the late intermediate constant and the late constant families in Table 9, where the late pure line of **G. P.** was one of the parents, take a distinctly later position than those in Table 10 where the early pure line of **G. P.** was one of the parents. This indicates very clearly the hereditary difference of the two pure lines of **G. P.** From the similarity of distribution of constant families, how-

ever, we can safely assume that the hereditary difference of the pure line character is qualitative rather than quantitative. In other words, if the heredity of flowering time may be interpreted by the Mendelian factor theory, the number of factors from both pure lines is not different, but the quality of factors is different.

In Table 11 (Pls. XV and XVI) the would-be constant families are comparatively few. There are no early constants. Only one case is met with in each of the late and the pseudo-late constants (Nos. 11 and 10 respectively). Among the intermediate constants, the 7 families from No. 1 to No. 7 appear to belong to the early intermediate group. The variation types of these families are not all similar, and the difference among them is not so wide as to divide them again into different groups. Two families, No. 8 and No. 9, have a peculiar variation type. From the position of the variation range, they may be considered as late intermediate constants, but from the type of frequency distribution they suggest rather that they are families variable within a narrow range. Their intrinsic nature must be determined, however, only by the actual raising of the F_4 offsprings (see Table 15).

Next, we shall dwell on the variable families. From the general characters of the variation types we may take 79 families, from No. 20 to No. 98, in Table 9, 38 families, from No. 17 to No. 54, in Table 10 and 73 families, from No. 12 to No. 84, in Table 11, as variable families. For the sake of easy comparison, they are arranged according to the similarity of the variation types. The following may be enumerated as remarkable facts.

1. None of the families which are the progenies of those F_2 individuals which belonged to the early flowering group (No. 20 to No. 44 except 32, 33, 37, 39 and 41 in Table 9; No. 17 to No. 27 in Table 10; No. 12 to No. 32 in Table 11) have variation ranges which reach the variation range of **G. P.** Some vary only within the combined range of the early constant and the early intermediate constant, and the others within the combined range of the early constant and the late intermediate constant.
2. Among the families descended from the late-flowered F_2 individuals,

there are only 6 families which vary like the above mentioned families (No. 32, 33, 37, 39 and 41 in Table 9, and No. 33 in Table 11). It is quite probable that the F_2 parent plants of these 6 families belonged to the early flowering group genetically, but for some cause their flowering time had been so retarded as to make them fall into the late flowering group.

3. The variation ranges of all other variable families descended from the late-flowered F_2 parents reach the variation range of **G. P.** Some vary from the range of **M. P.** to that of **G. P.**, as in the case of the F_2 families; some vary within a combined range of the early intermediate constant and **G. P.**, while some show such a narrow variation range as to begin from that of the late intermediate constant.
4. There are a few exceptional families descended from the late-flowered F_2 individuals, whose variation ranges do not reach that of **G. P.** but only that of the pseudo-late constant families (No. 60, 62, 67, 71 and 77 in Table 9, No. 34, 35, 47, 56 and 57 in Table 11).
5. Comparing the variation types of all variable families in Table 9 with those in Table 10 and Table 11, we did not find any difference in character between them. So, again, we can assume that the hereditary difference of the pure line character is qualitative and not quantitative.

F₄ Raisings.

In 1913.

This year, as it needed a comparatively large area for raising the F_3 , the results of which had already been shown in Table 11 (Pls. XV and XVI), and as the available space was limited, only the F_4 progenies of the following F_3 families in Table 10 (Pl. XIV) were grown, as preliminary raisings:—

No. 8	(I × 1.4.3)	(A)
No. 18	(I × 1.4.4)	(B)
No. 45	(I × 1.4.14)	(C)
No. 43	(I × 1.4.9)	(D)
No. 50	(I × 1.4.13)	(E)
No. 38	(I × 1.4.2)	(F)

The results are shown in Tables 12 and 13.

Table 12, **A**. The parent family of this raising was one of the families designated as the early intermediate constant. Now it is proved actually that this latter designation was well chosen. The variation types of all families are almost equal, in correspondence with the assumption that the F_2 grand-parent might be constant, and their variation means situated nearer to that of **M. P.** rather than in the intermediate position between **M. P.** and **G. P.**

Table 12, **B**. The parent family of this raising varied within the combined range of **M. P.** and the early intermediate constants; and within the range, there was a minimum frequency class, which makes it possible to divide the individuals into two groups, the early and late flowering. Now, in the table, it will be seen that all families descended from the early flowered parents (No. 1 to No. 6) show the variation type of the constant families which are very near to that of **M. P.** (pseudo-early)¹⁾, and among the families descended from the late flowered parents, there are two types of variation, one varying just like the early intermediate constant (from No. 21 to No. 25), the other varying within the combined range of the pseudo-early and early intermediate constants, exactly like the parent family. These facts suggest strongly that the F_2 grand-parent was monohybrid, being heterozygous in the determiners of the early (pseudo) flowering time and of the early intermediate flowering time. The ratios of the early constant, the variable, and the early intermediate constant families are 6 : 14 : 5, quite close to the expected ratios 1 : 2 : 1.

Table 13, **C, D, E, F**. All four parent families of the raisings shown here varied from the range of the early intermediate constant to that of the pseudo-late constant or of the late constant, and their variation types were all similar, having vacant classes near the middle of the range, which makes it possible to divide all individuals into two groups, the earlier and the later flowering. Now, in the actual raisings of the F_4 families, we see that all

1) One F_3 individual which flowered in 47 days produced too small a number of seeds and was discarded for the F_4 raising.

TABLE 12.—Frequency distribution in F_4 (1913)

Designation	Parent class	Class Centers																		Means of Constants										
		43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60		61	62	63	64	65	66	67	68	69	70
M. P. 4				43	15	16	1	2														1	2		13	21	35	11		45.75
G. P. 1																														67.41
A Table 10, No. 8 (IX-14.3)	1 (1)	51								5	7	8	4																	52.46
	2 (3)	51							1	3	8	6	2	1																52.38
	3 (4)	51								1	9	7	3	1																53.10
	4 (6)	50									5	10	3	1																52.33
	5 (7)	50									6	8	6	3																52.00
	6 (8)	50									12	8	5	1																51.85
	7 (9)	51									2	12	6	2																52.84
	8 (11)	50									3	18	4	2																52.61
	9 (13)	51									9	14	4	4																52.55
	10 (14)	50									9	14	4	4																52.10
	11 (15)	51								1	5	11	6	3																52.19
	12 (16)	51									6	10	9	9																52.41
	13 (17)	52									3	8	8	4																52.67
	14 (18)	53									5	13	5	1																52.24
	15 (20)	49									3	11	8	5																52.54
	16 (21)	50									12	11	2	4																51.60
	17 (22)	51									4	10	7	7																53.81
	18 (23)	51									4	10	7	7																52.58
	19 (24)	51								1	11	12	5	5																51.72
	20 (25)	49									6	14	5	2																52.11
	21 (27)	50									3	12	8	2																52.44
	22 (28)	51									13	10	2	2																51.56
	23 (29)	52									3	13	10	1																52.55
	24 (30)	51									12	13	1	1																51.70
																													av. 52.34	
B Table 10, No. 18 (IX-14.4)	1 (8)	46			3	16	5	2	1																				47.33	
	2 (22)	46		1	12	15	8	5																					47.13	
	3 (12)	46			4	15	8																						47.15	
	4 (27)	46			4	16	7	3																					47.30	
	5 (19)	47			2	14	6	8																					47.07	
	6 (5)	48			5	8	9	3																					47.50	
	7 (10)	49			1	3	2	2																					av. 47.25	
	8 (16)	49				4	2	2																						
	9 (18)	50				1	7	2																						
	10 (4)	50				1	1	1																						
	11 (9)	49				2	2	3																						
	12 (20)	49				4	2	2																						
	13 (28)	52				3	3	3																						
	14 (2)	50				3	4	2																						
	15 (6)	51				4	6	5																						
	16 (13)	50				2	4	2																						
	17 (23)	51				2	3	2																						
	18 (25)	50		1		2	4	2																						
	19 (3)	51				3	1	1																						
	20 (24)	51				2	3	1																						
	21 (17)	49				3	3	1																						
	22 (15)	49				7	18	4																					51.07	
	23 (1)	50				1	19	5																					50.90	
	24 (14)	50				1	19	7																					51.30	
25 (26)	53				4	10	13																					51.38		
																												51.45		
																												av. 50.12		

* No. in bracket indicates parent No.

TABLE 13.—Frequency distribution in F_4 (1913)

Designation	Parent Class	Class Centers																		Means and Ratios.										
		43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60		61	62	63	64	65	66	67	68	69	70
M. P. 4				43	15	16	1	2															1	2		13	21	35	11	45.75
G. P. 1																														67.41
C Table 10, No. 45 (IX-14.14)	1 (12)	50							4	17	7	1																	51.17	
	2 (24)	52							4	17	3																		52.08	
	3 (5)	52							1	10	12	3																	51.78	
	4 (8)	58							1	5	1	4																	av. 58.68	
	5 (11)	57								5	1	4																		
	6 (9)	58								5	1	4																		
	7 (15)	57								1	3	4																		
	8 (22)	58								1	3	4																		
	9 (23)	58								1	3	4																		
	10 (28)	56								3	1	1																		
	11 (6)	58								2	2	3																		
	12 (3)	56								1	2	2																		
	13 (7)	57								2	2	2																		
	14 (1)	56								2	2	2																		
	15 (27)	59								2	2	2																		
	16 (26)	57								2	2	2																		
	17 (18)	58								1	2	1																		
	18 (13)	57								6	10	6	3																61.69	
	19 (20)	57								5	5	4	10																62.75	
	20 (21)	58								1	4	5	10																63.04	
	21 (19)	58								2	6	10	2																63.08	
	22 (30)	58								5	9	9	2																	

parent individuals, which belonged to the early flowering group, produced the early intermediate constant families; and among the later flowered parent individuals, some produced the late or pseudo-late constant families, and some produced families which have almost equal variation types to those of the parent families. Here again, we see the variation types of segregation in the progenies of a monohybrid parent, and we can safely conclude that the F_2 grand-parents were monohybrids, being heterozygous in the determiners of the early intermediate flowering time and of the late or pseudo-late flowering time. By comparing the variation means of the constant families of four different F_4 progenies, however, we must assume that their F_2 grand-parents were more or less different in the flowering character genetically. There is no practical difference between the variation means of both the earlier and later constant families in **E** and **F**, but the variation means of both the earlier and later constant families in **D** are smaller (earlier) than those of both constants in the former two raisings, and the variation means of the earlier constant families in **C** are larger (later) than that in **D**, while the variation means of the later constants are almost equal to that in **D**.

