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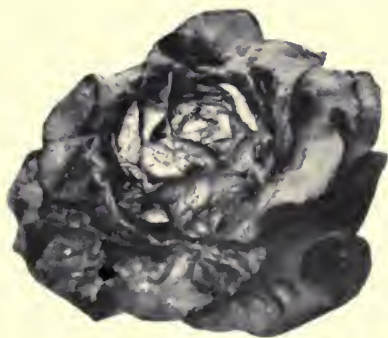
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INHERITANCE IN LETTUCE

By CHARLES E. DURST



UNIVERSITY OF ILLINOIS
AGRICULTURAL EXPERIMENT STATION
BULLETIN 356

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INHERITANCE IN LETTUCE¹

By CHARLES E. DURST, formerly Assistant Chief in Olericulture

THE INVESTIGATIONS described in this publication were conducted for the purpose of determining some of the facts of inheritance in lettuce (*Lactuca scariola* L.), a plant for which no extensive genetic investigations have been reported, so far as the author is aware. The experiments were conducted at the Illinois Agricultural Experiment Station at Urbana, Illinois. They were started in 1913 and were continued for five years. Crosses were made between typical varieties of the important cultivated types of lettuce, and between these and the wild forms of *L. scariola* found in the vicinity of Urbana.

The parental varieties and hybrids grown in this investigation were studied with reference to anthocyanin pigment, seed color, leaf form, prickliness, leaf length, leaf width, width index (leaf width divided by leaf length), leaf area, time required to reach the flowering period, height of plants at date of first bloom, and habit of growth in the rosette stage. The relations of these characters to one another have also been studied. Finally, some general conclusions have been drawn as a result of the study as a whole.

MATERIALS AND METHODS

Varieties Used in the Investigation

For the purposes of this investigation, typical forms of each of the important types of both wild and cultivated lettuce were selected.

Wild Forms.—For some of the early crosses the pinnatifid, or lobed form, of *L. scariola* was used. Later the unlobed form was used also. Typical specimens of each form were chosen after rather extended observation of the types prevalent in the vicinity of Urbana. Each specimen was taken from a location in which uniformity existed with reference to the type in general and to leaf form in particular. Photographs of each form in the rosette stage are shown in Fig. 1.

Cultivated Types.—Representative varieties of each of the important cultivated types of lettuce were selected for hybridization. For the heading type Big Boston and May King were used; for the leaf type, Grand Rapids; and for the Cos type, Paris White Cos.

¹The results presented in this bulletin form part of a thesis submitted by the author to the Graduate School of the University of Illinois in partial fulfillment of the requirements for the degree of doctor of philosophy in genetics, 1924.

Big Boston is second in commercial importance among the varieties of lettuce used in the United States (Morse, 1923). It was introduced by Peter Henderson in 1887 from Europe, where it was known as Trocadero. It was named Big Boston by Henderson because of its similarity to the variety Boston Market (Morse, 1923).

May King was introduced probably from Germany about twenty years ago. According to Morse (1923), it is tenth in commercial importance among the varieties used in America.

The Grand Rapids was developed by Eugene Davis of Grand Rapids, Michigan, from a cross between Hanson and an English variety, the identity of which Mr. Davis was unable to establish (Tracy, 1904; Morse, 1923). A hybrid was obtained by planting the two side by side. The Grand Rapids was later "fixed" by selection. The new variety was found better adapted for greenhouse culture than any other variety known. It is now practically the only variety of leaf lettuce grown in greenhouses in the United States, and it is also used to a considerable extent for outdoor culture. According to Morse (1923), it is third in commercial importance among the varieties used in America.

Paris White Cos is practically the only variety of Cos lettuce grown in America. According to Morse (1923), it is sixth in importance among the lettuce varieties grown in the United States. Vilmorin (1883) stated that it is "the most grown of all the Cos lettuces, and perhaps of all other kinds."

Detailed descriptions of each of these varieties, except that of May King, are given by Tracy (1904). Photographs of typical specimens of each are presented in Fig. 1.

Flowering Habits of Lettuce

The indications are that lettuce is very largely self-fertilized. Tracy (1904) says, "Lettuce does not readily cross-fertilize in the field and different varieties are planted side by side with little danger of mixture." Starr¹ states that the species is largely, if not entirely, self-fertilized; that uniformity of type is pronounced in varieties of lettuce; and that variations are rare, but when they occur they may be the result of mutation. Morse states (1924): "Lettuces do not easily cross-fertilize, but will do so.... We aim to make a division of not less than a rod between varieties, and do not have much trouble with mixtures." In examining lettuce in commercial greenhouses and in the fields, one is strongly impressed by the extreme uniformity in type; in fact, it is rare that an off-type plant is found. The evidence, therefore, is indicative of a high degree of self-fertilization.

Moreover, the structure and behavior of the flowers favor a high percentage of self-fertilization. The involucrens open early in the morn-

¹Starr, Geo. B. Personal conversation with author, Dec., 1923.



FIG. 1.—TYPICAL PLANTS OF THE VARIETIES EMPLOYED FOR HYBRIDIZATION

The two wild forms shown above were chosen from types prevalent in the vicinity of Urbana. Of the cultivated forms shown above, Big Boston and May King represent the heading type; Grand Rapids, the leaf type; and Paris White Cos, the Cos type.

ing, usually between 7 and 8 o'clock on a normal summer day. In strong sunlight the flower heads remain open only 20 or 30 minutes; on cloudy days the period is somewhat longer. Flowers open only in the morning, and a given flower head opens but once. Furthermore, when a flower head expands, the anthers have already dehisced and the unexpanded stigmas are covered with pollen. The stigmas begin to expand at their tips, and simultaneously an abundance of pollen falls on their inner surfaces, to which the pollen closely adheres. Thus, the chances of self-fertilization are decidedly increased both by the short period in which the flowers are exposed to cross-pollination and by the fact that "own" pollen is likely to be present in abundance while foreign pollen is likely to be present in limited quantity, if at all.

There are, however, some indications that even under these conditions cross-fertilization may occur. Cross-fertilization must have taken place in the experience of Eugene Davis in the development of the Grand Rapids variety, already described. It is possible that wind spreads the pollen. Morse (1924) thinks, however, that wind has little effect, if any, in spreading pollen, but he believes insects may cause some cross-fertilization. The writer has frequently seen small syrphid flies working among lettuce flowers with their bodies covered by pollen. Undoubtedly they spread pollen. The probabilities are, however, that under normal conditions self-pollination occurs before the flower heads are visited by them.

The chances of self-fertilization are increased by the fact that an abundance of "own" pollen is in practically every case presented to the stigmas before any foreign pollen can be presented. The author assumes, in making this statement, that "own" pollen has as good a chance as foreign pollen to effect fertilization. East (1918) has shown, however, that certain species of *Nicotiana* are more likely to be fertilized by foreign than by their own pollen. On the other hand, Jones (1920) has found that corn shows a decided preference for "own" over foreign pollen. The difficulty in securing crosses in this investigation indicates that self-fertilization is the rule in lettuce.

The wild forms of *L. scariola* show evidence of more cross-fertilization than the cultivated types. Besides the deeply lobed and unlobed forms existing at Urbana, there are intermediate forms which may be hybrids between the other two, tho this matter was not investigated by the writer. The wild forms bloom in the same manner as described for the cultivated forms, and this fact would seem to limit the chances of cross-fertilization.

Method of Artificial Hybridization

In making the crosses Oliver's method (1910) of depollination by means of a small stream of water was employed with certain modifications, the principal one being that the corollas of the ray flowers

were first trimmed off with small shears. This process seemed to give the stream of water better access to the flower head as a whole.

All plants used as female parents were grown in a greenhouse, as more favorable conditions could be provided there than on the outside. Most of the plants used as males were also grown in the greenhouse. A branch of a panicle of the female parent was used for a given cross. The branch was enclosed in a manila bag pinned on both sides, before the crossing was begun. Previous to the placement of the bags, all flower heads which had bloomed were removed. Each morning during the pollination period the bag was removed, the heads which had opened were pollinated, and the bag was then replaced. When enough pollinations had been made to yield a supposedly sufficient quantity of hybrid seed, the remaining flower heads, i.e., those which had not yet opened, were removed. The bags were left attached until the seeds were harvested.

In the case of the pollen-bearing parent a branch of a panicle was likewise bagged in order to prevent the flowers from carrying foreign pollen. For pollinating the female parent an entire head was removed from the male parent and the anthers were gently rubbed among the stigmas of the female flowers. A single flower head was often used to pollinate two or three flower heads on the female parent.

In order to insure self-fertilization in the F_1 and later generations, a portion of the panicle of each plant was bagged at about the time the first flowers appeared, precaution being taken to remove any flower heads which had opened.

Oliver (1910) states that in his experiments "all of the resulting seedlings proved to be intermediate between the two parents." In this investigation all seedlings were hybrids in some cases; in others only part were hybrids; and in still others none were hybrids.

The only means of determining whether or not crosses had been secured was to grow the seedlings. If they proved to be like the female parent in every respect and continued to breed true, it was considered fairly certain that they were not hybrids. If they were different from the female variety in appearance, it seemed likely that crossing had occurred. In all cases in which hybrids were secured, the F_1 plants were quite uniform in type and they were intermediate between the parents in appearance. In no case were more than two types secured, that is, one like the female parent and the other of an intermediate type. If in F_2 , the parental forms were practically recovered, this was considered further evidence that crosses between the two varieties had been secured.

Cultural Methods

In order to provide the plants with a longer period of cool weather in which to attain normal development, the seeds of the main plant-

ings were sown in a greenhouse in four- or six-inch pots each year about March 1. Sterilized soil was used for starting the seedlings, both for the purpose of controlling fungi and for preventing the growth of foreign seeds which might be present in the soil. The brown silt loam characteristic of the locality was used, a small quantity of sand and rotted manure being added to make it light and porous.

The seedlings were transplanted to 2½-inch pots in the cotyledon stage or while the first pair of rosette leaves was yet small. For this purpose a mixture of 4 parts of brown silt loam, 2 parts of rotted manure, and 1 part of sand was used. The plants were "hardened off" as a rule in cold frames. They were transplanted to the garden early in April. A distance of about 3 feet was allowed between rows, and the plants were set about 24 inches apart in the rows. In each season a location was selected which furnished apparently uniform conditions; the location was changed each year. The usual methods of cultivation were practiced.

When the plants began to produce seed stalks, rose stakes made of heavy galvanized wire, such as are used by florists, were forced into the ground at the side of each plant; to these the plants were tied loosely as they grew in height. These supports served the purpose excellently, since they sway readily with the wind.

Abbreviations and Numbering System

In this paper BB indicates the Big Boston variety; MK, May King; GR, Grand Rapids; Cos, Paris White Cos; and W is used for wild forms. The terms lobed and unlobed are frequently used in the text to distinguish the two wild forms. The numbers used in connection with the abbreviations are the plant numbers. Different generations are indicated by dashes.

The stocks of each of the above cultivated varieties were obtained from seed purchased from the W. Atlee Burpee Company, Philadelphia. The wild forms, as explained, were secured in the vicinity of Urbana, Illinois. In all cases extreme care was taken to secure typical specimens of each variety or form.

The hybrids are designated by initials and numbers. The letter represents the cross, and the number indicates the plant number of each generation. Thus, in the symbol A0-10-28, the letter A indicates a cross between May King and Wild; the number 0 indicates a cross between two particular plants of the parent varieties; and 10 and 28 are the numbers of single F₁ and F₂ plants respectively. The symbol A0-10 indicates the pedigree and number of a certain F₁ plant. This symbol is also used to designate the F₂ family. Likewise, A0-10-28 shows the pedigree and number of a certain F₂ plant. This symbol is also used to designate the F₃ family as a group.

Terms such as Cos1-1' indicate that the female parent of such a family was grown in the greenhouse.

The parentage of each cross is indicated in footnotes accompanying the tables. In the tables which present frequency distributions of quantitative characters the condition of the parent in the case of F_3 and F_4 is shown by the class set in italic type, except when the parents were grown in the greenhouse, in which case the data would not be comparable.

Methods of Taking and Assembling Data

The method of taking and assembling the data will be described in detail in connection with the discussion of results for each character. The author made all of the crosses here described in person. In order that a single standard might be followed thruout for each character, the author took all of the readings of the different characters, the results being recorded on specially prepared forms by an assistant. The constants have all been checked at least once.

RESULTS OF THE INVESTIGATION

Inheritance of Anthocyanin Pigment in Stems and Leaves

The inheritance of pigments has been studied in a great many species and varieties of plants. It is doubtful if any group of plant characters has received more attention. Perhaps this is due to the fact that pigments present such striking differences and because they are less influenced, on the whole, by environmental conditions than many other characters.

Miss Wheldale's excellent summary of the subject (1916) indicates that of the various kinds of pigments, the anthocyanins are more prevalent than any other and that it is the anthocyanins upon which most information has been accumulated.

Anthocyanin pigments manifest themselves in a variety of ways. They are responsible for color development in flowers, for pigments in the stems and leaves, for aleurone color in certain seeds and even for colors in such organs as styles, stamens, and pollen grains (Wheldale, 1916), varying of course in different species and varieties.

The inheritance of anthocyanin pigments occurs in a variety of ways. A single pair of allelomorphs may be involved, with complete or incomplete dominance; such factors may express themselves in one organ only or they may be manifested in two or more organs of the plant. In other cases two pairs of allelomorphs are present, which may result in a 15:1 or a 9:7 ratio. From these fairly simple modes of inheritance there are many variations, involving several pairs of allelomorphs in many cases and exhibiting practically every known form of modification of typical Mendelian cases (Wheldale, 1916).

The Big Boston, May King, and wild forms of lettuce carry anthocyanin pigment, while the Grand Rapids and Paris White Cos carry none.

The pigment appears to vary in intensity in different cultivated varieties, certain varieties being so conspicuous for the amount of pigment contained that they are called "red" varieties; such varieties, however, have little importance from a commercial standpoint. Most of the varieties in common use either have no pigment or carry it only in slight degree. Even in these, however, the presence of pigment sometimes becomes so pronounced following a period of cool spring weather that the redness of the leaves causes the variety to be discriminated against on the market.

The pigment is carried in different parts of the plant. It may be seen as a purplish-red color on the stems of seedlings below the cotyledons at a very early age, especially if the seedlings have been subjected to drouth or low temperatures. It may be seen on the leaves of the plant at any stage of growth. Under favorable growth conditions, however, it is quite inconspicuous in many varieties, but becomes conspicuous as a purplish-red color on the leaves following a period of cool weather. The pigment may, later in the life of the plant, cause a purplish-red coloration in the seed stalk and branches of the panicles.

The same pigment also appears to be responsible for blueness on the undersides of the ray florets.

Five crosses were made, involving differences in this character pair. In each cross all of the F_1 plants carried pigment, indicating that the presence of anthocyanin pigment (G) is dominant to its absence (g). In the F_2 generations of all crosses, segregation and recombination occurred. The results for four of these crosses in the F_2 and later generations are presented in Tables 1 to 4, inclusive. Only one F_2 family was grown of the fifth cross, and the results are described in the text.

In three of these crosses (Tables 1, 2, and 4), the F_2 generations produced pigmented and unpigmented individuals in the proportion of about 3 to 1. Both the individual F_2 families and the combined F_2 results for each cross show comparatively small deviations from a 3:1 ratio, and the deviations divided by the probable errors are fairly small in all cases but one (N1-2 in Table 4). In two of these three crosses (Tables 1 and 2), F_3 and F_4 families were grown. In both cases some of these families produced only pigmented plants (GG), others proved to be heterozygous (Gg), while still others consisted of only unpigmented offspring. The pigmented F_2 plants produced homozygous and *segregating populations* in proportions closely approximating a 1:2 ratio, as would be expected.

The cross between unlobed Wild and Paris White Cos produced

rather wide deviations from a 3:1 ratio (Table 3). It appears that in this cross, inheritance took place either on some other than a simple Mendelian basis or that disturbing influences were in operation which appreciably affected the ratios.

The F_2 family for which no table is presented (Grand Rapids ♀ X unlobed Wild ♂) consisted of 107 pigmented and 51 unpigmented plants. This is a deviation of 11.5 from a 3:1 ratio, and the deviation is 3.13 times the probable error. Further investigation of this cross should be made before final conclusions are drawn.

Inheritance of Anthocyanin in Ray Flowers

The strap-leaved corollas of the ray flowers of lettuce are yellow thruout in the varieties Grand Rapids and Paris White Cos, while in the Big Boston, May King, and wild forms the undersurfaces of the corollas are pale blue.

When these differences were first observed, it was thought that they might be due to a pair of factors independent of those responsible

TABLE 1.—INHERITANCE OF ANTHOCYANIN PIGMENT, MAY KING ♀ X GRAND RAPIDS ♂

Parent ¹	Generation	Condition of parent	(G) With anthocyanin pigment	(g) Without anthocyanin pigment	Total	Deviation ²	Deviation P. E.
E2-1.....	F ₂	G	150	45	195	4	.98
E2-4.....	F ₂	G	172	62	234	3.5	.78
E2-6.....	F ₂	G	140	39	179	6	1.54
E7-1.....	F ₂	G	129	42	171	1	.26
E7-3.....	F ₂	G	52	16	68	1	.42
E7-9.....	F ₂	G	10	2	12	1	.99
E7-5.....	F ₂	G	62	28	90	5.5	1.99
Subtotal.....	715	234	949	3	.33
E7-1-15.....	F ₂	G	15	0
E7-1-18.....	F ₂	G	21	1
E7-3-15.....	F ₂	G	11	3	14	.5	.46
E7-3-5.....	F ₂	G	38	11	49	1	.49
E7-1-67.....	F ₂	G	13	1	14	2.5	2.29
E7-3-65.....	F ₂	G	7	1	8	1	1.21
E7-3-22.....	F ₂	G	16	10	26	3.5	2.35
E7-3-3.....	F ₂	G	32	10	42	.5	.26
E7-3-47.....	F ₂	G	20	10	30	2.5	1.56
Subtotal.....	137	46	183	0	0
E2-4-10.....	F ₂	g	0	33
E2-4-10'	F ₂	g	0	55
E2-4-4.....	F ₂	g	0	107
E7-1-2.....	F ₂	g	0	55
E7-3-20.....	F ₂	g	0	57
E7-1-19.....	F ₂	g	0	24
E7-1-6.....	F ₂	g	0	40
Subtotal.....	371
E2-4-4'-4.....	F ₄	g	0	34
E2-4-4'-5.....	F ₄	g	0	35
E2-4-4'-6.....	F ₄	g	0	39
E2-4-4'-25.....	F ₄	g	0	35
E2-4-10-19.....	F ₄	g	0	34
Subtotal.....	0	177

¹E2 = MK15 ♀ X GR1 ♂; E7 = MK1-1' ♀ X GR2-3-1' ♂. ²All deviations in this table are calculated on a 3:1 basis.

TABLE 2.—INHERITANCE OF ANTHOCYANIN PIGMENT, BIG BOSTON ♀ X GRAND RAPIDS ♂

Parent ¹	Generation	Condition of parent	(G) With pigment	(g) Without pigment	Total	Deviation ²	Deviation P. E.
G4-9.....	F ₂	G	126	34	160	6	1.63
G4-13.....	F ₂	G	2	3	5	2	3.06
G4-23.....	F ₂	G	69	24	93	1	.36
G4-5.....	F ₂	G	95	44	139	9	2.61
Subtotal.....	292	105	397	6	1.03
G4-9-15.....	F ₃	G	21	0
G4-9-17.....	F ₂	G	19	0
G4-9-18.....	F ₂	G	30	0
G4-13-2.....	F ₃	G	11	0
G4-23-3.....	F ₃	G	30	0
G4-23-4.....	F ₂	G	12	0
Subtotal.....	123	0
G4-9-1.....	F ₃	G	3	1	4	0	0
G4-9-2.....	F ₃	G	17	3	20	2	1.53
G4-9-3.....	F ₃	G	22	3	25	3	2.06
G4-9-5.....	F ₃	G	18	11	29	4	2.54
G4-9-6.....	F ₃	G	27	17	44	6	3.10
G4-9-7.....	F ₃	G	26	6	32	2	1.21
G4-9-9.....	F ₃	G	18	5	23	1	.71
G4-9-10.....	F ₃	G	25	9	34	.5	.29
G4-9-13.....	F ₃	G	16	6	22	.5	.36
G4-9-16.....	F ₃	G	8	4	12	1	.99
G4-9-19.....	F ₃	G	15	3	18	1.5	1.21
G4-9-21.....	F ₂	G	22	5	27	2	1.32
G4-9-22.....	F ₃	G	33	13	46	1.5	.76
G4-13-1.....	F ₃	G	42	11	53	2	.94
G4-23-2.....	F ₃	G	18	6	24	0	0
G4-23-5.....	F ₃	G	17	2	19	3	2.36
G4-23-6.....	F ₃	G	61	18	79	2	.77
Subtotal.....	388	123	511	5	.76
G4-9-4.....	F ₃	g	0	12
G4-9-8.....	F ₃	g	0	80
G4-9-11.....	F ₃	g	0	12
G4-9-12.....	F ₃	g	0	5
G4-9-14.....	F ₃	g	0	113
G4-9-20.....	F ₃	g	0	26
G4-23-1.....	F ₃	g	0	21
Subtotal.....	269
G4-9-6-5.....	F ₄	G	20	7	27	0	0
Subtotal.....	20	7	27	0	0
G4-23-6-12' ²	F ₄	g	0	2
G4-27-6-1' ²	F ₄	g	0	5
G4-9-6-4' ²	F ₄	g	0	24
G4-9-8-6' ²	F ₄	g	0	75
G4-9-14-12' ²	F ₄	g	0	35
G4-23-6-67' ²	F ₄	g	0	53
G4-9-14-42' ²	F ₄	g	0	8
Subtotal.....	202

¹G4 = BB7 ♀ X GR2 ♂. ²All deviations in this table are calculated on a 3 : 1 basis.

for anthocyanin in stems and leaves. As the investigation progressed, however, it was found that plants with anthocyanin in stems and leaves always had blue ray florets. A diligent search was maintained in vain thruout the investigation for exceptions to this relationship.

The conclusion was reached, therefore, that anthocyanin in stems and leaves and blue undersurfaces of the ray flowers are due either to one and the same factor or to different factors located so closely together on the same chromosome that crossing-over rarely if ever occurs.

TABLE 3.—INHERITANCE OF ANTHOCYANIN PIGMENT, UNLOBED WILD ♀ X PARIS WHITE COS ♂

Parent ¹	Generation	Condition of parent	(G) With pigment	(g) Without pigment	Total	Deviation		Deviation P. E.	
						3 : 1 basis	9 : 7 basis	3 : 1 basis	9 : 7 basis
R1-2.....	F ₂	G	13	15	28	8	3	5.17	1.70
R1-3.....	F ₂	G	8	19	27	12	7	7.92	4.03
Subtotal.....	21	34	55	20	10	9.23	9.45
R1-2-80.....	F ₃	G	19	4	23	2	6	1.43	3.74
R1-2-88.....	F ₃	G	31	26	57	12	1	5.44	.40
Subtotal.....	50	30	80	10	5	3.83	1.67
R1-2-48.....	F ₃	g	0	5
Subtotal.....	0	5	5

¹R1 = Paris White Cos ♀ X W5 ♂.

TABLE 4.—INHERITANCE OF ANTHOCYANIN PIGMENT, BIG BOSTON ♀ X PARIS WHITE COS ♂

Parent ¹	Generation	Condition of parent	(G) With pigment	(g) Without pigment	Total	Deviation ²	Deviation
							P. E.
N1-2.....	F ₂	G	74	10	84	11	4.11
N1-4.....	F ₂	G	13	4	17	0	0
N1-5.....	F ₂	G	4	0	4	1	1.71
N1-1.....	F ₂	G	14	7	21	2	1.49
Subtotal.....	105	21	126	10.5	3.20

¹N1 = BB7-1' ♀ X Cos1-1' ♂. ²In this table all deviations are calculated on a 3 : 1 basis.

Evidence from a number of sources favors the single-factor hypothesis. A single factor was found to be responsible for anthocyanin in flowers, fruits, and stems of *Belladonna* by Bateson and Saunders (1901), for red stems and violet flowers in *Datura* by Bateson and Saunders (1902), for seed-coat color and flower color in garden beans by Shaw (1913), for orange-colored calyx-cup interiors and yellow-fleshed fruit in peaches by Hedrick (1913), and for seed-coat color and flower color in cowpeas by Spillman (1913).

On the other hand, there is some evidence in favor of two pairs of factors being involved. Pigments in flowers and in stems were found to be due to independent factors by Cockerell (1915) in the chestnut-red flowered *Helianthus annuus*. Keeble and Pellew (1910) showed that white-flowered varieties of *Primula sinensis* may have green or red stems. It must be said, however, that the literature indicates the existence of far fewer cases of this kind than of that first described.

The fact that the pigment in the leaves and stems of lettuce is purplish red, while that in the ray flowers is blue, rather strongly suggests the existence of separate factors for stem and flower color. The literature on the subject indicates that when one factor controls the presence of anthocyanin in flowers and stems the colors are usually similar except when the color is modified by the presence of another

color. It is possible that the differently colored pigments in the stems and ray florets of some varieties of lettuce may be due to one factor and that the pigment becomes blue in the ray flowers because it meets a different environment there.

Because of the complete correlation which prevailed, the inheritance of pigment in the ray flowers of lettuce took place in the same manner as described for pigment in the stems and leaves. Therefore, the data and discussion for the inheritance of anthocyanin in stems and leaves apply also to the inheritance of blueness on the undersurfaces of the ray flowers.

Inheritance of Seed Color

The ripened ovules of Composites are called achenes. According to Gray's Manual,¹ an achene is "A small dry and hard one-celled one-seeded indehiscent fruit," and contains "a single erect anatropous seed, with no albumin." Robbins (1917) described an achene as "a one-celled, dry indehiscent fruit in which the testa and pericarp are not firmly attached." In this paper the achenes will be called seeds, a term which is firmly established in practical usage for lettuce.

Lettuce seeds are classified by Tracy (1904) and Morse (1923) as whitish, purplish, and blackish. Each variety produces seeds of but one of these kinds, but the shade of color varies within a variety; possibly the shade is influenced by the conditions existing during harvesting and storage. Some varieties appear to have darker seeds on the average than others of the same group. Yellow-seeded varieties are less common than the blackish- or whitish-seeded sorts. In this investigation, only whitish- and blackish-seeded varieties were employed. For purposes of brevity the terms black and white will hereafter be used to designate seed color.

It is unfortunate that the records on inheritance of seed color are so meager for some families. The small numbers are due to the effect of hot, dry weather in destroying many plants before seeds were produced. Perhaps sterility was also responsible in part. This matter, however, was not investigated, since there seemed to be no reliable method of determining whether failure to produce seeds was due to weather conditions or to sterility. The death rate was high among the parent varieties as well as among the hybrids.

The Grand Rapids and wild forms of lettuce have black seeds, while May King, Big Boston, and Paris White Cos have white seeds. Six crosses were made involving different combinations of black- and white-seeded parents.

The seed color of lettuce is carried in the seed coats. We should therefore expect the seed color of the female parent to be uninfluenced

¹Robinson, B. L., and Fernald, M. L. (1908).

by crossing. There was no apparent effect from crossing on the color of the resulting seeds.

In F_1 all plants bore only black seeds, indicating that black seeds are dominant. Segregation took place in the F_2 of all crosses. The results for the F_2 and succeeding generations are presented in Tables 5 to 10.

The tables show that in all of these crosses, inheritance probably took place on a simple Mendelian basis. With only a few exceptions the F_2 families and the F_3 and F_4 families of heterozygous parentage consisted of black- and white-seeded plants in proportions closely approximating a 3:1 ratio. In only three of these did the proportions

TABLE 5.—INHERITANCE OF SEED COLOR, MAY KING ♀ X LOBED WILD ♂

Parent ¹	Genera- tion	Condition of parent	(W) Black seeds	(w) White seeds	Total	Deviation ²	Deviation P. E.
A0-1.....	F ₂	W	28	8	36	1	.57
A0-10.....	F ₂	W	23	9	32	1	.61
A0-12.....	F ₂	W	40	14	54	.5	.25
A0-17.....	F ₂	W	65	19	84	2	.75
A0-18.....	F ₂	W	32	2	34	6.5	3.82
Subtotal.....	188	52	240	8	1.77
A0-1-84.....	F ₃	W	31	0
A0-10-44.....	F ₃	W	10	0
A0-10-57.....	F ₃	W	5	0
A0-10-11.....	F ₃	W	27	0
A0-10-15.....	F ₃	W	24	0
A0-12-62.....	F ₃	W	18	0
Subtotal.....	117	0
A0-1-2.....	F ₃	W	2	1	3	0	0
A0-1-6.....	F ₃	W	27	8	35	1	.58
A0-1-20.....	F ₃	W	39	9	48	3	1.48
A0-10-28.....	F ₃	W	30	7	37	2	1.13
A0-12-45.....	F ₃	W	28	7	35	2	1.16
A0-17-10.....	F ₃	W	1	0 ³	1	0	0
A0-18-40.....	F ₃	W	3	0 ³	3	1	1.98
A0-1-41.....	F ₃	W	8	2	10	.5	.55
A0-1-15.....	F ₃	W	28	7	35	2	1.16
A0-10-28.....	F ₃	W	25	7	32	1	.61
A0-10-10.....	F ₃	W	10	4	14	.5	.46
A0-18-38.....	F ₃	W	6	2	8	0	0
Subtotal.....	207	54	261	11	2.33
A0-1-16.....	F ₃	w	0	21
A0-1-32.....	F ₃	w	0	9
A0-10-86.....	F ₃	w	0	4
Subtotal.....	0	34
A0-12-45-30.....	F ₄	W	19	0
A0-10-44-42.....	F ₄	W	28	0
Subtotal.....	47	0
A0-18-40-15.....	F ₄	W	13	1	14	2.5	2.29
A0-12-45-22.....	F ₄	W	9	4	13	1	.95
A0-17-10-15.....	F ₄	W	5	3	8	1	1.21
A0-1-20-38.....	F ₄	W	19	9	28	2	1.29
Subtotal.....	46	17	63	1	.43
A0-1-6-1.....	F ₄	w	0	22
A0-12-45-72.....	F ₄	w	0	29
A0-1-16-7.....	F ₄	w	0	3
A0-10-86-6.....	F ₄	w	0	7
A0-1-32-3.....	F ₄	w	0	20

¹A0 = MK1 ♀ X W4 ♂. ²All deviations in this table are calculated on a 3 : 1 basis. ³Bred impure in F₄; therefore belongs to this group.

TABLE 6.—INHERITANCE OF SEED COLOR, BIG BOSTON ♀ X LOBED WILD ♂

Parent ¹	Generation	Condition of parent	(W) Black seeds	(w) White seeds	Total	Deviation ²	Deviation P. E.
C0-1.....	F ₂	W	46	21	67	4	1.67
C0-3.....	F ₂	W	89	34	123	3	1.93
Subtotal.....	135	55	190	7.5	1.87
C0-3-99.....	F ₃	W	1	0	1	0	0
C0-3-103.....	F ₃	W	20	9	29	2	1.27
C0-1-26.....	F ₃	W	23	11	34	2.5	1.47
Subtotal.....	44	20	64	4	1.71
C0-1-124.....	F ₃	w	0	16
C0-1-62.....	F ₃	w	0	9
C0-3-17.....	F ₃	w	0	21
C0-3-10.....	F ₃	w	0	20
Subtotal.....	0	66
C0-3-99-13.....	F ₄	W	4	0
Subtotal.....	4	0	4

¹C0 = BB7 ♀ X W4 ♂. ²All deviations in this table are calculated on a 3 : 1 basis.

TABLE 7.—INHERITANCE OF SEED COLOR, BIG BOSTON ♀ X UNLOBED WILD ♂ AND RECIPROCAL

Parent ¹	Generation	Condition of parent	(W) Black seeds	(w) White seeds	Total	Deviation ²	Deviation P. E.
C3-1.....	F ₂	W	2	2	4	1	1.71
C1-27.....	F ₂	W	3	0	3	1	1.98
D1-1.....	F ₂	W	38	15	53	2	1.94
D1-2.....	F ₂	W	1	2	3	.5	1.21
D1-12.....	F ₂	W	3	0	3	1	1.98
Subtotal.....	47	18	65	2	.85
C3-1-2.....	F ₃	W	1	0
C3-1-15.....	F ₃	W	12	1
D1-1-21.....	F ₃	W	2	0
Subtotal.....	15	1
D1-1-10.....	F ₃	W	26	7	33	1	.60
Subtotal.....	26	7	33	1	.60
D1-2-2.....	F ₃	w	0	7
Subtotal.....	0	7

¹C3 = BB7-1' ♀ X W5 ♂; C1 = BB5-4 ♀ X W38 ♂; D1 = W5 ♀ X BB7-1' ♂. ²All deviations in this table are calculated on a 3 : 1 basis.

very widely from a 3:1 ratio. Family A0-18 (Table 5) produced only two white-seeded to 32 black-seeded plants, and its deviation from a 3:1 ratio was 3.82 times the probable error. Family G4-9-14 (Table 10) produced one black-seeded to four white-seeded plants. The wide deviations are probably due to the small numbers grown and the laws of chance rather than to irregularities in genetic behavior. Family E7-5 (Table 9) consisted of 35 black-seeded to 22 white-seeded plants (Dev. / P. E. = 3.63), but as will be shown below, an influence seemed to be in operation in this cross which caused a deficiency of black-seeded individuals in F₂.

Some of the black-seeded F₂ plants produced only black-seeded individuals in F₃, indicating that the parents were of the constitution

WW. Others produced mixed populations, proving that they were of the constitution Ww. The F₃ families were not grown in sufficient numbers to show whether or not the black-seeded F₂ parents were homozygous and heterozygous in the expected 1:2 proportions.

