

INTRODUCTION

Mendel's Life and Work.

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THE INHERITANCE OF COLOR AND OTHER CHARACTERS IN PHLOX DRUMMONDII.

Johann Gregor Mendel, near Brno, in Austria, was an agricultural laborer and attended a private school.

A Thesis Presented to the Graduate Committee of the Virginia Polytechnic Institute in Application for the Degree of Master of Science

by

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In 1847, he was ordained a priest, and from 1849 to 1853

May, 1915.

He studied mathematics, physics, and natural sciences at the University of Vienna. Between the years of 1853 and 1854, Mendel taught physics at Brno, and in the latter year was elected superior of the abbey at Brno. The last years of his life were troubled, due

to a disease of the nervous system, and he died on June 6, 1884, of chronic nephritis.

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his plant-breeding work in hybridization which was to make him famous. Mendel was preceded by older hybridists, as Kolreuter, Knight, and Milbert. These investigators could not

INTRODUCTION

Mendel's Life and Work.

Due to the wide application of Mendel's law to both breeding of plants and animals, a brief sketch of his life and works will not be out of place in this paper.

Johann Gregor Mendel was born on July 22, 1822, at Heinzendorf, near Odrau, in Austrian Silesia. His father was an agricultural laborer and owned a small farm. Mendel first attended a private school and later the public school in his home town. At eleven years of age he left to continue his studies at Leipnik, and later at Troppau and Olmutz. At Troppau one of his teachers was an Augustinian monk, and it is this fact which probably caused Mendel to enter the monastery of Saint Thomas in Brünn.

In 1847, he was ordained a priest, and from 1851 to 1853 he studied mathematics, physics, and natural science at the University of Vienna. Between the years of 1853 and 1868, Mendel taught physics at Brünn, and in the latter years was elected Abbot or Prolät. The last years of his life were troubled, due to the tax levied by the government on religious houses. He died on January 6, 1884, of chronic nephritis.

It was in the cloister garden at Brünn that Mendel did his plant breeding work in hybridization which was to make him famous. Mendel was preceded by older hybridists, as Kolreuter¹, Knight, Naudin, and Millardet. These investigators would have

made themselves distinguished had they only taken into account the proportions obtained in their experiments. They had the material before them, but from ignorance failed to grasp its importance. Mendel being preceded by these workers, profited by their mistakes. He was careful, painstaking, and thorough, and due to these facts his work was a success. His methods may be enumerated under the following heads:

(1) He considered the individual as made up of unit characters, and that one of these characters may be transmitted independently of the other. The work must be done with unit characters, and not individuals or species as was formerly the practice.

(2) Must keep each pair of characters separate and study only one pair at a time.

(3) Must select only those plants that are self-fertilized.

(4) Must study each parent before crossing, in order to decide whether the characters are constant.

(5) After crossing, must keep mother plant and offspring separate. In this way, Mendel was enabled to discover dominant and recessive characters.

(6) Must keep seed from the F_1 generation crosses separate.

(7) Must keep seed from the F_2 generation crosses separate.

In this way, he was able to decide which individuals were homozygous and which were heterozygous.

(8) He worked with large numbers so as to eliminate error as far as possible.

(9) He carried the experiments for many generations to determine whether the results obtained were conclusive.

Although work had been done in hybridization prior to Mendel, but little light had been thrown on the problems of heredity. However, since the classical investigations by Mendel the studies of inheritance have been placed on a different basis. Mendel's most famous experiment was done with the garden pea (*Pisum sativum*). He found that on crossing tall peas (six feet) with dwarf peas (one and a half feet), the offspring in the F_1 generation were all tall like the tall parent, and none dwarf like the other. In fact, they were slightly taller than the tall parent. In the F_2 generation, some were tall like the tall parent and some dwarf like the other parent, the ratio being 3:1 (approximately). In the F_3 generation, those like the dwarf parent or 25 per cent. of the whole bred true to dwarfness, while 25 per cent. of the whole or one third of the tall peas were pure and came true to tallness. However, 50 per cent. of the whole or two-thirds of the tall were hybrid and broke up into the 3:1 proportion obtained in the F_2 generation. From these results was formulated Mendel's law of monohybrids² as follows: When parents, differing in respect to a single pair of allelomorphs, are crossed, the offspring in the F_1 generation will be like one parent with respect to the character in question. The parent which impresses the character on the offspring is called the dominant one. When, however, the offspring of the F_1 generation are crossed with each other, there will be produced offspring, 25 per cent. of which will be like the dominant grandparent, 25 per cent. like the other grandparent, and 50 per cent. like the parents resembling the dominant grandparent.