In 1914.

For this year, as more space was available for the experiment than in the previous years, we selected the following 15 families raised in 1913 (Table 11, Pls. XV and XVI):—

No. 13 (XVI × 3.2.13) (G)	No. 79 (XVI × 3.3.12) (O)
No. 20 (XVI × 3.3.24) (H)	No. 76 (3 × XVI.2.11) (P)
No. 22 (XVI × 3.2.30) (I)	No. 82 (3 × XVI.2.30) (Q)
No. 4 (XVI × 3.3.6) (J)	No. 83 (XVI × 3.2.1) (R)
No. 7 (3 × XVI.2.6) (K)	No. 37 (XVI × 3.2.29) (S)
No. 8 (XVI × 3.2.2) (L)	No. 41 (3 × XVI.2.23) (T)
No. 58 (3 × XVI.2.4) (M)	No. 57 (3 × XVI.2.27) (U)
No. 73 (XVI × 3.35) (N)	

The sowing was done on May 4. A heavy drought followed the sowing and prevented the normal, even sprouting of the seeds. The first sprouting took place on the 14th of the month and continued gradually until the 6th of June.

In consequence of very uneven sprouting, irregularity in the flowering time followed. So we discarded all individuals which sprouted after the 24th of May, and selected those which had sprouted within the 10 days from the 14th to the 23rd of May. We calculated the representative value of their flowering times, by using the formula proposed already (page 239). The results thus obtained are shown in Table 14—18.

Table 14.

G and **H**. The parent families of the two raisings varied between the ranges of the early constant and early intermediate constant. Now we see in this table the same variation types as in Table 12 **B**, suggesting the former to be the variation type of the segregation in the offsprings of a monohybrid parent which was heterozygous in the determiners of the early flowering time and early intermediate flowering time.

I. The parent family of this raising had a similar variation type to the parent families of the above 2 raisings **G** and **H**, and the general types of variation in **I** are also similar to those shown in the case of **G** and **H**. In the present case, however, there is only one later constant family whose variation means is larger than the average means of the later constant families in **G** and **H**, suggesting it rather to be a late intermediate constant. Thus we may assume that the F_2 grand-parent of **I** raising was a monohybrid which is heterozygous in determiners of the early flowering time and the late intermediate flowering time. It is quite remarkable that in the variable families of **I** raising, the white-flowered individuals are distinctly numerous toward the early part of the range, while in those of **H** raising (family Nos. 6, 7, 8, 9, 12, 13, 14 and 17) the distribution of white-flowered individuals is uniform.

Table 15.

J. The parent family of this raising was one of the early intermediate constants, but its variation type was rather different from the other related constants. Its maximum frequency was in the class 50. In class 51 there

were no frequencies, but in classes 52 and 53 the frequencies increased. In **J** we see that the variation types of all families are not so uniform as we have seen in Table 12 **A**. The 18 families, from No. 1 to No. 18, are very similar in their variation types, but the remaining 8 families have different variation types. The variation means of the latter are greater than those of the former. From this we can assume that the F_2 grand-parent plant was not constant in a strict sense, but somewhat variable in its nature.

K. The parent family of this raising was also one of those which were to be designated as the early intermediate constants. Its variation range was wider than that of the parent family of **J**. Its maximum frequency class was 51, one day later than in the case of the parent family of **J**. By examining Table **K**, however, we can assume that the wider range of variation in the parent family was not genetic but environmental, because the variation types of all the families in **K** are narrower in range and very similar to one another, suggesting genetical constancy of the F_2 grand-parent plant. But the difference in the position of the maximum frequency class in the parent families of **K** and **J** might have genetic meaning, because the average variation means in the **K** raising is larger (later) than that of the majority of the families in **J**. From this inequality of the variation means in both raisings, we have to conclude that all F_3 families, which we have designated as the early intermediate constant, are not equal genetically.

L. The parent family of this raising, together with the family No. 9 in Table 11 (Pl, XV), had a peculiar variation type (see page 248). They were very likely to be the families which vary within the combined range of the early intermediate and the late intermediate constant, having their maximum frequency class in the latter constant. Now, by the actual raising of F_4 progenies, we see:—

1. All F_4 families are more or less different in variation type, suggesting that the F_2 grand-parent was not a strictly constant one,
2. All families, however, vary only within the combined range of the previous two raisings (**J** and **K**), suggesting that the occurrence of the maxi-

imum frequency class in the parent family later than in the parent families of **J** and **K** was not genetic but environmental, i. e. the flowering times of almost all individuals grown in one row were retarded by some surrounding condition, probably by the soil property of that row. (It is remarkable that the flowering times of two families, No. 68 and No. 83 in Table 11, which were grown in the two rows next to the present family, appeared also to be retarded, especially that of No. 68, whose variation range exceeded the variation range of **G. P.** in its upper end. But by raising F_4 offsprings of this latter family, it was found that this retarding in flowering was not genetic, see Table 17 **R.**).

Table 16.

M, N and **O**. In all three raisings shown in the present table, we meet with the variation types of segregation in offsprings of a monohybrid grandparent, producing three kinds of families, the earlier constant families, the later constant families, and the families variable within the combined range of the above two constants, just as we have seen in Table 13. According to our classification of constants, the earlier constants in this table must be of the early intermediate, while the later constants must be of the pseudo-late or late constant. The variation means of the later constants in all three raisings are very similar, but those of the earlier constants are more or less different, being in **M** the earliest, in **N** the medium, and in **O** the latest. The order of difference in the variation means in the present cases corresponds with the order of the difference in the beginning of the range in the F_3 parent families (see Table 11). This indicates that each of the F_2 grand-parent plants of the above three raisings contained a different determiner for the earlier constant character (early intermediate constant).

Table 17.

P. Here again we meet with the variation types of the monohybrid segregation. The parent family of this raising varied in a range earlier

than that of **O** in the previous table, but the earlier constant families of the present raising vary in a later range compared with **O**. It is probable that the parent family of **O** was retarded in its flowering time, as in the case of the parent family of **L**.

Q and **R**. The variation types of the present two raisings are also of the monohybrid segregation. The earlier constants among them are to be classified as the late intermediate constant, and the later constants have almost equal variation means as **G. P.** and are to be classified as the true late constant. The parent family of **R** (No. 83 in Table 11) varied in a later range compared with that of **Q** (No. 82), but in the table we can see practically no difference in variation between **Q** and **R**. So we can assume that the parent family of **R** was retarded in its flowering time, together with its neighbours (Families No. 8 and No. 68), probably by the soil property of the row.

Table 18.

S and **T**. The parent families of the 2 raisings varied within the combined range of **M. P.** and **G. P.**, as in the case of the F_2 families. Now, by raising the F_4 progenies, we obtained types of variation similar to the F_3 raisings shown in Tables 9, 10 and 11. There are early constants (No. 1 in **S**, Nos. 1 and 2 in **T**), pseudo-early constants (No. 2 in **T**), early intermediate constants (Nos. 3, 4 and 5 in **T**), late intermediate constants (Nos. 3, 4, 5 and 6 in **T**), and late constants (Nos. 6 and 7 in **S**, No. 7 in **T**). The rest are all variable families. Those descended from the F_3 individuals which were to be grouped as the early flowering, do not vary so widely as to reach the range of **G. P.**, while those which descended from the late flowering group vary in different grades of width of the variation range. (See pages 248 and 249) From these facts we may safely conclude that the F_2 grandparent plants of **S** and **T** were equal, or nearly so, in flowering character as the F_1 hybrid plant. And it is noticeable that the late constant in **S** has larger variation means than that in **T**, while the parent family of **S** varied more widely than that of **T** in the upper end of the range.

U. The parent family of this raising had a variation type somewhat similar to that of the parent family of **M** in Table 16, but the variation types in the F_4 progenies are quite different in these two raisings. The variation types in **U** are quite similar to those in **S** and **T**, except in the non-presence of the early constant. So we may assume that the F_2 grand-parent of this raising was similar to the F_1 hybrid plant in zygotic character, but in its F_3 offsprings did not produce any early constant individual.

Interpretation of the Experimental Results.

In the foregoing pages, we have recorded the results of our experimental work extending over eight years, and we now think that there has been accumulated sufficient material to enable us to propose an interpretation of the inheritance of the flowering time in peas.

In the first place, let us propose a hypothesis, and then let us apply it for the explanation of the results of our experiments, and see how far this hypothesis may work true. The hypothesis consists of two clauses.

1. The inheritance of flowering time in the varieties of peas which were used in the present experiments, is governed by two Mendelian alleromorphic pairs, each factor of which has a specific hereditary effect as follows:—
 - A** determines the proper flowering time of the late parent.
 - B** determines flowering a few days earlier than the proper time of the late parent and is hypostatic to **A**.
 - a** alleromorphic to **A**, determines the proper flowering time of the early parent and is epistatic to **b**.
 - b** alleromorphic to **B**, determines the flowering a few days later than the proper flowering time of the early parent.
2. Gametic contamination is caused by hybridization.

Two-factor Hypothesis and Experimental Results.