TABLE 8.—INHERITANCE OF SEED COLOR, UNLOBED WILD ♀ X PARIS WHITE COS ♂

Parent ¹	Generation	Condition of parent	(W) Black seeds	(w) White seeds	Total	Deviation ²	Deviation P. E.
R1-2.....	F ₂	W	8	1	9	1	1.14
R1-3.....	F ₂	W	16	2	18	2.5	2.01
Subtotal.....	24	3	27	4	2.64
R1-2-98.....	F ₂	W	13	0
Subtotal.....	13	0
R1-2-80.....	F ₃	W	6	5	11	2	2.06
R1-2-88.....	F ₃	W	9	2	11	1	1.03
Subtotal.....	15	7	22	1.5	1.09
R1-2-10.....	F ₃	w	0	11
Subtotal.....	0	11
All heterozygous families.....	39	10	49	2	.98

¹R1 = W5 ♀ X Cos1-1' ♂. ²All deviations in this table are calculated on a 3:1 basis.

TABLE 9.—INHERITANCE OF SEED COLOR, MAY KING ♀ X GRAND RAPIDS ♂

Parent ¹	Generation	Condition of parent	(W) Black seeds	(w) White seeds	Total	Deviation ²	Deviation P. E.
E2-1.....	F ₂	W	26	10	36	1	1.57
E2-4.....	F ₂	W	35	12	47	0	0
E2-6.....	F ₂	W	20	12	32	4	2.42
E7-1.....	F ₂	W	7	6	13	3	2.85
E7-3.....	F ₂	W	6	2	8	0	0
E7-5.....	F ₂	W	35	22	57	8	3.63
E2-4.....	F ₂	W	5	5	10	2.5	2.71
Subtotal.....	134	69	203	18	4.32
E2-4-10.....	F ₃	W	3	0
E7-1-2.....	F ₃	W	5	0
E7-1-6.....	F ₃	W	3	0
E7-3-3.....	F ₃	W	1	0
Subtotal.....	12	0
E7-3-5.....	F ₃	W	2	2	4	1	1.71
E7-3-22.....	F ₃	W	7	1	8	1	1.21
Subtotal.....	9	3	12	0	0
E7-3-20.....	F ₃	w	0	2
E7-1-18.....	F ₃	w	0	10
E7-1-19.....	F ₃	w	0	1
E7-3-47.....	F ₃	w	0	2
Subtotal.....	0	15
E2-4-10-19.....	F ₄	W	1	1	2	.5	1.21
Subtotal.....	1	1	2	.5	1.21
E2-4-4'-4.....	F ₄	w	0	2
E2-4-4'-5.....	F ₄	w	0	5
E2-4-4'-6.....	F ₄	w	0	9
E2-4-4'-25.....	F ₄	w	0	7
E2-4-4'-39.....	F ₄	w	0	2
Subtotal.....	25

¹E2 = MK15 ♀ X GR1 ♂; E7 = MK1-1' ♀ X GR2-3-1' ♂. ²All deviations in this table are calculated on a 3:1 basis.

TABLE 10.—INHERITANCE OF SEED COLOR, BIG BOSTON ♀ X GRAND RAPIDS ♂

Parent ¹	Generation	Condition of parent	(W)	(w)	Total	Deviation ²	Deviation
			Black seeds	White seeds			P. E.
G4-9.....	F ₂	W	21	9	30	1.5	.94
G4-13.....	F ₂	W	1	1	2	.5	1.21
G4-23.....	F ₂	W	11	5	16	1	.86
G4-5.....	F ₂	W	54	14	68	3	1.24
Subtotal.....	87	29	116	0	0
G4-9-14.....	F ₃	W	1	4	5	3	4.59
Subtotal.....	1	4	5	3	4.59
G4-13-1'.....	F ₃	w	0	1
G4-23-6.....	F ₃	w	0	4
G4-9-6.....	F ₃	w	0	2
G4-9-8.....	F ₃	w	0	1
G4-9-22'.....	F ₃	w	0	2
Subtotal.....	10
G4-9-8-6'.....	F ₄	w	0	2
G4-9-6-5.....	F ₄	w	0	2
G4-23-6-67.....	F ₄	w	0	1
G4-9-14-42.....	F ₄	w	0	1
Subtotal.....	6

¹G4 = BB7 ♀ X GR2 ♂. ²All deviations in this table are calculated on a 3 : 1 basis.

F₃ family C3-1-15 (Table 7) produced one white-seeded and 12 black-seeded plants. Possibly the single white-seeded plant was the result of a seed mixture; this family is classified as a pure dominant.

The crosses between May King and Grand Rapids produced somewhat unusual results. All the F₂ families (see Table 9) except one produced a deficiency of black-seeded plants. The combined results show a deviation from a 3:1 ratio (Dev. / P. E. = 4.32), which is significantly indicative of a disturbing influence of some kind.

Inheritance of Prickles

The wild forms of lettuce have conspicuous prickles on the undersides of the midribs. Prickles are also present on the seed stalks, and the leaf margins are spinulose-denticulate in character. For this reason *L. scariola* is often called prickly lettuce. All of the cultivated varieties are without prickles except for a few inconspicuous plant hairs near the bases of the midribs in most varieties.

The inheritance of prickles is interesting from the standpoint of cell structure and differentiation. In an analysis of the subject, Strasburger (1903) has shown that a fairly close relationship exists between plant hairs, bristles, pubescence, prickles, spines, and thorns. Plant hairs may be outgrowths of one or more epidermal cells, and they may either be: (1) unicellular in character, as in the cotton fiber of commerce and the stinging hairs of nettles; or (2) multicellular, as in the staminal hairs of *Tradescantia*. "Emergencies" (including prickles, thorns, and spines) are the result of combined activity of epidermal and subepidermal tissue and are multicellular in structure. Both plant hairs and emergencies may act as secreting organs, in which case they

are termed glands. In some cases these organs act merely in an exudatory capacity and at times absorb water, while in other cases the cuticle finally is ruptured because of the accumulation of resinous material, resulting in the glandular pubescence that is common to so many plant species. It is evident that these various organs have a close morphological relationship, each seeming to be a modification in the method of differentiation and growth. It would appear reasonable, therefore, to believe that genetic data pertaining to any member of this group may have a bearing on the other members.

The author is unaware of any reported investigations pertaining to the inheritance of prickles on the midribs of leaves. However, results are available on the inheritance of prickles on other organs of the plant. Bateson and Saunders (1902) have shown that prickles on the capsules of *Datura* are inherited in simple Mendelian fashion; prickliness proved to be dominant to smoothness. Harland (1920) reports that in *Ricinus communis* prickly capsules are dominant to smooth capsules and are inherited on a simple Mendelian basis. Babcock and Collins (1922a) state that glandular pubescence on the involucre bracts of *Crepis capillaris* is dominant to its absence and that inheritance takes place in simple Mendelian fashion. They also found (1922b) that pubescence on the lower sides of the midribs is inherited on a dihybrid basis, pubescence being dominant. White (1918) found that bloom (pubescence) on the foliage of castor beans is dominant to absence of bloom and that inheritance occurs on a simple Mendelian basis. Belling (1914) reports a rather complicated case of inheritance of hairiness in velvet beans, several factors being apparently involved and different genotypic combinations producing varying degrees of hairiness. Nagai and Saito (1923) report a case of simple Mendelian inheritance in soybeans in which glabrousness is dominant to pubescence. Stewart and Wentz (1926) report a glabrous recessive character in soybeans which arose as a mutation in the germ cells of one of the parents.

In the present investigation records for the prickly condition were taken at about the time of full rosette development. In most cases the results were checked at a later time.

At the beginning of the experiment records were taken of the number of prickles per inch in the belief that inheritance might occur in quantitative fashion. It soon became apparent that the presence or absence of prickles in F_2 was sharply defined and these records were discontinued.

Five crosses were made involving the prickly wild forms and the smooth-ribbed cultivated varieties. The F_1 plants were all prickly. Segregation occurred in F_2 and succeeding generations from heterozygous parents. The results are presented in Tables 11 to 14.

TABLE 11.—INHERITANCE OF PRICKLES, BIG BOSTON ♀ X LOBED WILD ♂

Parent ¹	Genera- tion	Condition of parent	(S) With spines	(s) Without spines	Total	Deviation ²	Deviation P. E.
C0-1.....	F ₂	S	204	62	266	2.5	.53
C0-3.....	F ₂	S	277	101	378	6.5	1.15
Subtotal.....	..	.	481	163	644	2	.27
C0-3-82.....	F ₃	S	15	0
C0-1-62.....	F ₃	S	45	0
C0-3-17.....	F ₃	S	32	0
C0-3-103.....	F ₃	S	57	0
C0-1-26.....	F ₃	S	55	0
C0-3-10.....	F ₃	S	42	0
Subtotal.....	..	.	246
C0-3-97.....	F ₃	S	17	6	23	0	0
C0-3-58'.....	F ₃	S	14	3	17	1	.83
Subtotal.....	..	.	31	9	40	1	.54
C0-1-124'.....	F ₃	s	0	26
C0-3-80'.....	F ₃	s	0	7
C0-3-67'.....	F ₃	s	0	2
C0-3-62'.....	F ₃	s	1 (?)	4
Subtotal.....	..	.	1 (?)	39
C0-3-99-13.....	F ₄	S	9	0
Subtotal.....	..	.	9	0

¹C0 = BB7 ♀ X W4 ♂. ²All deviations in this table are calculated on a 3 : 1 basis.

Big Boston ♀ X *Lobed Wild* ♂.—The results from the cross *Big Boston* X *lobed Wild* (Table 11) show that the inheritance of prickles took place on a simple Mendelian basis, the presence of prickles being dominant to their absence.

The results for the cross *Big Boston* X *unlobed Wild* and the reciprocal are presented in Table 12. Six F₂ families were grown. In four of these the deviations from a 3:1 ratio were within reasonable limits of the errors of random sampling; in the other two families they were not. The combined results show a wide departure from a 3:1

TABLE 12.—INHERITANCE OF PRICKLES, BIG BOSTON ♀ X UNLOBED WILD ♂ AND RECIPROCAL

Parent ¹	Genera- tion	Condition of parent	(S) With spines	(s) Without spines	Total	Deviation ²	Deviation P. E.
C1-2.....	F ₂	S	6	6	12	3	2.97
C1-27.....	F ₂	S	27	13	40	3	1.62
C3-1.....	F ₂	S	40	21	61	6	2.63
D1-1.....	F ₂	S	49	30	79	10	3.85
D1-2.....	F ₂	S	13	4	17	0	0
D1-12.....	F ₂	S	83	42	125	11	3.37
Subtotal.....	..	.	218	116	334	32.5	6.09
C3-1-15.....	F ₃	S	39	1 (?)
D1-1-10.....	F ₃	S	55	0
Subtotal.....	..	.	94
C3-1-2.....	F ₃	S	24	18	42	6.5	3.44
D1-2-2.....	F ₃	S	21	8	29	1	.64
Subtotal.....	..	.	45	26	71	8	3.25
D1-1-21.....	F ₃	s	0	14
Subtotal.....	..	.	0	14

¹C1 = BB5-4 ♀ X W38 ♂; C3 = BB7-1' ♀ X W5 ♂; D1 = W5 ♀ X BB7-1' ♂. ²All deviations in this table are calculated on a 3 : 1 basis.

ratio. Examination of the figures shows that in every case but one, the proportion of prickly plants was deficient in relation to the number of smooth plants for a 3:1 ratio. The two segregating F_3 families exhibited a similar relationship.

It is noteworthy that family D1-2 and one of its progeny, D1-2-2, consisted of prickly and smooth plants in proportions closely approximating a 3:1 ratio. The question arises as to whether these two families represented a line which was free from the disturbing influences which seemed to affect the other F_2 and F_3 families.

Apparently inheritance took place in this cross on a simple Mendelian basis, but disturbing influences seemed to be in operation, which caused a deficiency in the number of prickly plants in most of the segregating families grown.

The results for the cross between May King ♀ and lobed Wild ♂ are given in Table 13. The F_2 families appeared to produce different results in different seasons, and the data are therefore presented separately for each year. In 1915 all F_2 families exhibited a more or less wide departure from a 3:1 ratio, the number of prickly plants being deficient in each case. In 1916 and 1917, however, the F_2 families consisted of prickly and smooth plants in proportions closely approximating a 3:1 ratio. The seeds of 11 prickly F_2 plants were sown. Eight of these proved to be heterozygous, and three proved to be homozygous dominants; the proportions, therefore, closely approached the expected 2:1 ratio.

Ten other F_3 families consisted of only smooth plants with one exception—family A0-10-11 consisted of 10 prickly and 44 smooth plants—notwithstanding the fact that the parent plant was classified as smooth. This family also had some plants with lobed leaves notwithstanding the fact that the parent was classified as unlobed. An examination of the individual plant records for the family indicates that accidental crossing of the F_2 parent probably occurred; it also suggested that the foreign pollen was of different genetic constitution as regards the factors for leaf form and prickles. It is believed, therefore, that family A0-10-11 should be classified as a recessive with reference to this character.

Ten F_4 families were grown of this cross. Two consisted of only prickly offspring. Three families consisted of prickly and smooth plants in proportions closely approximating a 3:1 ratio. Five families, each from a smooth parent, were made up entirely of recessives.

The results from this cross indicate that inheritance probably took place on a simple Mendelian basis, but that disturbing influences were in operation in 1915 which reduced the proportions of prickly plants.

Unlobed Wild ♀ X *Paris White Cos* ♂.—The results from a cross between unlobed Wild and Paris White Cos are given in Table

TABLE 13.—INHERITANCE OF PRICKLES, MAY KING ♀ X LOBED WILD ♂

Parent ¹	Genera- tion	Condition of parent	(S) With spines	(s) Without spines	Total	Deviation ²	Deviation P. E.
A0-1 (1915).....	F ₂	S	52	31	83	1	3.77
A0-10 (1915).....	F ₂	S	54	30	84	9	3.36
A0-12 (1915).....	F ₂	S	35	37	72	19	7.67
A0-17 (1915).....	F ₂	S	54	27	81	7	2.66
A0-18 (1915).....	F ₂	S	56	32	88	10	3.65
Total 1915.....	F ₂	S	251	157	408	55	9.32
A0-12 (1916).....	F ₂	S	36	14	50	1.5	.73
A0-17 (1916).....	F ₂	S	65	14	79	6	2.31
Total 1916.....	F ₂	S	101	28	129	4	1.21
A0-12 (1917).....	F ₂	S	21	8	29	1	.63
A0-17 (1917).....	F ₂	S	18	6	24	0	0
Total 1917.....	F ₂	S	39	14	53	1	.47
Subtotal.....	F ₂	S	381	199	590	51.5	7.26
A0-1-16.....	F ₃	S	33	0
A0-10-44.....	F ₃	S	47	0
A0-10-57.....	F ₃	S	13	0
Subtotal.....	..	.	93	0
A0-1-2.....	F ₃	S	53	21	74	2.5	1.00
A0-1-6.....	F ₃	S	53	13	66	3.5	1.47
A0-1-20.....	F ₃	S	61	17	78	2.5	.97
A0-18-40.....	F ₃	S	66	23	89	1.0	.36
A0-1-41.....	F ₃	S	17	4	21	1.0	.75
A0-1-15.....	F ₃	S	49	9	58	5.5	2.47
A0-10-15.....	F ₃	S	22	14	36	5.0	2.85
A0-10-86.....	F ₃	S	6	1	7	1.0	1.29
Subtotal.....	F ₃	S	327	102	429	5.0	.83
A0-1-32.....	F ₃	s	0	11
A0-1-84.....	F ₃	s	0	52
A0-10-28.....	F ₃	s	0	70
A0-12-45.....	F ₃	s	0	74
A0-17-10.....	F ₃	s	0	40
A0-10-28.....	F ₃	s	0	48
A0-10-10.....	F ₃	s	0	51
A0-18-38.....	F ₃	s	0	15
A0-12-62.....	F ₃	s	0	40
A0-10-11.....	F ₃	s	10 ³	44
Subtotal.....	..	.	10	445
A0-10-44-42.....	F ₄	S	39	0
A0-1-16-7.....	F ₄	S	4	0
Subtotal.....	..	.	43	0
A0-18-40-15.....	F ₄	S	30	10	40	0	0
A0-1-6-1.....	F ₄	S	29	6	35	3	1.73
A0-10-86-6.....	F ₄	S	12	3	15	1	.88
Subtotal.....	..	.	71	19	90	3.5	1.26
A0-12-45-22.....	F ₄	s	0	60
A0-17-10-15.....	F ₄	s	0	17
A0-1-20-38.....	F ₄	s	0	35
A0-12-45-30.....	F ₄	s	0	34
A0-1-32-3.....	F ₄	s	0	35
Subtotal.....

¹A0 = MK1 ♀ X W4 ♂. ²All deviations in this table are calculated on a 3 : 1 basis. ³See text.

14. The ratios of prickly and smooth plants of the two F₂ families are inconsistent, one showing a large deficiency of smooth plants and the other a slight excess. In the first family, R1-2, the deviation was over six times the probable error, while in the second case, R1-3, it was 2.28 times the probable error. The combined results show a rather wide deviation from a 3:1 ratio (Dev. / P. E. = 4.32).

Progeny of five prickly F₂ plants were grown in F₃. Three of the

families consisted of only prickly plants while two consisted of prickly and smooth plants in proportions closely approximating a 3:1 ratio.

The results from this cross show that inheritance of prickles probably took place on a simple Mendelian basis, prickly leaves being dominant to smooth leaves. It appears, however, that influences were probably in operation which caused deviations from the expected ratio.

TABLE 14.—INHERITANCE OF PRICKLES, UNLOBED WILD ♀ X PARIS WHITE COS ♂

Parent ¹	Genera- tion	Condition of parent	(S) With spines	(s) Without spines	Total	Deviation ²	Deviation P. E.
R1-2.....	F ₂	S	114	11	125	20	6.13
R1-3.....	F ₂	S	23	13	36	4	2.28
Subtotal.....	..	.	137	24	161	16	4.32
R1-2-10.....	F ₂	S	23	0
R1-2-48.....	F ₂	S	5	0
R1-2-88.....	F ₂	S	57	0
Subtotal.....	..	.	85	0
R1-2-80.....	F ₂	S	20	3	23	3	2.14
R1-2-98.....	F ₂	S	42	12	54	1.5	.70
Subtotal.....	..	.	62	15	77	4	1.56

¹R1 = W5 ♀ X Cos1-1' ♂. ²All deviations in this table are calculated on a 3:1 basis.

Grand Rapids ♀ X *Unlobed Wild* ♂.—The cross between *Grand Rapids* and unlobed *Wild* was grown only to the F₂ generation. The one F₂ family consisted of 114 prickly and 58 smooth plants. These figures represent a deviation of 15 from a 3:1 ratio, and the deviation is almost four times (3.92) the probable error.

The results from this cross show that prickly plants were dominant to smooth ones, that inheritance probably took place on a simple Mendelian basis, and that disturbing influences were probably in operation which reduced the proportion of prickly plants.

Inheritance of Leaf Form

As already explained, the wild *L. scariola* L. has pinnatifid or deeply lobed leaves. The variety *integrata* Gren. and Godr. has unlobed leaves. There are other types in the vicinity of Urbana which have lobes of intermediate size; possibly these types represent hybrid conditions. Big Boston and May King have unlobed leaves.

Comparatively few definite investigations are on record involving leaf form. Bateson (1909) describes a cross between palmatifid (palm-leaved) and pinnatifid (fern-leaved) varieties of *Primula sinensis*. According to Bateson the fern-leaved type was dominant, altho some strains, probably heterozygotes, were noted as being intermediate in leaf form. Inheritance in this case occurred on a simple Mendelian basis. Correns (1905) crossed *Urtica odorata*, which has almost

entire leaves, with *U. pilulifera*, which has sharply dentate leaves. The F_1 plants were all dentate. Segregation occurred in F_2 on a simple Mendelian basis. Tedin (1923) reported a cross between one variety of *Camelina* having "pinnatifid" leaves with another having "entire leaves, scantily dentate." The F_1 plants were intermediate, inclining toward the pinnatifid parent. Two pairs of factors were found to be involved. Four pure-breeding types were secured eventually, as follows: AABB, pinnatifid; aabb, entire; aaBB, deeply dentate; and AAbb, pinnatifid, with shorter and thicker lobes than in aaBB. Jones and Rayner (1916) crossed varieties of *Bryonia dioica*, a species which is conspicuously polymorphic with regard to shape and incision of leaves. The varietal types, however, could be readily recognized. Segregation occurred in F_2 , and practically every gradation from one parental type to the other was secured. No definite interpretation was given, but it was concluded that variability in leaf shape due to environment probably caused different genotypes to overlap one another.

There seems to be no botanical term for the opposite of pinnatifid, i.e., an entirely unlobed condition. The terms entire and denticulate, which have been used in this connection by some geneticists, refer to the margins of the leaves rather than to leaf form. In view of these circumstances the terms lobed and unlobed have been adopted in the present publication to designate the differences involved in leaf form. The term "unlobed" is used occasionally in Gray's Manual¹ to denote the opposite of pinnatifid.

In the present investigation three crosses were made involving differences in leaf form. In each case the F_1 plants were lobed, tho not so deeply as the lobed Wild parent. Segregation took place in F_2 . The results for F_2 and succeeding generations are presented in Tables 15 and 16.

May King ♀ X *Lobed Wild* ♂.—Five F_2 families, all from the same original parents, were grown of the cross between *May King* and *lobed Wild* (Table 15). Plantings of families A0-12 and A0-18 were grown in the greenhouse in 1916-17, and since the records were not kept separately in this case the results are presented together.

As stated, segregation occurred in F_2 . Some plants apparently had as deeply lobed leaves as the lobed Wild parent, while some were entirely unlobed, like the *May King*. Between these extremes, practically every gradation was secured. These gradations may have been due to genetic variations in leaf form, but it seems quite likely that differences in size, shape, crumpling, and crinkling of the leaves may have had an effect on the expression of leaf form. Such conditions added to the difficulty in taking records. Plants which had no leaves that were lobed were classified as unlobed. All others were designated as lobed.

¹Robinson and Fernald, 1908.

The proportions of lobed to unlobed individuals in F_2 suggested a 9:7 ratio, and this ratio was further supported by the breeding results in F_3 . The deviations and probable errors have therefore been calculated on a 9:7 basis for the F_2 families and for part of those segregating in later generations.

The results in F_2 (Table 15) show that each family consisted of lobed and unlobed plants in the proportion of about 9:7. In every case the deviation was quite small in relation to the probable error, and

TABLE 15.—INHERITANCE OF LEAF FORM, MAY KING ♀ X LOBED WILD ♂

Parent ¹	Generation	Condition of parent	Lobed	Unlobed	Total	Deviation	Deviation P. E.
A0-1.....	F_2	L	50	30	80	9:7 basis	1.67
A0-10.....	F_2	L	45	33	78	5	.34
A0-12.....	F_2	L	79	70	149	5	1.23
A0-17.....	F_2	L	129	107	236	4	.78
A0-18.....	F_2	L	43	37	80	2	.67
A0-12 & A0-18 (1916-17)	F_2	L	56	40	96	2	.61
Subtotal.....	402	317	719	2	.22
A0-10-10.....	F_3	L	51	0
A0-1-84.....	F_3	L	50	2 (7)
Subtotal.....	101	2 (7)
A0-10-44.....	F_3	L	32	16	48	3:1 basis	1.98
A0-10-28.....	F_3	L	49	21	70	4	1.43
A0-1-41.....	F_3	L	14	7	21	3.5	1.50
A0-10-28.....	F_3	L	41	7	48	2	2.47
A0-12-82.....	F_3	L	2	1	3	5	0
Subtotal.....	138	52	190	0	1.12
A0-1-2.....	F_3	L	30	42	72	9:7 basis	3.70
A0-1-6.....	F_3	L	38	28	66	10.5	.37
A0-1-20.....	F_3	L	52	26	78	1	2.71
A0-18-40.....	F_3	L	37	47	84	8	3.26
A0-10-15.....	F_3	L	18	19	37	10	1.47
A0-12-50 ²	F_3	L	2	3	5	3	1.34
A0-12-62.....	F_3	L	22	18	40	1	.24
A0-12-101 ²	F_3	L	7	5	12	.5	0
Subtotal.....	206	188	394	0	.91
A0-18-38.....	F_3	l	0	15
A0-1-16.....	F_3	l	0	33
A0-10-57.....	F_3	l	0	14
A0-10-86.....	F_3	l	0	7
A0-12-45.....	F_3	l	0	80
A0-17-10.....	F_3	l	0	40
A0-1-15.....	F_3	l	0	58
A0-10-11.....	F_3	l	8 ²	46
Subtotal.....	8	293
A0-18-40-15.....	F_4	L	40	0
Subtotal.....	40	0
A0-10-44-42.....	F_4	L	28	11	39	3:1 basis	.55
Subtotal.....	28	11	39	1	.55
A0-12-45-22.....	F_4	l	0	60
A0-17-10-15.....	F_4	l	0	17
A0-1-6-1.....	F_4	l	0	35
A0-1-20-38.....	F_4	l	0	35
A0-12-45-30.....	F_4	l	0	34
A0-1-16-7.....	F_4	l	0	4
A0-10-86-6.....	F_4	l	0	15
A0-1-32-6.....	F_4	l	0	35
Subtotal.....	0	235

¹A0 = MK1 ♀ X W4 ♂. ²See text.

TABLE 16.—INHERITANCE OF LEAF FORM, BIG BOSTON ♀ X LOBED WILD ♂

Parent ¹	Genera- tion	Condition of parent	Lobed	Unlobed	Total	Deviation	Deviation P. E.
C0-1.....	F ₂	L	141	93	234	9 : 7 basis 9	1.76
C0-3.....	F ₂	L	237	98	335	49	8.00
Subtotal.....	378	191	569	58	7.27
C0-1-26.....	F ₃	L	50	2 (?)
C0-3-58.....	F ₃	L	4	0
Subtotal.....	54	2
C0-3-1'.....	F ₃	L	1	1	2	3 : 1 basis .5	1.21
C0-3-15'.....	F ₃	L	10	1	11	2	2.06
C0-3-42'.....	F ₃	L	4	2	6	.5	.70
C0-1-62.....	F ₃	L	32	11	43	0	0
C0-3-10.....	F ₃	L	32	9	41	1	.53
Subtotal.....	79	24	103	2	.68
C0-3-80'.....	F ₃	L	3	3	6	9 : 7 basis 0	0
C0-3-58'.....	F ₃	L	14	7	21	2	1.30
C0-3-52'.....	F ₃	L	1	2	3	1	1.73
C0-3-62'.....	F ₃	L	3	2	5	0	0
C0-1-124.....	F ₃	L	15	11	26	0	0
C0-3-17.....	F ₃	L	22	10	32	4	2.11
C0-3-103.....	F ₃	L	39	19	58	6	2.35
Subtotal.....	97	54	151	13	3.16
C0-3-23.....	F ₃	l	0	1
C0-3-8.....	F ₃	l	0	2
C0-3-82.....	F ₃	l	0	12
C0-3-67.....	F ₃	l	0	1
C0-3-99.....	F ₃	l	0	31
Subtotal.....	0	47
C0-3-99-13.....	F ₄	l	0	9
Subtotal.....	0	9

¹C0 = BB7 ♀ X W4 ♂.

the combined total of 719 individuals showed a deviation of only 2 from a 9:7 ratio, the deviation being .22 of the probable error.

If inheritance took place on a complementary factor basis with two pairs of factors involved, as was suggested by the F₂ results, the unlobed F₂ plants when selfed should have produced only unlobed plants in F₃. Table 15 shows that seven F₂ families, each from an F₂ unlobed parent, consisted entirely of unlobed individuals. Another F₂ family (A0-10-11, descended from an unlobed F₂ parent) consisted of eight lobed and forty-six unlobed plants; this is the same family which showed an irregularity in regard to prickles. It is believed, as explained in connection with the discussion of the inheritance of prickles, that accidental crossing occurred in the F₂ generation of this family, and the family is therefore classed as a recessive.

We should expect, furthermore, that unlobed F₃ families would, when selfed, continue to produce nothing but plants with unlobed leaves in F₄ and succeeding generations. In F₄ five of the eight unlobed families were from unlobed F₃ plants which in turn had unlobed F₂ parents. The other three unlobed F₄ families were from unlobed segregates of heterozygous F₃ parents. In no case did an unlobed plant throw lobed individuals (except in family A0-10-11, whose parent, as explained, was probably crossed accidentally).

Regarding the lobed F_2 plants, one out of nine of these on the average, when selfed, should have bred true; four should have produced lobed and unlobed plants in the proportion of about 9 to 7; and four should have produced lobed and unlobed plants in a ratio of about 3 to 1. As a matter of fact, two of the fifteen F_3 families from lobed F_2 parents bred as pure dominants; five apparently belonged to the 3:1 class; and eight apparently segregated on a 9:7 basis. These numbers are reasonably near the expected 1:4:4 proportions.

The five F_3 families which apparently segregated on a 3:1 basis both individually and collectively showed a small deviation from the expected ratio, and the deviation divided by the probable error is small enough in all cases to indicate that the results are reasonably significant.

Of the eight families which apparently segregated on a 9:7 basis, two showed deviations which were somewhat high in relation to the probable error. The figures from the other six families and the combined total closely approximate a 9:7 ratio.

It is true that in some families of both segregating F_2 groups the numbers were small, but these families could be shifted from one group to the other or omitted altogether without materially affecting the interpretation of inheritance on a complementary factor basis, with two allelomorphous pairs involved.

In addition to the eight recessive F_4 families discussed, one (A0-18-40-15, from a lobed F_3 parent) consisted of only lobed individuals, and another (A0-10-44-42, from a lobed F_3 parent) consisted of 28 lobed and 11 unlobed plants, which is a deviation of only one from a 3:1 ratio.

It is recognized that one additional test should have been applied. Crosses should have been made between various unlobed segregates of the F_2 or F_3 generations. By making several matings of this kind it should have been possible to find two unlobed plants which when bred together would have produced the fully lobed condition. Such a test, with the result described, would have served as final proof of inheritance on a complementary factor basis.

Big Boston ♀ X *Lobed Wild* ♂.—The results from the cross between *Big Boston* and lobed *Wild* (Table 16) also support the interpretation of inheritance on a complementary factor basis. One F_2 family (C0-1) showed a deviation from a 9:7 ratio which is small in comparison with the probable error. The other family (C0-3) showed a wide departure from a 9:7 ratio; in fact, the proportions approached a 3:1 ratio more closely than a 9:7 ratio.

In F_3 , two F_2 lobed plants were found to be pure dominants; five seemed to show segregation on a 3:1 basis; and seven appeared to segregate on a 9:7 basis. These figures are reasonably near the expected 1:4:4 ratio, considering the numbers involved.

Five F_3 families and one F_4 family, each from an unlobed F_2 parent, consisted of only unlobed individuals.

Unlobed Wild ♀ X *Lobed Wild* ♂.—A cross was made in 1915 between an unlobed and a lobed Wild form. W5 was used as the female parent, the same plant that was used for other crosses. W4-1' was used as the male parent; the parent of this plant (W4) was used as the male parent in the crosses just described with Big Boston and May King.

The F_1 plants were all lobed. In 1917, 104 F_2 plants were grown; 73 of these were lobed and 31 were unlobed. Since these figures represent a deviation of only 5 from a 3:1 ratio, it appears that inheritance occurred on a simple Mendelian basis.

The breeding results from plant W4 in the crosses with Big Boston and May King indicate that plant W4-1' must have been a pure dominant for both factor pairs. It will therefore be represented by the formula $U_1 U_1 U_2 U_2$. In order to make possible a 3:1 ratio in F_2 , the unlobed parent must have been of the constitution $U_1 U_1 u_2 u_2$ or $u_1 u_1 U_2 U_2$. Either of these crossed with the type $U_1 U_1 U_2 U_2$ would have produced a 3:1 ratio in F_2 .

Inheritance of Quantitative Characters

In addition to the characters described, studies were made of leaf length, leaf width, width index (width divided by length), leaf area, time required to reach date of first bloom, height of plants, heading habit, and color of leaves. In each of these character complexes inheritance was found to take place in a quantitative manner.

Our present methods of explaining the inheritance of quantitative characters are based on the analyses of Nilsson-Ehle (1908, 1909), East and Hayes (1912), Emerson and East (1913), Shull (1914, 1921), Jones (1918), East and Jones (1919) and others. While there are still differences of opinion among geneticists regarding details, the methods of interpretation now almost universally accepted would seem capable of accounting for all the results which have been observed to date. It appears inadvisable, therefore, to discuss each cross separately for each of the character complexes investigated or to enter into a detailed explanation regarding them. In the following discussion specific attention will be given only to such features as seem more or less out of the ordinary from a genetic standpoint or of particular value from an economic standpoint. Each of the character complexes will be discussed as a whole for all of the crosses.

Leaf Length

Since lettuce is cultivated largely for its leaves, a study of leaf sizes and shapes seemed particularly important in this investigation.

The parent types differed materially in leaf length. Marked differences were later observed in the hybrids, indicating that segregation and recombination had taken place.

In order to study leaf length, measurements were taken of the length of three of the largest rosette leaves from each plant. These measurements were all taken at the same time for a given family, but the time varied for different families. Each family was measured when the largest possible proportion of its plants seemed to have attained full rosette leaf development. It is realized that because of genetic variation in the F_2 and succeeding generations as to rate of growth, a certain amount of experimental error may have been introduced by this method, for manifestly all plants of a given family did not reach full rosette development simultaneously. To minimize this error as far as possible, the measuring was delayed until some of the plants in each family were developing seed stalks. This gave at least a portion of the slower growing plants an opportunity to attain maximum or near-maximum rosette leaf development. Since the rosette leaves practically stop development at the time the seed stalks appear and do not deteriorate appreciably for several days, more comparable measurements were probably secured by this method than could have been secured by any other. It is evident that if any error occurred because of the method of taking measurements, the chief result of it was to exaggerate the lower classes of the frequency distributions. No conspicuous effect of this kind was observed. All things considered, the method of taking measurements seemed the most practical one to use under the existing field conditions, and it is believed the experimental error from the cause described was reduced to negligible proportions.