The law for di-hybrids is simply the monohybrid proportion, (3:1), squared, thus giving a proportion of 9:3:3:1, or four gametes from each pair, making sixteen possible combinations. It is stated as follows: When two individuals are crossed, which differ with respect to two pairs of different characters, the hybrid (F_1 generation) are all of the same form, exhibiting the dominant character of each of the two pairs. While on the average in the F_2 generation, nine show both dominant characters, three show one dominant and one recessive character, three the other dominant and the other recessive, and one both recessive characters. This law is well illustrated in the case of the comb of fowls.³

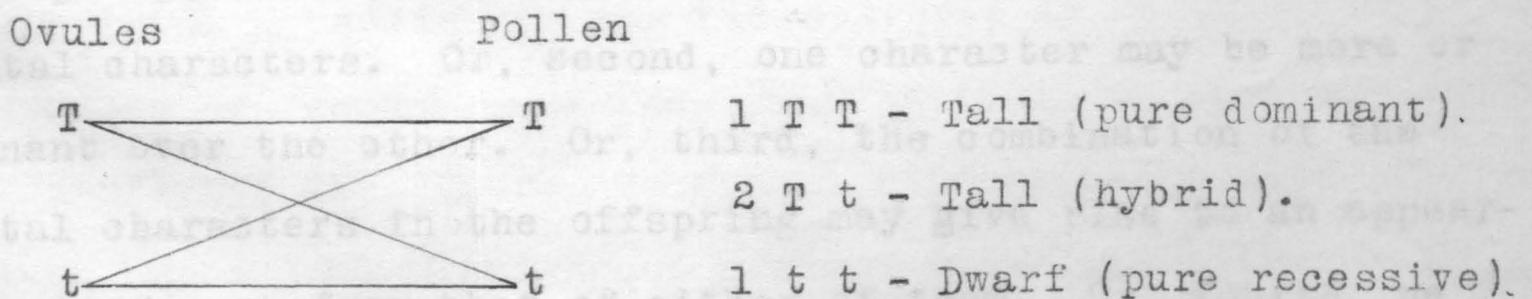
However, the 9:3:3:1 proportion sometimes becomes more complex, as Rogers⁴ found in his scarlet white cross of dwarf phlox, the proportion being 9:3:4, which will be explained later in this paper by the interaction of factors. The proportion is modified to 13:3 when white and brown leghorn fowls are crossed; 9:7 in the case of sweet peas⁵, when all the different colors of the latter are taken into consideration we obtain the tri-hybrid proportion (3:1)³. East⁶ obtained a 15:1 proportion when he crossed white and yellow corn. All of these seemingly aberrant cases are easily explained by the interaction of factors hypothesis, and Mendel's law still holds as true as ever.

In case the parents differ in respect to more than one pair of characters, we have the Law of Polyhybrids⁷—when parents differing with respect to more than one pair of characters are crossed, all the possible combinations of these characters will be

found in the F_2 generation and these combinations will occur in a definite numerical proportion.

To explain his law, Mendel offered the Theory of Gametic Purity. This theory is essentially as follows: gametes are bearers of something capable of giving rise to the characters of the individual. However, any individual gamete is able to carry one and only one of any alternative pair of characters. For instance, a given gamete may carry tallness or dwarfness, but not both. The two are mutually exclusive as far as the other of such a pair is concerned. The something in the gamete is now called a factor, and that which corresponds to the factor, in the individual, is called a unit character.

According to Mendel's theory of gametic purity, half of the gametes are pure for one or other of the factors producing the pair of allelomorphous characters. This is true for the pollen grains as well as for the ovules. Then hybrid plants must produce ovules and pollen grains carrying the character in question in equal numbers. For instance, take the characters of tallness and dwarfness. When plants of the F_1 generation are self-fertilized or fertilized ~~interse~~, there are four possible combinations as follows:



If we notice above, the three principles concerned in Mendel's

law are: independent unite characters, dominance, and segregation.

An organism acts together as a physiological and morphological whole, but from a standpoint of heredity is made up of individual heritable unit characters.

Every individual is made up of dominant and recessive characters, represented in its germplasm by factors or determiners. The dominant characters are the first to become apparent in the individual and the recessive ones remain hidden as long as the dominant determiner is present, but as soon as it becomes absent the recessive determiner forces its character into view.

Unit characters may be closely associated in the individual, but during the process of maturation separate or segregate out as if independent of each other and may unite into new combinations.