According to the proposed two-factor hypothesis, F_2 families must con-

TABLE 14—Frequency distribution in F_4 (1914)

Designation	Parent Class	Class Centers																																			Means and Ratios	
		31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65		
M. P.			1	2	11	7	9	13	7		1																											35.84
G. P.																																					56.72	
Table 11, No. 13 (XVII-32-13)	1 (3)	45		2	11	5	5	2	2	1	1																										35.31	
	2 (4)	45		2	4	1	3	1	1	1	1																									35.80		
	3 (9)	45	3	1	5	4	3	5	5	2																											35.31	
	4 (19)	45		6	3	3	5	5	2																												35.44	
	5 (24)	45		4	5	4	5	5	5	2																											35.44	
	6 (26)	45		4	4	5	4	5	5	7																											36.00	
	7 (27)	45		4	4	6	5	6	3	2																											35.00	
	8 (10)	48		4	4	4	6	3	2																												36.04	
	9 (7)	49			3	1		6	6																												av. 35.54	
	10 (21)	49				1		1	2	1																												
	11 (25)	49		1		1		4	2	2																												
	12 (28)	49				1		4	2	1																												
	13 (30)	50				4		2	1	2																												
	14 (17)	50				1		1	2	1																												
	15 (14)	50				1		1	2	2																												
	16 (1)	50				1		3	3	1																												
	17 (16)	52				2		2	3	3																												
	18 (2)	51				2		2	2																													
	19 (29)	50																																				
	20 (6)	51																																			41.41	
	21 (8)	51																																			42.04	
	22 (11)	51																																			43.80	
	23 (18)	51																																			42.52	
	24 (22)	51																																			40.91	
	25 (13)	50																																			40.58	
	26 (12)	50																																			43.89	
	27 (5)	50																																			44.26	
	28 (20)	52																																			42.75	
																																				45.34		
																																					av. 43.68	
Table 11, No. 20 (XVII-33-24)	1 (5)	45		2	8	6	14	2	3		1																									35.32		
	2 (8)	45		3	1	12	3	3	2																												36.35	
	3 (26)	45		2	2	7	4	5	3																												35.21	
	4 (20)	45			1	1	4	3	3																												35.96	
	5 (14)	47				1	5	3	5																												37.32	
	6 (1)	49				1	1	3	2																												av. 36.05	
	7 (6)	49				1	1	1	1																													
	8 (10)	49				1	1	1	1																													
	9 (22)	49				1	1	1	1																													
	10 (27)	49				1	1	1	1																													
	11 (16)	50				1	1	1	1																													
	12 (12)	50				1	1	1	1																													
	13 (15)	50				1	1	1	1																													
	14 (11)	50				1	1	1	1																													
	15 (9)	50				1	1	1	1																													
	16 (7)	50				1	1	1	1																													
	17 (4)	52				1	1	1	1																													
	18 (18)	53				1	1	1	1																													
	19 (28)	53				1	1	1	1																													
	20 (3)	49				1	1	1	1																													
	21 (19)	49				1	1	1	1																													
	22 (20)	49				1	1	1	1																													
	23 (21)	50				1	1	1	1																													
	24 (17)	50				1	1	1	1																													
	25 (13)	52				1	1	1	1																													
	26 (30)	53				1	1	1	1																													
	27 (2)	53				1	1	1	1																													
	28 (25)	52				1	1	1	1																													
	29 (23)	52				1	1	1	1																													
																																				av. 42.70		
Table 11, No. 22 (XVII-32-30)	1 (7)	45		1	2	5	2	3	2		1																									36.37		
	2 (13)	45		1	4	3	4	1	2		1																									37.05		
	3 (14)	45		1	1	1	1	1	1		1																											
	4 (23)	45		1	1	1	1	1	1		1																											
	5 (24)	45		1	1	1	1	1	1		1																											
	6 (30)	45		1	1	1	1	1	1		1																											
	7 (29)	47		1	1	1																																

TABLE 17.—Frequency distribution in F_4 (1914)

Designation	Parent Class	Class Centers																																			Means of Constants	
		31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65		
M. P.			1	2	11	7	9	13	7		1																											
G. P.																								5	11	10	11	10	7	10	1		3	2	1			
A Table 11, No. 76 (3×XVI.2.11)	1 (22)	54											3	5	3	4	1	3	1			2																45.46
	2 (26)	54											3	2	1	3	4	3	6	1	2		1														46.78	
	3 (14)	56											2	1	2	4	4	8	1	1		1															46.83	
	4 (10)	56											4	1	2	4	6	3	2	1	1																46.14	
	5 (15)	57												7	2	2	2	2	2																		45.23	
	6 (24)	59												3	3	3	4	1	1																		45.07	
	7 (29)	61												2	4	2	3	7	2																		46.48	
	8 (27)	62													1	1		2	2			1	1	3	4	3	6	1	1	2	1					av. 46.00		
	9 (5)	62												3	1		1	1			4	4	4	3	2	2	1											
	10 (4)	63												1	1		1	1	2	2	2	5	4	3	2	2	2	1										
	11 (6)	63												1	1		1	1	1	1	1	2	2	3	2	6	2	1										
	12 (7)	63												1	1		2	2	2	2	2	2	4	2	2	2	2	1	1	1								
	13 (8)	63													1							2	2	2	2	2	2	2	1	1	1							
	14 (16)	63												1				2	2	2	1	1	2	4	4	1	3	3	3	1	1							
	15 (17)	63														1		2	2		1	2	2	5	5	1	1	1	1	1								
	16 (19)	63													2	2	1	1	1	1	1	2	2	8	5	1	2	2	1	1								
	17 (20)	63												3	2	1	1	1	1			3	2	2	1	5	2	1	1	3								
	18 (13)	65												1			1	2	2	1	1	1	3	3	1	3	3	1	1	1								
	19 (11)	65														1	1	1	1	1	1	1	3	8	1	5	3	3	1	1								
	20 (3)	66												2	2	1	1	2	1	1		7	4	3	1	1	2	2	1									
	21 (21)	64																			1	4	10	2	3	1	2	2	1	2	1							
	22 (23)	62																				2	6	6	6	3	2	1	1	2	1							
	23 (1)	62																					3	1	7	7	6	1	1	1	1							
	24 (9)	63																					7	2	2	2	2	1	1	1	1							
	25 (25)	63																					10	2	4	5	2	1	6	1	1							
	26 (28)	63																					5	9	4	6	1	1	2	2	1							
	27 (2)	65																					4	4	5	10	3	1	1	1								
	28 (12)	67																					2	5	4	4	3	3	4	1	1							
																																				av. 54.09		
B Table 11, No. 82 (3×XVI.2.30)	1 (30)	58														3	3	4	3	2	2	6	2													49.18		
	2 (17)	60														2	3	3	2	2	4	4	8															
	3 (16)	60														1	2	5	6	4	4	5	3	1	1													
	4 (11)	60														1	1	2	2	2	2	8	3	1	1													
	5 (1)	60															1	2	2	5	4	5	1	1	1	3	5											
	6 (3)	65													1	1						4	4	4	5	3	2	4	1									
	7 (5)	65																				3	1	1	6	2	2	4	1	2	1							
	8 (8)	65																				1	7	5	2	2	1	1	3	1								
	9 (28)	66																				2	4	1	8	2	1	2	1	1	3							
	10 (10)	66																				1	2	2	4	3	3	1	1	1	1							
	11 (18)	68																					4	1	2	3	5	4	8	1	1							
	12 (13)	69																				2	2	2	2	1	1	1	1	1	2	1						
	13 (21)	66																					4	1	2	5	2	2	2	1	1							
	14 (25)	66																					2	7	4	2	4	2	2	1	1							
	15 (12)	69																					1	4	2	3	3	1	1	1	1							
	16 (19)	65																					1	1	10	7	4	1	2	1	1							
	17 (23)	66																					1	6	4	4	1	1	4	2	3	1						
	18 (24)	66																					1	2	3	6	5	1	2	3	1							
	19 (15)	66																					2	4	9	4	3	1	1	1	1							
	20 (26)	66																					3	6	6	4	4	3	3	3	2	1						
	21 (27)	66																					3	2	6	4	4	1	5	1	1							
	22 (22)	67																					1	2	2	2	4	2	2	2	4							
	23 (7)	66																					1	1	2	2	3	2	2	8	3	1						
	24 (29)	70																						3	4	4	1	1	2	2	3	1						
	25 (2)	65																						2	2	4	2	3	4	3	3	1						
	26 (9)	67																						4	4	4	2	3	3	3	3	1						
	27 (14)	69																						6	5	3	3	1	3	4	3	1						
	28 (20)	69																							9	4	4	3	4	4	1	2						
	29 (4)	69																							1	1	3	1	4	4	2	4						
																																				av. 57.57		
C Table 11, No. 83 (XVII×3.2.1)	1 (7)	59													1	1	2	2	6	5	5	1	1												49.38			
	2 (24)	60													1	1	2	2	4	5	2	6	3	2	1													
	3 (29)	61														3	1	3	3	5	4	5	4	2	2													
	4 (8)	62														1	1	1	1	3	4	4	6	3	2													

tain the following 9 different zygotic series, 5 heterozygous and 4 homozygous.

Homozygous		Heterozygous	
1 aabb	} Early flowering group	2 aabB	} Early flowering group
1 aaBB		2 aAbb	
1 AAbb	} Late flowering group	4 aAbB	} Late flowering group
1 AABB		2 aABB	
		2 AAbB	

Among the 5 heterozygous series, **aAbB** has the same zygotic constituent as F_1 , and its flowering time must incline towards that of the late parent rather than intermediate between those of both parents (page 233 and 242); **aABB** and **AAbB**, which have become partly homozygous on account of the introduction of a factor from the late parent, must flower later than **aAbB**; **aabb** and **aAbb**, which have become partly homozygous by the introduction of one factor from the early parent, must flower earlier than **aAbB**. Two homozygous series, **aabb** and **AABB**, have the same zygotic constitution as the early and the late parent respectively. As we have seen in F_1 that the dominance of lateness was incomplete, the following assumption on the flowering time of the remaining two homozygous series, **aaBB** and **AAbb**, is quite probable. **aaBB**, which is homozygous in the earlier determiners from both parents, may flower earlier, inclining towards the early parent, while **AAbb**, which is homozygous in the later determiners from both parents, may flower later, inclining towards the late parent.