In order that the measurements might be taken as accurately as possible, the leaves were removed from the plant. The length measurements were taken of the midribs, since those represented the greatest leaf length. No difficulty was experienced in obtaining these measurements. Relatively small differences were found in the length of the three leaves from each plant.

The leaf lengths of the three leaves from each plant were averaged, and the averages for the different plants were used in constructing frequency distributions. The results are presented in Tables 17 to 25.

Inspection of the data shows that all of the parents exhibited a relatively low variability for each season, except family W4-1' in 1916. In this particular population only 25 individuals were grown, and the increased variation may have been due to errors in random sampling or to the varying effects of environment. This same stock and one of its progeny (W4-1'-11) showed a relatively low variation in 1917.

The parental varieties exhibited about the same relations to each other in each cross for the different seasons, except that in 1917 the means were larger and the variabilities greater for the cultivated varie-

TABLE 17.—INHERITANCE OF LEAF LENGTH, MAY KING ♀ X GRAND RAPIDS ♂ AND RECIPROCAL

Parent ¹	Year grown	Generation	Class centers in centimeters															Total	Mean	S. D.	C. V.		
			10.0	11.5	13.0	14.5	16.0	17.5	19.0	20.5	22.0	23.5	25.0	26.5	28.0	29.5	31.0					32.5	34.0
			..	2	50	2	0	0	1	25	8	2
MK1-1'	1915	F ₂	55				
GR2-3-1	1915	F ₂	74				
E2-1, E2-4, and E2-6	1915	F ₂	323				
MK1-1'	1916	F ₂	66				
GR2-3-1'	1916	F ₂	75				
E4, E7, E0	1916	F ₁	116				
E0	1916	F ₁	7				
E7-1, E7-3, and E7-9	1916	F ₁	151				
E2-4-4'	1916	F ₂	70				
E2-4-10	1916	F ₂	33				
E2-4-10'	1916	F ₂	54				
MK1-1'	1917	F ₂	66				
GR2-3-1'	1917	F ₂	98				
E7-1	1917	F ₂	8				
E7-1-18	1917	F ₂	21				
E7-3-65	1917	F ₂	8				
E7-3-3	1917	F ₂	39				
E7-3-22	1917	F ₂	26				
E7-1-19	1917	F ₂	17				
E7-3-20	1917	F ₂	50				
E7-3-47	1917	F ₂	17				
E7-3-5	1917	F ₂	50				
E7-3-15	1917	F ₂	25				
E7-1-15	1917	F ₂	43				
E7-1-6	1917	F ₂	17				
E7-1-2	1917	F ₂	35				
E7-1-67	1917	F ₂	53				
			11				

¹E2 = MK15 ♀ X GR1 ♂; E4 = MK15 ♀ X GR2-3-1' ♂; E7 = MK1-1' ♀ X GR2-3-1' ♂; E0 = MK1 ♀ X GR2 ♂; F0 = GR2-2 ♀ X MK1-5 ♂.

TABLE 18.—INHERITANCE OF LEAF LENGTH, BIG BOSTON ♀ X PARIS WHITE COS ♂

Parent ¹	Year grown	Generation	Class centers in centimeters												Total	Mean	S. D.	C. V.			
			14.5	16.0	17.5	19.0	20.5	22.0	23.5	25.0	26.5	28.0	29.5	31.0					32.5	34.0	35.5
			6	17	22	14	2	5	8	19	21	13					4
BB7-1'	1916	P ₂	61	17.23 ± .13	1.50 ± .09	8.71 ± .53		
Cos1-1'	1916	P ₂	72	28.73 ± .17	2.08 ± .12	7.24 ± .41		
N1 and N2	1916	F ₁	08	27.49 ± .24	2.94 ± .17	10.69 ± .63		
N1-1, N1-2, N1-4, and N1-5	1916	F ₂	2	2	8	10	12	9	10	7	5	3	4	2	..	84	22.91 ± .31	4.27 ± .22	18.64 ± 1.00		
BB7-1'	1917	F ₂	1	3	11	22	22	1	1	1	0	4	10	14	11	60	19.25 ± .13	1.45 ± .09	7.53 ± .46		
Cos1-1'	1917	F ₂	1	1	4	6	5	1	1	1	0	4	10	14	7	51	30.94 ± .25	2.66 ± .18	8.60 ± .57		
N1-5	1917	F ₂	1	1	4	6	5	1	1	1	0	4	10	14	7	72	24.69 ± .33	4.13 ± .23	16.73 ± .97		

¹BB = Big Boston; Cos = Paris White Cos; N1 = BB7-1' ♀ X Cos1-1' ♂.

TABLE 19.—INHERITANCE OF LEAF LENGTH, GRAND RAPIDS ♀ X UNLOBED WILD ♂ AND RECIPOCAL

Parent ¹	Year grown	Generation	Class centers in centimeters												Total	Mean	S. D.	C. V.	
			14.5	16.0	17.5	19.0	20.5	22.0	23.5	25.0	26.5	28.0	29.5						
			1	0	2	6	14	28	14	6	4						
W5(unlobed)	1916	P ₁	75	22.02 ± .17	2.16 ± .12	9.81 ± .54
GR2-3-1'	1916	P ₃	6	15	33	20	1	75	20.40 ± .11	1.37 ± .08	6.72 ± .37
S1	1916	F ₁	4
W4-1' (lobed)	1917	P ₂	2	5	18	4	5	1	35	20.84 ± .19	1.68 ± .14	8.06 ± .65
GR2-3-1'	1917	P ₃	2	18	35	7	3	65	21.79 ± .20	1.23 ± .07	5.65 ± .33
T2-1	1917	F ₂	1	0	7	9	3	7	17	20	14	10	4	92	23.83 ± .24	3.40 ± .17	14.27 ± .72

¹W = Wild; GR = Grand Rapids; S1 = W5 ♀ X GR2-3-1' ♂; T2 = GR2-3-1' ♀ X W5 ♂. *No unlobed Wild were grown in 1917; the results from W4-1' (lobed) are included for comparison.

TABLE 20.—INHERITANCE OF LEAF LENGTH, GRAND RAPIDS ♀ X PARIS WHITE COS ♂

Parent ¹	Year grown	Generation	Class centers in centimeters												Total	Mean	S. D.	C. V.			
			11.5	13.0	14.5	16.0	17.5	19.0	20.5	22.0	23.5	25.0	26.5	28.0					29.5	31.0	32.5
		
GR2-3-1'	1916	P ₂	75	20.40 ± .11	1.37 ± .08	6.72 ± .37		
Cos1-1'	1916	P ₂	72	28.73 ± .17	2.08 ± .12	7.24 ± .41		
Y1	1916	F ₁	2		
Y1-1, Y1-2, and Y1-3	1916	F ₂	1	3	4	11	10	25	22	26	24	18	16	7	5	176	21.96 ± .21	4.04 ± .15	18.40 ± .68		

¹GR = Grand Rapids; Cos = Paris White Cos; Y1 = GR2-3-1' ♀ X Cos1-1' ♂.

TABLE 21.—INHERITANCE OF LEAF LENGTH, BIG BOSTON ♀ X UNLOBED WILD ♂ AND RECIPROCAL

Parent ¹	Year grown	Generation	Class centers in centimeters												Total	Mean	S. D.	C. V.
			Class centers in centimeters															
			8.5	10.0	11.5	13.0	14.5	16.0	17.5	19.0	20.5	22.0	23.5	25.0				
BB7-1'	1915	P ₂	
C2.....	1915	F ₁	
BB7-1'	1916	P ₂	
W5 (unlobed)	1916	F ₁	
C1 and C3	1916	P ₁	
D1.....	1916	F ₁	
C3-1.....	1916	F ₁	
D1-1 and D1-2.....	1916	F ₂	
BB7-1'	1917	P ₂	
W4-1' (lobed) ²	1917	F ₂	
C1-27.....	1917	F ₂	
D1-12.....	1917	F ₂	
C3-1-15.....	1917	F ₂	
D1-1-10.....	1917	F ₃	
D1-2-2.....	1917	F ₃	
C3-1-2.....	1917	F ₃	

¹C2 = BB5-5 ♀ X W38 (unlobed) ♂; C1 = BB5-4 ♀ X W38 ♂; C3 = BB7-1' ♀ X W5 (unlobed) ♂; D1 = W5 ♀ X BB7-1' ♂. ²No unlobed Wild were grown in 1917; the results from W4-1' (lobed) are included for comparison.

TABLE 22.—INHERITANCE OF LEAF LENGTH, UNLOBED WILD ♀ X PARIS WHITE COS ♂

Parent ¹	Year grown	Generation	Class centers in centimeters												Total	Mean	S. D.	C. V.
			Class centers in centimeters															
			10.0	11.5	13.0	14.5	16.0	17.5	19.0	20.5	22.0	23.5	25.0	26.5				
Cos1-1'	1916	P ₂
W5 (unlobed)	1916	F ₁
P1.....	1916	F ₁
R1.....	1916	F ₁
R1-2.....	1916	F ₂
Cos1-1'	1917	P ₂
R1-2.....	1917	F ₂
R1-2-48.....	1917	F ₂
R1-2-10.....	1917	F ₃

¹W = Wild; Cos = Paris White Cos; P1 = Cos1-1' ♀ X W5 ♂; R1 = W5 ♀ X Cos1-1' ♂.

TABLE 23.—INHERITANCE OF LEAF LENGTH, BIG BOSTON ♀ X GRAND RAPIDS ♂ AND RECIPROCAL

Parent ¹	Year grown	Generation	Class centers in centimeters												Total	Mean	S. D.	C. V.															
			7.0	8.0	10.0	11.0	13.0	14.0	15.0	16.0	17.0	18.0	19.0	20.0					22.0	23.0	25.0	28.0	29.5	31.0	32.5	34.0	35.0	37.0					
BB7-1'	1915	P ₂							7	27	3																	37	15.84 ± .08	.76 ± .06	4.80 ± .38		
GR2-3-1	1915	P ₂							1	7	13	5	4	2	9	17	13	21	19	14	8	6	4					74	19.73 ± .11	1.44 ± .23	7.30 ± .41		
G4-9 and G4-23	1915	P ₂							6	17	22	14	2															160	23.53 ± .32	6.02 ± .23	25.58 ± 1.03		
BB7-1'	1916	P ₂							6	15	33	20	1															61	17.23 ± .13	1.50 ± .09	8.71 ± .53		
GR2-3-1'	1916	P ₂												2	1	1	2	1										75	20.40 ± .11	1.37 ± .08	6.72 ± .37		
G0 and G2	1916	F ₁																										7	24.79 ± .56	2.19 ± .40	8.83 ± 1.59		
H2	1916	F ₁												3	1	1												6	23.50 ± .48	1.73 ± .38	7.36 ± 1.43		
G4-9-14'	1916	F ₃							1	2	4	2																13	14.96 ± .32	1.70 ± .23	11.36 ± 1.52		
G4-9-6	1916	F ₃							1	13	3	2																19	14.97 ± .17	1.09 ± .12	7.28 ± .80		
G4-9-14	1916	F ₃							1	9	26	22	6	3	0	0	0	0	0	0								67	16.72 ± .13	1.54 ± .09	9.21 ± .54		
G4-23-6	1916	F ₃							1	4	7	3	5	15	8	2												75	20.72 ± .14	1.74 ± .10	8.40 ± .46		
G4-9-8	1916	F ₃							1	9	7	3	5	15	7	5	3	1										75	21.06 ± .40	5.15 ± .28	24.45 ± 1.43		
G4-9-8-6'	1916	F ₄							7	6	18	13	16	12	4													76	17.52 ± .19	2.46 ± .14	14.04 ± .78		
G4-9-8-4'	1916	F ₄							1	3	2	1	9	7	4	1	1											23	19.59 ± .49	3.45 ± .34	17.61 ± 1.80		
G4-9-8-4'	1916	F ₄							3	11	22	9	2	1	1													60	19.26 ± .13	1.45 ± .09	7.53 ± .46		
BB7-1'	1917	P ₂																										60	21.79 ± .10	1.23 ± .07	5.69 ± .33		
GR2-3-1'	1917	P ₂							4	3	2	4	1	2	18	36	7	3										65	23.75 ± .36	4.34 ± .26	18.27 ± 1.12		
G4-5	1917	F ₂							4	2	4	1	9	5	17	7	4	8	0	1								29	20.40 ± .36	2.89 ± .26	14.17 ± 1.28		
G4-13-1'	1917	F ₂							4	2	8	3	6	4	1	0	1											36	30.88 ± .27	2.41 ± .19	7.80 ± 1.62		
G4-9-22'	1917	F ₃							1	0	7	9	4	2	1													24	13.00 ± .28	2.03 ± .20	15.62 ± 1.56		
G4-9-6-5	1917	F ₄							8	10	6	1																27	15.78 ± .19	1.46 ± .13	9.25 ± .85		
G4-9-14-12'	1917	F ₄							2	5	3	1																8	17.69 ± .28	1.17 ± .20	6.61 ± 1.11		
G4-9-14-42	1917	F ₄							2	1	15	12	15	2														47	21.87 ± .17	1.69 ± .12	7.73 ± .54		
G4-23-6-67	1917	F ₄																															

¹G4 = BB7 ♀ X GR2 ♂; G0 = BB5 ♀ X GR2 ♂; G2 = BB11 ♀ X GR1 ♂; H2 = GR2-3-2' ♀ X BB7-1' ♂.

TABLE 24.—INHERITANCE OF LEAF LENGTH, BIG BOSTON ♀ X LOBED WILD ♂

Parent ¹	Year grown	Generation	Class centers in centimeters																Total	Mean	S. D.	C. V.			
			8	10	11	13	14	16	17	19	20	22	23	25	26	28	29	31					32	33	34
W4 (lobed)	1915	P ₁	58
BB7-1'	1915	P ₂	37
CO-1 and CO-3	1915	F ₂	219
W4-1' (lobed)	1916	P ₂	25
BB7-1'	1916	P ₂	61
CO-1 and CO-3	1916	F ₂	1	0	4	8	13	14	21	19	23	19	15	4	2	1	154
CO-3-99	1916	F ₂	31
BB7-1'	1917	P ₂	60
W4-1' (lobed)	1917	P ₂	35
W4-1'-1 (lobed)	1917	P ₂	30
CO-1 and CO-3	1917	F ₂	20
CO-1-24	1917	F ₂	1	2	4	8	3	2	1	3	1	85
CO-1	1917	F ₃	28
CO-3-10	1917	F ₃	25
CO-3-103	1917	F ₃	49
CO-3-17	1917	F ₃	42
CO-3-17	1917	F ₃	53
CO-1-62	1917	F ₄	32
CO-3-99-13	1917	F ₄	41
..	1917	F ₄	7

CO = BB7 ♀ X W4 ♂.

ties than in the previous two years, while those of the wild form were reduced. The data in Table 26, which summarizes the means of all the parental types grown in more than one season, shows that no exception occurred in this regard. This circumstance caused the frequency distributions of the parents in the cultivated-wild crosses to overlap each other to a certain extent in 1917, while in 1915 and 1916

TABLE 26.—MEANS OF PARENTAL VARIETIES FOR EACH SEASON IN LEAF LENGTH

Name of variety	Means in leaf length (centimeters)		
	1915	1916	1917
Wild (lobed form).....	25.54 ± .19	25.54 ± .51	20.84 ± .19
May King.....	13.11 ± .08	13.55 ± .09	16.25 ± .13
Big Boston.....	15.84 ± .08	17.23 ± .13	19.25 ± .13
Grand Rapids.....	19.73 ± .11	20.40 ± .11	21.79 ± .10
Paris White Cos.....	28.73 ± .17	30.94 ± .25

they did not overlap. In other words, it appears that certain influences were in operation in 1917 which increased the length of leaves of cultivated varieties and at the same time decreased the leaf length of the wild *L. scariola* as compared with their respective leaf lengths in 1915 and 1916.

Because of the difficulty in obtaining hybrids, the F_1 plants of some crosses were grown in small numbers and in the greenhouse only. While measurements were taken in most of such cases, these obviously cannot be compared with measurements taken under field conditions, and they are therefore not presented.

The tables show that the F_1 generations exhibited practically as low variability as the parental types in every cross but May King X Grand Rapids in 1916 (Table 17).

The behavior of this cross in general leads the author to believe this exception was due to errors in random sampling or to environment rather than to genetic variation.

In the cross between Grand Rapids and Paris White Cos (Table 20), the F_1 mean occupied a position approximately intermediate between those of the parents, indicating a lack of dominance or the existence of positive- and negative-acting genes which practically neutralized the effects of each other. In no cross did the F_1 frequency distribution and mean occupy positions approximating those of the shorter-leaved parent.

In crosses between Grand Rapids and unlobed Wild (Table 19), Big Boston and Paris White Cos (Table 18), and unlobed Wild and Paris White Cos (Table 22), the F_1 frequency distributions and means closely approximated those of the longer-leaved parent of each cross, tho in some cases the number of F_1 's was too small to admit of definite conclusions. Such circumstances indicate either dominance of the

longer-leaved type or the bringing together in F_1 of genes which had an additive effect on leaf length. In the crosses between Big Boston and unlobed Wild (Table 21), May King and Grand Rapids (Table 17), and Big Boston and Grand Rapids (Table 23), the F_1 distributions and means ranged appreciably above those of the longer-leaved parent, which indicates that the frequency distribution of the longer-leaved parent did not occupy a position at the extreme upper limit of the genetic variability of the F_2 generation. Such a circumstance suggests the possibility of securing new types thru hybridization with longer leaves than those of the longer-leaved parent.

In all crosses in which reciprocal F_1 families were grown, the results were substantially the same.

The F_2 populations exhibited a greater variability in all cases than the parents or the corresponding F_1 families, indicating that segregation of leaf-length genes had taken place.

In the crosses between Big Boston and lobed Wild (Table 24) and between May King and lobed Wild (Table 25), the F_2 families exhibited different relations with respect to the original parents in the different seasons. In 1915, the F_2 of both crosses ranged from one class above the lowest class of the shorter-leaved (cultivated) parent to points several classes beyond the upper extreme of the longer-leaved parent; in 1916, both ranged from slightly below the lower extreme of the cultivated parent to points several classes above the upper extreme of the wild type; and in 1917, the F_2 range of May King X lobed Wild slightly overlapped the extremes of both parents. In Big Boston X lobed Wild the F_2 range extended from about the lower class of the Big Boston to a point five classes (7.5 centimeters) above the upper extreme of the wild. These facts again suggest that some environmental influence affected variously the expression of the genetic factors carried by the original parents.

The results with respect to dominance and ranges of variation are best explained by considering the F_1 and F_2 distributions jointly. In the cross between Grand Rapids and Paris White Cos (Table 20) the distributions of both the F_1 and F_2 families indicated a combination of genes which produced an effect in a minus direction. The two F_1 plants approached in leaf length somewhat closely the mean of the Grand Rapids parent. The F_2 showed a normal curve of error, ranging from the upper extreme of the Cos type to a point four classes (6 centimeters) below the lower extreme of the Grand Rapids. The spread of both the F_1 and F_2 distributions in a minus direction indicates a dominance of genes contributed by the shorter-leaved parent. Since a rather large number of F_2 's (176) of this cross was grown in 1916, it appears that the frequency distribution of the Cos parent may have stood at or near the upper extreme of the F_2 frequency distribution, while that of the Grand Rapids did not lie at the lower extreme.

In contrast to these results the F_1 and F_2 populations of all other crosses considered together indicate partial dominance of the longer-leaved form. In the crosses between Big Boston and Cos (Table 18), unlobed Wild and Cos (Table 22), and Grand Rapids and Wild (Table 19), the F_1 means and distribution frequencies approximately coincide with those of the longer-leaved parent. The F_2 of each of these approximately covered the combined frequency distributions of both parents altho that of Grand Rapids X unlobed Wild appeared to extend slightly above that of the longer-leaved parent. Furthermore, the F_2 distributions of each (except Big Boston X Cos in 1916) are more heavily weighted on the upper than on the lower sides, and there are also evidences of bi- or multi-modal effects.

No F_1 's of the crosses May King X lobed Wild and Big Boston X lobed Wild were grown in the open; but the F_2 distributions, while varying for different seasons, appear to extend from about the lower extreme of the shorter-leaved parent to a point beyond the upper limits of the longer-leaved variety. Both distributions are heavier on the upper than on the lower sides, and there are evidences of bi- or multi-modal effects. In addition to indicating partial dominance, such circumstances indicate a combination of growth genes from both parents in some of the F_2 plants, and the data also indicate that longer-leaved types than either of the parents could probably be isolated from these crosses.

The F_1 populations of Big Boston X unlobed Wild (Table 21), May King X Grand Rapids (Table 17), and Big Boston X Grand Rapids (Table 23) exhibited longer mean leaf lengths than those of the parents. While the F_2 's varied somewhat from season to season, their frequency distributions range in general from about the lower extreme of the shorter-leaved parent to a point beyond the upper limit of the longer-leaved parent. The F_2 distributions of each are more heavily weighted on the upper than on the lower sides and there are evidences of bi- and multi-modal effects. These results indicate that the longer-leaved type is partially dominant and that new types could probably be secured from each cross with longer leaves than either parent.

Further evidence of partial dominance and of bi- and multi-modal effects is furnished by some of the F_3 families.

The F_3 and F_4 families, in keeping with expectations, gave further evidence of segregation and recombination of genes affecting leaf length. Some of them showed practically as low variability as the original parents; others showed as much variation as, or slightly more than, the F_2 families; while still others exhibited different degrees of variation between these extremes.

In general the F_3 and F_4 means occupied positions between those of the parents, and the frequency distribution for the most part ranged

within those of the F_2 generations. There were, however, a few outstanding exceptions. Family A0-18-40-15, grown in 1917 (Table 25), had a distribution which extended slightly above that of the F_2 population for that season; it had a coefficient of variation of $8.62 \pm .66$ as compared with $9.60 \pm .56$ for the May King and $8.06 \pm .65$ for W4-1', suggesting a relatively high degree of homozygosity; and it had a mean of $27.25 \pm .25$ centimeters as compared with $20.84 \pm .19$ for W4-1' and $16.25 \pm .13$ for May King. Thus, the leaves of this family were over 30 percent longer on the average than those of the longer-leaved parent (P_1).

The cross between Big Boston and Grand Rapids (Table 23) showed two interesting families, one in F_3 and the other in F_4 , both grown in 1917. The distribution of one family extended decidedly below that of both the F_2 and the shorter-leaved (Big Boston) parent, and its mean was $13.00 \pm .28$ centimeters as compared with $19.25 \pm .13$ for Big Boston during the same season. Its variability was somewhat high (C. V. = 15.62 ± 1.56), but this was due in part to one plant with leaves 7 centimeters long, all others having leaves of 11.5 centimeters or above in length. Possibly this plant was either delayed in growth or injured. Without it the family would have had a mean of 13.26 centimeters and a coefficient of variation of 12.36, which would have made it still decidedly shorter-leaved than the Big Boston. The F_3 parent of this family had a leaf length of 14.5 centimeters, and the frequency distribution and mean in 1916 coincided rather closely with those of Big Boston. The F_3 parent had a leaf length of 16 centimeters. Thus this strain was short-leaved thruout, following its appearance in F_2 .

Another family of this cross, G4-9-22', produced 7 individuals out of a total of 36 which had longer leaves than any plants of the F_2 grown the same season, and it had two plants which had longer leaves than any other plants grown thruout the investigation of this cross. This family had a mean leaf length of $30.88 \pm .27$ centimeters as compared with $21.79 \pm .10$ for Grand Rapids and $19.25 \pm .13$ for Big Boston in the same season. Thus this strain had an average leaf length of over 41 percent above that of the longer-leaved parent. The standard deviation and coefficient of variation for this family compare favorably with those of the parents, indicating a high degree of homozygosity. Unfortunately the F_2 parent of this family was grown in the greenhouse, so that comparable measurements are not available.

The means of families G4-9-6-5 and G4-9-22' were $13.00 \pm .28$ and $30.88 \pm .27$ centimeters respectively. There is good reason for believing that types could be "fixed" which would approximately coincide with these for leaf length. The means of these two families differed by 14.88 centimeters and the mean of the longer-leaved family was about $2\frac{1}{3}$ times as large as that of the shorter-leaved one. On the

other hand, the parental varieties differed by only 2.54 centimeters in the same season. It is evident that growth genes for leaf length were combined, from parents which do not differ greatly in mean leaf length, which resulted in types having much longer and much shorter leaves than those of the parents.

Leaf Width

The parent varieties used in this investigation exhibited marked differences in regard to leaf width. These differences were particularly conspicuous between the cultivated and wild forms.

The measurements for leaf width were taken at the same time as those for leaf length. Because of the crinkling and crumpling of the leaves of some varieties, it was more difficult to secure the leaf-width measurements than the leaf-length measurements. In taking these the leaves were spread over the ruler to the greatest leaf width. The measurements for leaf width therefore represent, as far as conditions would permit, the full width of the leaf surface.

The frequency distributions for inheritance of leaf width are presented in Tables 27 to 35.

The results indicate that all of the parental varieties exhibited relatively little variation in each of the seasons grown, with the exception of Big Boston in 1916. The increased variation shown by this variety was probably due to errors in random sampling.

In all crosses the parent which had the wider leaves in one season had wider leaves in all the seasons grown. The frequency distribution and means of the parents, however, varied somewhat from season to season with reference to each other, apparently from environmental influences.

The F_1 hybrids exhibited variabilities which were practically the same as those of the parental forms, except those of the cross May King X Grand Rapids in 1916 (Table 27). The coefficient of variation of the combined F_1 families of this cross was intermediate between those of the parents and of the F_2 .

The F_2 generations of all crosses exhibited markedly increased variabilities compared with the parents and the F_1 populations, indicating that segregation had taken place.

With regard to dominance or lack of dominance the various crosses showed different conditions. In the crosses between May King and Grand Rapids (Table 27), Big Boston and Grand Rapids (Table 28), and Grand Rapids and Cos (Table 31), no dominance was apparent either in the F_1 or F_2 generations. In each of these crosses the F_1 distribution occupied a position about midway between those of the parents. The F_2 of Grand Rapids X Cos showed a wide variation (from 7.75 cm. to 28.75 cm.), equalling the combined distributions of both parents, notwithstanding the fact that only 176 individuals were

TABLE 27.—INHERITANCE OF LEAF WIDTH, MAY KING ♀ X GRAND RAPIDS ♂ AND RECIPROCAL

Parent!	Year grown	Generation	Class centers in centimeters																									Total	Mean	S. D.	C. V.
			8.75	9.75	10.75	11.75	12.75	13.75	14.75	15.75	16.75	17.75	18.75	19.75	20.75	21.75	22.75	23.75	24.75	25.75	26.75	27.75	28.75	29.75	30.75	31.75	32.75				
MK1-1'	1915	P ₂																													
GR2-3-1'	1915	P ₂																													
E2-4-10'	1915	F ₂																													
E2-4-4'	1916	P ₂																													
MK1-1'	1916	P ₂																													
GR2-3-1'	1916	P ₂																													
E7	1916	F ₁																													
F0	1916	F ₁																													
E7-1, E7-3, E7-9	1916	F ₂																													
E2-4-10'	1916	F ₂																													
E2-4-10'	1916	F ₂																													
E2-4-4'	1916	F ₂																													
MK1-1'	1917	P ₂																													
GR2-3-1'	1917	P ₂																													
E7-1	1917	F ₂																													
E7-1-18	1917	F ₂																													
E7-3-65	1917	F ₂																													
E7-3-19	1917	F ₂																													
E7-3-3	1917	F ₂																													
E7-3-20	1917	F ₂																													
E7-3-22	1917	F ₂																													
E7-3-15	1917	F ₂																													
E7-3-5	1917	F ₂																													
E7-1-6	1917	F ₂																													
E7-3-15	1917	F ₂																													
E7-3-47	1917	F ₂																													
E7-1-57	1917	F ₂																													
E2-4-4'-39	1917	F ₄																													

1MK = May King; GR = Grand Rapids; E2 = MK1-1' ♀ X GR2-3-1' ♂; E7 = MK1-1' ♀ X GR2-3-1' ♂; F0 = GR2-2 ♀ X MK1-5 ♂.

TABLE 28.—INHERITANCE OF LEAF WIDTH, BIG BOSTON ♀ X GRAND RAPIDS ♂ AND RECIPROCAL

Parent ¹	Year grown	Generation	Class centers in centimeters																				Total	Mean	S. D.	C. V.				
			9.75	10.75	11.75	12.75	13.75	14.75	15.75	16.75	17.75	18.75	19.75	20.75	21.75	22.75	23.75	24.75	25.75	26.75	27.75	28.75					29.75	30.75	31.75	32.75
BB7-1'	1915	P ₂										1	0	6	11	5	2	1									37	23.34 ± .15	1.34 ± .11	5.74 ± .45
GR2-3-1'	1915	P ₃										1	0	1	3	8	10	14	9	15	8	4	1				74	27.38 ± .17	2.11 ± .12	7.71 ± .43
G4-9 and G4-23	1915	P ₂										6	7	8	9	13	18	25	15	17	12	9	2				160	23.94 ± .16	2.06 ± .12	12.78 ± .49
BB7-5-1'	1916	P ₂										1	0	1	5	6	7	9	8	10	12	2	1				37	19.59 ± .23	2.62 ± .16	13.37 ± .83
G0 and G2	1916	P ₃										1	0	1	5	6	7	9	8	10	12	2	1				75	23.70 ± .17	2.12 ± .12	8.95 ± .49
H2	1916	F ₁										1	0	0	0	0	0	3	3								7	23.29 ± .77	3.01 ± .54	12.92 ± 2.37
G4-9-5	1916	F ₃										1	0	2	0	2	0	1									6	20.75 ± .68	2.45 ± .48	11.81 ± 2.33
G4-9-14'	1916	F ₃										1	3	4	4	1	2	0	1	2							19	17.75 ± .40	2.58 ± .28	14.54 ± 1.62
G4-9-14'	1916	F ₃										3	7	10	7	14	8	1	0	0	0	0					67	18.71 ± .17	2.08 ± .12	11.12 ± 1.66
G4-9-8	1916	F ₃										1	2	1	3	2	3	1									13	18.98 ± .33	1.76 ± .23	9.27 ± 1.23
G4-23-6'	1916	F ₃										1	0	0	3	4	4	12	9	11	14	9	5	3			75	20.40 ± .16	1.99 ± .11	9.75 ± .54
G4-9-8-6'	1916	F ₄										1	1	2	1	8	5	6	14	11	12	5	1				76	23.15 ± .22	2.88 ± .16	12.45 ± .70
G4-9-8-4'	1916	F ₄										2	1	2	0	4	3	0	3	4	3	0	1				23	17.14 ± .20	2.59 ± .14	15.11 ± .85
G4-23-6-1'	1916	F ₄										4	0	0	0	1											5	19.27 ± .43	3.05 ± .30	15.83 ± 1.61
BB7-1'	1917	P ₂										4	2	13	4	12	6	8	8	1	2						60	22.88 ± .20	2.28 ± .14	9.97 ± .61
GR2-3-1'	1917	P ₂										1	2	11	12	10	16	8	4	1							65	24.81 ± .14	1.71 ± .10	6.89 ± .41
G4-5	1917	F ₂										1	0	2	4	7	0	6	11	8	9	3	3	1			65	22.44 ± .22	2.61 ± .15	11.63 ± .70
G4-13-1'	1917	F ₂										3	3	1	4	3	3	3	1	3	1						29	24.54 ± .39	3.12 ± .28	12.71 ± 1.14
G4-9-29'	1917	F ₂										2	1	2	2	3	1	5	2	6	3	2	1				36	25.53 ± .31	2.76 ± .22	10.81 ± 1.14
G4-9-14-42	1917	F ₄										1	0	1	1	1	1	1	1	1	1						8	20.00 ± .63	2.73 ± .46	13.65 ± 2.34
G4-9-14-12'	1917	F ₄										3	1	2	4	7	0	1	4	3	1						97	20.27 ± .36	2.79 ± .26	13.76 ± 1.29
G4-9-5	1917	F ₄										1	2	3	3	2	1	5	2	3	0	0	0	0	0	1	24	21.46 ± .48	3.49 ± .34	16.26 ± 1.62
G4-23-6-6'	1917	F ₄										1	0	1	0	3	5	7	6	11	4	2					47	25.01 ± .22	2.22 ± .15	8.38 ± .62

¹BB = Big Boston; GR = Grand Rapids; G4 = BB7 ♀ X GR2 ♂; G0 = BB5 ♀ X GR2 ♂; G2 = BB1 ♀ X GR1 ♂; H2 = GR2-3-2' ♀ X BB7-1' ♂.