It is scarcely probable that all characters obey Mendel's law, but those which seem to be aberrant, have not been thoroughly proved that they are so. From a little study of Mendelian units, one will soon see that all characters do not behave in the simple manner as those of the earliest experiments. As a result of the meeting of the opposite characters in the pair, there may arise

in the offspring: first, the appearance of a simple blend of the two parental characters. Or, second, one character may be more or less dominant over the other. Or, third, the combination of the two parental characters in the offspring may give rise to an appearance quite different from that of either of them. Or, fourth, we may get further complications in which unsuspected characters, pre-

According to Mendel, a factor became apparent depend-
ing on whether it was dominant or recessive, the dominant character
sent in an invisible condition in one or both parents, take a part,
often giving rise to the appearance of a supposed reversion, as
the latter is present but remains hidden because of the presence of
seems to be the case in the scarlet-white⁴ cross.

Mendel worked first with one pair of alternate characters,
discovering his law of monohybrids. Later, in his experiments, he
took into consideration more than one pair, thus formulating his
law of polyhybrids. The result of his work with peas was published
in the Transactions of the Natural History Society of Brünn, an ob-
scure publication of only local importance, and here it was buried
to be rediscovered in 1900. It is surprising that his work was not
recognized, however, even Nügel failed to see the importance of
his old student's investigations, to whom Mendel wrote concerning
his experiments. Mendel's investigations were not limited to peas.
He also experimented with beans, bees, and hawkweed (Hieracium), as
his letters to Nügel give evidence. The results of these later ex-
periments have been destroyed. It must have been a source of dis-
appointment to Mendel when he was unable to obtain the same results
with Hieracium as with peas. However, after his death they were
found to reproduce parthenogenically, hence could not be cross fer-
tilized.

In 1900, Mendel's law was rediscovered by de Vries of
Holland, Correns of Germany, and Tschermak of Austria, each work-
ing independently of the other. To Mendel belongs the credit of
placing plant and animal breeding on a sound basis and bringing to
light the essential points of breeding.

According to Mendel, a factor became apparent depending on whether it was dominant or recessive, the dominant character owing its presence to its dominance over the recessive character. The latter is present but remains hidden because of the presence of the dominant character. Thus the characters of an alternate pair owe their presence to two separate factors. According to Bateson's Presence and Absence Hypothesis, the dominant character of an alternate pair owes its dominance to the presence of a factor which is absent in the recessive character. Instead of characters of an alternate pair being due to two separate factors, they are regarded as the expression of the only two possible states of a single factor - its presence or absence. For instance, the tall pea is tall owing to the presence in it of the factor for tallness, but in the absence of this factor, the plant remains a dwarf. All the plants are dwarf, but the tall pea is a dwarf plus a factor which turns it into a tall. Similarly, the case of the comb of fowls. All combs are single, but a single comb plus the factor for a pea comb produces a pea comb, single plus rose factor gives a rose comb. However, single plus pea and rose gives a walnut. If the factors for rose and pea are absent, the comb remains single.

All of the characters which I have mentioned above are probably of more scientific than practical importance. However, Mendel's law can be put to practical application. For instance, the coat color of horses is important, although the color of a horse has no effect on its real value but certain colors are demanded.

The inheritance of coat color in the horse obeys Mendel's law. When sorrel is mated with sorrel, all the offspring are sorrel, it being a recessive character. Gray is dominant to non-gray. Anderson⁸ gives the following series of colors, the color at the top of the series is dominant to all other members.

Gray	Roan	Dun
Bay	Bay	Bay
Black	Black	Black
Chestnut	Chestnut	Chestnut

Chestnut is recessive to all colors, bay is recessive to gray, roan and dun, but dominant to black and chestnut.

Still other more important facts have come to view, as in the case of diseases in the human. Epidermalysis, tylosis, presenile cataract, brachydactylous hands, and night blindness are dominant to their absence. Colorblindness and probably blindness are sex-limited, that is, a simplex dose is sufficient to produce the character in the male, but a duplex dose is required to produce the effect in the female.

Professor Biffen of Cambridge carried out an experiment with wheat which gives an excellent example of the practical application of Mendelian principles. English wheats are inferior in two respects; namely, their susceptibility to rust and lack of "hardness" of grain. On the other hand, their cropping power is equal to that of foreign wheats. It was thought impossible to raise a "hard" wheat in England, that is, one with high gluten content. Professor Biffen secured a wheat which retained its "hardness" but was low in cropping power and subject to rust. He found a variety immune to

rust and crossed it with the "hard" wheat and obtained a wheat of good cropping capacity, possessing a "hard" grain, and free from rust.

Many plants have been found to increase in vigor on crossing, for example, corn. The weight of the grain increases the current year, in the majority of cases, and the next year there is increased vigor both in grain and plant. However, in the F_2 generation, the yield begins to decrease, owing to Mendelian splitting.

Review of Roger's Work.