In actual raisings of F_2 families, we could always divide the individuals into two groups, the early flowering and the late flowering, by taking the minimum frequency class, which was at a nearly intermediate position between the parent varieties, as a line of demarkation. Now in the proposed hypothesis, we assume that the early flowering group consists of four series, **aabb**, **aaBB**, **aabB** and **aAbb**, and the late flowering group, of the remaining five series, **aAbB**, **aABB**, **AAbB**, **AAbb** and **AABB**. The ratio of the number of individuals in the former four series to those in the latter five series

must be 6 : 10. The ratio of the actual numbers in the early flowering group to those in the late flowering group is as follows:—

	Early group	:	Late group	
Table 2	112	:	259	
Table 8 A ₁	25	:	72	
Table 8 A ₂	26	:	43	
Table 8 B ₁	13	:	29	
Table 8 B ₂	32	:	64	
Table 8 C	50	:	90	
Sum	258	:	557	
Ratio	6	:	12.9	

The actual ratio exceeded the expected one, but this discrepancy is not so great as to be inadmissible. It is quite probable that such a discrepancy should occur, because, in the actual condition of plant raising, the hastening in flowering is rather rare, but its retardation is of very common occurrence, caused by environmental influences, both physiological and mechanical.

According to the present hypothesis, there must be, in the F₃ raisings, four kinds of constant families, **aabb**, **aaBB**, **AAbb**, and **AABB**. In Tables 9, 10 and 11 (Pls. XII—XVI), we were able to group constant families into four types,—the early constant, the early intermediate constant, the late intermediate constant, and the late constant (see page 247), except a comparatively few families, which we have designated as the pseudo-early or pseudo-late constant, and also two abnormal families, No. 8 and No. 9 in Table 11. The early constants might correspond to **aabb**, the early intermediate constants to **aaBB**, the late intermediate constant to **AAbb**, and the late constant to **AABB**, and the pseudo-early and the pseudo-late constants might be considered as contaminated early and late constants respectively. We shall discuss the two abnormal families, No. 8 and No. 9 in Table 11 later on.

In the F₃ variable families descended from the heterozygous F₂ plants, which belong to the early flowering group, we should expect two different variation types, the types of the progeny of **aabB** and of that of **aAbb**. The

type of the progeny of **aabB** should be that of the progeny of a monohybrid, varying between the early constant (**aabb**) and the early intermediate constant (**aaBB**), while that of the progeny of **aAbb**, being also of a monohybrid type, should vary between the early constant (**aabb**) and the late intermediate constant (**AAbb**). There should not occur any individuals which flower in the same period as the late constant. In actual F_3 raisings, we have seen that none of the variable families descended from the early flowered F_2 plants produced such a wide variation range as to reach the range of **G. P.** (page 248). It is quite difficult to divide all variable families from the early flowered F_2 plants into two distinct categories according to their variation types, as the actual variation types shown in Tables 9, 10 and 11 are too complicated and irregular. But we may say, that this difficulty in distinguishing two types of variation does not positively conflict with the proposed hypothesis, because we are concerned with experiments on such a physiological character as the flowering time, which even in homozygous progenies varies somewhat, according to environmental influences.

Among F_3 variable families descended from the late flowered heterozygous F_2 plants, we should expect three different types of variation, that of the progeny of **aAbB**, which varies from the early constant to the late constant, as in F_2 family; that of **aABB**, which, being of a monohybrid type, varies between the early intermediate constant and the late constant; and that of **AAbB**, which is between the late intermediate constant and the late constant. In Tables 9, 10 and 11, it is difficult to divide sharply all variable families descended from late flowered F_2 plants into three types, but it is certain that there are some families which represent each of the three expected types.

The upper end of the variation ranges of all F_3 variable families descended from the late flowered F_2 plants reaches the range of **G. P.** except a few cases as described in (2) and (4) on pages 248 and 249. Among these exceptional families, those described in (2) we have regarded already as the progenies of F_2 individuals which were in the early flowering group genetically but fell into the late group, owing to some environmental influences, and as

for those described in (4), we shall try to interpret them later on, by the contamination hypothesis.

So far as variation types are concerned, we could interpret approximately all experimental results in the F_3 raisings by the proposed two-factor hypothesis, admitted that some gametic contamination did take place. Now, we shall consider the numerical ratios among F_3 families assumed to be in different zygotic constitutions. As it is quite difficult to distinguish clearly between the progenies of **aabB** and **aAbb**, of **aAbB** and **aABB**, and of **aABB** and **AAbB**, we shall take the progenies of **aabB** and **aAbb** as one group (variable families descended from the early flowered F_2), and those of **aAbB**, **aABB** and **AAbB** as another (variable families from the late flowered F_2). The ratios between four constants and two groups of variables in Tables 9 and 10 are as follows:—

	aabb ¹⁾	aaBB	AAbb	AABB ²⁾	Early group variables	Late group variables
Table 9	4	6	5	4	25	55
Table 10	3	5	3	5	11	27
Sums	7	11	8	9	36	82
Actual Ratios	0.8	: 1.3	: 1.0	: 1.1	: 4.5	: 10.2
Expected Ratios	1	: 1	: 1	: 1	: 4	: 8

Here we do not see much difference between actual ratios and expected. In Table 11, however, we meet with a very singular distribution of constant families. There are only two families of the late constant, the early constant being entirely absent; while there are seven families of the early intermediate constant (No. 1—No. 7), and two families (No. 8 and 9) with peculiar variation types. To attribute to chance such a deviation of actual distribution from the expected, seems to be rather conventional, but to deny absolutely that such a deviation might occur by chance may be dogmatic. So, we believe that

1) Including "pseudo-early"

2) Including "pseudo-late"

the occurrence of such deviation does not militate against proposed two-factor hypothesis.

We shall next examine the experimental results in F_4 raisings. The variation types of **C**, **D**, **E** and **F** in Table 13, and **M**, **N** and **O** in Table 16 can be interpreted if we assume that the F_2 grand-parents were **aABB** in their zygotic constitution, taking gametic contamination as an admitted fact (pages 251 and 254). In the same way, we can assume **B** in Table 12 and **G** and **H** in Table 14 to be the variation types of the offsprings of **aabB** (pages 250 and 252); **I** in Table 14, of **aAbb** (page 252); **P**, **Q** and **R** in Table 17, of **AAbB** (page 254); and **S**, **T** and **U** in Table 18, of **aAbB** (page 255). **A** in Table 12 and **K** in Table 15 indicate the homozygosity of their F_2 grand-parents (the early intermediate constant **aaBB**). The variation types **J** and **L** in Table 15 might be interpreted as those of the progenies of the homozygous **aaBB**, if we assume that their F_2 grand-parents by gametic contamination produced such offsprings as vary within a small range.

Gametic Contamination.

It has been affirmed by the pedigree raisings of the parent varieties from 1910 to 1913, that the character of the flowering time was quite fixed and unchangeable in the parent varieties. (Tables 4, 5, 6) From this fixedness of the flowering character it should be expected, according to the common Mendelian interpretation, that all families descended from those individuals which had the same zygotic constitution, would produce the same variation type. But our actual experimental results do not fulfil this expectation, as long as we keep the proposed two-factor hypothesis.

In the F_3 raisings, there has been frequent occurrence of the pseudo-early and pseudo-late constants. Such is not admissible on the two-factor hypothesis when gametic purity is retained. We took **B** in Table 12, as variation types of the segregation of **aabB**, but the variation means of all six earlier constant families are larger than that of **M**. **P**. The variation types of four raisings, **C**, **D**, **E** and **F** in Table 13 and of three raisings, **M**, **N** and **O** in

Table 15 can be nothing but those of the segregation of **aABB**, according to the proposed hypothesis. Comparing the variation types of both earlier (would-be **aaBB**) and later (would-be **AABB**) constants of these raisings, however, we see some difference among them. From the variation types of **J**, **K** and **L** in Table 15, we can not take the F_2 grand-parents of these raisings as other than those with the zygotic formula **aaBB**, but within the variation types of the above three raisings we find complicated phenomena. The variation means of the majority of families in **J** are smaller than those of all families in **K**, and the variation types in **L**, in general, remind us of those types which fluctuate between two different early intermediate constants in **J** and **K**.

Now we are in a position to decide which is reasonable, to maintain the proposed two-factor hypothesis and to accept the occurrence of gametic contamination, or to assume gametic purity and propose the other hypothesis for the interpretation. Frequent occurrence of the distinct variation types of the monohybrid segregation in F_4 raisings disproved positively that the inheritance of flowering time is non-Mendelian. If the inheritance be Mendelian, more than one factor must be concerned. To propose a new interpretation other than the two-factor hypothesis, it is necessary to suppose the presence of more than two-factors. To assume the presence of more than three factors, however, conflicts with the actual results. The actual numbers of the early constant families are too great, as one would expect in case more than three factors were concerned. In Table 3, two families, Nos. 3 and 4, which had descended from the F_2 plants, flowered in 45 days, had almost equal variation means and ranges as **I. P.** (early constant), and two out of the three families (1, 2 and 11) which had descended from the F_2 plants, flowered in 46 days varied like **I. P.** It might be concluded that all F_2 individuals which had flowered in 45 days, and some of those flowered in 46, were early constant. In Table 2, there are 8 individuals flowered in 45, and 7 flowered in 46, and it might be assumed that in the F_2 raising there were present more than 10 early constant individuals among 372. Such a large number would not be

expected on the more-than-three-factor hypothesis, as, on the four-factor hypothesis, there is expected only one early constant individual among 254. In Table 9, there are three early constant and one late constant families (excluding the pseudo-early and-late) among 101 families (less than $254/2$), and in Table 10, 2 early constant and 3 late constant families among 54 families (far less than $254/4$). And moreover, by examining the variation types shown in Tables 9, 10 and 11, one will readily be convinced of the fact that the variation types are much too simple for those of F_3 progenies whose parents had more than three alleromorphic pairs.