TABLE 29.—INHERITANCE OF LEAF WIDTH, MAY KING ♀ X LOBED WILD ♂

Parent ¹	Year grown	Generation	Class centers in centimeters																							Total	Mean	S. D.	C. V.	
			2.5	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24					25
MK1-1'	1915	P ₃																2	9	7	16	10	7	3	1	55	17.86 ± .15	1.60 ± .10	8.96 ± .58	
W4	1915	P ₁	6	14	24	8	5	1																		58	6.66 ± .07	1.15 ± .07	17.27 ± 1.11	
A0-1, A0-10, A0-12, A0-17, A0-18	1915	F ₄	4	16	40	59	72	79	58	46	31	11	5	2	0	0	1									424	11.61 ± .07	2.17 ± .05	18.69 ± .45	
MK1-1'	1916	P ₂																1	9	10	22	13	6	5	65	17.89 ± .12	1.43 ± .08	7.99 ± .47		
W4-1'	1916	F ₁	2	0	10	7	6																			25	5.35 ± .15	1.10 ± .11	20.55 ± 2.04	
A0-12 and A0-17	1916	F ₃	2	9	18	19	42	8	19	16	20	22	9	2	4	1	2									129	11.01 ± .14	2.41 ± .10	21.89 ± .96	
A0-10-28	1916	F ₃																								70	5.61 ± .11	1.32 ± .08	23.53 ± 1.41	
A0-10-86	1916	F ₃																								7	7.04 ± .33	1.28 ± .23	18.18 ± 3.38	
A0-12-45	1916	F ₃	4	6	19	19	23	10	3	3																80	7.09 ± .14	1.85 ± .10	26.09 ± 1.48	
A0-18-40	1916	F ₃	1	0	2	1	5	5	0																	19	8.11 ± .12	1.72 ± .09	21.21 ± 1.12	
A0-10-57	1916	F ₃																								14	8.46 ± .26	1.44 ± .18	17.62 ± 2.23	
A0-10-44	1916	F ₃	1	13	18	18	8	4	0																	48	8.55 ± .18	1.82 ± .08	16.75 ± 1.95	
A0-1-20	1916	F ₃	2	4	7	10	9	5	4																	78	8.63 ± .11	1.39 ± .08	16.11 ± 1.57	
A0-1-16	1916	F ₃	3	7	22	24	12	7	2																	33	8.75 ± .14	1.18 ± .10	13.48 ± 1.14	
A0-1-32	1916	F ₃	1	0	11	12	5	3	1																	11	9.39 ± .16	.77 ± .11	8.20 ± 1.18	
A0-1-6	1916	F ₃	1	3	4	5	18	21	12	7	1															66	10.14 ± .13	1.56 ± .09	14.79 ± .89	
A0-1-84	1916	F ₃																								52	10.33 ± .14	1.40 ± .10	14.13 ± .95	
A0-17-10	1916	F ₃	1	0	1	3	10	5	3	2	4	0	1	1												66	12.38 ± .23	2.15 ± .16	17.37 ± 1.35	
MK1-1'	1917	P ₂	1	8	21	3	2																			35	20.89 ± .17	2.03 ± .12	9.72 ± .57	
W4-1'	1917	P ₃	1	12	6	1																				20	5.66 ± .09	.81 ± .07	14.31 ± 1.18	
W4-1'-11	1917	P ₃																								35	5.10 ± .10	.65 ± .07	12.75 ± 1.38	
A0-12 and A0-17	1917	F ₂	1	3	6	19	10	8	1	14	21	15	6	5	1	2	0	1									111	11.03 ± .16	2.47 ± .11	22.35 ± 1.06
A0-10-28	1917	F ₃	1	3	6	19	10	8	1	1	4	3	2													48	7.04 ± .12	1.24 ± .09	17.61 ± 1.25	
A0-10-11	1917	F ₃	1	3	5	7	17	9	7	1	4	3	2													53	8.49 ± .22	2.37 ± .15	27.92 ± 1.97	
A0-10-15	1917	F ₃																								38	9.25 ± .11	.99 ± .08	10.70 ± .84	
A0-10-15	1917	F ₃																								58	10.11 ± .12	1.32 ± .08	13.06 ± .83	
A0-10-10	1917	F ₃																								51	10.14 ± .13	1.40 ± .09	13.81 ± .94	
A0-1-41	1917	F ₃																								20	10.55 ± .25	1.66 ± .22	13.74 ± 1.72	
A0-10-15	1917	F ₃																								30	11.56 ± .31	2.78 ± .32	24.05 ± 2.02	
A0-10-15	1917	F ₃	1	3	5	4	4	3	7	5	1	0	1	1												11	13.30 ± .53	2.61 ± .38	19.02 ± 2.93	
A0-18-38	1917	F ₄																								15	3.02 ± .10	.57 ± .07	9.47 ± 1.17	
A0-12-45-22	1917	F ₄	1	9	5	4																				20	6.20 ± .09	.82 ± .06	13.23 ± 1.04	
A0-10-86-6	1917	F ₄	4	17	13	4																				33	8.39 ± .16	1.32 ± .11	15.73 ± 1.34	
A0-12-48-72	1917	F ₄	2	5	7	11	6	3																		35	9.61 ± .12	1.09 ± .09	11.58 ± .95	
A0-1-32-3	1917	F ₄	1	0	1	4	13	4	2																	35	9.61 ± .10	.87 ± .07	9.05 ± .73	
A0-1-20-38	1917	F ₄																								38	9.87 ± .16	.96 ± .11	9.74 ± 1.13	
A0-17-10-15	1917	F ₄																								17	10.33 ± .15	1.37 ± .11	13.26 ± 1.04	
A0-10-44-42	1917	F ₄	0	0	1	7	14	6	3	1	1															35	11.89 ± .20	1.73 ± .14	14.55 ± 1.44	
A0-1-6-1	1917	F ₄																								40	11.90 ± .23	2.17 ± .16	18.24 ± 1.44	
A0-18-40-15	1917	F ₄																												

¹MK = May King; W = Wild; A0 = MK1 ♀ X W4 ♂.

TABLE 30.—INHERITANCE OF LEAF WIDTH, BIG BOSTON ♀ X LOBED WILD ♂

Parent ¹	Year grown	Generation	Class centers in centimeters																Total	Mean	S. D.	C. V.						
			2.75	3.75	4.75	5.75	6.75	7.75	8.75	9.75	10.75	11.75	12.75	13.75	14.75	15.75	16.75	17.75					18.75	19.75	20.75	21.75	22.75	23.75
BB7-1'	1915	P ₂
W4	1915	F ₁	6	14	24	8	5	1
CO-1 and CO-3	1915	F ₂	1	2	4	12	21	33	32	35	24	21	8	15	8	1	0	1
BB7-1'	1916	P ₂
W4-1	1916	P ₂	2	0	10	7	6
CO-1 and CO-3	1916	F ₂	1	4	6	23	27	18	17	10	12	5	3	2	1	0	1
CO-3-99	1916	F ₂
BB7-1'	1917	P ₂
W4-1	1917	P ₂	1	8	21	3	2
W4-1'-11	1917	P ₂	1	12	6	1
CO-1 and CO-3	1917	F ₂	4	1	11	8	16	11	8	6	4	4	2	0	1
CO-1-124	1917	F ₂	1	0	2	6	4	8	2	2
CO-1-26	1917	F ₂	6	4	12	9	8	5	3	3
CO-3-103	1917	F ₂	2	2	7	9	7	8	9	2	2	4	1
CO-3-10	1917	F ₂	3	4	6	3	11	8	6	1	1	2
CO-3-17	1917	F ₂
CO-1-62	1917	F ₂
CO-3-99-13	1917	F ₂

¹BB = Big Boston; W = Wild; CO = BB7 ♀ X W4 ♂.

TABLE 31.—INHERITANCE OF LEAF WIDTH, GRAND RAPIDS ♀ X PARIS WHITE COS ♂

Parent ¹	Year grown	Generation	Class centers in centimeters																Total	Mean	S. D.	C. V.						
			7.75	8.75	9.75	10.75	11.75	12.75	13.75	14.75	15.75	16.75	17.75	18.75	19.75	20.75	21.75	22.75					23.75	24.75	25.75	26.75	27.75	28.75
Cos1-1'	1916	P ₂	1	0	1	2	7	13	19	16	7	3	2	1
GR2-3-1'	1916	P ₂
Y1	1916	F ₁
Y1-1, Y1-2, Y1-3	1916	F ₁	1	2	1	3	1	5	10	17	13	11	23	11	18	19	11	9	7	5	3	4	1	1

¹Cos = Paris White Cos; GR = Grand Rapids; Y1 = GR2-3-1' ♀ X Cos1-1' ♂.

TABLE 34.—INHERITANCE OF LEAF WIDTH, BIG BOSTON ♀ X UNLOBED WILD ♂ AND RECIPROCAL

Parent!	Year grown	Generation	Class centers in centimeters																		Total	Mean	S. D.	C. V.							
			3.75	4.75	5.75	6.75	7.75	8.75	9.75	10.75	11.75	12.75	13.75	14.75	15.75	16.75	17.75	18.75	19.75	20.75					21.75	22.75	23.75	24.75	25.75	26.75	27.75
			3.75	4.75	5.75	6.75	7.75	8.75	9.75	10.75	11.75	12.75	13.75	14.75	15.75	16.75	17.75	18.75	19.75	20.75					21.75	22.75	23.75	24.75	25.75	26.75	27.75
BB7-1'	1915	P ₂															1	0	6	11	11	5	2	1			37	23.34 ± .15	1.34 ± .11	5.74 ± .45	
C2	1915	F ₁																										23	12.40 ± .07	.48 ± .06	3.87 ± .39
BB7-1'	1916	P ₂																										61	19.59 ± .23	2.62 ± .16	13.37 ± .83
W5	1916	P ₁																										75	4.59 ± .04	.57 ± .03	12.42 ± .70
C1 and C3	1916	F ₁																										47	11.22 ± .10	1.01 ± .07	9.00 ± .63
D1	1916	F ₁																										36	11.19 ± .10	.86 ± .07	7.69 ± .61
C3-1	1916	F ₂																										62	9.86 ± .17	1.95 ± .12	19.78 ± 1.23
D1-1 and D1-2	1916	F ₂																										63	10.91 ± .16	1.85 ± .11	16.96 ± 1.06
BB7-1'	1917	P ₂																										35	22.88 ± .20	2.28 ± .14	9.97 ± .61
W4-1/2	1917	P ₂																										34	5.66 ± .09	.81 ± .07	14.31 ± 1.18
C1-27	1917	F ₁																										34	12.69 ± .30	2.58 ± .21	20.33 ± 1.73
D1-12	1917	F ₂																										62	12.57 ± .22	2.54 ± .15	20.21 ± 1.27
C3-1-16	1917	F ₃																										38	7.99 ± .11	.96 ± .07	12.02 ± .94
D1-1-10	1917	F ₃																										54	9.55 ± .18	1.93 ± .13	20.21 ± 1.36
D1-2-2	1917	F ₃																										26	13.71 ± .31	2.39 ± .22	17.21 ± 1.66
C3-1-2	1917	F ₃																										31	14.20 ± .28	2.34 ± .20	16.46 ± 1.45

1W = Big Boston; W = Wild; C1 = BB5-4 ♀ X W38 ♂; C3 = BB7-1' ♀ X W5 ♂; D1 = W5 ♀ X BB7-1' ♂. 2No unlobed Wild were grown in 1917; the results from W4-1', a lobed form, are included for comparison.

TABLE 35.—INHERITANCE OF LEAF WIDTH, GRAND RAPIDS ♀ X UNLOBED WILD ♂

Parent!	Year grown	Generation	Class centers in centimeters																		Total	Mean	S. D.	C. V.										
			3.75	4.75	5.75	6.75	7.75	8.75	9.75	10.75	11.75	12.75	13.75	14.75	15.75	16.75	17.75	18.75	19.75	20.75					21.75	22.75	23.75	24.75	25.75	26.75	27.75	28.75	29.75	30.75
			3.75	4.75	5.75	6.75	7.75	8.75	9.75	10.75	11.75	12.75	13.75	14.75	15.75	16.75	17.75	18.75	19.75	20.75					21.75	22.75	23.75	24.75	25.75	26.75	27.75	28.75	29.75	30.75
W5	1916	P ₁																											75	4.59 ± .04	.57 ± .03	12.42 ± .69		
GR2-3-1'	1916	P ₂																											75	23.70 ± .17	2.12 ± .12	8.95 ± .49		
S1	1916	F ₁																											35	22.00 ± .37	1.09 ± .26	4.95 ± 1.18		
W4-1/2	1917	P ₂																											45	5.66 ± .09	.81 ± .07	14.31 ± 1.18		
GR2-3-1'	1917	P ₂																											65	24.81 ± .14	1.71 ± .14	6.89 ± .41		
T2-1	1917	F ₂																											92	13.18 ± .19	2.73 ± .10	20.71 ± 1.07		

1W = Wild; GR = Grand Rapids; S1 = W5 ♀ X GR2-3-1' ♂; T2 = W5 ♂. 2No unlobed Wild were grown in 1917; the results from W4-1' (lobed) are included for comparison.

grown. The F_2 of Big Boston X Grand Rapids extended from about the upper class of the wide-leaved parent to a point below the lower class of the narrow-leaved parent; thus practically all the width classes of both parents and some new classes with narrower leaves than either parent were secured from populations of only 160 in 1915 and 65 in 1917. The F_2 of May King X Grand Rapids showed approximately the same distribution in 1915 (323 plants) and 1917 (98 plants) as the combined distributions of both parents. In 1916, however, the F_2 distribution of this cross occupied a decidedly lower position as a whole in comparison with the parents. The fact that all of the classes of the parents were recovered in these crosses, together with some new classes having leaves narrower than those of the narrow-leaved parent, may indicate either that relatively few genetic differences were involved or that the distributions of one or both of the parents did not occupy positions near the extreme limits of the distribution in F_2 . There are indications in the F_2 distributions of both May King X Grand Rapids and Big Boston X Grand Rapids that the latter was probably the case. The F_2 distributions of each of these crosses were of multi-modal nature, but the data are insufficient to admit of a more definite analysis.

The cross between Big Boston and unlobed Wild (Table 34) showed slight dominance of the wild type in F_1 and F_2 , while no dominance was apparent in either the F_1 or the F_2 of the cross between unlobed Wild and Cos (Table 32). In both of the crosses it appears that much larger populations would have to be grown in order to recover the parental types, since the distributions in F_2 failed to cover the combined distributions of both parents in both crosses.

In the cross between Big Boston and Cos (Table 33), the F_1 distribution approximately coincided with that of Big Boston. The F_2 distribution occupied an intermediate position. However, the F_2 distribution showed a bi-modal effect, with the larger proportion on the side of the Big Boston parent. An insufficient number of plants was grown to make possible the recovery of all the parental classes. The same conditions prevailed in the cross between Grand Rapids and unlobed Wild (Table 35), the former parent appearing to be partially dominant.

The crosses between May King and lobed Wild (Table 29) and between Big Boston and lobed Wild (Table 30) showed rather unusual results. In neither of these crosses were any F_1 plants grown outside of the greenhouse. The F_2 families of both crosses indicate partial dominance of the wild type. The distributions of both are weighted more heavily on the lower than on the upper sides. The parental classes were not all recovered, however, in any one of the three seasons grown, indicating that an insufficient number of plants was grown. In each cross the largest proportion of the parental classes

was recovered in the seasons when the largest number of plants was grown. This fact suggests that all the classes of the parents might have been secured if a sufficient number of individuals had been reared. As in the cross between Big Boston and unlobed Wild, the wild type proved partially dominant. In the last named cross, however, smaller numbers were grown than in the crosses Big Boston X lobed Wild and May King X lobed Wild. It is believed the F_2 distribution of these three crosses would have been generally similar if approximately equal numbers had been grown of each. The F_3 and F_4 generations produced results in accordance with expectations. In each case they furnished additional evidence of segregation. Some progenies exhibited a distribution approximately the same as that of the parents, indicating a relatively high degree of homozygosity. Others had a variability as great as that of the F_2 , while still others exhibited intermediate degrees of variation.

In the cross between Big Boston and Grand Rapids (Table 28) F_3 families were secured with mean leaf widths as great as that of the wider-leaved parent. In fact, the mean of family G4-9-22' slightly exceeded that of the Grand Rapids parent. This is the same family which had a decidedly greater *leaf length* than either of its parents. The mean of another family, G4-9-8-6', was lower in value than that of the narrow-leaved parent. The lower classes of this family extended three classes below the lowest of Big Boston for that season. The variability of both of these families, however, was greater than that of the parents.

Six F_3 families of the cross between May King and Grand Rapids (Table 27) had a lower mean than did the narrow-leaved parent, while one, E7-1-67, had a mean approximately equal to that of the wider-leaved parent. With the exception of the last named family, however, the variability of each was greater than that of the parental types. These results suggest the possibility of isolating types with narrower leaves from this cross, but not types with wider leaves than those of either of the parents, which is in keeping with the expectation as viewed in the light of the F_2 distributions.

Only one F_3 family was grown of the cross between Cos and unlobed Wild. In mean leaf width and amount of variation this family closely resembled the F_2 .

In the cross between Big Boston and unlobed Wild (Table 34), no F_3 families were secured, the means of which approximated the means of either of the parental forms. Apparently much larger numbers would have to be grown to insure the recovery of the parental types. One family, C3-1-15, showed a variability about as low as that of the parents.

A number of the F_3 and F_4 families of the cross between May King and lobed Wild (Table 29) indicated recovery or near-recovery of the

wild form. In F_3 no families were obtained with as narrow leaves, on the average, as those of the wild, but by continuing the selection for narrow leaves, three families were secured in F_4 which closely coincided in mean leaf width with that of the wild. Two of these families descended from the same F_2 plant. On the other hand, no F_3 or F_4 families were obtained which had a mean leaf width as great as that of the May King parent. In fact, the mean of the largest F_3 or F_4 was only slightly over half that of the May King. Such a condition, however, is to be expected when the pronounced dominance of the wild type, as indicated by the skew curve in F_2 , is taken into account. It appears that rather large numbers would have to be grown in F_2 and the most rigid selection for wide-leaved types maintained before a type could be isolated with a mean leaf width as large as that of May King.

The cross between Big Boston and lobed Wild (Table 30) gave similar results in F_3 . Only one F_4 family of this cross was grown. The variabilities of all of the F_3 and F_4 families were greater than those of the parents.

Width Index

It is obvious that along with the marked differences noted as to leaf length and leaf width, there would also be marked differences in leaf shape. As a matter of fact, the differences, particularly in hybrids of cultivated X wild varieties, were so various that no terminology could be devised to designate properly the many gradations observed.

In order to study the inheritance of shape of leaves the width average was divided by the length average for each plant, the result giving a "width index." The width indexes were arranged in frequency distributions. The same method was used by Hayes, East, and Beinhart (1913) to study "breadth index" in tobacco. The results for the inheritance of this character complex in lettuce are presented in Tables 36 to 44.

The tables show that the parental varieties exhibited relatively low variabilities thruout. It will be seen, however, that the wild forms had appreciably higher coefficients of variation, as a rule, than the cultivated varieties. As will be shown later, the wild forms were probably somewhat more heterozygous for leaf size and shape than the cultivated varieties. These conditions should be taken into account in studying the results.

The parental types varied somewhat from year to year in mean width index and distribution, but the parent with the larger index for one year had the larger index thruout the investigation, with one exception. In the cross between May King and Grand Rapids (Table 36), Grand Rapids had the smaller index for two years while May

King had the smaller for the third year. In this case, however, the parents did not differ greatly in width index in any season. The width indexes of Big Boston and Grand Rapids were also practically equal in all seasons.

TABLE 36.—INHERITANCE OF WIDTH INDEX, MAY KING ♀ X GRAND RAPIDS ♂ AND RECIPROCAL

Parent ¹	Year grown	Generation	Range of variation	Value of parent	Total number	Mean	S. D.	C. V.
GR2-3-1	1915	P ₂	1.08-1.58	74	1.38 ± .007	.09 ± .005	6.52 ± .36
MK1-1'	1915	P ₂	1.13-1.58	55	1.35 ± .010	.11 ± .007	8.15 ± .52
E2-1, E2-4, E2-6...	1915	F ₂	.73-1.98	323	1.22 ± .009	.23 ± .006	18.85 ± .52
GR2-3-1'	1916	P ₂	.93-1.53	75	1.17 ± .009	.11 ± .066	9.40 ± .52
MK1-1'	1916	P ₂	1.08-1.63	66	1.32 ± .010	.12 ± .007	9.09 ± .53
E0, E2, E7	1916	F ₁	.73-1.33	116	.97 ± .006	.10 ± .004	10.31 ± .46
F0	1916	F ₁	.88-1.18	7	.99 ± .023	.09 ± .016	9.09 ± 1.64
E7-1, E7-3, E7-9...	1916	F ₂	.58-1.53	151	1.21 ± .009	.16 ± .006	13.22 ± .52
E2-4-10'	1916	F ₃	.68-1.48	54	.96 ± .016	.17 ± .011	17.71 ± 1.19
E2-4-10	1916	F ₃	.58-1.68	1.37	33	.98 ± .029	.25 ± .021	25.51 ± 2.25
E2-4-4'	1916	F ₃	.78-1.43	70	1.14 ± .012	.15 ± .009	13.16 ± .76
GR2-3-1'	1917	P ₂	.98-1.33	65	1.15 ± .007	.08 ± .005	6.96 ± .42
MK1-1'	1917	P ₂	1.08-1.58	66	1.29 ± .009	.11 ± .007	8.53 ± .50
E7-1...	1917	F ₂	.78-1.63	98	1.10 ± .014	.20 ± .010	18.21 ± .91
E7-1-67	1917	F ₃	.78-1.38	.69	11	.93 ± .031	.15 ± .022	16.13 ± 2.38
E7-3-20	1917	F ₃	.58-1.28	.61	50	.93 ± .017	.18 ± .012	19.35 ± 1.35
E7-1-19	1917	F ₃	.63-1.38	.72	17	.94 ± .028	.17 ± .020	18.08 ± 2.16
E7-3-3	1917	F ₃	.68-1.23	.19	39	.94 ± .011	.10 ± .008	10.64 ± .82
E7-1-15	1917	F ₃	.63-1.23	.69	13	.95 ± .030	.16 ± .021	16.84 ± 2.29
E7-3-22	1917	F ₃	.63-1.43	.93	26	.99 ± .027	.20 ± .019	20.20 ± 1.97
E7-1-6	1917	F ₃	.68-1.58	.77	35	.99 ± .025	.22 ± .018	22.22 ± 1.88
E7-3-5	1917	F ₃	.73-1.53	.92	47	1.01 ± .016	.16 ± .011	15.84 ± 1.13
E7-3-15	1917	F ₃	.73-1.43	1.05	13	1.02 ± .043	.23 ± .030	22.55 ± 3.13
E7-1-2	1917	F ₃	.83-1.33	.86	53	1.07 ± .011	.12 ± .008	11.21 ± .74
E7-3-65	1917	F ₃	.68-1.38	.93	8	1.09 ± .060	.25 ± .042	22.94 ± 4.07
E7-3-47	1917	F ₃	.88-1.53	.83	25	1.16 ± .026	.19 ± .018	16.38 ± 1.60
E7-1-18	1917	F ₃	.98-1.43	.92	21	1.17 ± .016	.11 ± .011	9.41 ± .98

¹GR = Grand Rapids; MK = May King; E2 = MK15 ♀ X GR1 ♂; E0 = MK1 ♀ X GR2 ♂; E7 = MK1-1' ♀ X GR2-3-1' ♂; F0 = GR2-2 ♀ X MK1-5 ♂.

TABLE 37.—INHERITANCE OF WIDTH INDEX, BIG BOSTON ♀ X GRAND RAPIDS ♂ AND RECIPROCAL

Parent ¹	Year grown	Generation	Range of variation	Value of parent	Total number	Mean	S. D.	C. V.
BB7-1'	1915	P ₂	1.33-1.68	37	1.46 ± .009	.08 ± .006	5.48 ± .43
GR2-3-1	1915	P ₂	1.08-1.58	74	1.38 ± .007	.09 ± .005	6.52 ± .36
G4-9, G4-23	1915	F ₂	.68-1.73	160	1.08 ± .013	.24 ± .009	22.22 ± .88
BB7-1'	1916	P ₂	.88-1.48	61	1.14 ± .012	.14 ± .009	12.28 ± .76
GR2-3-1'	1916	P ₂	.93-1.53	75	1.17 ± .009	.11 ± .006	9.40 ± .52
G0, G2	1916	F ₁	.73-1.08	7	.93 ± .028	.11 ± .020	11.83 ± 2.16
H2	1916	F ₁	.78-0.98	6	.91 ± .019	.07 ± .014	7.69 ± 1.50
G4-9-8	1916	F ₃	.68-1.63	.98	75	1.02 ± .017	.22 ± .012	21.57 ± 1.24
G4-23-6	1916	F ₃	.83-1.43	1.08	75	1.11 ± .010	.13 ± .007	11.71 ± .65
G4-9-14	1916	F ₃	.88-1.48	.95	67	1.13 ± .012	.14 ± .008	12.39 ± .73
G4-9-6	1916	F ₃	.88-1.53	1.43	19	1.18 ± .025	.16 ± .018	13.56 ± 1.51
G4-9-14'	1916	F ₃	1.03-1.73	13	1.29 ± .036	.19 ± .025	14.73 ± 1.99
BB7-1'	1917	P ₂	1.03-1.38	60	1.20 ± .009	.10 ± .006	8.33 ± .51
GR2-3-1'	1917	P ₂	.98-1.33	65	1.15 ± .007	.08 ± .005	6.96 ± .41
G4-5	1917	F ₂	.63-1.58	65	.97 ± .018	.21 ± .012	21.65 ± 1.34
G4-9-22'	1917	F ₃	.58-1.08	36	.84 ± .013	.12 ± .010	14.29 ± 1.16
G4-13-1'	1917	F ₃	.98-1.43	29	1.21 ± .016	.13 ± .012	10.74 ± .96
G4-9-14-42	1917	F ₄	.98-1.28	1.03	8	1.14 ± .017	.07 ± .012	6.14 ± 1.04
G4-23-6-67	1917	F ₄	.98-1.43	.90	47	1.15 ± .010	.10 ± .007	8.70 ± .74
G4-9-14-12'	1917	F ₄	1.08-1.58	27	1.27 ± .017	.13 ± .012	10.24 ± .95
G4-9-6-5	1917	F ₄	1.33-2.68	1.03	24	1.67 ± .050	.33 ± .032	19.76 ± 2.00

¹BB = Big Boston; GR = Grand Rapids; G0 = BB5 ♀ X GR2 ♂; G2 = BB11 ♀ X GR1 ♂; H2 = GR2-3-2' ♀ X BB7-1' ♂; G4 = BB7 ♀ X GR2 ♂.

TABLE 38.—INHERITANCE OF WIDTH INDEX, MAY KING ♀ X LOBED WILD ♂

Parent ¹	Year grown	Generation	Range of variation	Value of parent	Total number	Mean	S. D.	C. V.
MK1-1'	1915	P ₂	1.13-1.58	55	1.35 ± .001	.11 ± .007	8.15 ± .52
W4	1915	P ₁	.13- .38	58	.26 ± .004	.05 ± .003	19.23 ± 1.25
A0-1, A0-10, A0-12								
A0-17, A0-18	1915	F ₂	.28-1.08	424	.46 ± .003	.10 ± .002	21.74 ± .53
MK1-1'	1916	P ₂	1.08-1.63	66	1.32 ± .010	.12 ± .007	9.09 ± .53
W4-1'	1916	P ₂	.13- .28	25	.21 ± .005	.04 ± .004	19.05 ± 1.88
A0-12, A0-17	1916	F ₂	.33- .93	129	.50 ± .007	.11 ± .005	22.00 ± .97
A0-18-40	1916	F ₂	.23- .53	.38	89	.36 ± .004	.06 ± .003	16.67 ± .87
A0-10-28	1916	F ₂	.23- .48	.38	70	.37 ± .005	.06 ± .003	16.22 ± .95
A0-10-44	1916	F ₂	.23- .53	.33	48	.37 ± .007	.07 ± .005	18.92 ± 1.35
A0-10-86	1916	F ₂	.28- .43	.43	7	.39 ± .013	.05 ± .009	12.82 ± 2.35
A0-12-45	1916	F ₂	.23- .73	.28	80	.40 ± .007	.09 ± .005	22.50 ± 1.26
A0-1-16	1916	F ₂	.33- .53	.43	33	.41 ± .006	.05 ± .004	12.19 ± 1.03
A0-1-32	1916	F ₂	.38- .53	.43	11	.45 ± .010	.05 ± .007	11.11 ± 1.62
A0-1-2	1916	F ₂	.33- .58	.43	74	.46 ± .005	.06 ± .003	13.04 ± .74
A0-1-20	1916	F ₂	.38- .73	.43	78	.46 ± .005	.07 ± .004	15.22 ± .84
A0-10-57	1916	F ₂	.38- .58	.53	14	.48 ± .009	.05 ± .006	10.42 ± 1.34
A0-1-84	1916	F ₂	.33- .78	.48	52	.51 ± .009	.10 ± .007	19.61 ± 1.35
A0-17-10	1916	F ₂	.33- .88	.48	40	.57 ± .013	.12 ± .009	21.05 ± 1.66
A0-1-6	1916	F ₂	.43- .88	.63	66	.62 ± .007	.08 ± .005	12.90 ± .77
MK1-1'	1917	P ₂	1.08-1.58	66	1.29 ± .009	.11 ± .007	8.53 ± .50
W4-1'	1917	P ₂	.18- .38	35	.28 ± .005	.04 ± .003	14.29 ± 1.18
A0-12, A0-17	1917	F ₂	.28- .78	111	.50 ± .006	.10 ± .005	19.63 ± .92
A0-10-11	1917	F ₂	.28- .63	.35	53	.44 ± .007	.07 ± .005	15.91 ± 1.07
A0-1-15	1917	F ₂	.38- .68	.46	58	.46 ± .005	.06 ± .004	13.04 ± .83
A0-10-15	1917	F ₂	.33- .78	.44	36	.51 ± .011	.10 ± .008	19.61 ± 1.62
A0-1-41	1917	F ₂	.38- .63	.39	20	.51 ± .008	.05 ± .005	9.80 ± 1.05
A0-10-10	1917	F ₂	.33- .83	.51	51	.53 ± .009	.09 ± .006	16.98 ± 1.17
A0-12-62	1917	F ₂	.43- .73	.57	38	.55 ± .008	.07 ± .005	12.73 ± 1.00
A0-18-38	1917	F ₂	.58-1.18	.89	11	.80 ± .028	.14 ± .020	17.50 ± 2.60
A0-12-45-22	1917	F ₄	.23- .48	.25	20	.33 ± .009	.06 ± .006	18.18 ± 2.00
A0-10-86-6	1917	F ₄	.28- .53	.38	15	.39 ± .010	.06 ± .007	15.38 ± 1.94
A0-12-45-72	1917	F ₄	.33- .48	.41	38	.40 ± .004	.04 ± .003	10.00 ± .78
A0-12-45-30	1917	F ₄	.33- .48	.43	33	.41 ± .005	.04 ± .003	9.76 ± .81
A0-18-40-15	1917	F ₄	.28- .58	.40	40	.44 ± .006	.06 ± .005	13.64 ± 1.05
A0-1-20-38	1917	F ₄	.38- .53	.40	35	.45 ± .005	.04 ± .003	8.89 ± .72
A0-17-10-15	1917	F ₄	.38- .53	.33	17	.45 ± .007	.04 ± .005	8.88 ± 1.03
A0-1-32-3	1917	F ₄	.33- .58	.39	35	.46 ± .006	.05 ± .004	10.87 ± .89
A0-10-44-42	1917	F ₄	.43- .68	.35	38	.51 ± .007	.06 ± .005	11.76 ± .92
A0-1-6-1	1917	F ₄	.48- .83	.72	35	.65 ± .008	.07 ± .006	10.76 ± .88

¹W = Wild; MK = May King; A0 = MK1 ♀ X W4 ♂.

TABLE 39.—INHERITANCE OF WIDTH INDEX, BIG BOSTON ♀ X LOBED WILD ♂

Parent ¹	Year grown	Generation	Range of variation	Value of parent	Total number	Mean	S. D.	C. V.
W4	1915	P ₁	.13- .38	58	.26 ± .004	.05 ± .003	19.23 ± 1.25
BB7-1'	1915	P ₂	1.33-1.68	37	1.46 ± .009	.08 ± .006	5.48 ± .43
C0-1, C0-3	1915	F ₂	.23- .98	219	.48 ± .005	.12 ± .004	25.00 ± .86
W4-1'	1916	P ₂	.13- .28	25	.21 ± .005	.04 ± .004	19.05 ± .88
BB7-1'	1916	P ₂	.88-1.48	61	1.14 ± .012	.14 ± .009	12.28 ± .76
C0-1, C0-3	1916	F ₂	.23- .88	154	.49 ± .007	.12 ± .005	24.49 ± 1.00
C0-3-99	1916	F ₂	.33- .98	.73	31	.67 ± .017	.14 ± .012	20.90 ± 1.87
W4-1'	1917	P ₂	.18- .38	35	.28 ± .005	.04 ± .003	14.29 ± 1.18
BB7-1'	1917	P ₂	1.03-1.38	60	1.20 ± .009	.10 ± .006	8.33 ± .51
C0-1, C0-3	1917	F ₂	.23- .88	85	.52 ± .008	.11 ± .006	21.15 ± 1.14
C0-1-24	1917	F ₂	.33- .63	.54	30	.43 ± .009	.07 ± .006	16.28 ± 1.45
C0-3-103	1917	F ₂	.28- .78	.35	53	.45 ± .007	.08 ± .005	17.78 ± 1.20
C0-1-62	1917	F ₂	.33- .58	.42	41	.46 ± .006	.06 ± .005	13.04 ± .99
C0-1-26	1917	F ₂	.33- .63	.54	19	.47 ± .012	.08 ± .009	17.02 ± 1.92
C0-3-17	1917	F ₂	.33- .63	.47	32	.47 ± .008	.07 ± .006	14.89 ± 1.28
C0-3-10	1917	F ₂	.33- .73	.35	42	.47 ± .008	.08 ± .006	17.02 ± 1.29
C0-1-124	1917	F ₂	.38- .68	.53	25	.52 ± .011	.08 ± .008	15.38 ± 1.50
C0-3-99-13	1917	F ₄	.58- .73	.80	7	.64 ± .015	.06 ± .011	9.38 ± 1.69

¹W = Wild; BB = Big Boston; C0 = BB7 ♀ X W4 ♂.