This experiment was started to confirm the results obtained by Mr. Rogers⁴ in 1911-12 with fiery scarlet, brilliant rose, and pure white varieties. Also to determine the inheritance of several other characters which will be enumerated later. His investigation was carried through the F_1 generation, but complete results from the F_2 generation were not obtained by June. However, the partial results obtained in the latter generation gave evidence that phlox would be of special interest to the Mendelian student. Mr. Rogers obtained on crossing fiery scarlet and brilliant rose a dominance of fiery scarlet in the F_1 generation. Brilliant rose and pure white gave a dominance of the former. Both of the crosses from the partial results obtained would have, no doubt, given the simple monohybrid ratio. All offspring of the same cross were similar, regardless of which parent was the seed parent.

The fiery scarlet-white cross was more complex in the F_2 generation than the others. However, fiery scarlet was dominant. When the paper was written only a small percentage of the plants

had bloomed, but from the partial results it appeared as if a di-hybrid proportion would have been obtained. There were 69 fiery scarlet, 17 brilliant rose, and 35 pure white. No doubt a larger number of plants would have shown a 9:3:4 proportion. The probable occurrence of the modified di-hybrid proportion is easily explained by the interaction of factors. Let us assume that the factor for brilliant rose is present in a cryptomeric condition in both parents it being recessive to scarlet in one parent and cannot become apparent in the other parent because of the absence of the factor for color. This is a case, if the supposed proposition proves to be true, of the interaction of complementary factors - brilliant rose from the white parent and color from the fiery scarlet parent. According to the presence and absence hypothesis, both parents are brilliant rose, but the scarlet is due to the addition of a factor for scarlet which is dominant to brilliant rose; the white parent being white due to the absence of the factor for color. Thus when the factors for scarlet and color are present, scarlet is produced, when the factor for brilliant rose and color are present but the factor for scarlet is absent, brilliant rose is produced. When the factor for color is absent, the individuals produced are white, although the factors for one or more different colors may be present.

Let S equal factor for fiery scarlet, B brilliant rose, C color, s the absence of fiery scarlet, and c absence of color or white.

History and Description.

P₁ Fiery Scarlet (♀) X Pure White (♂).

Gametes S B C

s B c

F₁ generation. S s B B C c (Heterozygous zygote).

Gametes S B C, S B c, s B C, s B c.

Gametes ♂	S B C	S B c	s B C	s B c
♀ S B C	S B C	S B c	s B C	s B c
S B c	S B C	S B c	s B C	s B c
s B C	S B C	S B c	s B C	s B c
s B c	S B C	S B c	s B C	s B c

9 fiery scarlet, 3 brilliant rose, and 4 pure white.

in the tube of the History and Description. 3-clert, 6-stigmas;

ovary 3-celled; capsule 3-celled, 3-valved; anthers introrse; seed
There are two types of phlox - annual or dwarf, and perenn-
two to three in number, dark grayish to black. (2/10)
nial. The latter includes many species and varieties and is found
growing wild, while the former is only one species - Phlox Drummon-
dii - which is found mostly under cultivation. Perennials reach the
height of two or three feet, while annuals grow from twelve to
eighteen inches high. Only the dwarf type will be considered in
this paper. (3) to determine the behavior of the star shaped

flowers in Phlox Drummondii is named for Professor Drummond, who
found it growing in Texas and sent seed to Europe. Great improve-
ment has been made among them; we now have single, double, and star
varieties. It is probable that their beauty has been enhanced by
crossing with perennial varieties. The colors vary from pure white
to fiery scarlet, however, there are no blue varieties. Their pro-
fusion of bloom is especially noteworthy, because of the fact that
blooming continues even when the flowers are not cut and the seed
are allowed to form throughout the season. Because of their beauty,
duration of bloom, brilliancy of color, and usefulness, phlox may
be arranged so as to make a very effective display in beds or bor-
ders.

The plants are erect or procumbent with opposite entire
leaves, or some of the upper ones alternate, 12 to 18 inches high.
Flowers showy, white to scarlet, borne in terminal cymes or cymose
panicles. Lobes of corolla obvate, orbicular, or obcordate, spread-
ing, 5-lobed. Corolla salver-formed with long tube, very much res-
tricted near the base. Stamens five in number, unequally inserted

in the tube of the corolla. Style filiform, 3-cleft, 3-stigmas; ovary 3-celled; capsule 3-celled, 3-valved; anthers introrse; seed two to three in number, dark grayish to black. (9X10)

Statement of Problem.

The purposes of the experiment were: (1) to determine the color inheritance in the F_1 and F_2 generation crosses. (2) to study the inheritance of halo or center character - commonly called the "eye". (3) to determine the behavior of the star shaped flowers when crossed with normal shaped ones. (4) to study the inheritance of double flowers.

Material Used.

All the varieties of phlox used were standard dwarfs; namely, fiery scarlet, brilliant rose, pure white, violacea, rosea aurea stellata, rosea alba oculata, chamois rose white eye, brilliant, double, purple-eyed white, soft lilac, primrose, star, and shell pink. A number of crosses were made with these varieties.