If we assume the presence of three factors, there are two ways of interpretation; (1) supposing that all three factors have the same hereditary effect, and (2) supposing that each of the three factors has a different hereditary effect. On the former assumption, there must be 4 kinds of constant families as shown in the following zygotic formula:—

$$\begin{array}{cccc}
 \text{I} \left\{ \begin{array}{l} \text{I} \text{ aabbcc} \end{array} \right. & \text{II} \left\{ \begin{array}{l} \text{I} \text{ AAbbcc} \\ \text{I} \text{ aaBBcc} \\ \text{I} \text{ aabbCC} \end{array} \right. & \text{III} \left\{ \begin{array}{l} \text{I} \text{ AABBcc} \\ \text{I} \text{ aaBBCC} \\ \text{I} \text{ AAbbCC} \end{array} \right. & \text{IV} \left\{ \begin{array}{l} \text{I} \text{ AABBCC} \end{array} \right.
 \end{array}$$

If we assume gametic purity, even on the above hypothesis, we should expect only 4 distinct constants and can not interpret the occurrence of the pseudo-early and pseudo-late constants in the F_3 raisings and of those constant families whose variation means are located in various places between the variation means of the parent varieties in F_4 raisings. If gametic contamination be granted, our two-factor hypothesis explains the facts obtained by our experiments far better than the three-factor hypothesis.

If we attribute a different hereditary effect to each of the three-factors, there must be 8 different constant families in F_3 raising. This conflicts with the fact that we could group the intermediate constant families into only two, the early intermediate and late intermediate, in Tables 9 and 10, especially in the former. And the variation types of the variable families in F_3 and F_4 raisings are too simple to be interpreted on this hypothesis. If we deduce,

from the zygotic series¹⁾ in F_2 , various variation types in F_3 and F_4 and compare those types with the actual variation types in F_3 and F_4 raisings, one will readily see that the two-factor hypothesis is more probable than the three-factor hypothesis.

As a natural outcome of the foregoing discussion, we are convinced that our proposed hypothesis of the presence of two alleromorphic pairs and of the occurrence of gametic contamination is the most reasonable interpretation of the inheritance of the flowering time in peas. To explain the nature and cause of contamination is difficult in such experiments as those on the inheritance of flowering time. But it is certain that the contamination in our case at least is not "inconstancy" in the sense of Castle (1912). In each of the F_4 raisings which showed the variation types of monohybrid segregation, all earlier constant families had almost the same variation means and ranges and also all later constant families had uniform variation types. This indicates gametic constancy in the F_2 grand-parents. The hypothesis of the presence of a secondary determiner or determiners might be maintained to some extent. If we assume that the gametes from an early parent carry with primary factors (**ab**) some secondary determiner or determiners which act on the factors from a late parent as an agent or agents having the power to hasten flowering time to a slight extent, and that those from the late parent carry a secondary determiner or determiners, acting on the primary factors from the early parent as a retarding agent or agents, we can explain the occurrence of both pseudo-early and pseudo-late constant families. The variation types in **J** and **L** in Table 14 can be interpreted if we assume that their F_2 grand-parents were homozygous in the primary factors (**aaBB**) but heterozygous in

1)	Constant	Monohybrid	Dihybrid	Trihybrid
	1 aabbcc	2 Aabbcc	4 AaBbcc	8 AaBbCc
	1 AAbbcc	2 aaBbcc	4 aaBbCc	
	1 aaBBcc	2 aabbCc	4 AabbCc	
	1 aabbCC	2 AaBBcc	4 AaBbCC	
	1 AABBcc	2 AabbCC	4 AaBBCc	
	1 AAbbCC	2 AABbcc	4 AABbCc	
	1 aaBBCC	2 AAAbCc		
	1 AABBCC	2 aaBbCC		
		2 aaBBCc		
		2 AABBCc		
		2 AABbCC		
		2 AABbCC		
		2 AaBBCC		

the secondary determiner or determiners. The difference of variation types between **D** and **E**, in Table 13 (see page 251), and **P** and **Q** in Table 17 (page 255) can be understood, if we assume that the F_2 grand-parents of **D** and **P** become homozygous in the earlier secondary determiner or determiners, while those of **E** and **Q** become homozygous in the late secondary determiner or determiners. But the variation types of **M**, **N** and **O** in Table 15 are not to be explained by a simple assumption of the presence of a secondary determiner or determiners, as each of the above three raisings has its own proper variation types in earlier constant families, while the variation types of the later constant families are uniform in all three raisings. We hope, by further experiments, to be able to cast a clearer light on this contamination hypothesis.

On Transgressive Inheritance.

Throughout our experiments with peas and also with rice, we did not find a single case of transgressive inheritance. On the proposed two-factor hypothesis, however, we might expect the occurrence of such an inheritance. In the crosses between the late and early constant, or between either of these two constants and either of two intermediate constants (the early intermediate and the late intermediate), we can not expect any transgressive inheritance, but when we cross two intermediate constants (**aaBB** and **AAbb**) we should expect transgressive inheritance to take place. To state it in general terms, transgressive inheritance occurs oftener in the case of crosses between the varieties with narrower difference of character than in the case of crosses between those with wider difference. From the address of Nilsson-Ehle at the Fourth International Conference of Genetics held in Paris, 1911, we find, although he did not state it in so many words, that among his several cross breeds in wheat and oats, those breeds which were the descendants of the crosses between the varieties with comparatively wider difference in their precocity did not show transgressive variation, while those descended from the crosses between the varieties with narrower difference did. Even a cross

between the varieties with the same precocity produced very clearly the transgressive inheritance (see pp. 142-147 of *Comptes Rendus et Rapports de la Conference*). We are now conducting experiments on crosses among derivative constants, hoping in the near future to have the pleasure of publishing the results.



II. EXPERIMENTS WITH RICE

The varieties of rice which can be grown in Sapporo, where the late frost ceases late in May and the early frost begins about the beginning of October, must be those which have extraordinary precocity. We have only a few varieties suitable for cultivation here. They are all local varieties specially bred. The difference of the ripening period among these varieties is quite insignificant. They flower and ripen at about the same time. Even the earliest varieties in southern Japan do not ripen in the vicinity of Sapporo.

In April 1907, the author procured a variety of rice, known by the name of **Kuro-Bozu**, through the kindness of Mr. S. Kato of Kinai Substation of the Imperial Agricultural Experiment Station near Osaka. We sowed the seeds in pots in a forcing house at the beginning of May, and after one month removed the pots into a glass house. But the shooting of its ears had delayed so much as to make it impossible for us to execute crossing between it and any of the local varieties. But we succeeded in the next year, 1908, in producing their hybrids.

Material Used and Experimental Methods.

1. Late flowering parent :— Variety name ; **Kuro-Bozu** (we shall denote it as **K. P.**) ; a variety of *Oryza glutinosa* ; awnless ; tip of glumes black and with black striations on ridges of stalk.
2. Early flowering parent :— Variety name **Akagé (A. P.)** ; one of the local varieties of *Oryza sativa* ; with reddish brown awn ; stalk without black striations.

Our experiments were carried on in a glass house. We used zinc pots 24 cm. in diameter and 35 cm. in height. In the three years,—1908, 1909 and 1910, the pots were filled with the soil from a paddy field, but from 1911 on, we filled them with fine river sand, adding a suitable quantity of artificial fertilizers. At first, 5 plants per pot were grown, but afterwards, 10 plants per pot. The space in the glass house available for the present experiments

was limited, and could accommodate 50 pots only; therefore we could not raise more than 500 individual plants each year.

Because it is difficult to record the time of flowering in the rice plant, we took a record of the time when the first spikelet appeared above the ligule of the sheath (shooting time) as the representative period of precocity. Mr. S. Kato, who has had much experience in the pollination of rice, informed the author that the rice plant is not absolutely self-pollinizing and that natural crossing often occurs. So we took care to envelope with paper bags all ears from which we were intending to take seeds for further raisings.

F₁ Raisings.

In 1909

As the result of the crosses between **K. P.** and **A. P.** in the previous year, we got 9 grains in ♀ **K. P.** × ♂ **A. P.** and none in ♀ **A. P.** × ♂ **K. P.** On the 7th of May, we soaked the nine hybrid seeds with some of both parents in a forcing house. When the plantlets began to grow, we planted them in pots and put them in the glass house.

The number of days from soaking to shooting was as follows:—

K. P. × A. P.		K. P.	A. P.		
Pot I	No. 1...92	Pot III	No. 1...115	Pot IV	No. 1...86
	No. 2...93		No. 2...115		No. 2...80
	No. 3...94		No. 3...116		No. 3...82
	No. 4...94		No. 4...112		No. 4...85
	No. 5...93		No. 5...108		No. 5...85
Pot II	No. 1...89	Av.113.2	Av.....83.8		
	No. 2...99				
	No. 3...95				
	No. 4...100				
	Av.....94	Average of the parents = 98.5			

From this result, we see that the shooting time of the hybrid F₁ is intermediate between those of both parents, but inclining rather towards that of the early parent. This inclination is in the opposite direction in the case of F₁ in pea hybrids (pages 233 and 242).

In 1910.

In the previous year, besides the raising of F₁, we made crosses again and got 6 hybrid grains in ♀ **K. P.** × ♂ **A. P.** and 7 grains in ♀ **A. P.** × ♂ **K. P.** We sowed these grains on May 18 directly in pots. There was one grain which failed to sprout in each of the reciprocal crosses, but we had 11 F₁ plants which came to maturity. The number of days from sowing to shooting of the F₁ plants and of the offsprings of the parents was as follows:—

Hybrid F ₁		Parents			
Pot No. 49	A. P. × K. P. 1...111 days	Pot No. 47	A. P. 1...90	Pot No. 48	K. P. 1...122
	" 2...105		" 2...90		" 2...119
	" 3...104		" 3...91		" 3...122
	" 5...102		" 4...90		" 4...121
	" 6...98		" 5...88		" 5...126
	" 7...102		" 6...88		" 6...126
	" 7...88		" 7...122		
Pot No. 50	K. P. × A. P. 1...98	Av..... 89.2	Av.....122.5		
	" 2...103	Av. of parents.....105.8			
	" 3...103				
	" 4...102				
	" 6...103				
Av.	102.8				

From the above results, we see that there is no difference between reciprocal crosses, and that the shooting time in F₁ is intermediate, inclining toward that of the early parent.

