THE INHERITANCE OF YELLOW-BERRY IN WHEAT

THESIS FOR DEGREE OF M. S.

ELMER WALKER BRANDES

1915

Wheat

Tells: [illegible]-berry in wheat

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ACKNOWLEGEMENT

I wish to thank Mr. Frank A. Spragg, head of the Office of Plant Breeding of the Michigan Agricultural College, under whose supervision the investigation was carried on, for kindly advice and assistance during the course of the work.

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THE CROP

Its Culture,Value and Maladies

In view of the vast economic importance of the wheat plant any factor which interferes with its maximum financial returns to the growers,even to a very slight extent,is bound to be of tremendous importance in the aggregate,provided that the disturbing factor is universally distributed. The condition known as "yellow-berry" is such a factor. Apparently no wheat growing region is absolutely free from it although the amount of damage caused by it varies considerably in different localities. The fact that millers object to wheat in this condition is apparent by their refusal to pay the top market price for grain which has any considerable amount of yellow kernels. In some cases they refuse to accept affected grain under any consideration when healthy grain is available,the reason given being that it affects the color and quality of the flour. A local investigation of the attitude of the millers on this subject has disclosed the fact that they regard the deterioration due to yellow-berry serious enough to discount from two to ten cents per bushel,depending on the percent of yellow-berry present,from the price which they would be willing to pay for healthy wheat.

Keeping these facts in mind,a short review of the wheat industry will reveal the enormity of the financial loss suffered by wheat growers on account of this depreciating factor.

Wheat is a plant which is widely distributed over the civilized world,and constitutes the main article of food wherever its culture is practiced. Its history is coincident with that of the human race. The United States leads all countries in the production of wheat and the maximum capacity for production has not yet been reached. Land suitable for raising this cerial is still available and more careful methods will increase the output from the land already in use. Figures from the "Statistical Abstract of the United States" indicate that we may expect a continued increase in production. The following table, taken from that source, and including a record of all the crops from the year 1870 to 1910 at ten year intervals and also the crop for 1913 shows a uniform increase up to the present time.

Year	Area acres	Production bushels	Farm Value dollars	Av.Yield per acre	Av.Farm Value
1870	18,992,591	235,884,700	222,766,969	12.4	94.4
1880	37,986,717	498,549,868	474,201,850	13.1	95.1
1890	36,087,154	399,263,000	334,773,678	11.1	83.8
1900	42,495,385	522,229,505	323,525,177	12.3	61.9
1910	45,681,000	635,121,000	561,051,000	13.9	88.3
1913	50,184,000	763,380,000	610,122,000	15.2	79.9

Estimating the loss due to yellow-berry at five percent, and there is reason to believe that it exceeds that amount, it may be seen by consulting the above tabe that the income of American farmers during the year 1913 was reduced by over thirty-five million dollars. Some states suffered more heavily than others, not only on account of the relative size of the crops, but because the percent of yellow-berry varies in different regions. During the last fifty years there has been a constant movement of the center of wheat production from east to west in the United States. This has proceeded much more rapidly than the center of population. In 1850 New York was one of the great wheat growing states, and the Genessee Valley was the greatest wheat growing region in the United States. Since that time the wheat production of New York has decreased over three million bushels, and its proportion of the entire crop has declined from 13.1% to 1.6%, while the four states which now produce the most wheat were, with the exception of Ohio, still unsettled. The latter state was also at one time the leader in wheat production, and the rich Miami Valley succeeded the Genessee Valley as a wheat region. But while Ohio is still a large producer of wheat, its relative production has declined from 14.4% to 7.6%. Southern Wisconsin and Northern Illinois was once the great wheat growing region of the country, but this was again supercedded by Minnesota and North Dakota. For the past few years Kansas has been producing more wheat than any other state. It seems probable that the great plains area of western Kansas and Nebraska and of eastern Colorado and Wyoming and perhaps northern Texas is destined to be the next great wheat growing region. Something more than a mere following up of the center of population may be observed from these facts. The culture of wheat is gradually moving away from the humid regions and toward the semi arid regions of the country, a point to which we will presently recur.

For purposes of comparison with yellow-berry, the damage caused by the other important maladies of wheat will be here considered. They may be classified as unfavorable environment insect pests and fungus diseases. The first of these, unfavorable environment, would include drought; hail, wind and rain storms; floods; fire; frosts; hot waves; excessive moisture and unfavorable soil. Very little specific information can be found as to the extent of the damage caused bt unfavorable environment. Loss occures every year from one or more of these factors but usually it is restricted to limited areas, and on account of the compensating distribution of favorable meteorological conditions, it is not felt much by the crop as a whole. The average loss for a period of fifty years in France occasioned by the most serious of these, the hailstorm, was 0.81%. There are about one hundred species of destructive insects which damage wheat to a greater or lesses degree. Less than a dozen however, occasion enough loss to be considered of very great importance.