TABLE 40.—INHERITANCE OF WIDTH INDEX, GRAND RAPIDS ♀ X PARIS WHITE COS ♂

Parent ¹	Year grown	Generation	Range of variation	Total number	Mean	S. D.	C. V.
Cos1-1'	1916	P ₂	.38-.63	72	.52 ± .003	.04 ± .002	8.54 ± .48
GR2-3-1'	1916	P ₂	.93-1.53	75	1.17 ± .009	.11 ± .006	9.40 ± .52
Y1	1916	F ₁	.83-.98	2
Y1-1, Y1-2, Y1-3	1916	F ₂	.48-1.38	176	.86 ± .011	.21 ± .008	24.42 ± .93

¹Cos = Paris White Cos; GR = Grand Rapids; Y1 = GR2-3-1' ♀ X Cos1-1' ♂.

TABLE 41.—INHERITANCE OF WIDTH INDEX, BIG BOSTON ♀ X UNLOBED WILD ♂ AND RECIPROCAL

Parent ¹	Year grown	Generation	Range of variation	Value of parent	Total number	Mean	S. D.	C. V.
BB7-1'	1916	P ₂	.88-1.48	61	1.14 ± .012	.14 ± .009	12.28 ± .76
W5	1916	F ₁	.13-.28	75	.20 ± .002	.03 ± .002	15.00 ± .84
C1 and C3	1916	F ₁	.38-.48	47	.41 ± .003	.03 ± .002	7.32 ± .51
D1	1916	F ₁	.33-.53	36	.41 ± .004	.04 ± .003	9.76 ± .78
C3-1	1916	F ₂	.33-.73	63	.50 ± .009	.11 ± .007	22.00 ± 1.38
D1-1 and D1-2	1916	F ₂	.38-.73	62	.49 ± .006	.07 ± .004	14.29 ± .88
BB7-1'	1917	P ₂	1.03-1.38	60	1.20 ± .009	.10 ± .006	8.33 ± .51
W4-1'	1917	P ₂	.18-.38	35	.28 ± .005	.04 ± .003	14.29 ± 1.18
C1-27	1917	F ₂	.33-.78	34	.53 ± .013	.11 ± .009	20.75 ± 1.77
D1-12	1917	F ₂	.33-.68	62	.50 ± .007	.08 ± .005	16.00 ± .99
C3-1-15	1917	F ₃	.33-.58	.44	38	.45 ± .006	.05 ± .004	11.11 ± .87
D1-1-10	1917	F ₃	.38-.63	.47	54	.50 ± .006	.06 ± .004	12.00 ± .79
C3-1-2	1917	F ₃	.43-.68	.58	31	.54 ± .007	.06 ± .005	11.11 ± .96
D1-2-2	1917	F ₃	.33-.73	.45	26	.56 ± .011	.08 ± .007	14.29 ± 1.36

¹BB = Big Boston; W = Wild; C1 = BB5-4 ♀ X W38 ♂; C3 = BB7-1' ♀ X W5 ♂; D1 = W5 ♀ X BB7-1' ♂.

TABLE 42.—INHERITANCE OF WIDTH INDEX, BIG BOSTON ♀ X PARIS WHITE COS ♂

Parent ¹	Year grown	Generation	Range of variation	Total number	Mean	S. D.	C. V.
Cos1-1'	1916	P ₂	.36-.63	72	.52 ± .003	.04 ± .002	8.54 ± .48
BB7-1'	1916	P ₂	.88-1.48	61	1.14 ± .012	.14 ± .009	12.28 ± .76
N1, N2	1916	F ₁	.63-.88	68	.72 ± .005	.06 ± .004	8.33 ± .48
N1-1, N1-2, N1-4, N1-5	1916	F ₂	.58-.93	84	.73 ± .008	.11 ± .006	15.07 ± .80
Cos1-1'	1917	P ₂	.48-.68	51	.57 ± .004	.04 ± .003	7.02 ± .47
BB7-1'	1917	P ₂	1.03-1.38	60	1.20 ± .009	.10 ± .006	8.33 ± .51
N1-5	1917	F ₂	.53-1.43	72	.83 ± .013	.16 ± .009	19.28 ± 1.12

¹Cos = Paris White Cos; BB = Big Boston; N1 = BB7-1' ♀ X Cos1-1' ♂.

TABLE 43.—INHERITANCE OF WIDTH INDEX, GRAND RAPIDS ♀ X UNLOBED WILD ♂ AND RECIPROCAL

Parent ¹	Year grown	Generation	Range of variation	Total number	Mean	S. D.	C. V.
GR2-3-1'	1916	P ₂	.93-1.53	75	1.17 ± .009	.11 ± .006	9.40 ± .52
W5	1916	P ₁	.13-.28	75	.20 ± .002	.03 ± .002	15.00 ± .84
S1	1916	F ₁	.88-1.08	4	.94 ± .027	.08 ± .019	8.51 ± 2.03
GR2-3-1'	1917	P ₂	.98-1.33	65	1.15 ± .007	.08 ± .005	6.96 ± .41
W4-1' ²	1917	P ₂	.18-.38	35	.28 ± .005	.04 ± .003	14.29 ± 1.18
T2-1	1917	F ₂	.28-1.13	92	.58 ± .013	.18 ± .009	31.03 ± 1.68

¹GR = Grand Rapids; W = Wild; S1 = W5 ♀ X GR2-3-1' ♂; T2 = GR2-3-1' ♀ X W5 ♂. ²No unlobed Wild were grown in 1917; the results from W4-1' (lobed) are included for comparison.

TABLE 44.—INHERITANCE OF WIDTH INDEX, UNLOBED WILD ♀ X PARIS WHITE COS ♂ AND RECIPROCAL

Parent ¹	Year grown	Generation	Range of variation	Value of parent	Total number	Mean	S. D.	C. V.
W5.....	1916	P ₁	.13 — .28	75	.20 ± .002	.03 ± .002	15.00 ± .84
Cos1-1'.....	1916	P ₂	.38 — .63	72	.52 ± .003	.04 ± .002	8.54 ± .48
R1.....	1916	F ₁	.33 — .48	13	.43 ± .006	.03 ± .004	6.98 ± .92
P1.....	1916	F ₁	.33 — .48	3
R1-2.....	1916	F ₂	.28 — .68	99	.41 ± .004	.06 ± .003	14.63 ± .72
W4-1' ²	1917	P ₂	.18 — .38	35	.28 ± .005	.04 ± .003	14.29 ± 1.18
Cos1-1'.....	1917	P ₂	.48 — .68	51	.57 ± .004	.04 ± .003	7.02 ± .47
R1-2.....	1917	F ₂	.28 — .63	25	.42 ± .011	.08 ± .008	19.05 ± 1.88
R1-2-10.....	1917	F ₂	.33 — .58	.33	23	.38 ± .008	.06 ± .006	15.79 ± 1.61

¹W = Wild; Cos = Paris White Cos; R1 = W5 ♀ X Cos1-1' ♂; P1 = Cos1-1' ♀ X W5 ♂. ²No unlobed Wild were grown in 1917; the results from W4-1', a lobed form, are included for comparison.

The F₁ populations exhibited a low variability in all cases, comparing favorably with the parents in this respect. The F₁'s also had a decidedly lower variability than the F₂ families. Reciprocal crosses, in cases where grown, exhibited approximately similar behavior.

The F₂ generations of each cross exhibited increased variation as compared with the parents and the F₁, except in the case of unlobed Wild X Cos in 1916 (Table 44). In this cross the F₂ distribution occupied an intermediate position, and the coefficient of variability of the wild form was high for the reason already stated. The behavior of all F₂ populations indicated that segregation of width-index genes had taken place.

In the cross between Grand Rapids and unlobed Wild (Table 43), the means of both the F₁ and F₂ were intermediate between those of the parents, and the distribution of the F₂ almost embraced the combined distributions of the two parents.

In the crosses between May King and Grand Rapids (Table 36) and between Big Boston and Grand Rapids (Table 37), the F₁ distributions occupied positions below those of both parents, while the F₂ distributions extended appreciably beyond those of both parents. In both crosses the F₂ distributions appeared to be weighted more heavily on the lower side, and there were also evidences of multi-modal effects.

The crosses between Big Boston and Cos (Table 42) produced F₁ and F₂ populations with means and distributions intermediate between those of the parents. Neither of the parental extremes was recovered in F₂; probably an insufficient number of individuals was grown.

Similar behavior was exhibited by the crosses between May King and lobed Wild (Table 38), Big Boston and lobed Wild (Table 39), and Big Boston and unlobed Wild (Table 41). No F₂'s of the first two crosses were grown in the open, but the means and frequency distributions of the reciprocal F₁'s of the last cross named were intermediate between those of the parents, but inclining

slightly toward those of the wild form. The F_2 means and frequency distributions of each of these three crosses resembled more closely those of the wild than those of the cultivated forms. In no case were the parental extremes recovered. The F_2 distributions for each cross are weighted more heavily on the lower than on the upper sides, indicating partial dominance or a predominance of repressive genes contributed by the wild parents.

In each cross of which reciprocal F_1 and F_2 generations were grown, the behavior of the two was substantially similar.

The F_3 and F_4 populations produced results in accordance with expectations. Some of them showed relatively small variabilities, comparing favorably with the parents and the F_1 generations in this respect; others showed variabilities practically as great as those of the F_2 families; while still others showed intermediate amounts of variation. In general, those crosses which had F_2 families giving evidence of skew or multi-modal curves also had some F_3 or F_4 families which exhibited similar phenomena.

In the crosses between May King and lobed Wild (Table 38), Big Boston and lobed Wild (Table 39), and Big Boston and unlobed Wild (Table 41); neither parental form was duplicated by an F_3 or F_4 family. None of the F_3 or F_4 families had classes which even closely approached the extremes of the parents. Some F_3 families contained a few individuals with smaller width indexes than the mean of the F_2 in the cross May King X lobed Wild. In the crosses Big Boston X unlobed Wild (Table 41), and Big Boston X lobed Wild (Table 39), none of the F_2 individuals reached the lower limits of the F_2 distributions. None of the F_3 or F_4 families of this group had a distribution which approached very closely the upper extreme of the corresponding F_2 distribution.

These results seem to indicate that long-continued selection of individuals with low or high width indexes, from families showing segregation for this character, would probably be necessary in order to recover the parental types.

In the cross unlobed Wild X Cos, the one F_3 family grown (R1-2-10), rather closely resembled the Cos parent in mean width index and in spread of the frequency distribution (Table 44).

The results from the cross between May King and Grand Rapids (Table 36) shows that some F_3 families were secured with lower means and lower extremes of variation than the Grand Rapids parent, but none with means as large as those of the May King. One family (E7-1-6) had a distribution which extended to the upper limits of the May King parent, but it failed by an appreciable amount to extend to the upper limits of the F_2 .

In the cross between Big Boston and Grand Rapids (Table 37) the means and frequency distributions of the parents as to width index

differed only slightly. Some F_3 families were secured with means and distributions which fell below those of either parent. Some of these showed a low coefficient of variability, indicating a reasonably high degree of homozygosity. Other F_3 families exhibited higher means than either parent. These circumstances indicate that the two parents, while closely resembling each other in width index, are in reality quite different genetically so far as genes affecting width index are concerned. Furthermore, the results show that the frequency distribution of neither parent occupied a position near either extreme of the frequency distribution of the F_2 generation. It should therefore be possible to establish types from this cross with both smaller and larger mean width indexes than those of the parents.

Leaf Area

When the plants for this investigation were grown, measurements were taken of the leaf length and leaf width, but no determinations were made of leaf area. When the data were being assembled, it seemed desirable to study the inheritance of leaf area, so far as the data at hand would permit.

Photographs of leaves of plants of the parental varieties and of plants of most of the F_1 and F_2 generations had been taken. From these and the leaf-length and leaf-width data, a factorial method of determining leaf area was developed which, it is believed, provided a fairly reliable means of studying the inheritance of leaf area.

With the aid of an enlarging camera, tracings were made, to the same scale, of the outline of all leaves of which photographs had been taken. A rectangle was then drawn into which the leaf tracing exactly fitted. By means of a planimeter the areas of the leaf tracings and corresponding rectangles were then determined.

A leaf-area factor was next determined for each parental type or hybrid family by using the formula $\frac{T}{R} 100$, in which T is the sum of the areas of the leaf tracings of a given generation and R the sum of the areas of the corresponding rectangles.

When the factors had been determined for the various generations, it was noted that by making slight changes, in no case exceeding 2.2 percent, the factors could be arranged in a few groups. Such groupings were made. It is recognized that a certain amount of experimental error accompanied the method, but it is believed the differences in leaf area between the parents of most crosses were great enough to make the experimental error reasonably insignificant from the standpoint of interpretation of results. Table 45 shows for each variety or generation the number of leaves from which the factor was determined, the actual factor determined, and the factor assumed for calculating leaf areas.

TABLE 45.—NUMBER OF LEAVES FROM WHICH LEAF AREA FACTORS WERE DETERMINED, ACTUAL FACTORS DETERMINED, AND THE FACTORS EMPLOYED

Variety or hybrid	Generation	Number of leaves from which factor was calculated	Actual factor determined	Factor used in calculating areas
Big Boston.....	P	1	74.8	75
Lobed Wild.....	P	2	45.9	46
Unlobed Wild.....	P	1	63.8	62.5
May King.....	P	2	69.5	68
Grand Rapids.....	P	1	68.4	68
Paria White Cos.....	P	1	66.9	68
Big Boston X lobed Wild.....	F ₁	1	52.3	53
Big Boston X lobed Wild.....	F ₂	23	59.4	58.5
Big Boston X lobed Wild.....	F ₃	0	58.5
Big Boston X lobed Wild.....	F ₄	0	58.5
Big Boston X unlobed Wild.....	F ₁	2	64.5	62.5
Big Boston X unlobed Wild.....	F ₂	7	66.6	68
Big Boston X unlobed Wild.....	F ₃	0	68
May King X lobed Wild.....	F ₁	1	58.9	58.5
May King X lobed Wild.....	F ₂	42	59.7	58.5
May King X lobed Wild.....	F ₃ , F ₄	0	Unlobed, 68 Heterozygous, 58.5 Lobed, 53
May King X Grand Rapids.....	F ₁	2	67.3	68
May King X Grand Rapids.....	F ₂	0	68
May King X Grand Rapids.....	F ₃	0	68
Big Boston X Grand Rapids.....	F ₁	2	68.4	68
Big Boston X Grand Rapids.....	F ₂	0	68
Big Boston X Grand Rapids.....	F ₃	0	68
Big Boston X Grand Rapids.....	F ₄	0	68
Big Boston X Cos.....	F ₁	0	68
Big Boston X Cos.....	F ₂	7	64.3	62.5
Big Boston X Cos.....	F ₃	0
Grand Rapids X Cos.....	F ₁	1	60.3	62.5
Grand Rapids X Cos.....	F ₂	12	60.5	62.5
Grand Rapids X Cos.....	F ₃	0	62.5
Grand Rapids X unlobed Wild.....	F ₁	1	53.2	53
Grand Rapids X unlobed Wild.....	F ₂	0	62.5
Cos X unlobed Wild.....	F ₁	2	62	62.5
Cos X unlobed Wild.....	F ₂	7	58.5	58.5
Cos X unlobed Wild.....	F ₃	0	62.5

No photographs had been taken of leaves of any of the F₃ or F₄ families, and it was necessary to determine factors arbitrarily for these, which was done by taking into account the factors of the parents, the F₁'s and the F₂'s of each cross. Following this, the areas of the leaves were determined by the formula $\frac{P(LW)}{100}$, in which *P* is the leaf-area factor used for the family in question, *L* the leaf length, and *W* the leaf width.

The task of calculating was much reduced by preparing certain tables in advance. One of these showed the rectangular area for different combinations of leaf lengths and leaf widths, being arranged on the principle of the Punnett square. The class ranges were decided upon in advance. By means of other tables, one for each factor used, the limiting areas of rectangles whose corresponding leaves would be included in each class, were shown. From these tables the classes into which the leaf area for each plant would fall could be determined at a glance.

It is recognized that this method of determining leaf area is subject to more or less experimental error because: (1) only one leaf was photographed of some of the varieties and hybrid generations; (2) no photographs were taken of any F_3 or F_4 leaves, thus making estimated determinations necessary, based on the factors of the parents, the F_1 and the F_2 , of the cross in question; and (3) because of the segregation of leaf-form genes in F_3 and succeeding segregating generations in the crosses between Big Boston and lobed Wild and between May King and lobed Wild. In the latter cross an attempt was made to reduce the error in the F_3 and F_4 families by using a factor of 53 for homozygous lobed families, a factor of 68 for homozygous unlobed families, and a factor of 58.5 for segregating families. The possibility of experimental error should be kept in mind in examining the results, and no attempt should be made to draw conclusions from relatively small differences in breeding behavior. It is believed, however, that in most crosses the differences in leaf area were sufficiently large in comparison with the probable error that the results are significant. It should be borne in mind also that more or less error would have been involved, even if measurements had been taken from actual leaves, owing to the pronounced crinkling and crumpling of the leaves of some varieties.

The study of leaf area is, in the opinion of the author, an important matter from an economic standpoint. It is believed the method described will provide an improved means of studying this character in many instances. Especially would this seem to be true in crosses involving no leaf-form differences, and in which the leaf shapes are fairly uniform. By taking leaf-length and leaf-width measurements of all plants and by making enough actual leaf-area determinations from which to secure accurate leaf-area factors, the work can be reduced to fairly small proportions. Having these measurements the areas can be determined, by the aid of the tables described, much quicker and easier than actual areas can be determined, and the calculations can be made at any convenient time.

The results for the inheritance of leaf area are presented in Tables 46 to 53.

It is again apparent in this character complex that the wild forms exhibited greater variability than the cultivated varieties. This fact should be taken into consideration in studying the results.

The parental varieties exhibited relatively low variabilities in comparison with the hybrids, except in the case of Cos 1-1' in 1917. It is believed that the greater variability of this variety was due to environmental effects rather than to irregularities in genetic behavior.

The F_1 generations of all crosses were of comparatively low variability, except those of Big Boston X Cos (Table 53) and May King X Grand Rapids (Table 51) in 1916; the distributions suggest that a few

TABLE 46.—INHERITANCE OF LEAF AREA, MAY KING ♀ X LOBED WILD ♂

Parent ¹	Year grown	Gener- ation	Class centers in square centimeters								Area factor used	Total	Mean	S. D.	C. V.					
			25	50	75	100	125	150	175	200						225	250	275	300	325
W4	1915	P1													57	81.14 ± 1.44	16.08 ± 1.02	19.82 ± 1.30		
MK1-1'	1915	P2	11	33	12	2	16	21	11	3	2				40	176.36 ± 2.47	27.16 ± 1.75	15.40 ± 1.01		
A0-1, A0-10, A0-12, A0-17, A0-18	1915	P3													435	47.57 ± 1.54	47.57 ± 1.09	27.70 ± .68		
W4-1	1916	F1	3	9	10	3		33	67	92	78	69	46	29	6	4	2	66.00 ± 2.88	21.36 ± 2.04	33.90 ± 3.59
MK1-1'	1916	F2													46	26.91 ± 1.97	23.69 ± 1.39	14.28 ± .86		
A0-12 and A0-17	1916	F2	1	4	22	24	24	13	8	2	3	1	1		129	155.02 ± 3.17	53.33 ± 3.23	34.27 ± 1.60		
A0-10-28	1916	F3	15	16	17	1	2								58.5	51.45 ± 1.42	17.47 ± 1.24	33.96 ± 2.16		
A0-10-86	1916	F3	2	2	1		2								68	88.75 ± 2.46	32.60 ± 1.74	36.73 ± 2.21		
A0-12-45	1916	F3	1	16	27	19	11	4	1	1					68	97.41 ± 1.77	23.20 ± 1.25	23.82 ± 1.36		
A0-1-20	1916	F3	1	2	24	31	27	0							58.5	99.25 ± 1.92	26.35 ± 1.35	23.43 ± 1.43		
A0-1-6	1916	F3	6	12	27	22	0								68	112.60 ± 4.75	26.35 ± 1.35	23.43 ± 1.43		
A0-10-57	1916	F3	2	1	4	6	1								68	111.82 ± 4.87	26.58 ± 1.61	23.43 ± 1.43		
A0-1-2	1916	F3	4	4	21	23	8	2	0	2					68	115.36 ± 2.98	24.58 ± 1.61	21.80 ± 2.00		
A0-18-4	1916	F3	1	5	21	22	2	1	1	0	0				53	125.56 ± 2.88	40.00 ± 2.02	31.89 ± 1.77		
A0-18-40	1916	F3	1	14	22	22	16	8	3	1	2				68	127.35 ± 2.89	42.45 ± 1.79	19.07 ± 1.67		
A0-1-6	1916	F3	1	9	11	8	3								68	136.38 ± 2.53	12.45 ± 1.79	9.13 ± 1.32		
A0-1-32	1916	F3	3	1	13	9	8	6	7	1					68	136.46 ± 4.24	43.60 ± 3.00	31.95 ± 2.41		
A0-10-44	1916	F3	1	3	1	10	9	6	1	1					68	180.00 ± 4.03	37.83 ± 2.85	21.02 ± 1.65		
A0-17-10	1916	F3	29	6			2	10	9	6	1	1			46	54.30 ± 1.08	9.44 ± .76	17.31 ± 1.42		
MK1-1'	1917	F2													75	232.95 ± 3.24	38.97 ± 2.29	16.73 ± 1.01		
A0-12 and A0-17	1917	F2	2	4	6	14	23	27	17	5	11	2	0	1	58.5	54.18 ± 3.34	59.10 ± 2.57	38.33 ± 1.90		
A0-10-11	1917	F2	1	10	16	6	4	1	3	2					53	102.83 ± 4.35	46.97 ± 3.08	45.08 ± 3.56		
A0-10-10	1917	F3	1	1	11	18	17	2	1	5					53	104.41 ± 2.54	26.93 ± 1.80	25.79 ± 1.83		
A0-12-62	1917	F3	7	19	7	3	2								38	107.90 ± 2.70	33.45 ± 3.57	23.86 ± 1.95		
A0-1-41	1917	F3	2	2	5	3	7	2	1	1					58.5	131.25 ± 5.04	55.74 ± 4.19	25.49 ± 2.89		
A0-18-38	1917	F3	1	1	1	1	5	7	1	1	1	0	1	58.5	150.70 ± 8.12	39.92 ± 5.74	26.61 ± 3.02			
A0-10-15	1917	F3	4	5	7	5	8	3	2	1	1	0	1	58.5	150.70 ± 8.12	39.92 ± 5.74	26.61 ± 3.02			
A0-1-15	1917	F4	6	9	1	3	13	15	8	1					56	155.36 ± 2.82	31.23 ± 2.00	20.10 ± 1.33		
A0-10-80-6	1917	F4	1	6	9										68	65.00 ± 2.13	12.95 ± 1.51	18.85 ± 2.40		
A0-12-45-73	1917	F4	1	16	21	8	7	5	4						40	65.00 ± 1.66	15.61 ± 1.18	24.02 ± 1.91		
A0-12-45-22	1917	F4	2	6	4	5	7	1	6	2	1				30	104.86 ± 4.86	43.23 ± 3.44	41.23 ± 3.79		
A0-12-45-30	1917	F4	0	1	10	17	10								33	121.97 ± 3.60	30.63 ± 2.54	25.11 ± 2.21		
A0-10-44-2	1917	F4	1	1	9	14	12	4	1						38	123.98 ± 2.17	19.83 ± 1.53	16.03 ± 1.27		
A0-1-32-3	1917	F4	2	1	9	14	12	4	1						35	137.14 ± 2.84	24.91 ± 2.01	18.16 ± 1.51		
A0-1-30-38	1917	F4	2	1	12	16	4								35	138.57 ± 2.67	23.41 ± 1.89	16.89 ± 1.40		
A0-1-6-1	1917	F4	2	8	5	12	10	3	1	1	1	1	1	68	152.86 ± 3.78	33.17 ± 2.67	21.70 ± 1.83			
A0-18-40-15	1917	F4	3	3	10	9	9	3	1	1	1	1	1	53	176.25 ± 4.62	43.30 ± 3.27	24.57 ± 1.96			

¹W = Wild; MK = May King; A0 = MK1 ♀ X W4 ♂.

TABLE 47.—INHERITANCE OF LEAF AREA, BIG BOSTON ♀ X LOBED WILD ♂

Parent ¹	Year grown	Generation	Class centers in square centimeters																Total	Mean	S. D.	C. V.	
			25	50	75	100	125	150	175	200	225	250	275	300	325	350	375	400					425
			11	33	12	1	1	..	6	8	7
W4	1915	P ₁	57	81.14 ± 1.44	16.08 ± 1.02	19.82 ± 1.30	
BB7-1'	1915	P ₂	23	270.65 ± 3.69	26.22 ± 2.61	9.69 ± .97	
C0-1, C0-3	1915	F ₂	219	190.41 ± 2.59	56.79 ± 1.83	29.83 ± 1.04	
W4-1'	1916	P ₂	3	9	10	3	25	69.00 ± 2.88	21.36 ± 2.04	33.90 ± 3.59	
BB7-1'	1916	P ₂	61	254.10 ± 4.18	48.35 ± 2.85	19.03 ± 1.20	
C0-1, C0-3	1916	F ₂	1	5	18	28	36	27	14	13	5	0	2	1	150	133.83 ± 2.72	49.38 ± 1.92	36.90 ± 1.62	
C0-3-99	1916	F ₂	68	147.58 ± 4.44	36.65 ± 3.14	24.63 ± 2.25	
W4-1'	1917	P ₂	35	54.30 ± 1.08	9.44 ± .76	17.31 ± 1.42	
BB7-1'	1917	P ₂	35	330.75 ± 4.39	50.87 ± 3.11	15.35 ± .96	
C0-1, C0-3	1917	F ₂	1	3	11	5	8	16	16	9	3	0	1	2	0	1	86	174.96 ± 4.47	61.40 ± 3.16	35.09 ± 2.01	
C0-1-124	1917	F ₂	2	8	7	2	25	70.00 ± 3.76	27.84 ± 2.66	37.62 ± 4.07	
C0-3-103	1917	F ₂	49	104.08 ± 3.02	31.33 ± 2.13	30.01 ± 2.22	
C0-3-10	1917	F ₂	54	141.74 ± 4.70	51.24 ± 3.33	36.15 ± 2.64	
C0-3-17	1917	F ₂	1	2	9	10	9	5	6	1	5	3	42	144.05 ± 3.10	29.70 ± 2.19	20.68 ± 1.50	
C0-1-62	1917	F ₂	32	164.84 ± 5.57	46.70 ± 3.94	28.33 ± 2.57	
C0-1-62	1917	F ₂	41	211.88 ± 7.74	73.48 ± 5.47	34.73 ± 2.88	

¹W = Wild; BB = Big Boston; C0 = BB7 ♀ X W4 ♂.

TABLE 48.—INHERITANCE OF LEAF AREA, BIG BOSTON ♀ X UNLOBED WILD ♂ AND RECIPROCAL

Parent ¹	Year grown	Generation	Class centers in square centimeters																Total	Mean	S. D.	C. V.	
			25	50	75	100	125	150	175	200	225	250	275	300	325	350	375	400					425
			1	33	41
W5	1916	P ₁	62.5	63.33 ± 1.02	13.13 ± .73	20.73 ± 1.19	
BB7-1'	1916	P ₂	75	254.10 ± 4.18	48.35 ± 2.95	19.03 ± 1.20	
C1	1916	F ₁	38	204.61 ± 2.34	21.35 ± 1.65	10.43 ± .82	
D1	1916	F ₁	35	180.72 ± 2.73	23.97 ± 1.93	12.57 ± 1.03	
C3-1	1916	F ₂	1	7	18	10	10	5	2	1	1	68	139.28 ± 4.04	47.50 ± 2.85	34.10 ± 2.34	
D1-1 and D1-2	1916	F ₂	61	172.89 ± 3.63	42.05 ± 2.57	24.31 ± 1.37	
BB7-1'	1917	P ₂	78	330.75 ± 4.39	50.87 ± 3.11	15.35 ± .96	
W4-1'	1917	P ₂	35	54.30 ± 1.08	9.44 ± .76	17.31 ± 1.42	
C1-27	1917	F ₂	34	207.35 ± 6.82	58.95 ± 4.82	28.43 ± 2.51	
D1-12	1917	F ₂	62	221.77 ± 5.51	64.37 ± 3.90	29.03 ± 1.96	
C3-1-15	1917	F ₂	38	98.03 ± 2.21	20.18 ± 1.56	20.59 ± 1.60	
D1-1-10	1917	F ₂	54	140.09 ± 3.91	42.58 ± 2.76	30.39 ± 2.15	
D1-2-2	1917	F ₂	24	220.83 ± 7.80	56.68 ± 5.25	25.67 ± 2.66	
C3-1-2	1917	F ₂	31	260.47 ± 8.87	73.19 ± 6.27	28.10 ± 2.59	

¹W = Wild; BB = Big Boston; C1 = BB5-4 ♀ X W38 ♂; D1 = W5 ♀ X BB7-1' ♂; C3 = BB7-1' ♀ X W5 ♂.

TABLE 49.—INHERITANCE OF LEAF AREA, BIG BOSTON ♀ X GRAND RAPIDS ♂ AND RECIPROCAL

Parent ¹	Year grown	Generation	Class centers in square centimeters																Total	Mean	S. D.	C. V.					
			75	100	125	150	175	200	225	250	275	300	325	350	375	400	425	450					475	500	525	550	575
BB7-1'	1915	P ₂	1	1	1	6	8	7	11	9	16	10	9	4	0	1	75
GR2-3-1'	1915	P ₃	68
G4-9, G4-23'	1915	F ₂	4	8	13	11	5	4	5	9	7	15	10	16	14	7	12	5	4	2	3	1	1	74
BB7-1'	1916	P ₂	1	0	6	5	10	10	13	10	4	2	7	4	1	88
GR2-3-1'	1916	F ₂	61
G0, G2	1916	F ₁	75
H2	1916	F ₁	7
G4-9-6	1916	F ₁	6	6	5	7	1	68
G4-9-14	1916	F ₃	6	11	12	22	13	2	0	1	19
G4-9-8	1916	F ₃	1	4	4	10	7	6	3	7	4	10	4	7	0	2	1	67
G4-9-8	1916	F ₃	1	0	4	10	7	6	9	7	4	12	5	3	3	77
G4-9-8-6'	1916	F ₄	1	3	7	14	13	10	7	6	65
G4-9-6-4'	1916	F ₄	76
BB7-1'	1917	P ₂	4	1	1	3	2	1	3	7	0	1	68
GR2-3-1'	1917	P ₂	75
G4-5	1917	F ₂	61
G4-5	1917	F ₂	23
G4-13-1'	1917	F ₂	65
G4-9-22'	1917	F ₂	1	3	2	6	4	7	5	6	5	8	6	7	0	1	64
G4-9-6-5	1917	F ₂	34
G4-23-6-5'	1917	F ₂	1	4	6	2	4	2	4	0	3	4	1	2	0	1	68
G4-23-6-5'	1917	F ₂	1	3	4	6	4	1	1	35
G4-23-6-5'	1917	F ₂	24
G4-23-6-5'	1917	F ₂	47

¹BB = Big Boston; GR = Grand Rapids; G4 = BB7 ♀ X GR2 ♂.

TABLE 50.—INHERITANCE OF LEAF AREA, UNLOBED WILD ♀ X PARIS WHITE COS ♂ AND RECIPROCAL

Parent ¹	Year grown	Generation	Class centers in square centimeters																Total	Mean	S. D.	C. V.					
			25	50	75	100	125	150	175	200	225	250	275	300	325	350	375	400					425	450	475	500	525
Cos1-1'	1916	P ₂	72
W5	1916	F ₁	1	1	1	1	5	12	12	17	13	3	5	2	75
R1	1916	F ₁	13
R1-2	1916	F ₂	1	1	3	9	23	18	25	15	3	0	1	109
Cos1-1'	1917	P ₂	58
W4-1/2	1917	F ₂	55
R1-2	1917	F ₂	2	3	1	4	5	8	1	35
R1-2-10	1917	F ₂	25
			1	0	0	10	6	2	3	1	23

¹Cos = Paris White Cos; W = Wild; R1 = W5 ♀ X Cos1-1' ♂. ²No unlobed Wild were grown in 1917; the results from the lobed Wild are included for comparison.