On the Inheritance of Morphological Characters.

1. Awn: Awned dominated awnless in F₁. The dominance of the awned character over the awnless in the rice hybrids is widely known to the circle of Japanese experimenters, but, as far as we know, this seems not yet to have been published in any scientific paper. It is interesting to notice that in wheat the awnless character is dominant, but in rice the opposite is true.

2. Colour: Black colour of **K. P.** dominated F₁ and all F₁ plants had black awns and black striations on stalk.

3. Endosperm character: The distinction between *Oryza sativa* and *O. glutinosa* is based only on the difference of their endosperm character. The endosperm of the former contains common starch, while that of the latter contains a kind of dextrin. By husking, we can easily distinguish two kinds of endosperm at a glance. Husked grains of *O. sativa* present a light brownish and glassy appearance, and those of *O. glutinosa* a whitish and opaque appearance. We took one ear from every F_1 plant, husked all grains and examined their endosperm characters. In every ear there were two kinds of grains and the ratio of *sativa* grains to *glutinosa* grains was approximately 3 : 1. These facts show that in the endosperm of rice there appears *xenia* as in the case of maize. The starch character dominates the dextrin character and these characters segregate according to the simple Mendelian law.

At this point, the author wishes to take the liberty of claiming *his priority in investigation on the existence of the immediate effect of pollen on the rice endosperm*. Having been interested in the fact that the rational interpretation of the occurrence of *xenia* in grains of some cereal crosses, such as in maize and rye, had become possible by the discovery of double fecundation by Nawaschin (1898) and Guignard (1899), the author made two crossings of rice, ♀ *glutinosa* × ♂ *sativa*, one in a green house of the College Botanic Garden in May 1901, and another in a paddy field in August of the same year. In the former crossing, he got 6 hybrid grains and in the latter, 12 hybrid grains. As these crossings were executed by cutting off the upper part of the glumes, and as the hybrid grains were exposed to the air, their color had become so darkened that it was impossible to distinguish by outward appearance whether their endosperms were starchy or of dextrin. So the hybrid grains were cut and soaked in iodine solution. All hybrid grains turned violet just as in the case of the grains of *sativa*, while self-fertilized *glutinosa* grains changed to brown color. It showed perfectly the presence of *xenia* in the rice endosperm, and the author published this result in a Japanese journal, the Journal of the Sapporo Agricultural Society, Vol. III, pp. 90-92, April, 1902. As the author left Sapporo for America and Europe

the following year, further experiments on this interesting subject were not carried out. In 1905, Moquette's paper appeared and confirmed the author's observations.

F₂ Raising.

In 1910, the pressure of other work prevented the sowing of the seeds from the F₁ plants of the previous year at the same time with the cross grains on May 18, and we were obliged to sow them 10 days later. Adopting the method which is followed by practical farmers when the sowing has been delayed, we sowed all the grains after husking them. Germination was not bad, but many of the young plantlets were injured by mould and some were killed. So the F₂ raising of 1910 did not give any reliable results.

In 1911, we took 43 pots filled with river sand and sowed 20 seeds in each pot. After the young plants had grown 2 inches, half of them were thinned out. During the experiments, 5 pots, Nos. 4, 28, 30, 34 and 36, began to leak and could not be mended. So those plants which were grown in these pots were discarded. When **K. P.** began to shoot, a lowering of the temperature evidently affected the vegetative force of the plant. Therefore the variation range of the shooting time in **K. P.** became far wider than that in **A. P.**

Table 19 shows that the F₂ offsprings varied within the combined range of **A. P.** and **K. P.**, and there was no transgressive variation. By summing up the number of individuals in each class, we get the minimum frequency class (104), midway between the variation ranges of **A. P.** and **K. P.**, and can divide all individuals into two groups, the early-shooting and late-shooting, as we divided the early-flowering and late-flowering in the F₂ of pea hybrids. But in the present case, where the shooting period of F₁ inclined toward that of the early parent, there were a greater number of individuals in the early group than in the late group (220 : 120); while in the case of peas, where the flowering period of F₁ inclined toward the late parent, the number of individuals was greater in the late group than in the early group. (Tables 2

and 8)

Tschermak records in Fruwirth's "Züchtung der landwirtschaftlichen Kulturpflanzen" Vol. 4, (2 Auf.) pp. 176, 238 and 314, that in wheat, barley and rye, the early ripening character seems to be partially dominant, and in Table 39 of Emerson and East's work (1912) on maize, we see that there is a minimum frequency class within the variation ranges of the two F_2 progenies (1127) and (1128), and the number of individuals in the early flowering group is greater than that in the late flowering group. From these facts, we venture to propose that, in cereals, incomplete dominance of the early ripening may be a law. We did not forget to observe the relation between morphological characters and shooting time in the F_2 , but could not find any correlation between them, as we had seen in the case of peas between the flowering time and the colour of their flowers.

F_3 Raising.

From 80 offsprings of **K. P.** \times **A. P.** 1 (Table 19), we selected 46 individuals with different shooting dates, and raised 10 F_3 offsprings of each individual, together with 20 individuals of each parent variety. In this year, the lowering of the temperature during the shooting time of **K. P.** was greater than in the previous year. Consequently, the shooting of **K. P.** individuals occurred slowly, and one of them and three of hybrid F_3 individuals (in families 35, 45 and 46) did not eventually shoot.

The frequency distributions of the number of days from sowing to shooting is shown in Table 20. From this table, we can not draw any definite conclusion, except that there occurred four families, Nos. 1, 2, 45 and 46, which produced variation types quite similar to that of either of the parent varieties, suggesting that their F_2 parents had returned, in shooting character, to the original parents.

F_4 Raising.

From the result of the F_3 raising in the previous year, we were convinced

that it would be rather impossible to expect any definite interpretation of the inheritance of shooting character in rice, by raising such a small number of F_4 individuals as 500. But hoping that we might reach some interesting conclusion by comparing the results obtained in rice with those in peas, we took four F_3 families, Nos. 4, 5, 10 and 16 (Table 20), which showed some similarity in variation types and selected 23 individuals from them, taking care to select those which were different in shooting dates. Twenty offsprings of each selected plant were raised.

As the shooting of **K. P.** was too late in the two previous years, the sowing of the seeds was done in wooden boxes placed in a forcing house on April 20. After the temperature in the glass house had become high enough for rice, the plantlets were transplanted in pots. In spite of this precaution, the plants did not shoot early, because of the unusually low temperature which prevailed during the summer, and which caused an almost total failure in the paddy culture in the vicinity of Sapporo. In our raising, **A. P.** came to shoot a little later than in the previous two years, and **K. P.** did not shoot at all, even in the glass house. Five individuals of the family No. 5 of **C** Table 21, also failed to shoot.

Table 21 shows the results of this F_4 raising. F_2 grand-parents of two raisings of **A** and **B** appeared on the same day and their F_3 parent families varied in a similar type, but in the present table their variation types are not similar. Those of **B** suggest strongly monohybrid segregation, family No. 2 being an earlier constant, families Nos. 3 and 7 later constants, and the three families, Nos. 5, 1 and 10, variable between two constants. In **A**, the variation types are quite different. There is one family which seems to be a constant (No. 6). And the variation types of the remaining variable families are not those which would be expected in monohybrid segregation. In both raisings of **C** and **D**, we see also variation types of non-monohybrid segregation.

Interpretation.

By comparing the experimental results in rice with those in peas, we see

a parallelism between them to some extent. The flowering time (shooting time in rice) of the first generation of a hybrid was not just intermediate between parent varieties. It inclined towards one of the parents, in peas towards the late parent and in rice towards the early parent. In F_2 , the variation range extended within the combined ranges of both parents, having the minimum frequency class in the middle. When all F_2 individuals were arranged into two groups, the early flowering and the late flowering, using the minimum frequency class as a demarkation line, the group towards which F_1 inclined contained a greater number of individuals than the other group,—in the rice the early group and in peas the late group. In F_3 raisings of rice hybrids, there appeared few families which seemed to be constant, though the distribution of these apparently constant families was not similar to that in the peas, and in F_4 raisings we had one case of variation types closely suggesting those of monohybrid segregation (**B** Table 21).

From the above cited facts, we may safely assume that the inheritance of the shooting character in rice is not different from that of the flowering character in peas in its underlying principle and is interpretable by the multiple-factor hypothesis. But the two-factor hypothesis which was proposed for the interpretation of the inheritance of the flowering time in peas is not applicable in the case of rice, because of the following two facts.

1. The actual number of F_2 individuals which seem to be in the same zygotic constitution as the original parents is much smaller than would be expected on the two-factor hypothesis. From actual results in F_3 raising, we might assume those F_2 individuals which shot forth within the variation range of the late parent as the late constant, and those which shot forth during the two days, 88 and 89, as the early constant. The actual number of the former is 4 and that of the latter 5, while the expected number of each of the early and late constant on the two-factor hypothesis is $340/16=21.2$.

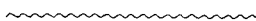
2. According to the two-factor hypothesis, all variable families in F_3 have to be divided into two categories, monohybrid segregates (descendants of **aabB**, **aAbb**, **aABB** or **AAbB**) and dihybrid segregates (descendants of

aAbB, same as F_1). From the results of the raising of F_4 offsprings of those F_3 families such as No. 4 and No 5 of Table 20 which could be assumed, from their parent classes and their variation types, not to be descendants of F_2 having the same zygotic constitution as F_1 (**aAbB**), we should expect variation types of monohybrid segregation only. In the actual F_4 raisings, however, this expectation was not fulfilled. In Table 21, the variation types in **B** suggest those of monohybrid segregation, but those in **A** are too complicated to be regarded as monohybrid segregation.