Description of Varieties.

All names of colors used in the descriptions have been taken from Ridgway.¹¹

Violacea - dark soft bluish violet, with white eye, border of dark dahlia purple around edge of corolla tube or eye, white halo.

Rosea alba oculata - light rose with white eye, pansy violet border around edge of corolla tube, white halo.

Rosea aurea stellata - pink with white eye, cream halo.

Chamois-rose white eye - pink with white eye, rose red halo.

Brilliant - rose color with white eye, rose red halo.

set seed.

Later, the flowers to be used as the pistillate parents were allowed to become older before emasculation. At this time, normal number.

Double - white with 6 to 10 petals. Five is the normal number. Two days before opening, the corolla was removed entire with the fingers or a pair of forceps, and pollinated with pollen the next day. However, the stigmas remained receptive for two or three days.

Purple-eyed white - white with white eye, phlox purple halo. By this latter method practically every flower which was pollinated border around edge of corolla tube, large white halo.

Soft lilac - phlox purple with white eye, true purple border around edge of corolla tube, large white halo.

Primrose - cream. The stigmas were probably cut off or injured in the first case, while in the second method they remained intact. As soon as emasculation was effected, the flower was covered with a thin paper bag and securely tied. The bag was removed when pollen was applied, then replaced. After pollination, the flowers remained covered until the seed had set.

Star - fringed, borders of petals distinctly white.

Shell Pink - soft shell with white eye, rose red halo.

Fiery Scarlet - rose red with whitish eye, deeper rose red halo.

Brilliant rose - deep rose pink with white eye, rose red halo.

Notes on Pigment Formation.

The formation of pigments in plants is due to the presence of two factors, chromogen and oxydase. Oxydase is an enzyme, the constituents being a peroxidase and a peroxid. The peroxidase behaves as an activator to the peroxidase in that it supplies oxygen. The activating action can be supplied by hydrogen peroxide. In order to produce color or pigmentation, the colorless chromogen is oxidized by the oxydase. However, the former exists in the plant as a constituent of a glucoside, and in this combined form resists oxidation. By a reversible reaction, enzymes of the emulsion type hydrolyze the glucoside and liberate chromogen. The chromogen is then oxidized by an oxidizing enzyme or oxydase to anthocyanin. Anthocyanins are the soluble pigments of flowering plants.

Methods Used.

The flowers are perfect and self-fertilized. The first emasculations were made by cutting off the end of the bud three or four days before time for pollination. The anthers were removed with a sharp pointed needle. In those cases in which it was thought probable pollen had fallen on the stigmas during the process of emasculation, they were thoroughly washed with a syringe and clear water or discarded. At the proper time, in two or three days, pollen was removed with a sharpened pine stick from the flower to be used as the staminate parent and applied to the stigmas of the emasculated flower. Four to five hundred flowers were emasculated and pollinated with pollen in this manner, but only about 4 per cent.

set seed.

Later, the flowers to be used as the pistillate parents were allowed to become older before emasculation. At this time, two days before opening, the corolla was removed entire with the fingers or a pair of forceps, and pollinated with pollen the next day. However, the stigmas remained receptive for two or three days. By this latter method practically every flower which was pollinated set seed. The stigmas were probably cut off or injured in the first case, while in the second method they remained intact. As soon as emasculation was effected, the flower was covered with a thin paper bag and securely tied. The bag was removed when pollen was applied, then replaced. After pollination, the flowers remained covered until the seed had set.

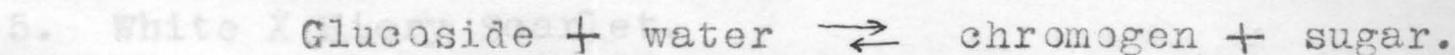
In order to: Notes on Pigment Formation.

The formation of pigments in plants is due to the presence of two factors, chromogen and oxydase. Oxydase is of a dual nature, the constituents being a peroxydase and a peroxide. The peroxide behaves as an activator to the peroxydase in that it supplies oxygen. The activating action can be supplied by hydrogen peroxide. In order to produce color or pigmentation, the colorless chromogen is oxidized by the oxydase. However, the former exists in the plant as a constituent of a glucoside, and in this combined form resists oxidation. By a reversible reaction, enzymes of the emulsion type hydrolyse the glucoside and liberate chromogen. The chromogen is then oxidized by an oxidizing enzyme or oxydase to anthocyanin.

Anthocyanins¹² are the soluble pigments of flowering plants

Matings.