TABLE 51.—INHERITANCE OF LEAF AREA, MAY KING ♀ X GRAND RAPIDS ♂ AND RECIPROCAL

Parent ¹	Year grown	Generation	Class centers in square centimeters																										Area factor used	Total	Mean	S. D.	C. V.
			75	100	125	150	175	200	225	250	275	300	325	350	375	400	425	450	475	500	525	550	575	600	625	650							
MK1-1'	1915	P ₂			2	16	21	11	3	2																	55	176.36 ± 2.47	27.16 ± 1.75	15.40 ± 1.01			
GR2-3-1'	1915	P ₃																									74	364.86 ± 3.94	50.21 ± 2.78	13.76 ± .78			
E2-1, E2-4, E2-6	1915	F ₂			1	8	24	21	20	24	22	20	28	33	27	24	17	20	9	8	4	1	0	0	1		68	341.87 ± 3.84	101.84 ± 2.72	29.79 ± .86			
MK1-1'	1916	P ₂			8	22	22	14																			66	165.91 ± 1.97	23.09 ± 1.39	14.28 ± .86			
GR2-3-1'	1916	F ₂			1	2	0	2	5	4	3	5	2	3	6	1	1										68	326.00 ± 3.40	43.65 ± 2.40	13.39 ± .75			
E0, E2, E7	1916	F ₁			1	2	0	2	5	4	3	5	2	3	6	1	1										68	297.93 ± 9.08	80.78 ± 6.42	27.11 ± 2.31			
F0, F2	1916	F ₁			1	2	4	9	10	15	28	21	23	13	12	6	2	3	0	1	2						68	379.55 ± 10.38	51.05 ± 2.72	13.45 ± 1.17			
E2-1, E7-3, E7-9	1916	F ₂			1	0	1	3	6	17	8	10	7	2	3	0	2										68	250.00 ± 3.85	70.40 ± 2.72	28.16 ± 1.17			
E2-4-10	1916	F ₂			1	0	1	0	1	7	5	6	3	0	0	1											68	269.45 ± 3.66	39.84 ± 2.59	14.79 ± .92			
E2-4-1'	1916	F ₂			1	0	2	2	6	14	17	8	10	5	2	4											68	289.70 ± 7.64	65.05 ± 5.40	24.12 ± 2.12			
MK1-1'	1917	P ₂			1	1	3	17	15	14	10	3	2														70	286.08 ± 4.17	51.73 ± 2.95	18.08 ± 1.06			
GR2-3-1'	1917	F ₂			1	1	3	17	15	14	10	3	2														66	232.96 ± 3.24	38.97 ± 2.39	16.73 ± 1.01			
E7	1917	F ₁			1	2	6	5	2	0	9	4	6	12	11	13	7	2	1	1							68	389.22 ± 3.27	39.13 ± 2.31	10.60 ± .63			
E7-1	1917	F ₁			1	2	6	5	2	0	9	4	6	12	11	13	7	2	1	1							80	350.00 ± 4.97	65.90 ± 3.51	18.83 ± 1.04			
E7-1-18	1917	F ₁			3	3	4	4	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	98	328.06 ± 7.72	113.33 ± 2.31	34.56 ± 1.85			
E7-3-3'	1917	F ₃			1	1	1	2	7	12	7	4	2	0	1												68	250.20 ± 5.07	54.32 ± 5.65	30.22 ± 3.42			
E7-1-19	1917	F ₁			1	0	1	0	2	6	5	1	0	1													68	179.75 ± 8.00	46.37 ± 3.59	18.53 ± 1.48			
E7-3-22	1917	F ₃			1	0	2	3	2	4	1	1	0	1	1	0	2										68	251.48 ± 7.74	47.30 ± 5.47	18.81 ± 2.25			
E7-3-20	1917	F ₃			1	1	1	3	2	4	1	1	6	6	12	6	7	2	4								68	269.50 ± 6.08	63.09 ± 4.30	23.63 ± 1.68			
E7-3-5	1917	F ₃			1	1	0	1	1	0	1	1	6	6	12	6	7	2	4								68	327.13 ± 5.78	58.74 ± 4.09	17.96 ± 1.29			
E7-3-47	1917	F ₃			3	1	0	2	3	3	1	4	2	2	2	4	3	0	0	1							68	356.25 ± 16.03	116.43 ± 11.33	32.68 ± 3.50			
E7-1-6	1917	F ₃			3	1	0	2	3	3	1	4	2	2	2	4	3	5	3	4	1	0					68	359.58 ± 8.81	76.20 ± 6.23	21.19 ± 1.81			
E7-1-2	1917	F ₃			2	1	1	1	1	0	1	2	1	6	12	9	7	5	1	3	1						53	427.83 ± 7.55	81.51 ± 5.34	19.05 ± 1.29			

1MK = May King; E2 = MK1 ♀ X GR2 ♂; E7 = MK1-1' ♀ X GR2-3-1' ♂; F0 = GR2-2 ♀ X MK1-5 ♂; F2 = GR2-3 ♀ X MK1-5 ♂.

TABLE 52.—INHERITANCE OF LEAF AREA, GRAND RAPIDS ♀ X PARIS WHITE COS ♂

Parent ¹	Year grown	Generation	Class centers in square centimeters												Area factor used	Total	Mean	S. D.	C. V.			
			Class centers in square centimeters																			
			75	100	125	150	175	200	225	250	275	300	325	350						375	400	425
Cos1-1'	1916	P ₂	1	1	1	5	12	12	17	13	3	5	2	..	68	72	291.67 ± 3.89	48.03 ± 2.75	16.78 ± .97
GR2-3-1'	1916	P ₃	2	11	13	17	17	7	4	1	1	75	326.00 ± 3.40	43.65 ± 2.40	13.39 ± .75	
Y1	1916	F ₁	68	
Y1-1, Y1-2, Y1-3	1916	F ₂	3	4	3	8	18	10	27	25	18	13	14	6	7	2	..	62.5	255.68 ± 3.88	76.40 ± 2.75	29.88 ± 1.17	

¹Cos = Paris White Cos; GR = Grand Rapids; Y1 = GR2-3-1' ♀ X Cos1-1' ♂.

TABLE 53.—INHERITANCE OF LEAF AREA, BIG BOSTON ♀ X PARIS WHITE COS ♂

Parent ¹	Year grown	Generation	Class centers in square centimeters												Area factor used	Total	Mean	S. D.	C. V.				
			Class centers in square centimeters																				
			100	125	150	175	200	225	250	275	300	325	350	375						400	425	450	475
Cos1-1'	1916	P ₂	1	1	5	12	12	17	13	3	5	2	68	291.67 ± 3.89	48.03 ± 2.75	16.78 ± .97
BB7-1'	1916	P ₂	..	1	0	6	5	10	10	12	10	4	2	75	284.10 ± 4.18	48.35 ± 2.65	19.08 ± 1.20
N1	1916	F ₁	68	394.94 ± 8.34	108.48 ± 6.80	29.73 ± 1.75
N1-1, N1-2, N1-4, N1-5	1916	F ₂	3	3	8	9	10	9	10	5	3	5	3	4	2	..	0	1	..	62.5	244.28 ± 6.06	81.90 ± 4.29	33.53 ± 1.94
Cos1-1'	1917	F ₂	1	1	2	0	2	2	2	2	2	7	13	7	5	0	0	1	..	68	347.43 ± 7.52	84.93 ± 5.32	24.45 ± 1.62
BB7-1'	1917	F ₂	75	330.75 ± 4.39	50.87 ± 3.11	15.38 ± .96
N1-3	1917	F ₂	..	2	0	4	..	2	4	9	6	12	9	11	5	3	62.5	325.35 ± 6.83	86.60 ± 4.87	26.62 ± 1.60

¹Cos = Paris White Cos; BB = Big Boston; N1 = BB7-1' ♀ X Cos1-1' ♂.

plants of these crosses had been held in check by some environmental influence. If this is the case, the results indicate that the parent plants were fairly homozygous for leaf-area genes. In crosses in which reciprocal F_1 families were grown the breeding behavior was practically similar.

All of the F_2 generations exhibited increased variation compared with that of the parents and F_1 generations, denoting segregation and recombination of factors.

In the crosses May King X lobed Wild (Table 46), Big Boston X lobed Wild (Table 47), and Big Boston X unlobed Wild (Table 48), the F_1 populations had mean leaf areas and frequency distributions which more nearly resembled those of the cultivated type than those of the wild. The spreads of the distributions practically equalled the combined spreads of the two parents in two of these crosses, and in the third, May King X lobed Wild, the F_2 distributions extended from about the lower extreme of the wild type to beyond the upper extreme of the May King. In all cases, however, the F_3 distributions were weighted more heavily on the lower than on the upper sides, indicating partial dominance of the wild type. It appears that from the cross May King X lobed Wild, types can probably be developed which will have greater leaf areas than the May King parent.

In crosses between May King and Grand Rapids and between Big Boston and Grand Rapids (Tables 51 and 49), the F_1 and F_2 distributions indicate lack of dominance. The F_2 distributions in both crosses extended beyond the combined distributions of both parents in both directions, indicating that the frequency distributions of the parents do not occupy the opposite extremes of the F_2 distributions and that new types can probably be established with both larger and smaller mean leaf areas than those of the parents.

In the cross Big Boston X Cos (Table 53), the parents were somewhat similar in leaf area. The F_1 mean leaf area was greater than those of both parents, indicating the bringing together of positive growth factors. The spread of the F_2 distribution was as great as the combined distributions of both parents and was weighted more heavily on the lower than on the upper side. These circumstances again indicate partial dominance of the wild type.

In the cross Grand Rapids X Cos (Table 52) the parents were nearly alike in leaf area. The two F_1 plants grown were intermediate in leaf area. The F_2 distribution covered the combined distributions of both parents, and produced some classes of smaller leaf area than that of the Cos. The F_2 distribution indicated a lack of dominance.

The cross unlobed Wild X Cos produced an F_1 and an F_2 which were intermediate between the parents in means and in spread of the frequency distributions. The F_2 distribution failed to reach either extreme of the combined distributions of the parents. Apparently larger

numbers of the F_2 of this cross would have to be grown to make probable the recovery of all of the parental classes. The F_2 distributions closely approximated a normal curve.

In accordance with expectations some of the F_3 families exhibited variabilities which compared favorably with those of the parents; others were practically as variable as the F_2 ; while still others exhibited intermediate amounts of variability. The F_3 families had different mean leaf areas, which provided further evidence of segregation and recombination.

In the crosses May King X lobed Wild (Table 46), Big Boston X lobed Wild (Table 47), and Big Boston X unlobed Wild (Table 48) the smaller-leaved (wild) type seems to have been practically recovered in only one case, Family A0-10-28, grown in 1916. In none of these crosses was an F_3 or F_4 family obtained which closely approximated the larger-leaved type. This result is in keeping with the skewed distribution shown by the F_2 of these crosses. Apparently quite large numbers of individuals would have to be grown to render reasonably certain the recovery of the parental classes. It is not indicated by these results that larger- and smaller-leaved types than the parents can be developed from the crosses named.

No F_3 or F_4 families were secured in the crosses May King X Grand Rapids and Big Boston X Grand Rapids, which had both larger and smaller mean leaf areas than those of either parent. Family E7-1-18 had a mean leaf area of 179.75 ± 8.00 as compared with 232.95 ± 3.24 for the M K 1-1' (the smaller-leaved parent), grown the same season. Family E7-1-2 had a mean leaf area of 427.83 ± 7.55 as compared with that of 369.22 ± 3.27 for Grand Rapids, the larger-leaved parent.

In the cross Big Boston X Grand Rapids (Table 49) the F_4 family G4-9-6-5 had a mean leaf area of 189.57 ± 6.59 as compared with a leaf area of 330.75 ± 4.39 for Big Boston, the smaller-leaved parent, grown in the same season. It is significant to note that the parent of family G4-9-6-5 belonged to the smallest-leaved F_3 family grown in 1916 and that its F_2 parent was the smallest-leaved plant from which F_3 progeny were grown. Family G4-9-22', on the other hand, had a mean leaf area about 45 percent larger than that of the larger parent, grown in the same season. The results from these two crosses are quite interesting in view of the close similarity of the parents in leaf area. The frequency distributions of the parents do not occupy the opposite extremes of the F_2 distributions. It appears quite certain, therefore, that types could be established from these crosses with leaf areas both larger and smaller than those of the parents.

Only one F_3 family was grown of the cross between unlobed Wild and Cos. Its mean leaf area and distribution spread were intermediate between those of the parents.

Time Required to Reach Flowering Stage

Lettuce has a flowering period which extends over a considerable time. Marked differences existed with reference to the time required for different varieties to reach the flowering stage. Especially were these differences marked between parents used in wild X cultivated crosses. It should be borne in mind that in nature *L. scariola* is an annual, and that in this investigation the wild seeds were sown in the spring. It was observed that *L. scariola* plants growing wild bloomed earlier on the average than those grown under culture. The cultivated forms, on the other hand, have been developed and are grown as ordinary annuals in this vicinity.

It seemed that this character could probably be studied best by securing data on the number of days required for the plants to present their first flowers. Accordingly all of the plants were carefully inspected every second morning during the blooming period, and the date was recorded on which the first flowers appeared on each plant. Each plant was tagged when it reached the blooming stage. From these data the number of days ensuing between seeding time and the time of presentation of flowers was determined for each plant. The figures for different plants of the various families were used in constructing frequency distributions. The results are presented in Tables 54 to 61.

Unfortunately the climate in central Illinois is too warm in the summer for the most successful maturity of lettuce, and many plants died before blooming. For this reason, the numbers from which data were obtained for this character complex were quite small in some families.

It should be borne in mind that, other things being equal, hot weather is more likely to destroy late-maturing plants than early ones. This may account in most instances for the depression of the frequency distributions on the upper sides.

The tables show that in all crosses the parents were of comparatively low variability, indicating relatively high homozygosity. The parents of given crosses also bore the same general relation to each other when grown more than one season.

The F_1 generations showed practically the same variability as the parental types, indicating comparatively pure parental material. An apparent exception is family C2, grown in 1916, which exhibited greater variability than the Big Boston but not more than the wild (Table 56). But even in this family, as the table shows, if one plant were omitted, the variation would be materially reduced; the larger variation is therefore probably due to errors in random sampling.

While there are exceptions, due in all probability to the small numbers, the F_2 populations in general exhibited increased variation as

TABLE 55.—INHERITANCE OF TIME REQUIRED TO REACH DATE OF FIRST BLOOM, BIG BOSTON ♀ X LOBED WILD ♂

Parent ¹	Year grown	Generation	Class centers in days from date of seeding ²																Total	Mean	S. D.	C. V.			
			112.5	116.5	120.5	124.5	128.5	132.5	136.5	140.5	144.5	148.5	152.5	156.5	160.5	164.5	168.5	172.5					176.5	180.5	184.5
			1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1					1	1	1
BB7-1'	1915	P ₂	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1						
W4	1915	P ₁	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1						
C0-1 and C0-3	1915	F ₂	5	6	10	9	21	30	14	4	5	1	1	1	3						
BB7-1'	1916	F ₂						
C0-1 and C0-3	1916	F ₂						
C0-3-99	1916	F ₄						
BB7-1'	1916	F ₄						
W4-1' and W4-1-11	1917	P ₂						
C0-1 and C0-3	1917	F ₂						
C0-1-26	1917	F ₂						
C0-3-17	1917	F ₂						
C0-1-124	1917	F ₃						
C0-1-62	1917	F ₃						
C0-3-103	1917	F ₃						
C0-3-10	1917	F ₃						
C0-3-99-13	1917	F ₄						

¹BB = Big Boston; W = Wild; C0 = BB7 ♀ X W4 ♂. ²In order to economize space, the distributions are presented in 4-day classes; the constants were calculated from distributions based on 2-day classes.

TABLE 56.—INHERITANCE OF TIME REQUIRED TO REACH DATE OF FIRST BLOOM, BIG BOSTON ♀ X UNLOBED WILD ♂ AND RECIPROCAL

Parent ¹	Year grown	Generation	Class centers in days from date of seeding ²												Total	Mean	S. D.	C. V				
			120.5	124.5	128.5	132.5	136.5	140.5	144.5	148.5	152.5	156.5	160.5	164.5					168.5	172.5	176.5	180.5
BB7-1'	1915	P ₂	..	1	11	13	128.88 ± .34	1.82 ± .24	1.41 ± .19
W4	1915	F ₁	5	129.63 ± .99	5.89 ± .70	4.54 ± .54
C2	1915	F ₁	2	3	4	5	1	16	134.41 ± .48	3.34 ± .34	2.48 ± .25
BB7-1'	1916	P ₂	4	6	10	2	22	133.50 ± .54	3.87 ± .39	2.90 ± .29
C1 and C3	1916	F ₁	9	4	6	4	23	135.86 ± .48	3.32 ± .34	2.44 ± .25
D1	1916	F ₁	1	8	8	4	1	22	132.5 ± .75	4.42 ± .53	3.34 ± .40
C3-1	1916	F ₂	1	1	4	2	5	2	2	2	17	124.47 ± 1.04	6.33 ± .73	5.09 ± .59
D1-1 and D1-2	1916	F ₂	9	139.06 ± .46	2.06 ± .33	1.49 ± .24
BB7-1'	1917	P ₂	5	3	1	17	171.74 ± 1.53	9.33 ± 1.08	5.43 ± .63
W4-1' and W4-1'-11	1917	P ₂	4
C1-27	1917	F ₂	1	0	0	1	0	1	1	1	3
D1-12	1917	F ₂	3
C3-1-15	1917	F ₃	8	4	7	2	0	1	19	195.18 ± .70	5.08 ± .53	4.06 ± .43
D1-2-2	1917	F ₃	8	7	1	0	0	0	1	12	126.17 ± 1.53	7.85 ± 1.08	6.22 ± .86
D1-1-10	1917	F ₃	2	5	15	6	6	2	1	0	1	38	130.87 ± .69	6.28 ± .49	4.80 ± .37
C3-1-2	1917	F ₃	0	1	0	1	0	1	0	0	1	4

¹BB = Big Boston; W = Wild; C2 = BB5-5 ♀ X W38 (unlobed) ♂; C1 = BB5-4 ♀ X W5 (unlobed) ♂; C3 = BB7-1' ♀ X W5 (unlobed) ♂; D1 = W5 ♀ X BB7-1' ♂. ²In order to economize space the distributions are presented in 4-day classes; the constants were calculated from distributions based on 2-day classes.

TABLE 57.—INHERITANCE OF TIME REQUIRED TO REACH DATE OF FIRST BLOOM, MAY KING ♀ X GRAND RAPIDS ♂ AND RECIPROCAL

Parent ¹	Year grown	Generation	Class centers in days from date of seeding																Total	Mean	S. D.	C. V.			
			Class centers in days from date of seeding																						
			111.5	113.0	115.0	117.5	119.0	121.0	123.0	125.0	127.5	129.0	131.0	133.0	135.0	137.5	139.0	141.0					143.0	145.0	147.5
GR2-3-1	1915	P ₂	1	131.41 ± .74	5.26 ± .52	4.00 ± .40	
MK1-1'	1915	P ₂	23	122.74 ± .33	6.53 ± .23	5.32 ± .19
E2-1, E2-4, E2-6	1915	F ₂	9	12	16	13	16	29	21	16	20	7	9	10	1	2	2	1	184	138.10 ± .51	3.36 ± .39	1.72 ± .26
GR2-3-1'	1916	P ₂	10	136.83 ± .55	3.17 ± .39	2.31 ± .28
MK1-1'	1916	P ₂	15	129.86 ± .21	2.25 ± .15	1.73 ± .11
E7, E0	1916	F ₁	55	129.86 ± .21	2.25 ± .15	1.73 ± .11
F0	1916	F ₁	3	127.85 ± .39	4.15 ± .27	3.25 ± .22
E7-1, E7-3, E7-9	1916	F ₂	1	2	5	7	14	8	6	3	4	52	126.25 ± .31	2.63 ± .22	2.08 ± .18
E2-4-4'	1916	F ₂	1	2	5	6	13	4	1	32	141.32 ± .87	4.30 ± .62	3.04 ± .44
GR2-3-1'	1917	P ₂	11	136.03 ± .44	2.82 ± .31	2.07 ± .23
MK1-1'	1917	P ₂	19	134.77 ± 1.83	9.00 ± 1.29	6.68 ± .96
E7-1	1917	F ₂	11	124.90 ± 1.40	6.58 ± .99	5.27 ± .79
E7-3-47	1917	F ₂	10	126.83 ± .66	3.40 ± .47	2.68 ± .37
E2-4-4'	1917	F ₂	12	127.82 ± .77	5.00 ± .52	3.91 ± .41
E7-3-22	1917	F ₂	19	134.50 ± .86	4.77 ± .61	3.55 ± .45
E7-1-18	1917	F ₂	14	130.10 ± .71	3.35 ± .51	2.58 ± .39
E2-4-4'-25	1917	F ₄	10	130.10 ± .71	3.35 ± .51	2.58 ± .39

¹GR = Grand Rapids; MK = May King; E2 = MK15 ♀ X GR1 ♂; E7 = MK1-1' ♀ X GR2-3-1' ♂; E0 = MK1 ♀ X GR2 ♂; F0 = GR2-2 ♀ X MK1-5 ♂.

TABLE 58.—INHERITANCE OF TIME REQUIRED TO REACH DATE OF FIRST BLOOM, GRAND RAPIDS ♀ X PARIS WHITE COS ♂

Parent ¹	Year grown	Generation	Class centers in days from date of seeding																Total	Mean	S. D.	C. V.			
			Class centers in days from date of seeding																						
			133.5	135.5	137.5	139.5	141.5	143.5	145.5	147.5	149.5	151.5
Cos1-1'	1916	P ₂	6	138.10 ± .50	2.37 ± .36	1.72 ± .26
GR2-3-1'	1916	P ₂	1	10	139.79 ± .52	2.88 ± .37	2.06 ± .26
Y1-1, Y1-2, Y1-3	1916	F ₂	14	139.79 ± .52	2.88 ± .37	2.06 ± .26

¹Cos = Paris White Cos; GR = Grand Rapids; Y1 = GR2-3-1' ♀ X Cos1-1' ♂.

TABLE 59.—INHERITANCE OF TIME REQUIRED TO REACH DATE OF FIRST BLOOM, BIG BOSTON ♀ X GRAND RAPIDS ♂ AND RECIPROCAL

Parent ¹	Year grown	Generation	Class centers in days from date of seeding															Total	Mean	S. D.	C. V.
			Class centers in days from date of seeding																		
			117.5	119.5	121.5	123.5	125.5	127.5	129.5	131.5	133.5	135.5	137.5	139.5	141.5	143.5	145.5				
BB7-1'	1915	P ₂	1	4	7	0	1	13	128.88 ± .34	1.82 ± .24	1.41 ± .19
GR2-3-1'	1915	P ₂	1
G4-9 and G4-23	1915	F ₂	1	5	2	2	6	7	8	0	12	4	3	1	0	1	..	52	134.41 ± .48	3.34 ± .34	2.48 ± .25
BB7-1'	1916	F ₂	4	3	3	6	4	1	1	..	22	138.10 ± .51	2.37 ± .36	1.72 ± .26	
GR2-3-1'	1916	F ₂	1	1	4	2	10	
G2	1916	F ₁	1	
H2	1916	F ₁	1	
G4-9-14	1916	F ₂	6	5	1	3	1	7	22	127.32 ± .49	3.41 ± .35	2.68 ± .27	
G4-23-6	1916	F ₂	5	5	5	1	3	1	20	131.00 ± .46	3.03 ± .32	2.31 ± .25	
G4-9-8	1916	F ₃	1	0	3	0	1	1	..	6	
G4-9-8-6'	1916	F ₄	2	1	0	0	3	0	2	0	1	9	134.83 ± 1.20	5.33 ± .85	3.95 ± .63	

¹BB = Big Boston; GR = Grand Rapids; G4 = BB7 ♀ X GR2 ♂; G2 = BB11 ♀ X GR1 ♂; H2 = GR2-3-2' ♀ BB7-1'.

TABLE 60.—INHERITANCE OF TIME REQUIRED TO REACH DATE OF FIRST BLOOM, GRAND RAPIDS ♀ X UNLOBED WILD ♂

Parent ¹	Year grown	Generation	Class centers in days from date of seeding															Total	Mean	S. D.	C. V.
			Class centers in days from date of seeding																		
			128.5	132.5	136.5	140.5	144.5	148.5	152.5	156.5	160.5	164.5	168.5	172.5	176.5	180.5	184.5				
GR2-3-1'	1917	P ₂	3	4	3	0	1	11	141.32 ± .87	4.30 ± .62	3.04 ± .44	
W4-1' and W4-1'-11'	1917	P ₂ and P ₃	17	171.74 ± 1.53	9.33 ± 1.08	5.43 ± .63	
T2-1	1917	F ₇	2	4	3	4	0	4	1	18	139.06 ± 1.29	8.10 ± .91	5.82 ± .65		

¹GR = Grand Rapids; W = Wild; T2 = GR2-3-1' ♀ X W5 ♂. ²N₀ unlobed Wild were grown in 1917; the results from the lobed Wild are included for comparison purposes.

compared with those of the parents and the F_1 , indicating segregation and recombination of genetic factors for time required to mature flowers. Further evidence of segregation and recombination is furnished by the F_3 and F_4 families.

As to dominance, distribution spread, and possibilities for developing new forms, the various crosses exhibited different behavior. In the cross May King X lobed Wild (Table 54), no F_1 plants were grown in the open field. The F_2 generation in 1915 had a spread from about the upper extreme of the distribution of the wild parent to a point well below (12 days) the lower extreme of the May King. The frequency distribution is heavier on the lower than on the upper side, but this may be due in part to the effect of hot weather in killing late blooming plants. The F_2 distribution indicates that at least the range of variability of the earlier flowering (May King) parent is not located at the lower extreme of the potential F_2 variability, and this fact suggests the possibility of producing new types of earlier flowering habit than either of the parents.

The results in F_3 and F_4 lend confirmation to this suggestion. In 1916 several F_3 families were produced which were earlier in flowering habit than the May King for that season. One of these families, A0-1-32, had a mean date of first bloom about 15.5 days earlier than that of May King. In 1917 the progeny of A0-1-32-3 (one of the plants of A0-1-32) had a mean date of first bloom about 15 days earlier than May King, showing that the strain is more or less homozygous for maturity factors. Another F_4 family, A0-1-20-38, had a mean date of first bloom about the same as that of A0-1-32-3. Both of these families had a low variability, as did a number of F_4 and some F_3 families. On the other hand, no F_3 or F_4 families were secured with a mean date of first bloom even approximating that of the wild form. It would appear possible, therefore, to establish new types which are of earlier flowering habit than the May King, but it would probably be a difficult matter to recover the late flowering habit of the wild.

The cross Big Boston X lobed Wild (Table 55) gave results quite similar to those of the cross just discussed, as did also the cross Big Boston X unlobed Wild (Table 56).

The parents of the cross Big Boston X Grand Rapids (Table 59) were practically similar as to time of flowering. The two F_1 plants grown, bloomed at about the same time as the parent types. The F_2 distribution appreciably overlapped the combined distributions of both parents. In F_3 , types with lower variability and of earlier mean date of first bloom than the Big Boston, were obtained. Others were recovered which in these respects approximately resembled the parents. None of the F_3 families, however, had distributions extending as

low as that of the F_2 . It appears likely that types could be developed from this cross with earlier and later flowering habits than either of the parents.

In the cross May King X Grand Rapids (Table 57) the parents were quite similar in blooming habit. The reciprocal F_1 's showed an earlier date of first bloom than either parent, indicating the combination of additive early-maturing factors. The F_2 distribution extended from the upper extreme of the combined parental distributions to six classes (12 days) below their lowest class in 1915 and 1916 and seven classes lower in 1917. One F_3 family, E-2-4-4', bloomed on the average 10 days earlier than the May King (the earlier parent); furthermore, this family had a low variability. No F_3 families were secured which were as late blooming on the average as the parental varieties. The results indicate that new types could be developed with earlier flowering habits than those of the parents, tho it appears uncertain as to whether later-flowering types than the later (Grand Rapids) parent could be established from this cross.

In the cross unlobed Wild X Cos (Table 61), the F_1 plants were of earlier-flowering habit than both parents. The F_2 in both seasons produced a distribution extending far below that of both parents, but it failed even to reach the *lower* limits of the wild type in 1917. Three of the four F_3 families grown in 1917 had earlier blooming plants than any of the F_2 's in either season. One of the F_3 families, R1-2-80, had a mean date of first bloom 25 days earlier than that of the Cos in 1917. None of the F_3 's represented even near-recovery of either parental type. One F_3 , R1-2-88, had a greater variability than the F_2 in both seasons. In this cross, dominant genes for earliness of bloom were apparently brought together in the hybrids. It appears that earlier-blooming types than both parents may readily be established from this cross, but it would seem to be difficult or impossible to secure types of later-flowering habit than the wild.

No F_1 plants of the cross Grand Rapids X Wild (Table 60) reached the flowering stage outside of the greenhouse. Of the 18 F_2 plants grown, six bloomed earlier than any plants of the Grand Rapids. New types can no doubt be established from this cross with earlier-flowering habits than that of Grand Rapids.

The parents of the cross Big Boston X Cos (Table 62) differed from each other in mean flowering time. The F_1 was intermediate. The F_2 in 1917 practically covered the combined distributions of both parents. No F_3 's were grown. Because of the small numbers of plants reaching the flowering stage definite conclusions cannot be drawn other than that apparently both parental forms could be recovered from the hybrids.

In the cross Grand Rapids X Cos (Table 58) no F_1 plants grown in the field reached the blooming stage. The F_2 distribution almost

covered the combined distributions of the parents. Definite conclusions cannot be drawn because of the small numbers of plants reaching the blooming period.

Plant Height at Date of First Bloom

Differences in plant height are found between the varieties of numerous species. Morphologically these differences are due to differences in the lengths of internodes or the number of nodes or both. Genetically the differences in many cases have been explained on a rather simple basis. For instance, Mendel (Castle, 1916) found tallness and dwarfness in *Pisum sativum* to be accounted for by a single pair of genes, tallness being dominant. Emerson (1916) crossed dwarf lima beans, in which the main axis is terminated by an inflorescence when from four to eight nodes have developed, with pole limas which have no terminal inflorescence and are indeterminate in growth habit. These differences result in large differences in plant height, but yet are accounted for by a single pair of genes, the indeterminate condition being fully dominant.

On the other hand, the differences in numerous other species have been found to be quite complex from the standpoint of genetic constitution, including tobacco, Indian corn, and many others.

Rather marked differences were found in the height of the mature lettuce plants. No attempt was made to study the length of internodes or the numbers of nodes, chiefly because of the extreme shortness of the internodes in the rosette stage and because removal of the leaves would probably have destroyed many of the plants and reduced the data for other characters.

For the purpose of studying plant height the greatest height, in inches, was determined on the date each plant was observed to produce its first flowers, the plants being inspected every two days during the flowering period.

It should be stated that this measurement does not in most cases represent the absolute height attained. In varieties which have a compact panicle, like May King and Grand Rapids, there is little if any increase in height after the first flowers appear, but in the wild forms, which have loose, open panicles, there is usually an appreciable increase in height after the first blossoms appear. It would have been better to take the measurements in absolute height had it not been for the fact that many plants died during the blooming period because of hot weather. It appears, therefore, that comparable measurements could not have been secured for absolute plant height. Everything considered, the method employed seemed the best one to use under the circumstances.

In taking the measurements the panicle branches were gathered together and the greatest length of growth attained was determined.

The data for the inheritance of plant height are presented in Tables 63 to 71.

Owing to the large proportion of plants which died before reaching the flowering stage, the numbers in most families were small; this fact should be kept in mind in considering the results.

The tables show that the parental types exhibited a low variability in all cases in comparison with the hybrids. Furthermore, the parents of given crosses occupied approximately the same positions with reference to each other when grown more than one season.

The F_1 generations exhibited variations which compared favorably with those of the parents. There was no indication in the F_1 of any cross that the parent stocks were conspicuously impure.

Except in the crosses Grand Rapids X Cos (Table 67) and Big Boston X Cos (Table 69), in both of which the numbers of F_2 were small and the parental differences slight, the variabilities in F_2 exceeded those in F_1 and the parental forms, indicating that segregation and recombination of genes for plant height had taken place. Further evidence of segregation was provided by the F_3 and F_4 families.

In all crosses except May King X lobed Wild (Table 63) the F_2 frequency distributions did not extend beyond the combined distributions of the parents. Failure to do so, however, may have been due to the small number of plants involved in some crosses; in fact, the behavior of the F_3 families in certain crosses strongly supports this view. In the single apparent exception named the F_2 populations, consisting of 232 individuals in 1915 and 68 in 1917, had distributions extending from slightly above the mean of the shorter parent to several classes beyond the upper extreme of the taller parent.

All the F_2 distributions seem to simulate practically normal curves; such differences as exist can probably be accounted for by errors in random sampling.

In the crosses in which F_3 and F_4 families were grown, the different families showed variabilities ranging in degree from about those of the parents to that of the F_2 , all of which are in accord with expectations.

Tables 68 and 71 show that from the crosses Big Boston X Grand Rapids and May King X Grand Rapids, F_3 and F_4 families were secured which closely approximated the parents in mean plant height and in spread of the frequency distributions; others showed intermediate means and frequency distributions; while some were secured with a higher or lower mean than either parent. While the numbers were quite small, this circumstance in connection with the F_2 results suggests that the frequency distributions of the parents of these crosses may not lie at the extreme limits of the potential variability of the F_2 generation.