Then, by assuming the three-factor hypothesis, can these facts be explained? Although our experiments were conducted on too small a scale to supply enough material for a discussion of this subject, so far as our experiments go, the three-factor hypothesis does not conflict with actual results. As we have noted above, among 340 F_2 individuals (Table 19), 5 which shot forth during the two days 88 and 89, might be taken as the early constants and 4 which shot forth within the variation range of the late parent, as the late constants. These numbers of both early and late constant F_2 individuals are in admirable correspondence with the calculated number 5.3 (340/64), according to the three-factor hypothesis. The variation types of **A** and **B** in Table 21, which were not conceivable on the two-factor hypothesis, are quite acceptable on the three-factor hypothesis, when we take F_2 grand-parent of **B** as monohybrid such as **aabBcc**, **aabbC**, or **aAbbcc**, (see foot notes on page 264), and that of **A**, as a dihybrid such as **aabBcC**, **aAbbcC** or **aAbBcc**.

Here we wish to propose the three-factor hypothesis for the interpretation of the inheritance of the shooting character in the rice varieties which we have used in our present work.

Owing to climatic conditions in Sapporo, experiments on a sufficiently large scale were not possible by the author, but he hopes at some future date, with the co-operation of some investigator in southern Japan, to obtain more conclusive results.



III. ON THE GAMETIC COUPLING BETWEEN FLOWERING TIME AND FLOWER COLOUR IN PEAS.

Lock (1904 and 1905) noticed in his experiments with pea hybrids the correlation between white flowers and early flowering, red flowers and late flowering. Afterwards Tschermak (1910) saw the same correlation in his experiments. But neither tried to explain this correlation genetically. Throughout the present experiments we also have noticed this correlation. In all F_2 families, there was excess of white-flowered to red-flowered individuals in the early flowering group, but in the late flowering group, on the contrary, a very small number of white flowers was present (Tables 2 and 8). In variable families of F_3 and F_4 raisings, the same phenomenon prevailed, except in a very few cases. We shall consider now whether this correlation may be interpreted on the hypothesis of gametic coupling or not.

For the interpretation of the inheritance of the flowering time in peas, we proposed two alleromorphic pairs, **a, A** and **b, B**. If we assume that one character is determined by two Mendelian factors, our method of treatment must be different from that in the cases of gametic coupling hitherto investigated. We must consider at first, whether the flower colour couples exclusively with either one of the two factors, or independently with each of them, or whether the coupling takes place when two-factors are present together in the gametes. Studying carefully the distribution of different coloured individuals throughout the experimental results, we are quite convinced, that the latter two assumptions must be abandoned. By assuming that the factor for red colour couples with the more powerful factor **A** from the late parent, all the observed results can be adequately explained. We shall show in the following paragraphs the possibility of this interpretation.

If we assume gametic coupling between the factor for red colour and the factor **A** for flowering time on the 7 : 1 basis, we should expect a distribution of whites and reds in the two flowering groups of F_2 families as follows:—

Early flowering group		Late flowering group	
	W. R.		W. R.
1 abab	$= 7+1 \times 7+1 = 49 : 15$	1 ABAB	$= 1+7 \times 1+7 = 1 : 63$
2 abaB	$= 2(7+1 \times 7+1) = 98 : 30$	2 ABAb	$= 2(1+7 \times 1+7) = 2 : 126$
2 abAb	$= 2(7+1 \times 1+7) = 14 : 114$	2 ABaB	$= 2(1+7 \times 7+1) = 14 : 114$
1 aBaB	$= 7+1 \times 7+1 = 49 : 15$	1 AbAb	$= 1+7 \times 1+7 = 1 : 63$
		2 ABab	$= 2(1+7 \times 7+1) = 14 : 114$
		2 AbaB	$= 2(1+7 \times 7+1) = 14 : 114$
<hr/>			
Sums	210 : 174	:	46 : 594
Ratios	4.6 : 3.8	:	1 : 12.9

Counting the numbers of whites and reds in actual F_2 raisings, we get the following results:—

	Early flowering group		Late flowering group	
	white	red	white	red
Table 2	64	48	12	247
Table 8 A 1 ...	14	11	7	65
A 2 ...	19	7	3	40
B 1 ...	10	3	0	29
B 2 ...	24	8	5	59
C	26	24	8	82
<hr/>				
Sums	157	101	35	522
Ratios	4.5	: 2.9	: 1.0	: 14.9

These observed ratios are sufficiently close to the expected ones. Next, when we take some of the F_3 families (Tables 9—11, Pls. XII—XVI), which vary from the early constant to the late constant and which are assumed to be the progenies of F_2 plants, whose zygotic constitution might be **aAbB**, and when we examine the distribution of different coloured individuals in each of them, we get the following results:—

	Early flowering group		Late flowering group		
	white	red	white	red	
Table 9	Family 45	6	2	3	19
	„ 46	6	5	5	14
	„ 47	5	8	0	13
	„ 48	6	5	1	14
	„ 59	7	7	0	12
	„ 50	4	5	0	19
	„ 51	0	8	6	13
	„ 52	8	5	1	16
	„ 54	4	6	4	16
	„ 56	6	5	0	14
	„ 57	6	4	0	17
	„ 58	5	4	1	20
	„ 69	7	7	2	14
„ 60	6	1	0	16	
„ 61	7	1	0	18	
Table 10	Family 28	8	4	2	15
	„ 29	8	6	3	12
	„ 30	4	7	0	18
	„ 31	6	7	0	16
	„ 32	7	4	0	19
	„ 33	4	5	1	19
	„ 34	9	4	1	14
	„ 35	9	5	1	13
	„ 37	1	10	2	18
Table 11	Family 34	3	2	1	23
	„ 35	4	5	2	18
	„ 36	3	5	2	18
	„ 37	3	4	5	17
	„ 38	8	1	9	12
	„ 41	9	0	1	16
	„ 42	5	3	4	17
	„ 43	5	2	1	21
	„ 44	9	4	1	14
	„ 45	6	2	4	19
„ 46	1	4	5	17	
„ 47	4	1	3	22	
	Sums	199	158	71	593
	Ratios	2.8	2.2	1.0	8.4

In the above table, we meet with so large a number of whites in the late flowering group, that, when we take it as the unit and calculate ratios, the result differs much from the expected. By considering, however, that on account of environmental influences the retarding of the flowering time is of common occurrence and that some individuals belonging to the early group genetically may very often fall thereby into the late group, we may take the number of reds in the early group as the unit and calculate ratios. Then we get the following ratios:—

	Early group		Late group	
	W.	R.	W.	R.
Observed	1.3	1.0	0.45	3.8
Expected	1.2	1.0	0.26	3.3

Here, except whites in the late group, the ratios are quite close to the expected.

Thus, our proposed gametic coupling is practically confirmed, but before we draw a definite conclusion, we have to prove the following two propositions:—

1. Non-presence of the correlation in F_3 and F_4 variable families, which are the descendants of the F_2 plants which have become homozygous in the factor **A** or **a** (**aabB** or **AAbB**).
2. The occurrence of the zygotic series 49 : 15 : 15 : 177 in F_3 and F_4 variable families which are the descendants of the F_2 plants heterozygous only in the factor **A** (**aAbb** or **aABB**).

(1) As we have already noted on page 259, the distinction between the supposed **aabB** families and the supposed **aAbb** families in F_3 raisings (Tables 9, 10 and 11) is not clear, but by careful examination of the variable families descended from the early-flowered F_2 plants, we see that those families which have relatively narrow ranges of variation and which suggest the progenies of **aabB** parents, have uniform distribution of white-flowered individuals and indicate non-presence of the correlation (families, Nos. 26, 27 and 28 in Table 9; Nos. 19, 20, 21 and 22 in Table 10; No. 20 in Table 11). In Table 14 **H**, where the results of the raising of F_4 progenies of the family No. 20 Table

11 are shown, we see again uniform distribution of whites in variable families (page 252). Family No. 21 in Table 11 appears to conflict with the present hypothesis, because the distribution of whites in it is quite uneven, while from its parent class and variation type we have to assume it to be progeny of **aabB**. On the other hand, we may also assume it to be the progeny of **aAbb**, deducing from the example of the similar typed family No. 22 which are shown to be the segregates of **aAbb** by raising F_4 progenies (Table 14).

Among those F_3 families which are to be taken as the segregates of **AAbB**, the majority are homozygous red. Only one family, No. 81 of Table 11, which is variable in colour, has uniform distribution of whites. No. 79 of Table 11 seems to be the segregates **AAbB**, but by F_4 raising it was proved to be those of **aABB** (Table 16 O).

(2) According to the proposed hypothesis, F_2 plants which were homozygous in the factor **B** or **b** but heterozygous in the factors **A** and **a** and also in colour, must produce such F_3 families which have the following distribution of different coloured individuals.

Early group (earlier constants)		Late group (variables & later constants)	
white	red	white	red
49	15	15	177

And when we raise F_4 progenies of these F_3 families, there must appear the same distribution of different coloured individuals in variable families.

As the variation types of the supposed **aAbb** segregates in F_3 raising in 1913 (Table 11) are irregular and do not allow us to distinguish two groups, the early flowering and the late flowering, by taking a definite minimum frequency class, we shall take only Tables 9 and 10, and examine the distribution of different coloured individuals in those families which suggest the segregates of **aAbb**.

		Early group		Late group	
		white	red	white	red
Table 9 (Min. Fr.=48)	Family 31	7	0	1	20
	„ 32	6	5	0	18
	„ 33	8	1	1	20
	„ 34	7	1	2	20
	„ 35	3	1	2	13
	„ 36	4	1	0	23
	„ 37	1	1	0	25
	„ 38	7	0	1	20
	„ 39	5	0	1	14
	„ 40	2	2	2	17
Table 10 (Min. Fr.=49)	Family 24	7	2	1	18
	„ 25	5	0	3	25
	„ 26	5	2	2	22
Sums		67	16	16	255

Here we see an exactly equal number of early reds and late whites, as was expected, but the number of both early whites and late reds is greater than the expected. Then, turning to **I** Table 14 in which the variation types were assumed to be those of the descendants of **aAbb** F₂ plant, let us examine the distribution of whites and reds in variable families.