1. *Roses Alba Oculata X Violacea.*
and are produced by the oxidation of colorless chromogens of an aromatic nature which are present in the living tissues in combination with sugar as glucosides as follows:



7. *Or* From the above equations it can be seen that the amount of pigmentation is inversely proportional to the concentration of the sugar and directly proportional to the concentration of the glucoside in the tissue. The local formation of pigments in the same plants is due to the local concentration of free sugars or glucosides. The abnormal pigmentation of plants under altered conditions is also due to degrees of concentration of these substances due to changes in the plant brought about by the new environment.

15. *Ch* In order to test the truth of the above hypothesis, Miss Wheldale¹² has classified her evidence under the following heads:

17. *B*(1) Analogous reactions.

18. *R*(2) Distribution of anthocyanin.

19. *C*(3) Concentration of sugars and glucosides in various tissues.

20. *B*(4) Existence of enzymes.

(5) Sugar feeding.

Description of F₂ Generation crosses.

Gortner¹³ holds that the same hypothesis is true for animals as well as for plants.

The lack of pigmentation is due to one or both of the following reasons: (1) inhibition of the action of oxydase on the chromogen, (2) inhibition of the processes which go to form chromogen.

Matings.

1. Rosea Alba Oculata X Violacea.
2. Brilliant X Violacea.
3. White X Brilliant Rose.
4. Brilliant Rose X Scarlet.
5. White X Fiery Scarlet.
6. Violacea X Fiery Scarlet.
7. Cream X Purple Eyed White.
8. Cream X Shell Pink.
9. Cream X Double White.
10. Cream X White.
11. Cream X Brilliant Rose.
12. Cream X Fiery Scarlet.
13. Lilac X Cream.
14. Shell Pink X Lilac.
15. Chamois Rose White Eye X Star.
16. Rose Aurea Stellata X Star.
17. Brilliant X Star.
18. Rose Alba Oculata X Star.
19. Cream X Star.
20. Shell Pink X Star.

Description of F₁ Generation crosses.

Before taking up the description of the individual crosses, a word of explanation of the terms used will be of some benefit. The term "eye" has reference to the color of the inside of the corolla tube; "halo" to the color immediately bordering the edge of the corolla tube and extending varying distances on the petals. The halo may be of two colors as in violacea, lilac, and rosea alba oculata.

Rosea Alba Oculata X Violacea.

Dark rhodomine purple with pansy violet and white halo; white eye.

Brilliant X Violacea.

Brilliant completely dominant, with exception of eye and halo, the cross being rose color with white eye and dark dahlia purple and white halo from violacea.

White X Brilliant Rose.

Brilliant rose dominant, being a deep rose pink with white eye and rose red halo.

One of these crosses is dilute brilliant rose, being pale pink with ~~typical~~ rose eye and white halo.

Brilliant Rose X Scarlet.

Scarlet dominant, being rose red with deeper rose red halo and white eye.

White X Scarlet.

Scarlet dominant, being rose red with deeper rose red halo and white eye.

Violacea X Scarlet.

Dark dahlia purple with pansy purple halo and white eye.

Cream X Purple-Eyed White.

Purple-eyed white dominant, being white with true purple halo and white eye. Some of the flowers have star shaped phlox purple halos radiating into each petal from a true purple border of halo around edge of corolla tube. Others are phlox purple in the entire, with white and phlox purple halo and white eye. However, some have phlox purple eyes.

Cream X Shell Pink.

Shell pink dominant, being rose color with rose red halo and white eye.

Cream X Double White.

Single whites are dominant, only a very few are double whites, no creams of any description.

Cream X White.

Cream, in this instance, is dominant. This is probably a false cross, as in all other crosses of white and cream parentage, white is dominant.

Cream X Scarlet.

In one series, a majority of the flowers are dark dahlia purple with auricular purple and white eye. However, some of the flowers are rose red with deeper rose red halo, white eye.

In another series, all of the flowers are rose red with deeper rose red halo and whitish eye.

Lilac X Cream.

Lilac is dominant, being phlox purple with true purple and white halo, white eye. In some of the flowers, phlox purple intergrades into white but the true purple and white halo and white eye are retained.

Shell Pink X Lilac.

Lilac is dominant, but a deeper shade than the lilac described in the last cross, the color being true purple with true purple and white halo, white eye.

Cream X Brilliant Rose.

Brilliant rose completely dominant, being deep rose pink with rose red halo and pinkish eye.

Star Crosses.

The seed of the star phlox planted to produce the parental varieties were mixed and thus produced various colors. When these star flowers were crossed with flowers of normal form a still greater range of colors was obtained. However, in every instance the star form is dominant to the normal. The colors are so varied that it is next to impossible to explain their appearance, and for this reason they will not be given in this paper. In the next two or three generations we shall attempt to isolate and fix some of the most promising star phlox.

Discussion of F₁ Generation Crosses.