The cross Big Boston X unlobed Wild (Table 64) produced no F_3 families which closely resembled the shorter parent in mean plant

TABLE 63.—INHERITANCE OF PLANT HEIGHT, MAY KING ♀ X LOBED WILD ♂

Parent:	Year grown	Genera- tion	Class centers in inches																Total	Mean	S. D.	C. V.								
			16.5	19.0	21.5	24.0	26.5	29.0	31.5	34.0	36.5	39.0	41.5	44.0	46.5	49.0	51.5	54.0					56.5	59.0	61.5	64.0	66.5	69.0	71.5	
W4	1915	P ₁	1	3	7	6	2	2	8	11	17	31	42	35	26	23	14	8	0	1	0	0	1	6	42.75	1.72	6.25	1.22	14.62	± 2.91
MK-1'	1915	P ₂	1	3	7	6	2	2	8	11	17	31	42	35	26	23	14	8	0	1	0	0	1	23	25.41	.40	2.84	.28	11.18	± 1.13
A0-1	1915	F ₁	1	3	7	6	2	2	8	11	17	31	42	35	26	23	14	8	0	1	0	0	1	232	43.47	.30	0.66	.21	15.32	± .49
W4-1'	1916	P ₁	1	4	3	5	1	2	7	6	1	0	1	1	1	1	1	1	1	1	1	1	1	15	33.67	.57	3.28	.40	13.86	± 1.74
A0-12 and A0-17	1916	F ₂	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	33	33.77	.66	5.59	.46	16.55	± 1.41
A0-12 and A0-17	1916	F ₂	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	11	29.91	.82	4.03	.58	13.48	± 1.97
A0-12 and A0-17	1916	F ₂	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	48	30.51	.37	3.84	.26	12.58	± .88
A0-12-45	1916	F ₃	1	3	9	8	13	10	5	1	1	0	1	1	1	1	1	1	1	1	1	1	1	51	32.61	.39	4.13	.28	13.36	± .91
A0-10-28	1916	F ₃	1	1	4	8	14	8	5	3	1	0	0	1	1	1	1	1	1	1	1	1	1	49	33.74	.60	4.70	.33	14.41	± 1.05
A0-1-84	1916	F ₃	2	2	4	8	6	7	6	7	4	1	1	1	1	1	1	1	1	1	1	1	1	10	35.00	.43	2.00	.30	5.71	± .86
A0-1-32	1916	F ₃	1	1	2	5	4	13	8	9	6	6	3	1	1	1	1	1	1	1	1	1	1	59	37.05	.52	5.86	.36	15.82	± 1.01
A0-10-86	1916	F ₃	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	6	40.67	2.24	8.12	1.58	19.97	± 4.04	
A0-10-44	1916	F ₃	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	18	41.22	.98	6.18	.69	14.99	± 1.72	
A0-18-40	1916	F ₃	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	7	43.29	1.24	4.86	.88	11.23	± 2.05	
A0-1-16	1916	F ₃	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	25	46.50	.69	5.10	.49	10.96	± 1.06	
W4-1' and W4-1'-11	1916	F ₃	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	19	41.06	.93	5.70	.66	13.88	± 1.64	
W4-1' and W4-1'-11	1917	P ₂	1	4	9	2	1	1	1	1	1	3	2	4	3	0	1	1	1	1	1	1	1	17	26.76	.41	2.68	.29	10.01	± 1.09
MK-1'	1917	P ₂	1	4	9	2	1	1	1	1	1	1	3	2	4	3	0	1	1	1	1	1	1	68	40.66	.59	7.22	.42	17.76	± 1.06
A0-12 and A0-17	1917	F ₂	1	0	3	4	0	10	0	14	7	7	3	2	1	1	1	2	1	1	1	1	1	7	30.07	1.59	6.25	1.13	20.73	± 3.90
A0-18-38	1917	F ₂	1	0	3	4	0	10	0	14	7	7	3	2	1	1	1	2	1	1	1	1	1	41	32.66	.47	4.42	.33	13.53	± 1.03
A0-10-10	1917	F ₂	1	0	3	4	0	10	0	14	7	7	3	2	1	1	1	2	1	1	1	1	21	33.29	.87	5.93	.51	17.81	± 1.91	
A0-12-62	1917	F ₂	1	0	3	4	0	10	0	14	7	7	3	2	1	1	1	2	1	1	1	1	23	34.43	.44	3.10	.31	9.00	± .90	
A0-10-15	1917	F ₂	1	2	6	2	3	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	14	35.07	.63	3.50	.45	9.98	± 1.24	
A0-1-41	1917	F ₂	1	3	7	8	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	35	37.36	.64	5.60	.45	14.98	± 1.24	
A0-10-11	1917	F ₂	1	2	1	2	3	9	8	4	3	7	0	1	1	1	2	2	0	0	0	0	47	46.50	.52	4.31	.37	11.42	± .80	
A0-1-15	1917	F ₂	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	31	30.69	.41	3.38	.29	11.01	± .95	
A0-12-45-72	1917	F ₄	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	22	34.83	.49	3.39	.34	11.00	± 1.13	
A0-12-45-30	1917	F ₄	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	24	34.83	.49	3.39	.34	11.00	± 1.13	
A0-1-32-3	1917	F ₄	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14	34.83	.49	3.39	.34	11.00	± 1.13	
A0-1-6-1	1917	F ₄	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	24	34.83	.49	3.39	.34	11.00	± 1.13	
A0-12-45-22	1917	F ₄	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14	36.68	.50	2.75	.35	7.50	± .96	
A0-1-20-38	1917	F ₄	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	31	42.23	.28	2.30	.20	6.12	± .63	
A0-10-44-42	1917	F ₄	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	30	42.23	.28	2.30	.20	6.12	± .63	
A0-18-40-15	1917	F ₄	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	18	43.58	1.20	7.56	.85	17.35	± 2.01	

W4 = Wild; MK = May King; A0 = MK1 ♀ X W4 ♂.

TABLE 64.—INHERITANCE OF PLANT HEIGHT, BIG BOSTON ♀ X UNLOBED WILD ♂ AND RECIPROCAL

Parent ¹	Year grown	Generation	Class centers in inches												Total	Mean	S. D.	C. V.					
			Class centers in inches																				
			19.0	21.5	24.0	26.5	29.0	31.5	34.0	36.5	39.0	41.5	44.0	46.5					49.0	51.5			
BB7-1'	1915	P ₂	1	4	7	0	0	1	13	28.42 ± .52	2.80 ± .37	9.85 ± 1.30
C2	1915	F ₁	16	38.06 ± .51	3.04 ± .36	7.99 ± .95
BB7-1'	1916	P ₂	1	2	12	6	1	..	4	3	22	24.45 ± .30	2.08 ± .21	8.51 ± .87
C1	1916	F ₁	23	33.13 ± .57	4.08 ± .41	12.31 ± 1.24
D1	1916	F ₁	1	1	0	2	1	7	5	4	21	32.57 ± .66	4.47 ± .47	13.72 ± 1.46
C3-1	1916	F ₂	3	0	2	1	4	0	6	0	1	1	16	31.97 ± .90	5.32 ± .63	16.64 ± 2.04
D1-1 and D1-2	1916	F ₂	3	0	2	0	5	3	1	1	1	17	29.15 ± 1.05	6.44 ± .75	22.09 ± 2.68
BB7-1'	1917	P ₂	1	0	4	2	2	..	1	1	9	25.11 ± .65	2.91 ± .46	11.59 ± 1.87
W4-1' and W4-1'-11 ²	1917	P ₂ and P ₃	17	41.06 ± .93	5.70 ± .66	13.88 ± 1.64
C1-27	1917	F ₂	4
D1-12	1917	F ₂	1	0	0	1	0	1	1	1	3
D1-2-2	1917	F ₂	12	30.88 ± .53	2.72 ± .37	8.81 ± 1.21
C3-1-15	1917	F ₃	19	30.97 ± .54	3.50 ± .37	11.30 ± 1.20
D1-1-10	1917	F ₃	38	39.26 ± .60	5.49 ± .42	13.98 ± 1.10

¹BB = Big Boston; W = Wild; C2 = BB5-5 ♀ X W38 ♂; C1 = BB5-4 ♀ X W38 ♂; D1 = W5 ♀ X BB7-1' ♂; C3 = BB7-1' ♀ X W5 ♂. ²No unlobed Wild were grown in 1917; the results from the lobed Wild families are presented for comparison.

TABLE 65.—INHERITANCE OF PLANT HEIGHT, GRAND RAPIDS ♀ X PARIS WHITE COS ♂

Parent ¹	Year grown	Generation	Class centers in inches												Total	Mean	S. D.	C. V.					
			Class centers in inches																				
			26.5	29.0	31.5	34.0	36.5	39.0	41.5	44.0	46.5	49.0	51.5	54.0									
GR2-3-1'	1917	P ₃	1	1	0	2	4	1	2	11	35.59 ± .90	4.43 ± .64	12.45 ± 1.82
W4-1' and W4-1'-11 ²	1917	P ₂ and P ₃	17	41.06 ± .93	5.70 ± .66	13.88 ± 1.64
T2-1	1917	F ₂	18	39.14 ± 1.12	7.04 ± .79	17.99 ± 2.09

¹GR = Grand Rapids, W = Wild; T2 = GR2-3-1 ♀ X W5 ♂. ²No unlobed Wild were grown in 1917; the results from the lobed Wild are presented for comparison.

TABLE 66.—INHERITANCE OF PLANT HEIGHT, BIG BOSTON ♀ X LOBED WILD ♂

Parent ¹	Year grown	Generation	Class centers in inches												Total	Mean	S. D.	C. V.												
			14.0	16.5	19.0	21.5	24.0	26.5	29.0	31.5	34.0	36.5	39.0	41.5					44.0	46.5	49.0	51.5	54.0	56.5	59.0					
BB7-1'	1915	P ₂	1	4	7	0	0	1	13	28.42 ± .52	2.80 ± .37	9.85 ± 1.30
W4	1915	P ₁	6	42.75 ± 1.72	6.95 ± 1.22	14.62 ± 2.91
C0-1 and C0-3	1915	F ₂	1	1	1	8	9	6	14	17	18	12	10	8	4	5	1	115	42.70 ± .44	7.04 ± .31	16.46 ± .75
BB7-1'	1916	P ₂	1	2	6	1	22	28.45 ± .30	2.08 ± .21	8.51 ± .87	
W4-1'	1916	P ₂	1
C0-1 and C0-3	1916	F ₂	3	4	6	4	7	2	3	1	1	33	30.89 ± .72	6.15 ± .51	19.91 ± 1.72
C0-3-99	1916	F ₃	1	1	0	0	0	3
BB7-1'	1916	P ₂	1	1	0	2	9	25.11 ± .65	2.91 ± .46	11.59 ± 1.87	
W4-1' and W4-1'-11	1917	P ₂ and P ₃	17	41.06 ± .93	5.70 ± .66	13.88 ± 1.64	
C0-1 and C0-3	1917	F ₂	1	1	1	3	2	4	3	2	3	2	0	2	0	1	21	40.07 ± 1.09	7.43 ± .77	18.54 ± 2.00	
C0-1-124	1917	F ₃	2	4	3	0	1	0	1	19	24.39 ± .94	6.08 ± .67	24.93 ± 2.89	
C0-1-26	1917	F ₃	1	2	3	3	0	1	0	1	0	1	40	34.69 ± .50	4.71 ± .36	13.58 ± 1.04	
C0-3-10	1917	F ₃	1	3	4	3	4	3	2	4	1	1	0	1	0	0	0	24	38.27 ± .93	6.75 ± .66	17.64 ± 1.77	
C0-3-103	1917	F ₃	33	38.70 ± .86	7.33 ± .61	18.94 ± 1.63	
C0-3-17	1917	F ₃	20	46.13 ± .72	4.76 ± .51	10.32 ± 1.11	
C0-1-62	1917	F ₃	15	46.33 ± 1.35	7.77 ± .96	16.77 ± 2.12	
C0-3-99-13	1917	F ₄	5

1BB = Big Boston; W = Wild; C0 = BB7 ♀ X W4 ♂.

TABLE 67.—INHERITANCE OF PLANT HEIGHT, GRAND RAPIDS ♀ X PARIS WHITE COS ♂

Parent ¹	Year grown	Generation	Class centers in inches						Total	Mean	S. D.	C. V.					
			24.0	26.5	29.0	31.5	34.0	36.5					39.0	41.5			
Cos1-1'	1916	P ₂	6	33.58 ± 1.40	5.09 ± .99	15.16 ± 3.02
GR2-3-1'	1916	P ₂	1	1	1	5	2	0	1	1	1	1	1	10	29.50 ± .67	3.12 ± .47	10.58 ± 1.61
Y1-1, Y1-2, Y1-3	1916	F ₂	1	1	3	5	2	1	1	2	14	34.89 ± .65	3.61 ± .46	10.35 ± 1.33	

1Cos = Paris White Cos; GR = Grand Rapids; Y1 = GR2-3-1' ♀ X Cos1-1' ♂.

TABLE 70.—INHERITANCE OF PLANT HEIGHT, UNLOBED WILD ♀ X PARIS WHITE COS ♂ AND RECIPROCAL

Parent ¹	Year grown	Generation	Class centers in inches															Total	Mean	S. D.	C. V.
			24.0	26.5	29.0	31.5	34.0	36.5	39.0	41.5	44.0	46.5	49.0	51.5	54.0	56.5	59.0				
Cos1-1'	1916	P ₂	1	0	3	0	0	1	1	2	2	2	2	2	2	2	2	33.58 ± 1.40	5.09 ± .99	15.16 ± 3.02	
R1	1916	F ₁	38.50 ± 1.13	6.47 ± .80	16.81 ± 2.13		
R1-2	1916	F ₂	44.00 ± .42	2.57 ± .30	5.84 ± .68		
Cos1-1'	1917	P ₂	41.06 ± .93	5.70 ± .66	13.88 ± 1.64		
W4-1' and W4-1'-11 ²	1917	P ₂ and P ₃	35.72 ± .69	4.12 ± .49	11.53 ± 1.39		
R1-2	1917	F ₂	1	0	0	0	1	2	4	0	0	0	1	40.46 ± .61	3.14 ± .43	7.76 ± 1.07		
R1-2-98	1917	F ₂	46.74 ± .58	3.93 ± .41	8.41 ± .88		
R1-2-80	1917	F ₂	47.50 ± 1.38	7.90 ± .97	16.63 ± 2.10		
R1-2-88	1917	F ₃		
R1-2-10	1917	F ₃		

¹Cos = Paris White Cos; W = Wild; R1 = W5 ♀ X Cos1-1' ♂. ²No unlobed Wild were grown in 1917; the results from the lobed Wild are included for purposes of comparison.

TABLE 71.—INHERITANCE OF PLANT HEIGHT, BIG BOSTON ♀ X GRAND RAPIDS ♂ AND RECIPROCAL

Parent ¹	Year grown	Generation	Class centers in inches												Total	Mean	S. D.	C. V.		
			16.5	19.0	21.5	24.0	26.5	29.0	31.5	34.0	36.5	39.0	41.5							
BB7-1'	1915	P ₂	1	4	7	0	0	1	13	28.42 ± .52	2.80 ± .37	9.85 ± 1.30
GR2-3-1	1915	P ₃	1	34.60 ± .37	3.87 ± .26	11.16 ± .76
G4-9 and G4-23	1915	F ₂	51	24.45 ± .30	2.08 ± .21	8.51 ± .87
BB7-1'	1916	P ₂	22	29.50 ± .67	3.12 ± .47	10.58 ± 1.61
GR2-3-1'	1916	P ₃	10
G2	1916	F ₁	1
H2	1916	F ₁	1
G4-9-14	1916	F ₃	21	25.36 ± .34	2.35 ± .24	9.26 ± .94
G4-23-6	1916	F ₃	22	28.17 ± .58	3.96 ± .41	14.09 ± 1.49
G4-9-8	1916	F ₃	6	29.83 ± .86	3.11 ± .61	10.43 ± 2.06
G4-9-8-6'	1916	F ₄	1	0	5	1	1	1	2	2	1	9	22.61 ± .76	3.36 ± .53	14.86 ± 2.41

¹BB = Big Boston; GR = Grand Rapids; G4 = BB7 ♀ X GR2 ♂; G2 = BB11 ♀ X GR1 ♂; H2 = GR2-3-2' ♀ X BB7-1' ♂.

height. No unlobed Wild family was grown in 1917 due to loss of stock, but one of the F_3 families, D1-1-10, had a mean ($39.26 \pm .60$) practically equal to that of W4-1' and W4-1'-11 ($41.06 \pm .93$), the results from which are included in Table 64 for purposes of comparison.

In the cross May King X lobed Wild (Table 63) no F_3 or F_4 families were secured which compared closely with the shorter parent (May King) in mean plant height. Some contained classes as low in plant height as those of May King, but none extended below. On the other hand, one F_3 family (A0-1-15) and two F_4 families (A0-10-44-42 and A0-18-40-15) had average plant heights higher than those of the wild forms, but the variability was somewhat high in the case of A0-18-40-15. It is pertinent to note that F_4 lots A0-18-40-15 and A0-10-44-42 came from F_3 families which were of higher mean plant height than any other F_3 families except one (A0-1-16). Furthermore, each of these two F_3 families was descended from a noticeably high F_2 plant.

The cross Big Boston X lobed Wild (Table 66) produced one F_3 family, C0-1-124, which had a mean plant height lower than that of the shorter (Big Boston) parent, but it exhibited a higher variability; this family would no doubt have been a good one from which to make selections in a minus direction, because of its apparently heterozygous nature. The parent of this family had a lower plant height (19 inches) than any other F_2 plant from which an F_3 generation was grown. Two other F_3 families, C0-3-17 and C0-1-62, averaged about 5 inches higher than the wild in the same season; the latter family, however, had a high variability. These results indicate that new types, both of lower and higher mean plant height than either parent, can probably be isolated from crosses between these varieties.

Habit of Growth in the Rosette Stage

The wild forms of lettuce have a distinctly spreading rosette habit of growth; there is no tendency whatever toward the formation of heads, such as are produced by some cultivated varieties. The Grand Rapids (leaf type) forms no heads, but the leaves have a more upright habit than the wild forms; perhaps this is due wholly or in part to the crinkling and crumpling of the leaves. The Big Boston and May King, on the other hand, form fairly solid, compact heads under favorable conditions. The Paris White Cos forms a tall, rather loose head. Photographs of each of these types are shown in Fig. 1.

In crosses involving the heading and non-heading types the F_1 plants were intermediate in habit, inclining perhaps toward the non-heading parent. In F_2 , segregation and recombination occurred, and the parental forms were practically recovered in most crosses. In addi-

tion, numerous gradations between the parental extremes were obtained. It therefore seemed apparent that inheritance of habit occurred in a quantitative manner.

No method could be devised for securing exact measurements of this character, as was done with leaf length and other characters. After studying the forms of segregates in relation to the parental types, two series of visual standards were adopted, one for the wild X heading-type crosses and another for the Grand Rapids X heading-type crosses. The plants of the F_2 , F_3 , and F_4 generations were classified according to the type they most closely resembled. No attempt was made to calculate statistical constants because of the inexactness of the method employed.

Crosses Between the Wild and Heading Types. For studying crosses between the wild forms and heading varieties, seven classes were adopted. The heading habit was designated as +3; the open spreading habit of the wild as -3, the intermediate type as 0, and the intervening types were indicated by -1, -2, +1, and +2. Fig. 2 shows the parental types and typical plants of the F_1 and seven F_2 classes for the cross May King X lobed Wild. No plants recorded as +3 were recovered, and therefore the picture of a plant rated as +2½ is presented in its place, and plants of this rating are included in the +3 column in the tables. The crosses between Big Boston and lobed Wild and between unlobed Wild and Paris White Cos displayed substantially similar results.

The results for the F_2 , F_3 and F_4 generations for these four crosses are presented in Tables 72 to 75, inclusive. It will be seen that in each cross the F_2 generation varied from one extreme to the other. In the crosses between May King and lobed Wild the +1 class was larger than the -1 class, suggesting partial dominance of the heading type, but this condition is believed to be the result of a tendency to designate as +1 some plants which should have been classified as 0. As a matter of fact, the plants in the field indicated partial dominance of the Wild forms, and the tables for all of these crosses show that the Wild type was recovered more frequently than the cultivated type.

The F_3 and F_4 generations exhibited further evidence of segregation and recombination. Some families were obtained in the crosses between May King and lobed Wild and between Big Boston and lobed Wild which closely approximated the type of the wild parent, and family A0-18-36 closely resembled the cultivated type in habit. Other families occupied intermediate positions. There were also differences in the amount of variability of various F_3 and F_4 families, as would be expected.

Crosses Between Grand Rapids and Heading Varieties.—Grand Rapids is somewhat more upright in habit than the wild forms, and

therefore the same standards would not suffice for the crosses between Grand Rapids and the heading varieties as were used for the wild X heading-type crosses. For studying habit in crosses between Grand

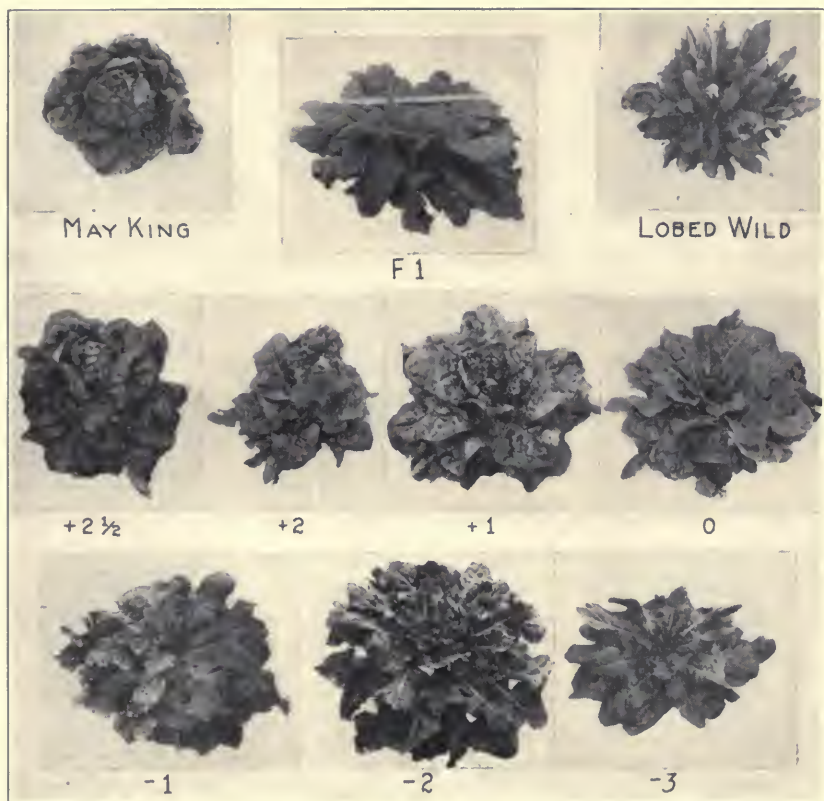


FIG. 2.—TYPICAL PLANTS OF THE PARENTS, F_1 , AND OF EACH HABIT CLASS IN F_2 OF THE CROSS MAY KING ♀ X LOBED WILD ♂

In the top row (center) is a typical plant of the F_1 . Below are seven plants of the F_2 class. The heading habit was designated as +3, the open spreading habit of the wild as -3, the intermediate type as 0, and the intervening types were indicated by -1, -2, +1 and +2. No plants recorded as +3 were recovered, and therefore the picture of a plant rated as +2½ is shown.

Rapids and heading varieties, the Grand Rapids was designated as A, the heading type as F, and the intervening classes as B, C, D, and E. Fig. 3 shows the parent type, the F_1 , and typical plants of each class of the F_2 for the cross between May King and Grand Rapids. The crosses between Big Boston and Grand Rapids and between Grand

Rapids and Paris White Cos gave substantially similar results, and photographs are therefore not presented for these. The results for the F_2 and later generations are presented in Tables 76 to 78.

The F_2 generations of all three crosses showed a wide variation. In each of these crosses both parental types were recovered, and nu-

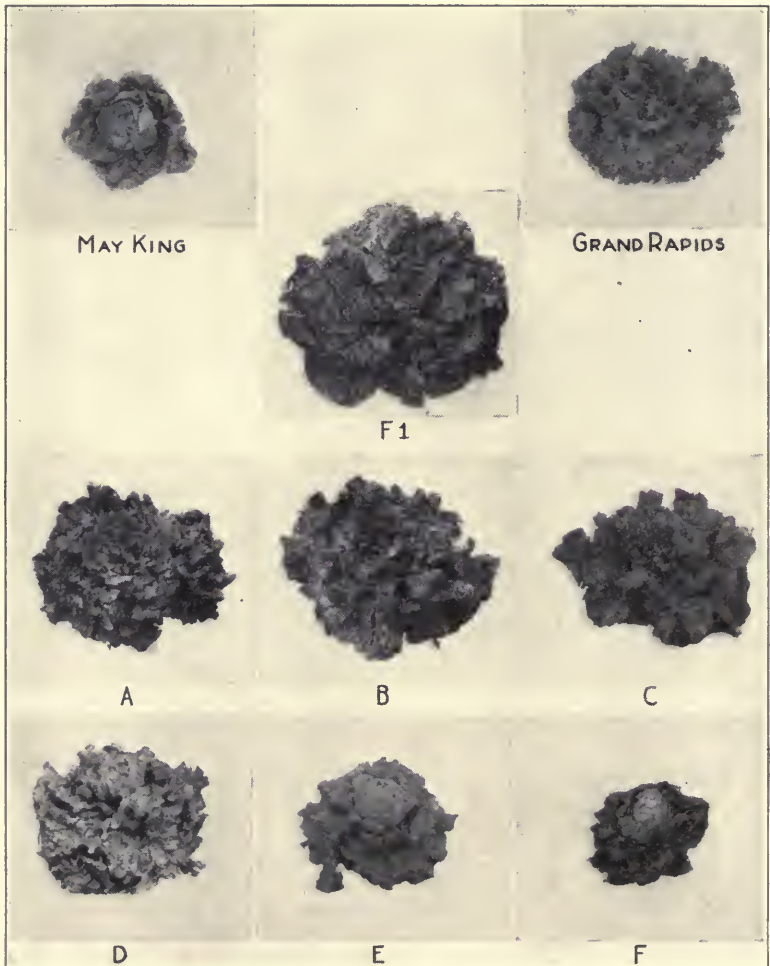


FIG. 3.—CROSSES BETWEEN MAY KING (HEADING) ♀ AND GRAND RAPIDS (LEAF TYPE) ♂

The six F_2 plants indicated by *A*, *B*, *C*, *D*, *E*, and *F* show that both the leaf type of the Grand Rapids (*A*) and the heading type of the May King (*F*) were recovered, together with all gradations between.

TABLE 72.—INHERITANCE OF HABIT, MAY KING ♀ X LOBED WILD ♂

Parent ¹	Generation	Year grown	Habit of parent	Number of plants in each class						
				-3	-2	-1	0	+1	+2	+3
A0-1	F ₂	1915	12	42	57	130	147	27	2
A0-10			3	26	39	28	22	9	2
A0-12			3	17	31	30	21	7	2
A0-17			3	17	31	30	21	7	2
A0-18			3	17	31	30	21	7	2
Subtotal	F ₂	18	85	127	189	190	43	6
A0-10-28	F ₂	-3	28	15	5
A0-10-11	F ₃	-2	6	21	14	6	6
A0-10-10	F ₃	-1	6	22	5	7	10	1	...
A0-1-41	F ₃	+1	..	2	3	10	9
A0-1-15	F ₃	+1	6	25	27
A0-10-15	F ₃	+1½	5	9	17	5	...
A0-12-62	F ₃	+2	2	19	18	...
A0-18-38	F ₃	+2	13	2
A0-12-45-72	F ₄	-2	36	3
A0-12-45-22	F ₄	-2	18	3
A0-12-45-30	F ₄	-2	8	18	7
A0-1-16-7	F ₄	0	..	4
A0-18-40-32	F ₄	0	..	3	15	22
A0-10-44-42	F ₄	-2	16	13	10
A0-17-10-15	F ₄	+1	4	13

¹A0 = MK1 ♀ X W4 ♂.

TABLE 73.—INHERITANCE OF HABIT, BIG BOSTON ♀ X LOBED WILD ♂

Parent ¹	Generation	Year grown	Habit of parent	Number of plants in each class						
				-3	-2	-1	0	+1	+2	+3
C0-1, C0-3	F ₂	1915	...	3	6	22	57	119	13	..
C0-1, C0-3	F ₂	1916	...	5	28	48	32	30	9	2
C0-1, C0-3	F ₂	1917	...	2	12	23	23	23	3	1
Subtotal	F ₂	10	46	93	122	172	24	3
C0-1-26	F ₃	1917	+1	31	20	4
C0-3-103	F ₃	1917	+1	8	24	14	9
C0-1-124	F ₃	1917	-3	2	6	8	4	5
C0-1-62	F ₃	1917	0	2	8	9	16	8
C0-3-17	F ₃	1917	0	2	8	15	4	3
C0-3-10	F ₃	1917	0	1	9	16	8	8

¹C0 = BB7 ♀ X W4 ♂.

TABLE 74.—INHERITANCE OF HABIT, BIG BOSTON ♀ X UNLOBED WILD ♂ AND RECIPROCAL

Parent ¹	Generation	Year grown	Habit of parent	Number of plants in each class						
				-3	-2	-1	0	+1	+2	+3
C3-1, D1-1, D1-2..	F ₂	1916	...	1	11	37	36	38	3	..
C1-2, C1-27, D1-2.	F ₂	1917	...	2	7	30	42	35	4	..
Subtotal	F ₂	3	18	67	78	73	7	..
D1-1-10	F ₃	1917	-1	..	7	30	15	2
D1-1-21	F ₃	1917	-1	2	5	7

¹C3 = BB7-1' ♀ X W5 ♂; C1 = BB5-4 ♀ X W38 ♂; D1 = W5 ♀ X BB7-1' ♂.

TABLE 75.—INHERITANCE OF HABIT, UNLOBED WILD ♀ X PARIS WHITE COS ♂

Parent ¹	Generation	Year grown	Habit of parent	Number of plants in each class						
				-3	-2	-1	0	+1	+2	+3
R1-2.....	F ₂	1916	...	2	19	30	27	20	1	..
R1-2.....	F ₂	1917	3	9	5	6	4	..
Subtotal.....	F ₂	2	22	39	32	26	5	..
R1-2-48.....	F ₃	+2	3
R1-2-80.....	F ₃	-1	6	13	4	..
R1-2-88.....	F ₃	-1	1	..	16	20	10	2	1
R1-2-98.....	F ₃	-2	..	1	7	40	6

¹R1 = W5 ♀ X Cos1-1' ♂.

merous intervening gradations in habit were produced. Arranged in accordance with the system of standards adopted, the distributions simulated normal curves in most cases. In the cross between Grand Rapids and Cos the Grand Rapids appeared to manifest slight dominance, but there was no evidence of dominance in the other crosses of this group.

In the F₃ and F₄ of the crosses between May King and Grand Rapids and between Big Boston and Grand Rapids (Tables 76 and 77) the different families showed differences in the extent of variability, and their frequency distributions occupied different positions in the distribution spread. This is in accordance with expectation, and it furnished further proof of segregation and recombination in regard to this character.

TABLE 76.—INHERITANCE OF HABIT, MAY KING ♀ X GRAND RAPIDS ♂

Parent ¹	Generation	Year grown	Habit of parent	Number of plants in each class					
				A	B	C	D	E	F
E2-1, E2-4, E2-6.....	F ₂	1915	..	10	73	87	69	78	8
E7-1, E7-3, E7-9.....	F ₂	1916	..	3	51	59	22	15	3
E7-1.....	F ₂	1917	..	7	28	24	23	12	3
Subtotal.....	F ₂	20	152	170	114	105	14
E7-1-2.....	F ₃	1917	B	7	42	4
E7-3-5.....	F ₃	1917	B	..	25	19	4	1	..
E7-3-3.....	F ₃	1917	B	..	2	39	1
E7-3-47.....	F ₃	1917	C	..	2	18	8	2	..
E7-1-6.....	F ₃	1917	B	..	8	17	10	3	..
E2-4-10.....	F ₃	1916	E	..	4	20	2	6	1
E7-1-67.....	F ₃	1917	C	..	2	9	2	1	..
E7-1-15.....	F ₃	1917	B	..	2	10	2	2	..
E7-3-20.....	F ₃	1917	B	..	8	25	18	6	..
E7-3-22.....	F ₃	1917	C	..	6	14	5	1	..
E7-3-65.....	F ₃	1917	C	..	1	3	2	2	..
E2-4-10'.....	F ₃	1916	2	42	4	5	1
E7-3-15.....	F ₃	1917	C	10	2	2	..
E2-4-4'.....	F ₃	1916	5	30	37	..
E7-1-18.....	F ₃	1917	D	13	8	..

¹E2 = MK15 ♀ X GR1 ♂; E7 = MK1-1' ♀ X GR2-3-1' ♂.

TABLE 77.—INHERITANCE OF HABIT, BIG BOSTON ♀ X GRAND RAPIDS ♂

Parent ¹	Genera- tion	Year grown	Number of plants in each class					
			A	B	C	D	E	F
G4-9, G4-23.....	F ₂	1915	9	50	51	32	17	2
G4-5.....	F ₂	1917	1	11	39	9	7	..
Subtotal.....	F ₂	10	61	90	41	24	2
G4-9-5.....	F ₂	1915	2	6	1	..	1	2
G4-13-1.....	F ₂	1915	2	5	2	..	2	..
G4-9-15.....	F ₂	1915	1	9	1	1
G4-23-5.....	F ₂	1915	..	5	7
G4-9-9.....	F ₂	1915	..	4	7	..	1	..
G4-9-7.....	F ₂	1915	..	3	8	1
G4-9-1.....	F ₂	1915	..	1	3	..	1	..
G4-9-12.....	F ₂	1915	..	1	3	..	1	..
G4-9-11.....	F ₂	1915	..	2	4	0	4	2
G4-9-8.....	F ₂	1916	..	13	31	15	14	..
G4-23-4.....	F ₂	1915	8	1	2	1
G4-9-6.....	F ₂	1916	3	12	5	..
G4-9-14.....	F ₂	1916	3	50	12	..
G4-23-6.....	F ₂	1915	2	1	1	1
G4-23-6.....	F ₂	1916	2	38	25	9
G4-9-8.....	F ₂	1915	2	3
G4-9-6.....	F ₂	1915	2	1	2	..
G4-9-2.....	F ₂	1915	7	1	..
G4-9-4.....	F ₂	1915	6	6	..
G4-9-13.....	F ₂	1915	1	..	4	..
G4-9-14.....	F ₂	1915	8	8	2
G4-9-14 ¹	F ₂	1916	8	5	..
G4-23-1.....	F ₂	1915	5	..
G4-23-2.....	F ₂	1915	3	8	1
G4-9-3.....	F ₂	1915	1	4	..
G4-13-1 ¹	F ₂	1915	1	4
G4-9-6-4 ¹	F ₄	1916	..	10	10	1	2	..
G4-9-8-6 ¹	F ₄	1916	4	48	22	..
G4-23-6-1 ¹	F ₄	1916	4	1	..
G4-23-6-12 ¹	F ₄	1916	2	..