Perhaps the most important of the destructive insects is the Hessian Fly. In 1900 the Ohio loss was placed at over sixteen million dollars. The Chinch Bug is next in destructiveness. In years when the Chinch Bug has been unusually severe the loss to single states has been variously estimated at from ten to twenty million dollars. The Wheat Midge has been known to cause the loss of from one half to two thirds of the crop in single states. Plant Lice are thought to cause an annual damage of about two percent in some regions. Locusts or grasshoppers used to devastate extensive areas, but of late years have ceased to be of great economic importance. Large portions of their breeding grounds are now cultivated and this restricts their multiplication. The Grain Aphis, popularly known as the "Green Bug" can be found in the wheat fields any year but it is rather erratic in its serious outbreaks. These generally occur after a mild open winter followed by a cold wet spring, due to the fact that it can stand a lower temperature than its natural enemies. Other insect enemies are the Wheat Straw Worm, the Joint Worm, the Wheat Bulb Worm, the Cut Worm, several species of Saw Flies and the Army Worm, the damages from which are local and can be controlled.

While these losses seem to be enormous,it must be remembered that the occurence of most of the pests is epidemic,and the interval between outbreaks is erratic. Probably the aggregate loss occasioned by all of the destructive insects would average less than twenty percent of the annual crop.

There are several important fungus diseases of wheat. The Wheat Scab(Gibberella Saubinetii) causes a loss which is usually light but which may reach a maximum of ninety percent in some fields. Stinking Smut(Tilletia foetans and T.tritici) has ruined half of the crop in Wisconsin.Loose Smut(Ustilago tritici) is said to be responsible for the loss of over half of the crop in North Dakota in 1905. The rusts Of wheat are another source of loss. Two kinds are common. The Leaf Rust (Puccinia rubigo-vera)causes a loss in North Dakota which was estimated by Bolley to be ten percent of the crop annually. The well known Stem Rust(Puccinia graminis)causes an annual loss of over five million dollars in the United States.Leaf Blight(Leptosphaera tritici)and Powdery Mildew(Erisiphe graminis) occasionally cause slight losses in certain localities. What is true of the destructive insects in regard to the epidemic nature of the outbreaks is also true of the fungus diseases.

The occurence of yellow-berry is constant and uniformly distributed over the years. The devastations of insects and fungi are more sensational than the losses which can be attributed to yellow-berry,but the loss occasioned by them if taken on the average will be found not nearly so great as would be suspected by an examination of the foregoing figures.

It is probable that yellow-berry causes at least one tenth of the average annual loss sustained by the wheat crop of the United States. This tremendous loss has been overlooked largely because it does not affeet the size of the crop but merely the quality of the grain.

THE YELLOW-BERRY PROBLEM

Abnormal Anatomy

Yellow-berry is a term used to designate a condition of the wheat kernel which gives it a spotted or mottled appearance, due to an abnormal condition of the internal structure of the kernel. It is most conspicuous in the type known as hard winter wheat, and is variously termed "yellow-berry", "white-belly", "Starchy Kernels", "Mealy Kernels", "piebald", "off color" etc. The normal kernel of a hard winter wheat is more or less translucent, hard and vitreous. The spots of an affected kernel vary in size, shape and location, often being very small but sometimes involving the entire kernel. These spots are seen to be opaque when viewed in transmitted light. The gross appearance of an affected kernel may be compared with a cake of clear transparent ice which has been kicked violently with the heel or struck with some blunt instrument, causing air spaces to appear between the ice crystals and making the area opaque. The microscopic examination of an affected berry reveals the fact that there actually are larger and more numerous air vacuoles in the cells of the affected spots than in the healthy tissue. The spots may be near the surface, in which case they aresharply outlined, or they may be internal, when they are not so conspicuous. They may occur anywhere in the endosperm. A distinction is made between a "soft" wheat such as is grown in the Pacific coast region, and a yellow-berry kernel of a hard wheat. Some confusion seems to exist between these two in the minds of many, and some writers have considered them identical,i.e.,they have regarded the soft wheats as merely one hundred percent yellow-berry. That this opinion is erroneous is brought out by Lyon and Keyser's investigation(Nebraska Station Bulletin 89),on the specific gravities of the several types of wheat. For a clearer understanding of this experiment the chemical contents of the kernels must be first considered. Analysis has determined the soft wheats to be rich in starch but deficient in protein, a condition which is also true of the yellow kernels of the the hard type. Now the true soft(starchy)wheats are found to posses the highest specific gravity on account of the higher specific gravity of the carbohydrates(starch 1.53,sugar 1.60, cellulose 1.53),as compared with the proteids(gluten 1.297). The hard wheats therefore,on account of their larger percent of proteids,are lighter than the soft wheats. On the assumption that the yellow-berry kernels of the hard wheats are identical with the soft wheats we would expect to find a higher specific gravity in the yellow-berries than in the healthy kernels from the same source. But the reverse of this is true. Experiment has demonstrated that the yellow-berries, notwithstanding their relatively larger starch content,are actually lighter than the healthy berries with their larger percent of proteins. The presence of the numerous air vacuoles previously alluded to,may be offered as an explanation for this apparent anomaly. At any rate it is evident that a sharp distinction exists between the internal structure of the soft wheats and the yellow-berry kernels of the hard wheats.