It seems from the varying results obtained in this generation that the seed were no doubt in some instances, at least, heterozygous for the color in question. On account of the lack of time results from the F₂ generation could not be obtained before this paper was finished. For this reason, it is impossible to give scarcely any explanation for the behavior of the different crosses. However, the dominant and recessive characters can be determined. Brilliant rose is dominant to pure white, fiery scarlet to both pure white and brilliant rose, that is, pure white is recessive to both. Cream is recessive to color and non-color in all instances, save in one - cream-white cross - and ^{the next generation results} this will prove whether this assumption is proper. Lilac is dominant to shell pink. Brilliant is completely dominant to violacea with the exception of the halo.

at the center. such a case is found in the "bushosa" type of *Primula sinensis*.¹² The action of the inhibitor factor is to inhibit the action of the color factor, color only appearing at the periphery of the petals. Yellow or cream color due to the presence of yellow chromoplasts is recessive to the colorless condition of the chromoplast. It seems that in phlox the cream color is due to the presence of yellow chromoplasts.

Some plants as *Primula sinensis*, have dominant white flowers. These flowers differ from the true albinos in that the factor for color is present but in addition there is present an inhibitor factor which inhibits the action of the color factor. When dominant whites are crossed with colored types, white is dominant in the F_1 generation. The presence of the inhibitor has been proved in an experimental way for *Primula sinensis*.¹³

In all crosses between violacea and scarlet, purple is obtained in this generation. When scarlet is crossed with cream, in one instance scarlet is dominant, in the other, a purple color resulted. From these crosses, it would seem that scarlet is carrying a factor for purple in a cryptomeric condition. However, this cannot be decided until the F_2 generation results are obtained.

In the cream - purple eyed white crosses, some of the flowers prove to be lilac or phlox purple in the entire. The purple eyed white flowers carry the factor for lilac which in contrast with white appears to be purple. However, it is probable that the white flower carries a factor inhibiting the appearance of the lilac color in the petals, only allowing it to become evident

at the center. Such a case is found in the "Duchess" type of *Primula sinensis*.^{1b} The action of the inhibitor factor is localized in the periphery of the petals, color only appearing at the center. On the other hand, some of the flowers are lilac in the entire. It is probable that in the later case there is an interaction between the inhibitor factor of the white parent and a supplementary factor in the cream parent. Thus the lilac color is allowed to appear in the entire flower.

The large white centers or halos of the lilac parent is dominant in all crosses. In those instances in which purple eyed white was used as a parent, the halo of the white parent is dominant. Gregory^{1b} found, in *Primulas*, large yellow eye dominant to small eye, white eye to small yellow, and white eye to large yellow. In the F_2 generation a simple monohybrid proportion was obtained. In the brilliant - violacea crosses, brilliant is completely dominant to violacea except in the halo or center character. The purple and white center of violacea is dominant to the scarlet or rose red halo of brilliant. This shows that factors for color in the flower and in the halo are inherited independently of each other. In all crosses in which fiery scarlet is dominant, the deeper fiery scarlet halo present in this parent is dominant. When purple eyed white is crossed with cream, the halo is dominant. No crosses of purple eyed white and other parentage were made.

In all star crosses, the star or fringed form is completely dominant to the normal forms. Because of the mixed parentage of all the star flowers, no attempt was made to classify the different colors.

The normal number of petals in phlox is five, however, in some plants flowers are found having six to ten petals. Doubleless is only noticed in the increased number of petals and in none of the other organs as is the case with petunias.¹⁶ Nearly all the plants from normal-double crosses are single, that is, normal. Double phlox, unlike petunias and stocks (*Matthiola*), are fertile. All attempts to use double petunias as seed parents proved unsuccessful. However, the double character can be introduced on the male side. Miss Saunders¹⁶ found that when singles are crossed with doubles, doubles as well as singles occur in the F_1 generation. Such is the case with phlox. When F_1 singles are self-fertilized or fertilized inter se, the offspring are all single. This is due to the fact that the female organs are sterile. On the other hand, both organs are functional in the phlox. Doubles are only produced when pollen from doubles is used to fertilize the seed parent, so the operation must be repeated from year to year. This is not true with phlox, the doubles are able to reproduce themselves. The proportion of singles in a mixed family is probably always in excess in petunias, this also being true in phlox, at least in the F_1 generation.

With stocks, Miss Saunders¹⁷ obtained different results. The double flowers are always sterile, forming neither pollen nor ovules. They are always obtained from seed set by singles. Two strains occur, double and single, throwing strains. In the double throwing, all the pollen grains carry doubleness while the ovules are heterozygous for this character. This explains the fact that when double throwing forms are self-fertilized or fertilized inter se a majority of doubles is obtained, although the character is recessive to singleness. In the F_2 generation a proportion of 9 doubles to 7 singles is obtained.