¹G4 = BB7 ♀ X GR2 ♂.

TABLE 78.—INHERITANCE OF HABIT, GRAND RAPIDS ♀ X PARIS WHITE COS ♂

Parent ¹	Genera- tion	Year grown	Habit of parent	Number of plants in each class					
				A	B	C	D	E	F
Y1-1.....	F ₂	1916	..	7	22	18	5	2	1
Y1-2.....	F ₂	1916	..	2	6	11	4	1	..
Y1-3.....	F ₂	1916	..	7	38	38	13	1	..
Subtotal.....	F ₂	1916	..	16	66	67	22	4	1

¹Y1 = GR2-3-1¹ ♀ X Cos1-1¹ ♂.

DISCUSSION AND INTERPRETATION

The results obtained in this investigation show that inheritance takes place in lettuce in accordance with the principles of inheritance commonly accepted by geneticists. It is altogether unnecessary to discuss in detail each modification of Mendelian inheritance observed in this study. Attention will here be given only to certain features of inheritance as related to lettuce which appear to deserve special consideration.

Deviations in Mendelian Ratios

Significant variations in Mendelian ratios are frequently met with. Such results are generally believed to be due: (1) to errors in random sampling, (2) to production of functional gametes in unequal numbers, (3) to selective mating, (4) to partial or complete extermination of certain genotypes, and (5) to linkage and crossing over.

Such deviations may, in a general way, be divided into those which consistently modify the ratios in a given direction and those which produce variable effects under different conditions. Several cases of the first kind were observed in this investigation, but it was impossible to make tests designed to explain the reasons for these modifications. Miss Tammes (1914) analyzed a similar case in flax. In crosses between white- and blue-flowered varieties she obtained a consistent deficiency in the number of white-flowered (recessive) plants. She found that the number of seeds producing white-flowered plants was deficient. This cause, however, was insufficient to account for the entire deficiency. On further investigation it was found that the germinating power of seeds producing white-flowered plants was less than that of seeds producing blue-flowered plants. Thus the deficiency of white-flowering plants was due to two causes acting in the same direction.

It has been shown by East and Park (1918), Jost (1907), Stout (1916), and Jones (1920) that gametes of certain factorial constitutions have a better chance than others to fertilize a given ovule in some cases.

In contrast to cases in which the ratios are modified only slightly, there are some in which entire genotypes are exterminated, as shown by Little (1913) for yellow mice and Baur (1910) for snapdragons. In the first of these two instances the young of one class were found to die in embryo, while in the latter the plants of one class were devoid of chlorophyll.

It would seem reasonable to expect some cases to occur in which the ratios deviate variously at different times and under different conditions. A few instances of this kind have been reported. In describing variable ratios in *Oenothera* crosses, deVries (1924) states, "It is evident that such a process may be influenced strongly by external conditions, and therefore that we may expect the deviations to be variable in amount." Plough (1917) has shown that the amount of crossing over in *Drosophila* is appreciably affected by changes in temperature, which fact would cause variable deviations in dihybrid ratios. Lindstrom (1918) has reported that viriscent-white maize seedlings are almost without chlorophyll and may mature seeds. It is clear that in instances like this, in which an organism stands near the border line between death and life, slight changes in environment may cause quite variable deviations in Mendelian ratios. It seems reason-

able to believe that in cases like that described by Miss Tammes (1914), changes in environment may cause variable deviations in the germination and amount of seed produced of the deficient class, thus causing variable deviations in the Mendelian ratios.

In each of the instances cited it should be noted that the deficient ratios were apparently associated more or less directly with genes having to do with fertility and sterility, in their broader sense. Linkage of qualitative genes with sterility or fertility genes may account for some of the cases of variable deviations in Mendelian ratios which have been observed.

There is abundant evidence to show that fertility and sterility in plants are modified appreciably by changes in environment. Lewis and Vincent (1909) found that certain varieties of apples exhibited different degrees of self-sterility in different localities. Fletcher (1909-10) reported similar conditions for pears. Tufts (1919) found the Bartlett pear self-sterile in the foothills of California and partially self-fertile under valley conditions. Stout (1923) succeeded in increasing the self-compatibility of *Brassica pekinensis* from less than 10 to 65 percent, in the first flowers that opened, by growing the plants in small pots. He believes there may be cyclic changes in the sterility of a species in the course of a given season. Darwin (1876) recognized that exotic plants may become sterile when grown out of their natural habitat. East (1923) has shown that certain species of *Nicotiana* are self-sterile in the early part of their flowering period, but that late in the flowering period a few seeds are produced from self-pollination; East has termed this condition "pseudo-fertility." Shaw (1916) determined that in beets self-fertility decreased with proximity of flowers to each other on the same plant; it appears that in this case the degree of self-sterility varied in different parts of the same plant at a given time. There seems to be no question that sterility and fertility in plants may vary in degree in response to changes in environment.

Evidence is accumulating which shows that sterility and fertility in plants may be accounted for on a Mendelian basis, in many cases at least, as shown by Compton (1913), Baur and Lotsy (Babcock and Clausen, 1918), Correns (1912), East (1918), and others. While only one or two pairs of genes appear to be involved in some instances, the inheritance of fertility or sterility is apparently more or less complicated in most cases, and several genes as a rule are involved. East (1918) appears to have succeeded in isolating pure lines for fertility (or sterility), altho he does not call them such.

If sterility and fertility are controlled by genetic factors, these characters must be represented in the chromosomes by genes. In the case of characters for which several pairs of genes are involved, the genes are in all probability distributed among the various chromo-

somes of the organism. It follows that linkage relations must exist between the genes responsible for sterility and fertility and those responsible for other characters.

Our present-day conception of living organisms is that they are the result of their genetic complexes acting in relation to the environment. Each gene of the organism probably influences the genetic complex and is in turn influenced by it. The different genes, both individually and collectively, are probably influenced by the environment to a greater or less extent.

Many cases are now known in which qualitative genes influence the expression of one another. It seems reasonable to believe, therefore, that genes concerned with fertility and sterility and with qualitative characters may influence one another and that their genetic complexes may be influenced variously by different environments.

In presenting the results for the inheritance of prickles it was shown that segregation occurred apparently normally in F_2 in 1916 and 1917, but that in 1915 there was a marked deficiency in the number of prickly plants. The numbers grown and the method employed in securing the data leave no doubt as to the significance of the differences.

If the inheritance of prickles takes place on a simple Mendelian basis, as seems probable, then the deficiency of prickly plants must be associated directly or indirectly with fertility and sterility in their broader sense. Three hypotheses may be advanced to account for the deficiency of prickly plants as follows:

1. The deficiency in the number of prickly plants may be due entirely to the effect of fertility (or sterility) genes plus linkage of the gene responsible for prickles with a sterility gene of high specificity in its response to environment. The sterility factor may be more susceptible to environmental influence when present in homozygous condition. Such a state of affairs, however, would entail reduced viability of the parent which contributed the sterility gene in question.

2. Possibly our varieties of lettuce, particularly the wild forms, are more or less heterozygous for fertility and sterility factors, as seems to be the case for leaf-size factors. Such a condition was apparently found by East (1918) in certain species of *Nicotiana*. If such be the case, it is possible that some combinations of genes may produce highly viable zygotes, others may produce zygotes incapable of development, while still others may produce zygotes of intermediate degrees of vitality. It is conceivable that at certain intermediate stages the vitality of zygotes may be quite susceptible to environmental influences, as postulated by Emerson (1924) for sex in plants. In this case, however, it would be necessary, as above, to assume linkage in part of the zygotes at least, of the gene determining the prickly char-

acter with a fertility gene which is highly responsive to changes in environment. This and the above hypothesis, therefore, are essentially similar except that, if much heterozygosity exists, it is more difficult under this hypothesis to account for a very wide range of deviation in Mendelian ratios.

3. A third hypothesis is that the gene for the prickly character in conjunction with a gene or genes concerned with fertility, and possibly others also, sets up a genetic condition which is highly specific to environmental influence when the gene for prickles is present in homozygous condition.

The evidence is insufficient to show which of these three hypotheses is the most probable. Whatever explanation is the correct one, it appears that the May King parent must have contributed partly to the cause for the deficiency of prickly plants in the cross May King X lobed Wild, for none of the other crosses showed deviations of the same nature. Possibly the May King supplied fertility genes which were responsible for the variable deviations in prickliness.

It seems reasonable to believe that certain qualitative factors may be so linked with sterility or fertility factors that marked deviations in their ratios may result, while other qualitative factors may be inherited independently of such fertility factors. Such a situation would account for the occurrence of variable ratios of prickly and smooth plants, for seed color and anthocyanin were not so affected.

The evidence strongly suggests that sterility and fertility in plants are influenced in their expression by environmental causes. Since sterility and fertility are apparently determined by genetic factors, it seems likely that linkage of certain qualitative factors with factors which influence fertility and sterility may cause some of the variable Mendelian ratios which are observed in breeding experiments.

Variability of Quantitative Characters in Lettuce

The results for the inheritance of quantitative characters show that the growth of lettuce is influenced to a marked extent by environment. The parental types and F_1 generation of some crosses exhibited different variability in different seasons. Some of the F_2 hybrids also manifested differences in variability in different seasons. These results are in accord with the practical conception of lettuce culture, namely, that the plant is quite responsive to environmental conditions.

The effect of environment is clearly shown by comparing the means of F_3 and F_4 families with the condition or value of their parents. In the tables which present the results for the inheritance of quantitative characters the class to which the parent belonged has been underscored, except when the parent was grown in the greenhouse. The results show that the value of an F_2 or F_3 parent corresponded in a gen-

eral way with the mean value of its progeny, but that there were many marked deviations in this respect. While these deviations were no doubt due partly to genetic variation, there is reason to believe that some of them were caused by environment.

Such results are to be expected when one bears in mind the nature of the Compositae as a whole. They are recognized by many botanists as being a highly adaptable family of plants. It is for this reason that the family has spread over practically the entire world and that it consists of more species than any other family of the Spermatophyta. The family is quick to respond to the many environments in which the species find themselves. One would expect a member of such a family of plants to be affected appreciably by environment.

Variable Behavior of Wild and Cultivated Lettuce in Response to Environment

In connection with the discussion of leaf-length inheritance it was shown that the wild and cultivated forms of lettuce displayed different behaviors with respect to each other in different seasons. Certain influences were apparently in operation in 1917 which increased the length of leaves of cultivated varieties and at the same time decreased the length of leaves of the wild *L. scariola*, as compared with the respective leaf lengths in 1915 and 1916. The genetic complexes of the two forms as to leaf length obviously responded differently to the environment of a given season.

It is believed that these results are best explained by the relation of the weather conditions of the different seasons to the genetic constitutions of the parental types involved. Under central Illinois conditions cultivated lettuce makes its rosette growth chiefly during the latter half of May and the first half of June. The weather records (University of Illinois, Soil Physics Department, 1915, 1916, 1917) show that between May 15 and June 15 there were 6.51 inches of rain at Urbana in 1915, 7.87 inches in 1916, and 8.53 inches in 1917. Furthermore, both the maximum and minimum temperatures ranged lower in May in 1917 than in 1915 and 1916, and conspicuously chilly weather was noticeably lacking during the last 20 days of May, 1917. In short, the growing conditions were more favorable in 1917 than in 1915 or 1916 for cultivated lettuce, which is generally considered by horticulturists to thrive best in a moist, fairly cool environment.

On the other hand, the Compositae are recognized as being best adapted to hilly or mountainous habitats where the conditions are fairly dry. They are found in abundance rarely in swampy or prairie environments (Bentham and Hooker, 1873-76; Small, 1917). Small states that "The Compositae, indeed, seem to have been formed with the mountains by the mountains for the mountains."

The wild *L. scariola*, furthermore, is found in greatest abundance

in waste ground, vacant lots, railroad right-of-ways, roadsides, etc., which environments furnish fairly dry rather than moist conditions for growth. The fact that the plant is found most commonly in such places is evidence of its ability to thrive under adverse conditions.

It appears probable, therefore, that the weather conditions which provided a more favorable environment for cultivated varieties in 1917, produced an opposite effect on the wild form. If this be the correct explanation, it follows that if our cultivated varieties developed from the wild *L. scariola*, they consist of genetic factor combinations which exhibit appreciably different responses to varying weather conditions than those exhibited by the wild forms.

Greater Variability of Wild As Compared With Cultivated Lettuce

In presenting the results for leaf size and leaf area, it was stated that the coefficients of variation were larger for the wild than for the cultivated forms. In order to show these conditions more clearly, the constants for 1916 for the parental forms as to leaf length and leaf width are presented in Tables 79 and 80. Substantially similar relations prevailed in 1915 and 1917.

The figures show that the lobed wild form (W4-1') was more variable than any other cultivated variety in both leaf length and leaf width. The unlobed form (W5) exhibited a greater variation in leaf length than any other cultivated variety and practically equalled the two most variable cultivated varieties as to leaf width.

From these results it appears either that the coefficient of variation is not a reliable medium for comparing the variability of cultivated and wild forms of lettuce or that the cultivated forms are more nearly homozygous than the wild forms. The data do not furnish a firm foundation for the former hypothesis, for the results fail to show that the coefficient of variation becomes consistently larger as the mean increases in size. For instance, there were cultivated varieties which had mean leaf lengths both larger and smaller than both wild forms (Table 79), and yet the coefficients of variation were larger for the wild forms than for either cultivated variety. The second hypothesis seems the more plausible.

In regard to the wild forms it should be remembered that the Compositae as a whole are quite adaptable to new situations, as indicated by the general behavior and the large number of species of this family. We should therefore expect new forms of wild lettuce to appear occasionally by mutation. As a matter of fact, the existence of various types as to leaf form is evidence that mutations probably have occurred in regard to that character. With the large number of factors apparently involved for leaf sizes and areas we should expect mutations to take place even more frequently in the genes responsible for

such characters. These circumstances, together with occasional cross-fertilization and the total absence of any artificial agency favoring the production of homozygous types, would account for more or less heterozygosity as to leaf-size factors, even tho the leaves of wild lettuce in general of a given form appear to be much alike.

TABLE 79.—CONSTANTS OF PARENTAL VARIETIES FOR LEAF LENGTH, 1916

Variety	Mean (centimeters)	S. D.	C. V.
W5.....	22.02 ± .17	2.16 ± .12	9.81 ± .54
W4-1'.....	25.54 ± .51	3.77 ± .36	14.76 ± 1.44
BB7-1'.....	17.23 ± .13	1.50 ± .09	8.71 ± .53
MK1-1'.....	13.55 ± .09	1.13 ± .07	8.34 ± .49
GR2-3-1'.....	20.40 ± .11	1.37 ± .08	6.72 ± .37
Cos1-1'.....	28.73 ± .17	2.08 ± .12	7.24 ± .41

In cultivated lettuce the same general conditions no doubt prevail with reference to mutation and occasional cross-fertilization, but there is a distinct difference so far as artificial agencies favoring the production of homozygous types are concerned. The bulk of the lettuce seed of the country is grown by C. C. Morse and Company of San Francisco, and the Wheeler Seed company of Gilroy, California. Extreme care is taken by them in respect to the development and maintenance of pure types. The plants are planted in large blocks, and strips of vacant ground are left between different varieties. The plants are rogued carefully, and all other precautions are taken to promote the production of the purest strains possible.

TABLE 80.—CONSTANTS OF PARENTAL VARIETIES FOR LEAF WIDTH, 1916

Variety	Mean (centimeters)	S. D.	C. V.
W5.....	4.59 ± .04	.57 ± .03	12.42 ± .69
W4-1'.....	5.35 ± .15	1.10 ± .11	20.56 ± 2.04
BB7-1'.....	19.39 ± .23	2.62 ± .16	13.37 ± .83
MK1-1'.....	17.89 ± .12	1.43 ± .08	7.99 ± .47
GR2-3-1'.....	23.70 ± .17	2.12 ± .12	8.95 ± .49
Cos1-1'.....	14.88 ± .15	1.82 ± .10	12.23 ± .70

It appears, therefore, that in lettuce we have a plant which has a natural tendency to develop new forms, and that there is no restraint, other than that offered by natural selection, to the perpetuation of such forms in the wild lettuce, while in cultivated varieties the practical methods of seed production employed are constantly promoting the development and maintenance of homozygous types. These circumstances, it is believed, account largely, if not entirely, for the larger coefficients of variation shown for the wild forms as to leaf size and area.

Estimating the Number of Pairs of Genes Involved in Quantitative Inheritance

The data for the inheritance of quantitative characters suggests in a number of instances that there may be a relatively small number of pairs of genes involved for the differences in size between the parents used in this investigation. It has seemed desirable, therefore, to apply to the data the method proposed by Castle (1921) for estimating the number of factors involved in quantitative inheritance.

Castle's method, including a correction suggested by Wright, consists in using the formula $n = \frac{D^2}{8(\sigma_2^2 - \sigma_1^2)}$ in which n is the number of pairs of genes involved; D , the difference between the means of the parents; σ_1 , the standard deviation of F_1 ; and σ_2 , the standard deviation of F_2 . The method is based on the difference in variability shown by the F_1 and F_2 generations.

The method has been applied to the data from four crosses as to leaf length and leaf width. In all of them the F_1 and F_2 populations were the progeny of the same parents which were used for comparison (see footnote to Table 81). The results are presented in Tables 81 and 82.

Table 81 indicates that for the crosses May King and Grand Rapids and unlobed Wild and Cos, less than one pair of genes was involved for the differences in each case, and that between one and two pairs were involved for the differences in the crosses Big Boston X unlobed Wild and Big Boston X Cos.

TABLE 81.—NUMBER OF PAIRS OF GENES INVOLVED FOR LEAF LENGTH ACCORDING TO CASTLE'S PROPOSED METHOD

Parent	Generation	Number of plants	Mean leaf length (centimeters)	S. D.	Number of pairs of genes indicated
MK1-1'	P ₂	66	13.5576
GR2-3-1'	P ₂	75	20.40	
E7 ¹	F ₁	80	2.42	
E7-1, E7-3, E7-9	F ₂	151	3.68	
Cos1-1'	P ₂	72	28.7336
W5	P ₁	75	22.02	
R1 ²	F ₁	1378	
R1-2	F ₂	99	4.09	
BB7-1'	P ₂	61	17.23	1.59
W5	P ₁	75	22.02	
D1 ³	F ₁	36	2.26	
D1-1, D1-2	F ₂	62	2.62	
BB7-1'	P ₂	61	27.23	1.72
Cos1-1'	P ₂	72	28.73	
N1 ⁴	F ₁	68	2.94	
N1-1, N1-2, N1-4, N1-5	F ₂	84	4.27	

¹E7 = MK1-1' ♀ X GR2-3-1' ♂. ²R1 = W5 ♀ X Cos1-1' ♂. ³D1 = W5 ♀ X BB7-1' ♂. ⁴N1 = BB7-1' ♀ X Cos1-1' ♂.

In Table 82 the results for leaf width indicate a difference of less than one pair of genes in one cross and differences of from 5 to 10.5 pairs in three other crosses. In describing the method, Castle emphasized that it would give reliable indications only in cases of pure blending inheritance, that is, cases in which dominance is absent. He also stated that the various quantitative factors involved would have to exert about the same effect on size expression and that the parents must be homozygous. He recognized, however, that such conditions might not always prevail.

TABLE 82.—NUMBER OF PAIRS OF GENES INVOLVED FOR LEAF WIDTH ACCORDING TO CASTLE'S PROPOSED METHOD, 1916

Parent	Generation	Number of plants	Mean leaf width (centimeters)	S. D.	Number of pairs of genes indicated
MK1-1'	P ₂	66	17.89	5.28
GR2-3-1'	P ₁	75	23.70	
E7.....	F ₁	80	2.57	
E7-1, E7-3, E7-9.....	F ₂	151	2.72	
Cos1-1'	P ₂	72	14.88	5.88
W5.....	P ₁	75	4.59	
R1.....	F ₁	1386	
R1-2.....	F ₂	99	1.73	
BB7-1'	P ₂	61	19.59	10.50
W5.....	P ₁	75	4.59	
D1.....	F ₁	3686	
D1-1, D1-2.....	F ₂	62	1.85	
BB7-1'	P ₂	61	19.5964
Cos1-1'	P ₂	72	14.88	
N1.....	F ₁	68	2.21	
N1-1, N1-2, N1-4, N1-5.....	F ₂	84	3.04	

Notwithstanding the requirements enumerated by Castle, he illustrated the use of the method by applying it to data which do not meet these requirements. He used the data of Emerson and East on seed weight in maize. Emerson and East themselves stated with reference to these data (1913, p. 59) that small numbers in the frequency distributions and hybridity in one parent undoubtedly made the coefficients of variation too high. Furthermore, maize varieties are generally regarded as heterozygous. With such parental material one cannot be certain that he has typical F₁ and F₂ populations in the sense that they are commonly understood. Castle used for a second illustration his own data on weight inheritance in rabbits, another cross-fertilized organism. The question arises as to whether the method might not have been better illustrated by using data from the many investigations with approximately homozygous plants which are on record.

Castle's method has been criticized by Shull (1921), who points out that the method would indicate accurately the number of pairs of

factor differences involved only in cases of complete blending inheritance in which the different factors have equal weight in size expression, and in which the frequency distributions of the parental populations occupy positions at the opposite extremes of the "total potential genetic variability" of the F_2 generation of the hybrids. He states that if 15 pairs of factor differences were involved, the odds would be 633,477,184,000 to 1 that the parents would *not* occupy the extreme positions.

Shull also shows that situations might arise in which symmetrical curves may be obtained: (1) when dominance is complete, allowing for varying effects of different factors in size expression; and (2) from the interplay of positively and negatively acting factors when dominance is absent. Such cases would make it appear as tho pure blending inheritance were in operation, when in fact the curves of error in both cases would vary from the normal; therefore, the standard deviation and in turn the number of pairs of genes indicated by the method, would be materially affected.

There is one other factor not mentioned by Castle and Shull which deserves special emphasis, in the opinion of the writer. In addition to meeting the other requirements mentioned one would need to grow in the F_2 generations sufficient numbers of individuals to provide a reasonable chance for the appearance of all possible genotypes. If all possible extreme classes should not appear in F_2 , the variability shown by the curve of error would be reduced, and a larger number of pairs of genes would be indicated as a result.

In connection with the maize data Castle drew rather definite conclusions as to the number of factor differences involved from populations of 54 individuals in F_1 and 286 in F_2 . In his rabbit experiments he grew 16, 25, and 27 individuals respectively in F_1 ; and 50, 62, and 112 in F_2 . If very many pairs of genes were involved, these numbers were far too small compared with the number it would be necessary to grow to render probable the appearance of all genotypes in F_2 , even tho no linkages were involved.

If linkages were involved, much larger numbers would have to be grown. It is quite probable that the different genes governing size are distributed among the various chromosomes, and it follows that some chromosomes may carry more than one gene having to do with a single character complex. Linkage may therefore exist between some, perhaps many, size genes. With linkages involved the chances of appearance of all genotypes in F_2 , and especially of the extreme classes, become very small.

If an insufficient number of individuals were grown to render probable the appearance of all genotypes, Castle's method could not indicate with reasonable accuracy the number of pairs of factor differences involved even tho all the other requirements emphasized by Castle and

Shull were met. With the relatively few individuals grown in the populations used by Castle for illustrating the method, the chances are that frequency distributions would be secured in which only a few of the middle classes would be represented, that is, if as many pairs of factor differences were involved as he concluded. As a result, the standard deviation would be materially reduced for the F_2 , and this in turn would increase the number of pairs of factor differences indicated.

So far as the lettuce data presented herewith are concerned, they probably meet the requirements of Castle's method fairly well as to homozygosity, but they do not appear to meet the other requirements. The skewed and multi-modal character of the frequency distributions indicate partial dominance, or unequal effect of genes affecting size expression, or unequal effect of positively and negatively acting factors. It is quite apparent also that most, if not all, of the frequency distributions of the parents do not occupy the opposite extremes of the total potential variability in F_2 , for there were numerous instances in which the frequency distributions in F_1 , F_2 , and F_3 extended beyond one or both extremes of the combined distributions of the parents. It is also recognized that the lettuce populations were too small in number to permit reliable determinations by Castle's method even tho all other requirements had been met by the data. The results in Tables 81 and 82 are therefore regarded as having no value for indicating the number of pairs of factor differences involved in the crosses in question.

In conclusion, it is believed that the conditions assumed by Castle exist rarely if ever in crosses between animals or plants. In the author's opinion, the method should not be depended upon for indicating the number of factor differences involved, even tho the data should appear to meet all requirements, for influences may be in operation whose effects are not apparent. The method is believed to possess no value for indicating the number of factor differences involved in quantitative inheritance.

Probable Origin of Cultivated Lettuce

Many botanists and horticulturists have expressed the view that cultivated varieties of lettuce originated from the wild *L. scariola*. Some believe that all the cultivated types had a common origin, but Sturtevant (1886) believed that the important types had independent origins. There is no positive evidence, however, to support either view.

This investigation indicates that, with the possible exception of the Cos type, the cultivated lettuces may have originated from the wild *L. scariola*. There are no good grounds for believing otherwise.

In the first place the results for the inheritance of leaf form indicate that the forms with unlobed leaves probably originated from the lobed forms by mutations in dominant genes. Such mutations have

apparently repeated themselves at different times and in different places. There is good reason for believing that four types of the formulae $U_1 U_1 U_2 U_2$, $U_1 U_1 u_2 u_2$, $u_1 u_1 U_2 U_2$, and $u_1 u_1 u_2 u_2$ exist at the present time, together with the various heterozygotes resulting from hybridization of these forms.

The change from black seed color to white can be accounted for in a similar manner. This change has taken place in some cultivated varieties, and in others it has not. The same is true of anthocyanin pigment. The change from a prickly to the smooth condition can also be accounted for by the modification of a dominant gene.

As to leaf length, leaf width, leaf area, and leaf shape, the changes can be accounted for to an appreciable extent by the modification of dominant additive or inhibitory factors, for the wild forms appear to be more or less dominant over the cultivated forms in these respects. In all probability the diligence of man in perpetuating by selection the mutations which have suited his purposes has played an important part in the changes which have occurred in these characters. The changes in plant height and in time required to reach the flowering stage can be accounted for either by the loss of additive factors or by mutations in dominant genes, or by both.

The development of the heading habit is in all probability the result of man's efforts in selection together with the appearance of desirable mutations. Since the wild forms appear to exhibit partial dominance as to rosette habit, the changes in rosette habit can probably be accounted for in part by modifications in dominant genes.

While no data have been presented for leaf color and the crinkling and crumpling of leaves, evidence has been obtained which indicates that the changes which have occurred in these characters can be accounted for also by modifications in genetic constitution.

The Cos type alone appears to present some exceptions. The Paris White Cos variety has longer leaves than the wild and it appears to carry some genes which are dominant to their respective allelomorphs carried by the wild form. It is the only cultivated variety used in this investigation which appears to carry any factors which are dominant to those of the wild forms. These conditions may indicate that some dominant factors have arisen by mutation in the Cos type, or they may indicate an independent origin of the Cos type, as suggested by Sturtevant (1886). It may be also that the Cos type originated from *L. scariola* but has at some time in the past been intercrossed with certain other species of the Compositae; for it appears to carry a bitter principle which is lacking in the heading and leaf types. Its flower heads are somewhat larger than those of other types, and it has a distinctly different rosette habit and type of head.

Other facts in favor of the origin of cultivated types of lettuce from the wild *L. scariola* are the general similarity of the floral and seed structures, the fact that they intercross, and the fact that they have many points in common as to morphology and general behavior.

Nomenclature of Lettuce

Grenier and Godron (Robinson and Fernald, 1908) gave the name *L. scariola* var. *integrata* to the unlobed form of wild lettuce. This has been accepted generally by systematic botanists. The old school of systematists called the heading, leaf and Cos types of lettuce *capitata*, *crispa* and *longifolia*, respectively. The terms were used by some as specific names and by others as the names of botanical varieties of the cultivated *L. scariola*, which was then called *L. sativa*. However, modern systematists have almost universally refused to recognize these names, no matter how used.

It has been shown that the change from the lobed to the unlobed form may occur thru a modification in a single dominant gene and that at best the differences involve changes in not more than two dominant genes. In contrast to this, the differences between the cultivated types and the wild forms involve far more numerous and complicated changes, including modifications in seed color, prickles, anthocyanin, leaf size and shape, plant height, time required to produce flowers, leaf color, habit, and no doubt several other characters. It is recognized, of course, that the change in leaf form involves a morphological character which is sometimes used as a basis for classification. From a genetic standpoint, however, there is far more justification for recognizing the three cultivated types as botanical varieties than the unlobed *L. scariola*.

Bailey recently pointed out (1923) that if substantial progress is to be made in classifying cultivated plants, we must perfect our means of botanical classification. He has proposed the name *cultigen* for a species which has appeared under cultivation and the term *cultivar* for a botanical variety of a *cultigen*.

A method of nomenclature involving the use of these terms has been utilized by Bailey (1924) in his *Manual of Cultivated Plants*. He has revised, as a *cultigen*, the *L. sativa*, L. as a name for cultivated lettuce, and he has designated the important cultivated types as cultivars. Thus the four cultivated types are named by him as follows:

- Heading type..... *L. sativa*, L. var. *capitata*, L.
- Leaf type *L. sativa*, L. var. *crispa*, L.
- Cos type..... *L. sativa*, L. var. *longifolia*, Lam.
- Asparagus type *L. sativa*, L. var. *angustana*, Irish

This method of classification gives to cultivated types of lettuce higher specific rank than that which has been given *L. scariola*, var.

integrata, Gren. & Godr. The results of this investigation show that the method of nomenclature used by Bailey is fully justified so far as the heading, leaf, and Cos types are concerned, and the nomenclature of Bailey is therefore supported by the author.

SUMMARY AND CONCLUSIONS

1. In this investigation crosses were made between varieties of the important types of cultivated lettuce and between these and the wild *L. scariola*.

2. Lettuce was found to be largely self-fertilized.

3. Five crosses were made involving pigmented and unpigmented parents. Anthocyanin was dominant. Inheritance occurred on a simple Mendelian basis in four of these crosses. In the fifth cross an influence was apparently in operation which interfered with normal segregation and recombination, and the data are insufficient to show conclusively how inheritance occurred.

4. Anthocyanin pigment in the ray flowers and in the stems and leaves was found to be due either to a single factor or to two completely linked factors. The single-factor hypothesis appears to be the more probable.

5. Six crosses were made involving black- and white-seeded parents. Black seeds were dominant. Inheritance took place on a simple Mendelian basis, but in one cross an influence was in operation which consistently caused a deficiency of black-seeded plants in F_2 .

6. Five crosses were made between prickly and smooth varieties. The prickly condition was dominant. Inheritance apparently occurred in simple Mendelian fashion, but in four crosses the ratios deviated markedly from the expected proportions. In one cross the F_2 ratios deviated variously in different seasons.

7. In two crosses between heading and wild forms, with unlobed and lobed leaves respectively, two pairs of factors acting in a complementary manner were apparently involved. In a cross between lobed and unlobed forms of wild lettuce inheritance occurred on a simple Mendelian basis. In both cases the lobed condition was dominant.

8. The differences in leaf length, leaf width, width index, leaf area, time required to produce flowers, plant height, and rosette habit were found to be due to a number of factors inherited in a quantitative manner. The wild forms appeared to exhibit greater impurity than the cultivated varieties. The F_1 generations were found to be no more variable, as a rule, than the parental types. Increased variability and segregation were shown by the F_2 generations. The genes of the wild forms were dominant to those of the cultivated varieties with respect to some characters. Paris White Cos is the only cultivated variety

which gave evidence of having quantitative factors dominant to those of the wild. The F_3 and F_4 generations gave further evidence of segregation. In practically all crosses it was found that the frequency distributions of the parents did not respectively coincide with the opposite extremes of the potential variability of the F_2 generation; thus, it should be possible to establish new types with higher or lower mean values, or both, than those of the parent varieties.

9. The growth of lettuce is highly responsive to environmental influences.

10. Cultivated varieties apparently are the result of genetic combinations which respond more favorably to moist weather conditions than those of the wild forms.

11. Modified and deviating Mendelian ratios are apparently caused in many cases by linkage of qualitative genes with genes which influence fertility or sterility that are responsive to changes in environment.

12. Castle's proposed method of estimating the number of pairs of genes involved in quantitative inheritance is probably inadequate for the purpose in practically all cases.

13. The results indicate that cultivated lettuce probably developed from the wild *L. scariola* L. The differences can be accounted for largely if not entirely, by mutations in dominant genes.

14. The method of nomenclature proposed by Bailey is supported by the results of this investigation.

SUGGESTED TERMINOLOGY

In view of the results obtained in this investigation, the following symbols are proposed for the qualitative characters enumerated:

G for anthocyanin in stems and leaves; g for its absence, i. e., the green-leaved condition.

Y for anthocyanin (blue) on undersides of ray flowers; y for absence of anthocyanin or the yellow condition. This pair of genes is the same as G and g or is completely linked with that pair.

W for blackish seeds; w for whitish seeds.

S for prickly stems and midribs of leaves; s for smooth stems and midribs.

U_1 for lobed leaves; u_1 for unlobed leaves.

U_2 for lobed leaves; u_2 for unlobed leaves. This pair of genes is apparently associated with the pair U_1 and u_1 in some crosses, thus causing inheritance on a complementary factor basis.

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