PREVIOUS WORK

In regard to the chemical analysis of the contents of the kernels from a common source, Snyder, Minnesota Station Bulletin 95, found the difference in protein content to range from 1.6% to 4.87% in favor of the glutinous(healthy) kernels. That he was dealing with what we define as yellow-berry is evident whe he says, "In many cases it was possible to distinguish starchy and glutinous seeds in the same wheat head.". He found that dark colored, glutinous grains from the same source contained a higher percent of nitrogen than the light colored starchy grains. In regard to the relative value of these two types he says, "For purposes of nutrition wheats with the maximum amount of protein or gluten are the most valuable. Wheat of maximum gluten content contains as much protein as average beef, while that of minimum content contains no more than rice."

An explanation of the opaque and dead whit appearance of the affected grains or spots is offered by Hackel, who says, "If the albumenoids so fill up the intervals between the starch grains that the latter appear to be embedded in cement, the albumen appears translucent and the fruit is called corneous, but if the union is less intimate, there remain numerous small air cavities, and the albumen is opaque and the fruit mealy. Both conditions occur in the same variety(wheat)and they seem to be occasioned by differences in climate and soil."

The yellow kernels are known to contain more moisture than the flinty kernels of the same variety, even in grain which has been standing for several months. This would tend to confirm the theory of a more condensed accumulation of proteid in the flinty kernels.

T.L.Lycn and Alvin Keyser carried on an in vestigation of the yellow-berry problem the results of which were published in 1900 in Nebraksa Bulletin 89. An experiment to determine the part which weathering and bleaching plays in the production of yellow-berry was carried on by them as follows;half sheaves were taken from the field and cured in a dry room,moderately lighted,and the other halves were allowed to remain in the field from July 10 until August 21. The bundles were then threshed and separated into two portions,"yellow-berry" and "horny red". The bundle kept in the dry dark room had only twenty-five percent of yellow-berry,while the exposed bundle had 97.2 percent of yellow-berry.

Cuttings were made of the same wheat at intervals of four days and it was discovered that the percent of yellow-berry increased as the grain became riper. That there is a definate relation between the percent of yellow-berry and the character of the season,insofar as the latter affects the date of ripening was determined by the amount of yellow-berry in the crops of different seasons. The amount of yellow-berry increases with the lateness of ripening,and it was further indicated that crops of large yield and low nitrogen content contained more yellow-berry than crops of the opposite kind. Analysis of samples in every case substantiated the millers statements that the horny red type contained more gluten than the yellow-berry wheat(i.e.it had a larger nitrogen content). The authors attribute the presence of yellow-berry in wheat to failure to stack sheaves,and base their suggestions for alleviating the condition on these conclusions. They recommend early cutting and prompt stacking.

Professors Roberts and Freeman of the Kansas Experiment Station, Bulletin 156, 1908, attack the problem from a different standpoint and arrive at entirely different conclusions. In regard to climatic influence they draw attention to the fact that it has long been known that in cool moist climates, such as the maritime regions of western Europe and our own north Pacific coast, the wheats there grown have larger grains, are softer and lower in percent of proteid nitrogen than the wheats grown in continental areas such as the interior of Russia, the Balkan States, Hungary and the central western states of our own country. In their discussion of the internal structure of the wheat kernel they quote Lyon and Keyser as follows, "The protoplasmic network of the cells in the sections from the very horny kernels showed only an occasional vacuole; sections from the markedly yellow kernels showed very much m more numerous and larger vacuoles, measuring on the average less than 0.001 millimeter. Medium yellow-berries had fewer and smaller vacuoles than the markedly yellow kernels." Their investigation of temperature and vegetative period in relation to the percent of yellow-berry would seem to indicate that ripens later and at a higher mean temperature has the least amount of yellow-berry. These investigators are the first to discuss the possibility of yellow-berry being an hereditary tendency. In regard to this possibility the authors consider the elimination of yellow-berry by the method of plah plant breeding as wholly dependent upon the extent to which yellow berry is distinctly a heritable product, and not a fluctuating variation common to all the strains of glutinous wheats when grown under certain seasonal conditions. From the data gathered it was found that the minimum amount of yellow-berry in the groups studied in 1907 came from those groups showing the minimum amount in 1906. This points to a certain degree of actual inheritance of the yellow-berry tendency. A study of pedigreed wheats in 1906 and their progeny in 1907 showed a correlation in the amount of yellow-berry,which could be ascribed only to an inheritance of the condition on the part of the individual plants. Their deductions are summed up in the following words;"In view of the fact that but one head from each plant of the pedigree parent stocks had to furnish the grains upon which an estimate of the percentage yield of yellow-berry in the plants as a whole was based,the result is surprisingly confirmatory of our hypothesis that the yellow berry is a 'tendency' which finds expression in certain strains or races more markedly than in others and is heritable".

G.W.Shaw and E.H.Walters,California Station Bulletin have brought out some interesting facts in regard to the relation of soil and climate to the gluten content of wheat,and to the percent of "starchy kernels". Realizing that most of the earlier work had been done in the presence of two variables soil and climate,they set about to bring two types of soil under identical climatic conditions. This was accomplished by shipping a sufficient amount of Kansas soil in bags to the test plat in California. The chemical and mechanical analyses of the soils were determined and also the analysis of the wheats grown. The tabulated results do not show that the soil had any marked effect on the gluten content of the wheat.

They found that the soil nitrogen content had little if any direct influence on the nitrogen content of the crop,but that some climatic factor completely overshadowed the soil factor.