		Early group		Late group (Min. Fr.=39)	
		white	red	white	red
Family	10	6	1	0	11
„	11	7	2	4	15
„	12	3	5	3	9
„	13	2	0	1	14
„	14	3	5	2	19
„	15	6	2	1	16
„	17	4	2	1	18
„	18	6	1	3	17
„	19	4	0	2	16
„	20	8	1	2	14
„	21	3	2	1	17
„	23	2	0	1	13
„	24	5	0	5	18
	Sum	59	21	26	197

Here again we see that the numbers of early reds and late whites are quite close, but the numbers of early whites and late reds are smaller than the expected. Now let us add the above two sums, then we shall get a very close correspondence between the observed and the expected.

	Early		Late	
	white	red	white	red
	67	16	16	255
	59	21	26	197
	126	37	42	452
Expected	137	42	42	495

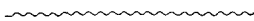
Next, let us look at the distributions of whites and reds in the families which were assumed to be the segregates' of **aABB**. To do this, we shall take only those families of F_4 raisings, because it is quite difficult to distinguish **aABB** families from **aAbB** families in F_3 raisings.

	Early group		Late group			Early group		Late group					
	white	red	white	red		white	red	white	red				
Table 13, D Min. Fr. = 55	Family 4	8	2	2	15	Table 13, F Min. Fr. = 59	Family 11	5	0	1	25		
	" 5	11	2	3	12		" 12	5	4	3	17		
	" 6	8	1	3	20		" 13	3	1	1	25		
	" 7	5	0	2	20		" 14	3	3	0	21		
	" 8	4	1	2	21		" 15	6	0	1	23		
	" 10	10	0	2	17		" 17	7	1	1	20		
	" 11	6	0	3	19		" 18	8	0	0	21		
	" 12	5	0	0	24		" 19	9	1	0	18		
	" 13	5	2	0	21		" 20	9	4	0	17		
	" 14	8	1	1	14		" 21	2	2	0	24		
	" 15	9	0	0	21		" 22	7	0	2	21		
	" 16	3	0	0	24		" 23	3	0	2	25		
	" 17	5	0	1	24		Sums	67	16	11	257		
	Sums	87	9	19	252								
	Table 13, E. Min. Fr. = 58	Family 8	2	2	2		24	Table 16, M. Min. Fr. = 47	Family 10	5	0	2	9
		" 9	9	1	0		18		" 11	4	1	0	20
		" 10	5	3	0		20		" 12	6	0	3	14
" 11		5	2	1	20	" 14	1		0	4	21		
" 12		8	0	0	17	" 15	5		1	6	16		
" 13		3	0	1	24	" 16	8		0	1	19		
" 15		3	0	1	25	" 17	7		0	2	19		
" 16		6	1	0	23	" 18	8		1	1	15		
" 17		2	1	3	24	" 19	3		0	3	16		
" 18		7	2	0	20	" 20	11		2	2	14		
" 19		5	1	1	20	" 21	2		4	2	20		
Sums	55	14	9	235	" 22	4	0	1	21				
					" 25	5	0	1	12				
					Sums	69	9	28	216				

		Early group		Late group				Early group		Late group		
		white	red	white	red			white	red	white	red	
Table 16, N , Min. Fr. = 50	Family	10	4	3	1	18	Total Sums	D 87 9 E 55 14 F 67 16 M 69 9 N 48 29 O 61 27 Sums 387 104	19	252		
	"	11	4	2	3	18			9	235		
	"	12	7	0	2	21			11	257		
	"	13	6	2	0	13			28	216		
	"	14	6	3	1	18			14	166		
	"	16	4	0	2	21			40	235		
	"	17	6	7	0	12			121	1361		
	"	18	5	3	3	17			395	121	121	1428
	"	20	4	5	1	17			340	104	104	1227
	"	21	2	4	1	11			Av. 368	112	112	1328
		Sums	48	29	14	166						
Table 16, O , Min. Fr. = 49	Family	6	8	2	5	14	Expected					
	"	7	2	0	2	19						
	"	9	4	1	4	15						
	"	10	3	3	3	13						
	"	11	6	3	2	17						
	"	12	2	1	4	19						
	"	13	5	3	5	19						
	"	16	11	1	1	18						
	"	17	8	1	1	17						
	"	18	4	2	1	16						
	"	19	2	6	4	17						
	"	20	2	3	2	17						
	"	21	3	1	5	18						
"	22	1	0	1	16							
	Sums	61	27	40	235							

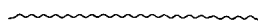
Here again, we see a remarkable correspondence between the observed and the expected.

Thus, all of our expectations have been fulfilled and *it would be quite safe for us to conclude that our proposed gametic coupling between flowering time and flower colour is justified. And this conclusion will give strong support, in its turn, to our proposed two-factor hypothesis for the inheritance of the flowering time in peas.*



SUMMARY.

1. The fixity of the character of the flowering time in the original varieties of peas is established experimentally and the presence of two pure lines in the population of one variety is also established.
2. The flowering time of the F_1 is not intermediate between the parents, but inclines towards one of the parents ; in peas towards the late parent, and in rice towards the early parent.
3. The variation range of F_2 families covers the combined range of both parent varieties, but their variation type is not the ordinary one. Individuals, whose flowering time is just intermediate between those of the parents, are very few in number and sometimes absent (minimum frequency class), while in the ordinary variation type there should be the largest number of flowering individuals.
4. By raising F_3 and F_4 families in peas, it is ascertained that the inheritance of the flowering time follows the Mendelian law.
5. The inheritance of the flowering time in peas can be interpreted by proposing (1) the presence of two Mendelian factors which differ in their effects, and (2) gametic contamination caused by hybridization whose nature is not yet explainable.
6. From variation types of F_1 , F_2 and F_3 families in peas, it is seen that the hereditary difference of the two pure lines is not quantitative but qualitative : i. e. the number of the factors is not different but the quality of the factors is different in both pure lines.
7. Our material was not sufficient to propose a definite interpretation for the inheritance of shooting time in the rice varieties, but the hypothesis of three alleromorphic pairs does not positively conflict with the actual results, as far as our experiments go.
8. The correlation between flower colour and flowering time in peas can be satisfactorily explained by assuming gametic coupling between colour factor and one of the two factors for flowering time.



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TABLE 10—Frequency distribution of number of days from sowing to flowering in F_3 of crosses between *M. P.* and early line of *G. P.* (1912).

No.	Patent Designation	Patent Class	Class Centers																							
			42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65
	<i>Mp</i> — <i>Gp</i>																									
	<i>Mp</i> — <i>Gp</i>																									
1	<i>I</i> × <i>I</i> · 4 · 29	39																								
2	<i>I</i> × <i>I</i> · 4 · 24	(53)*																								
3	<i>I</i> × <i>I</i> · 4 · 26	(54)																								
4	<i>I</i> × <i>I</i> · 4 · 1	(56)																								
5	<i>I</i> × <i>I</i> · 4 · 12	45																								
6	<i>I</i> × <i>I</i> · 4 · 19	46																								
7	<i>I</i> × <i>I</i> · 4 · 8	44																								
8	<i>I</i> × <i>I</i> · 4 · 3	49																								
9	<i>I</i> × <i>I</i> · 4 · 27	(66)																								
10	4 × <i>XVI</i> · 2 · 27	52																								
11	4 × <i>XVI</i> · 2 · 1	55																								
12	<i>I</i> × <i>I</i> · 4 · 17	56																								
13	<i>I</i> × <i>I</i> · 4 · 23	56																								
14	<i>I</i> × <i>I</i> · 4 · 16	56																								
15	<i>I</i> × <i>I</i> · 4 · 6	58																								
16	<i>I</i> × <i>I</i> · 4 · 5	59																								
17	<i>I</i> × <i>I</i> · 4 · 7	44																								
18	<i>I</i> × <i>I</i> · 4 · 4	(56)																								
19	<i>I</i> × <i>I</i> · 4 · 22	43																								
20	4 × <i>XVI</i> · 2 · 13	(54)																								
21	4 × <i>XVI</i> · 2 · 23	52																								
22	4 × <i>XVI</i> · 2 · 8	43																								
23	4 × <i>XVI</i> · 2 · 25	46																								
24	4 × <i>XVI</i> · 2 · 7	47																								
25	4 × <i>XVI</i> · 2 · 6	48																								
26	4 × <i>XVI</i> · 2 · 11	48																								
27	4 × <i>XVI</i> · 2 · 10	48																								
28	<i>I</i> × <i>I</i> · 4 · 11	53																								
29	<i>I</i> × <i>I</i> · 4 · 23	(69)																								
30	4 × <i>XVI</i> · 2 · 26	55																								
31	<i>I</i> × <i>I</i> · 4 · 10	(63)																								
32	4 × <i>XVI</i> · 2 · 24	53																								
33	<i>I</i> × <i>I</i> · 4 · 21	54																								
34	<i>I</i> × <i>I</i> · 4 · 20	56																								
35	4 × <i>XVI</i> · 2 · 3	53																								
36	4 × <i>XVI</i> · 2 · 5	55																								
37	4 × <i>XVI</i> · 2 · 23	53																								
38	<i>I</i> × <i>I</i> · 4 · 2	53																								
39	4 × <i>XVI</i> · 2 · 20	51																								
40	4 × <i>XVI</i> · 2 · 29	54																								
41	4 × <i>XVI</i> · 2 · 21	51																								
42	4 × <i>XVI</i> · 2 · 22	54																								
43	<i>I</i> × <i>I</i> · 4 · 9	55																								
44	4 × <i>XVI</i> · 2 · 2	51																								
45	<i>I</i> × <i>I</i> · 4 · 14	56																								
46	4 × <i>XVI</i> · 2 · 4	55																								
47	4 × <i>XVI</i> · 2 · 13	54																								
48	4 × <i>XVI</i> · 2 · 12	54																								
49	<i>I</i> × <i>I</i> · 4 · 15	53																								
50	<i>I</i> × <i>I</i> · 4 · 13	56																								
51	4 × <i>XVI</i> · 2 · 14	54																								
52	4 × <i>XVI</i> · 2 · 16	56																								
53	4 × <i>XVI</i> · 2 · 19	(68)																								
54	<i>I</i> × <i>I</i> · 4 · 25	(69)																								

* () late-sprouted.