No d-single x d-single = F_1 all single, F_2 singles and doubles. d-single x d-single = F_1 single and doubles, F_2 singles and doubles.

The white flowers are single, small percentage double. Creams are all double, no single creams. The behavior of phlox in this respect will be discovered in the next generation.

Gregory¹⁵ found doubleness in *P. sinensis* to be an ordinary recessive to singleness, obtaining the monohybrid proportion.

Doubleness is dominant to singleness in carnations.

In a cross of scarlet on white, two plants were produced which gave scarlet flowers splashed with white, this being unlike anything which was obtained in any other cross. The portion of the flower which contains pigment, according to Miss Wheldale's hypothesis, possesses both chromogen and oxydase, while the splashes lack chromogen or oxydase, or contains an inhibitor factor which prevents pigment formation. Keeble and Armstrong¹³ found in flaked or ever-sporting types of *P. sinensis* an inhibition of oxydase reaction in

For methods of calculation see Havenport.

the white areas. In the colored areas reactions for the formation of pigment takes place. Flashing or spotting is common in cultivated plants, being found in azaleas, sweet williams, stocks, and carnations. In the eversporting varieties of sweet williams, the amount of pigment formed is strictly proportional to the amount of oxydase present.

Miscellaneous.

It is expected in an experiment of this nature that some statistical calculations should be introduced. Biometry was discovered by Francis Galton and brought to its present importance by Karl Pearson and his associates. By statistical methods, not only different characters of the same individuals, but different characters of different individuals can be compared. The degree of correlation between characters can be calculated, and from this we can learn whether the factors which effect certain characters will change or modify other characters of the individual. If there is a correlation between the characters in question such will be the case, and vice versa.

In order to determine the correlation between height of plant and diameter of corolla, the height of the plant was measured to .5 of a centimeter and the diameter of the corolla to .1 of a centimeter. The measurements were then arranged in class centers to obviate complications in calculations.

For methods of calculation see Davenport.¹⁸

Correlation between height of plant and diameter of corolla of *Phlox Drummondii*.

Height of plant in centimeters.	Diameter of corolla in centimeters.									
	1.3	1.7	1.9	2.1	2.3	2.5	2.7	2.9	3.1	F _H
14.5					1					1
19.5			1	1	1	3				6
24.5	1		1	1	7	3	2	1		16
29.5			2	5	5	7	12	6	2	39
32.5		1	2	8	8	12	12	8		51
39.5		3	4	9	7	11	11	5	3	53
44.5		1	3	4	3	9	7	4	1	32
49.5				5	3	9	4	3		24
54.5			1		4	6	7	2		20
59.5					1	4	2	1		8
64.5						1	3			4
69.5							1			1
74.5							1			1
F _D	1	5	14	33	40	65	62	30	6	256

Diameter of Corolla

Height of Plant

M = 2.47 ± .021

M = 39.08 ± .444

S.D. = .507 ± .015

S.D. = 10.55 ± .314

Coef. Cor. = .072 ± .042.

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1. Deak, R. H., "Variation and Heredity", pp. 150-162. (1906)

2. Walter From the above, a slight positive correlation is noted between height of plant and diameter of corolla. The data was obtained from the F_1 generation plants without regard to the cross on account of the small number of plants of each cross. If it had been possible to obtain the data from plants of a single cross, there would no doubt have been a strong positive correlation.

3. East and Hayes, "Conclusions. Maize". Conn. Exp. Sta. Bull. 167

4. Price Without data from the F_2 generation, explanations of the results can but barely be touched upon.

5. Anders Fiery scarlet is dominant to brilliant rose and pure white, and brilliant rose ~~and~~ pure white. Cream is recessive to color in all instances, and to white in all crosses save one, and this one is probably false. Brilliant is dominant to violacea except in regard to halo character. The halo seems to be inherited independently of flower color. H., "On the formation of Anthocyanin", Jour. Gen. Vol. I

6. In those crosses in which fiery scarlet is dominant, the deeper fiery scarlet eye is also dominant. In the cream-purple-eyed white crosses, the purple eye is dominant. The white and purple center of violacea and lilac are dominant to their absence and to the fiery scarlet halo of shell pink. However, in the cross of fiery scarlet on violacea neither parent is dominant, a purple flower resulting. Vol. I, p. 73. (1911).

7. Single star forms are dominant in all crosses. ~~dominant in~~

8. There is incomplete dominance of singleness over doubleness.

9. There is a slight positive correlation between the height of plant and diameter of corolla. ~~greater in cross~~ Jour. Gen.

The comparatively meager results obtained give evidence that Phlox Drummondii will be of special interest to the Mendelian student.

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