This conclusion is in direct opposition to the deductions made by Headon, Colorado Station Bulletin 205, who states that tha elements of the soil is the one and only controlling factor in the production of yellow-berries. Shaw and Walters go farther in stating that it appears as though the nitrogen content of the original seed, when grown elsewhere than in a climate within which it has been acclimated has little or no influence on its progeny, and that even if it be acclimated, still some seasonal climatic factor is sufficient either to lower the nitrogen content of a high gluten wheat, or raise the nitrogen content of a low gluten original. Another interesting result of the experiment was the presence of more "starchy berries"(8%) in the check plat than in the plat where the soil had been disturbed, i.e. the soil had been removed for a depth of three feet and the same soil replaced to make the conditions the same as for the imported soil. The grain from this disturbed soil plat was of high milling quality and contained no "starchy berries". No reason was assigned for this very interesting development.

Headon, Wm.P., Col.Sta.Bul.205 states, "I do not think that the there can be any question of the identity of the affection of our wheats with that of Kansas, Nebraska or North Dakota, and almost no queation but that the starchy, opaque wheats of California and the Pacific coast states, in general, are identical in their character with extreme cases of yellow-berry in Colorado and have the same cause." This statement is not at al in harmony with the results of the experiment previously cited concerning the difference in microscopic anatomy and specific gravity between these two wheats. There is reason to believe that there is a sharp distinction between the internal structure of a true starchy wheat,and that of a yellow-berry kernel of a hard glutinous wheat,and that yellow-berry may occur in the true starchy wheats just as it does in the hard wheats,but is not so noticeable by a superficial examination. Dr.Headon apparently bases his opinion upon the macroscopic appearance of these two types of wheat,which are very similar as far as their gross anatomy is concerned. The investigation which Dr.Headon conducted during the years of 1913 and 1914 included thirty-six experiments each year,the the results of but twelve each year being published for the sake of brevity. In 1913 he planted twelve plats of wheat, four plats of each of the three varieties tested. The first plot of each variety was treated with nitrogen fertilizer at the rate of eighty pounds to the acre,the second plot with soluble phosphorus,forty pounds per acre,the third plot with potassium,one hundred and fifty pounds per acre and the fourth plot of each variety was grown as a check. The following year the experiment was repeated,using the same plots for the respective varieties,and using the 1913 crop for seed in 1914. The results may be best shown in tabular form.

Percentage of Yellow-berry in Crops of 1913 and 1914

Variety	Fertilizer	%yellow-berry in 1913	%yellow-berry in 1914
Defiance	Nitrogen	none	none
	Phosphorus	10.0	50.0
	Potassium	30.0	63,0
	Check	24.0	36.0
Red Fife	Nitrogen	none	24.0
	Phosphorus	24.0	97.0
	Potassium	42.0	98,0
	Check	31.0	98.0
Kubanka	Nitrogen	none	23.0
	Phosphorus	35.0	94.0
	Potassium	37.0	96.0
	Check	31.0	97.0

In discussing these results Dr.Headon says,"The only causes heretofore assigned for the appearance of this affection in wheat are over-ripeness of the grain,standing too long ih the shock,exposure to the action of moisture,air and sunshine,a heritable 'tendency',the action of fungi and the climatic and weather conditions,- no one of which can be considered as the cause in our case.*** The question of a tendency which is heritable is fully set aside by the fact that we can,from the same lot of seed,under identical conditions of climate,grow crops affected with or free from yellow-berry.*** We can see that in every case,the application of nitrogen,which was in the form of sodic nitrate,greatly reduced the amount of yellow berry,in some cases preventing it altogether." Again in the summary of this bulletin he says,"Yellow-berry can be very much lessened or entirely prevented by the application of a sufficient amount of available nitrogen.Yellow-berry can be greatly intensified or increased by the application of available potassium."

These results are very interesting and show beyond a doubt that the soil elements influence the evident or perceptible amount of yellow-berry to a large extent.

The complicated, and in many cases contradictory results secured in this line of investigation have resulted in a wide divergence of opinion as to the factors which influence this condition of the wheat kernel. Some consider it the result of degeneration in the variety, others believe it to be due to soil and climatic conditions, or regard it as the consequence of growing the same seed year after year, while still others attribute it to the condition of the crop at the time of harvesting. The possibility of its being a character inherent in the individual has been considered and it is the apparent logic of this latter solution, resulting from observations covering a period of years, that lead to the inception of the present investigation.

MENDELISM AND EXPLANATION OF TERMS

Before entering into the technical details of this problem it will be well to briefly summarize the rules governing the more important phases of heredity, especially those which have a direct bearing on dominance and segregation. The most signal achievements in this field were accomplished in an unostentatious manner by Gregor Johann Mendel, and Austrian monk, who in the privacy of hid cloister garden carried on experiments with the common garden pea which resulted in his publishing in 1866 the first fundamental contribution to the laws which govern the inheritance of unit characters. His work consisted in the hybridization of the several varieties of Pisum, the two parents of which were selected on account of differences in the same unit characters, such as white or colored flowers, green or yellow endosperm, elongated or shortened stems etc. The progeny of these crosses, termed by Mendel the first filial (F_1) generation, were carefully watched, and a careful record kept of the proportions in which the unit characters appeared in the offspring. He discovered that in most cases one of the two opposing characters was dominant while the other was recessive, i.e. the character in the offspring was not intermediate between those of the twp parents, but was to all appearances identical with that of the dominant parent. In the next generation however, it was found that the progeny were not all like the dominant grandparent, but had segregated into the two types which had been mated together in the first place. The most remarkable part was that they had segragated according to definate numerical ratios in every experiment which Mendel performed and these results have given rise to what is known as "Mendel's Law". It may be briefly formulated as follows; When two organisms that are unlike in respect to any unit character are crossed, all of the offspring, composing the F_1 generation will resemble one of the parents identically in their somatic constitution, but will differ in their germinal constitution. In the F_2 generation, however ther will be 25% of the offspring like the dominant grandparent, 25% like the recessive grandparent and 50% like the parents, which, it will be remembered <u>resembled</u> the dominant grandparent. Since the first and last of these groups are to all appearances identical, the apparent ratio will be three to one of dominants and recessives respectively. Mendel's original experiment will serve to illustrate the actual working of this law. Tall and dwarf peas were crossed and the seeds from this union planted. They gave rise to tall plants only. The seeds from this crop were planted, and the offspring were observed to be in the proportion of 75% of talls to 25% of dwarfs. Mendel explains this result diagramatically as follows;

(Tall) TT — tt (Dwarf)

Tt — F_1

TT Tt Tt tt — F_2

The unit characters or genes represented by T and t are double because every sexual individual is made up of contributions from each of the two parents. When these contributions are alike, as is the case in both parents here shown, the condition is known as homozygous. If they are unlike, as is the case in the F_1 generation the condition is known as heterozygous. The phenomena of segregation arises from the union of two of these heterozugous individuals. It may be represented graphically in this manner;

	T	t
T	TT	Tt
t	Tt	tt

Every possible combination of the gametes of the male and female parent is shown in the proportion in which they would occur no matter what numbers were involved, 1 TT:2Tt:1 tt. This is due to the law of chance which alone governs the union of pollen grain and ovule.

When the homozygous individuals breed, their offspring will come true, but when heterozygous individuals breed their offspring will segregate in exactly the same manner as was shown for the F_2 generation. Since the promulgation of the "Presence and Absence Hypothesis", which has been generally accepted, the terms duplex, simplex and nulliplex have replaced homozygote and heterozygote. According to this hypothesis a character determiner (gene) is either present or absent in an individual. If two germ cells possessing the character for tallness unite, they produce a duplex (TT), if one parent has the character and the other has not they produce a simplex (Tt), if neither parent has the character they produce a nulliplex (tt).

An allelomorph is the reaction of a gene with its absence in a Mendelian distribution. Yellow-berry and absence of Yellow-berry might be assumed to be the allelomorphic pair in the following discussion.

Autogamy (self marriage) is a term used in plant breeding to designate self fertilization in plants. The wheat plant is autogamous.

A population is all the decendents of a single seed,whether they are genotypically alike or not.

Progeny usually refers to the immediate offspring of a plant

SELECTION

It has been demonstrated that the selection of kernels free from spots for use in propogating has not resulted in establishing strains which have no yellow-berry. For years the Michigan Agricultural Experiment Station has culled the "off colors" and planted nothing but kernels of the ideal type and yet the progeny of these healthy kernels contained varying amounts of yellow-berry. This disproves the theory that the spotted condition is dominant, for in that case the healthy kernels would be recessive, consequently nulliplex, and would breed true, under natural conditions because wheat is a self fertilized plant. If the healthy condition were dominant, considering healthy and yellow-berry as the allelomorphic pair, we would expect to find in autogamy under no selection, a slight preponderance of healthy berries. The following chart in which healthy berries are represented by the duplex HH, and simplex Hh, and the yellow-berries by the nulliplex hh, will show the expected proportions.

CHART I

Generation	2	3	4	5	6	7	8	9	10	n
HH	1	3	7	15	31	63	127	255	511	$2^{n-1}-1$
Hh	2	2	2	2	2	2	2	2	2	2
hh	1	3	7	15	31	63	127	255	511	$2^{n-1}-1$
Summation	4	8	16	32	64	128	256	512	1024	2n

At the end of ten generations the proportion would be 513 to 511 of healthy to yellow-berries and at the end of n generations the difference would be practically negligible. This approximate proportion is met with in many pure lines which have been bred with no selection for a number of generations at this station.

Assuming the same condition of dominance, if mass selection were practiced we would expect the duplexes and simplexes (healthy) to gain an overwhelming preponderance over the nulliplexes (yellow-berry) in a few generations according to the formula;

CHART II

Generation	2	3	4	5	6	7	8	9	10	n
HH	1	3	7	15	31	63	127	255	511	$2^{n-1}-1$
Hh	2	2	2	2	2	2	2	2	2	2
hh	1	1	1	1	1	1	1	1	1	1
Summation	4	6	10	18	34	68	130	258	514	$2^{n-1}+2$

In the experiments conducted at this station, mass selection has resulted in no such preponderance of healthy berries, so it would seem that the healthy condition is not at least a simple dominant of an allelomorphic pair. At the same time it does not disprove that yellow-berry is inherited according to some definate Mendelian ratio, as there are many exceptions to the law of dominance. The mathematical precision with which dominance was found to act by Mendel in his experiments with the garden pea has been found to break down in some cases of other organisms. Imperfect dominance, as in the case of the blue Andalusian fowl, reversed dominance, illustrated by Lang's experiments with snails (Helix), in which snails with yellow shells were found to be sometimes dominant over those with red shells although the reverse of this was generally the case, the phenomena of potency and blending inheritance are some of the factors which are exceptions to the general rule of simple dominance.

Selection has resulted in strains which vary greatly in the amount of yellow-berry present. Red Rock, a variety originated at this station is singularly free from yellow-berry, while other strains have been dropped altogether on account of the large percentage of affected kernels. These wheats were all grown under the same environmental conditions. This would tend to show that the amount of yellow-berry is influenced by other than environmental factors.

Until last fall no yellow kernels were planted, all of the selections being made from the ideal type of kernel, but at that time yellow-berries as well as healthy berries were planted in an attempt to discover the proportions of healthy and yellow kernels resulting from yellow-berry seed. These results of course will be very important but unfortunately they cannot appear in this paper, which must be presented befor the crop is harvested.

CROSSING

The work upon which the opinions of the present paper are based was undertaken by the Experiment Station of the Michigan Agricultural College, not as a study of the inheritance of yellow-berry, but for the general improvement of Michigan wheat. This was started in 1912 with the crossing of several different types of wheat the progeny of which were planted the following year and individual records kept of every plant. This method has been pursued until the present time at which the progeny of those of the original crosses that were retained amounts to about seven hundred and fifty thousand seeds. During the course of this work it was observed that yellow-berry occured very unevenly in different individuals grown under identical conditions of soil and climate. Until last year no accurate counts were made of the proportions in which yellow-berry occured in the individual plants. The 1914 crop was harvested and stored, as in previous years, in manilla paper envelopes, each envelope containing the seeds from a single plant, whose ancestry could be traced back three years. The plants were all numbered according to the systemmin use by the plant breeding office of the farm crops department. The harvest from each plant is placed in an envelope and an entry made in the record book, noting all the characteristics under consideration of the plant in question. Individual populations were grown in separate plots which measured approximately three by five feet. This fact is important in what is to follow as it, indicates that the plants were in close enough proximity to eliminate any differences due to environmental influence, such as waves of soil fertility,

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uneven distribution of fertilizer,moisture and so forth.

A hereditary tendency has been offered as a possible solution of the yellow-berry problem,and observations by Mr.Frank Spragg,head of the plant breeding office of the College tended to confirm this theory. Consequently the present work was undertaken under Mr.Spragg's direction in the hope that it might contribute to the knowlege of this condition of wheat,which has been such a serious problem to the improvers of grain during the past few years.A study of the various types of Michigan wheats revealed the fact that none of them are free from yellow-berry,and most of them are affected to an alarming extent. As before stated,the extent to which an individual may be affected ranges from a single minute spot,which may be located anywhere in the interior of the grain to a condition whereby the entire endosperm is involved.The spots are conspicuous and can be readily detected when located near the periphery,but it is extremely difficult to detect an affected berry when the spot is situated near the center of the grain. Owing to this fact it is easy for error to creep in when separating the grains by inspection into yellow-berry and healthy classes. It is desireable for the operator to section a number of grains of the various classes in order to become thouroughly familiar with the correlation between internal structure and outside appearance,as it would be impossible to section every kernel on account of the numbers involved and becouse the seed would of course be destroyed and the experiment terminated. Thus it may be seen that there will be numerous individuals of uncertain classification and unavoidable error will enter to a slight extent. It is hoped however that this error is more or less compensating and that the proportions will be found quite accurate. On account of the persistence whth which all the affected grains of some progenies tented toward partial yellow-berry while others tended toward complete yellow-berry it was decided to separate the seeds of each progeny into three classes,termed for the sake of convenience,healthy berries,spotted berries and yellow-berries. Those grains which were apparently unaffected were put into the healthy class,those which were entirely affected were put into the yellow-berry class and those which were intermediate between the two extremes,i.e.those which exhibited an affected area ranging from a minute spot to almost total yellow-berry were put into the spotted class.The progeny of each plant was examined separately and the seeds sorted into these three clas classes. The progenies were found to have segregated into all three classes in most cases,but some were entirely healthy some entirely yellow-berry and some had segregated into any two of the three classes.Apparently neither the elements of the soil nor the climatic conditions were the controlling factors because there could be found plants included in the small area of a test plat exhibiting a most startling range in the percent of yellow-berry. It might be argued that an unequal distribution of fertilizer or a cow dropping here and there might account for these differences,but the root system of a wheat plant is sufficiently large to insure individuals, whose maximum distance apart is from three to five feet (the size of the plot) feeding on the same soil elements. An examination of some of the seed counts of the individual plants grown in the same plots, taken at random from the note book, which is much too voluminous to reproduce here in full show that these differences were not occasional, but frequent and uniformly distributed.

TABLE I

Results of Count in Plot II of 1914

Plant No.	Red Grains			Pearl Grains		
	Healthy	Spotted	Yellow	Healthy	Spotted	Yellow
40201	36	74	33			
40202		7	164			
40203	14	9	87			
40204	7	13	84			
40205	23	70	34			
40206	105					
40207	98	10				
40208	73					
40209	97	95	27			
40210	154	45	30			
40211	94	66	26			
40212	57	37				
40213	3	11	66			
40214	56	8				
40215	26					
40216	4	3	32			
40217	48	65	44			
40218	15	29	12			

Plant No.	Red Grains			Pearl Grains		
	Healthy	Spotted	Yellow	Healthy	Spotted	Yellow
40219	89	72	21			
40220	88	2				
40221				74	16	6
40222	13	71	114			
40223				77	3	
40224	58					
40225	4	9	19			
40226	66	13				
40227		4	269			
40228	13	33	63			
40229	27	81	42			
40230	50	66	25			
40231	10	27	38			
40232	25	44	13			
40233		24	293			
40234	21					
40235	6	19	82			
40236				39	22	33
40237	6	33	104			
40238	33					
40239	34	14	43			
40240	60	3				
40241	26	21	54			
40242	139					
40243	190	4				
40244				137	20	41
40245	105	13				

Plant no.	Red			Pearl		
	Healthy	Spotted	Yellow	Healthy	Spotted	Yellow
40246	32					
40247	2	3	132			
40248	16	34	24			
40249	52					
40250	23	25	167			
40251	8	12	192			
40252	63	32	136			
40253	8	10	17			
40254	9	41	45			
40255	7	17	48			
40256	167	33	[illegible]			
40257			196			
40258	48	1				
40259	101					
40260	88					
40261	19		1			
40262	74					
40263	30	39	51			
40264	7	32	72			
40265	49	26	16			
40266			44			
40267			44			
40268	4	4	34			
40269	5	28	126			
40270	29	5	124			
40271	6	21	240			
40272	43					
40273	62	33	34			

Plant No.	Red Healthy	Red Spotted	Red Yellow	Pearl Healthy	Pearl Spotted	Pearl Yellow
40274	25	30	124			
40275	92	46	136			
T0tal	1464	1441	2886			

RATIO - .9799 : 1.0058 : 2.014
EXPECTED RATIO - 1.0000 : 1.0000 : 2.000

This populatioh represents the F_2 generation of a cross between wheats number 60101 and number 60801,pearl and red wheats respectively. The totals given are the totals of those progenies which segregated into all three classes. They can be seen to have segregated in regard to color also,but we are not concerned with that fact beyond its proving the strain to be a true hybrid. The term "expected ratio" is used advisedly. It is not meant to convey that an undivided ratio of 1 : 1 : 2 will finally be found correct,but merely is used because the tendency of the material seems to be in that direction,and it will serve for purposes of discussion. This population is seen to come very close to this expected ratio. The difference between spotted and complete yellow-berry may be merely quantitative,so that these two groups can be lumped together in which the ratio would be one to three of healthy and yellow-berries. They were separated originally on the assumption that the spotted condition was intermediate between healthy and complete yellow kernels. Assuming that this is a normal Mendelian segregation,it would indicate that the yellow-berry condition is dominant over the healthy grain. Our present knowlege of the phenomena of segregation,however, does not uphold this assumption,since it has been shown that the healthy berries do not breed true(p.21)as they would if they were nulliplex.

There is absolutely no uniformity in the amount of yellow-berry to be found in the individual plants to indicate that it is the result of soil elements or climatic conditions alone. On the other hand the great variation in the percent of yellow-berry seems to point out very forcibly that it is due to differences in the individual germ cells.

The fòllowing tables are extracts taken at random from the data of various populations, which, for the sake of brevity will not be given in full.

TABLE II

Result of Count in Plot III of 1914

	RED			PEARL		
Plant No.	Healthy	Spotted	Yellow	Healthy	Spotted	Yellow
403001	6	18	134			
403002	35	49	121			
403003				11	11	176
403004	1	6	26			
403005	42	38	48			
403006				2	28	179
403007	12	13	126			
403008	5	9	26			
403009	60	25	193			
403010	14	18	111			
	*		*		*	
403063		7	200			
403064	72					
403065			131			
403066	142	39	65			
403067			187			
	*		*		*	
403077	26		1			
403080			159			

Plant No.	Red Healthy	Red Spotted	Red Yellow	Pearl Healthy	Pearl Spotted	Pearl Yellow
403081		1	118			
	*		*		*	
403109				32	3	3
403110	35	46	87			
403111	28					
403112	100	46	51			
403113	15	4	254			
Total	2948	1755	10546			

RATIO - .7733 : .4604 : 2.7663

The extreme variation in amount of yellow-berry is exhibited by the individual plants of this population as was the case in the previous one. This was the result of a cross between the same two wheats that were the parents of the preceeding.

TABLE III

Result of Count in Plot IV of 1914

Plant No.	RED Healthy	RED Spotted	RED Yellow	PEARL Healthy	PEARL Spotted	PEARL Yellow
404033	118	31	9			
404034	127	31	3			
404035	1	4	106			
404036			62			
404037		1	62			
404038	16	52	83			
404039				44	70	62
404040			181			
404041					1	48
404042			168			
	*		*		*	
404187	104					
404188	150	112	17			
404189	6	101	100			

Plant No.	R. Healthy	R. Spotted	R. Yellow	P. Healthy	P. Spotted	P. Yellow
404190	3	136	125			
404191	4	20	7			
404192	2	18	30			
404193	2	12	80			
404194				2		159
404195	46					
404196	3	51	50			
Total	2687	3297	6599			

RATIO - .8541 : 1.0485 : 2.0974

The ratio here has a tendency toward the expected ratio of one to one to two. Here again the cross was between the same wheat was in the previous populations. The abrupt change from all healthy progenies to all yellow progenies in consecutive plants is again illustrated.

TABLE IV

Result of Count in Plot VII of 1914

Plant No.	R. Healthy	R. Spotted	R. Yellow	P. Healthy	P. Spotted	P. Yellow
407032				117		59
407033						129
407034	42	9	3			1
407035	111				1	1
407036						186
407037						168
407038						191
	*		*		*	
407081				2	51	50
407082				3	28	150
Total				977	1540	2917

RATIO - .7205 : 1.136 : 2.151

This was a cross between wheats 913302 and 60101, both of which were pearls. The progenies which did not segregate ran pretty uniformly toward yellow-berry. It is interesting to note that two of the plants in this series produced red grains although both parents were supposedly pure pearls. This fact is the more inexplicable on account of the fact that red was clearly shown to be the dominant in the previous crosses. Of course there is always the possibility that they may be mutations.

TABLE VI

Result of the Count in Plot XIV of 1914

Plant No.	R.			P.		
	Healthy	Spotted	Yellow	Healthy	Spotted	Yellow
41401	115	65	50			
41402	7	20	229			
41403	136		20			
41404	84	7	31			
41405				37	10	83
41406	190	67	90			
41407	210	21	60			
41408	10	15	262			
41409	13	10	171			
41410	220	23	31			
41411	170	16	44			
41412	4		271			
Total	1638	360	2071			

RATIO - 1.633 : .3539 : 2.036

This was a cross between wheats 03417 and 95201, pearl and red respectively. There were only twenty three plants in the population, hardly enough to base any deductions upon. Every plant segregated into healthy and yellow berry grains and in most of them all three classes were represented.

TABLE VI

Result of Count in Plat XV of 1914

Plant No.	R.			P.		
	Healthy	Spotted	Yellow	Healthy	Spotted	Yellow
41501	37	5	97			
41502	128	2	5			
41503	169	2	6			
41504	46		152			
41505	47	3	8			
41506	125		29			
41507	115	2	7			
41508	27	73	73			
41509	34	68	150			
41510	5	10	246			
41511	152	6	14			
41512	46	25	160			
41513	27	90	126			
41514	34	50	150			
41520	*		* 238		*	
41521				39	72	110
41522	125	48	100			
41523	12		263			
Total	798	450	1240			

RATIO - 1.223 : .7235 : 1.993

This population was a cross between the same wheats as the preceeding. The ratio here approaches the expected one to one to two pretty closely.

TABLE VII

Result of Count in Plot XVIII of 1914

Plant No.	R Healthy	R Spotted	R Yellow	R Healthy	R Spotted	R Yellow
41801				72	75	77
41802	185	3	3			
41803	141	23	40			
41804	64	10	26			
41805	23	8	12			
41806	30	10	10			
41807	9	64	80			
41808	35	1				
41809	51	61	48			
41810	218	3	1			
41811				229	6	6
41812	95	2	2			
41813	36	26	40			
41814	37	1				
41815	129	65	65			
41816	130	5	6			
	*		*		*	
418136	5	7	150			
418137	164	34	1			
418138	65	7	29			
Total	4156	2960	4062			

RATIO - 1.497 : 1.059 : 1.453

The two parents here were 60101, a pearl wheat and 95201, a red wheat. As far as variation in the individual plants is concerned it is not very different from the other populations cited.

TABLE VIII

Result of Count in Plot XIX of 1914

Plant No.	R. Healthy	R. Spotted	R. Yellow	P. Healthy	P. Spotted	P. Yellow
419117	56	9	1			
419118	140	34	168			
419119	72	40	165			
419120				8	59	40
419121	102	43	205			
419122	19	12	3	10	20	95
419123	70	75	71			
419124			124			
419125		2	60			
419126	50	18	40			
419127	1	1	99			
419128	102		2			
419129	13	30	224			
419130	40	38	130			
419131	117	34	66			
419132	8	4	156			
419133	40	95	102			
419134	60	16	200			
419135	49	35	65			
419136	39	70	403			
419137	20	42	350			

TABLE VIII (continued)

Total	7287	3628	8344

RATIO - 1.472 : .692 : 1.836

This population and the preceeding, both of which came from the cross 60101X95201 do not approach the expected ratio of three to one very closely. However they show the same variation in percent of yellow-berry in adjacent plants which has been characteristic of all of the populations. It is very evident that some innate element in the individual plant is responsible for these variations. It would be manifestly wrong, however, in the face of the evidence of other investigators to ascribe the presence of yellow-berry to inheritance unreservadely.

Judging by the results of these other investigations it would seem probable that certain factors, such as soil and climate, influence the degree to which the characteristic becomes evident. However it is not overstepping the bounds justified by our evidence to assert that the fundamental factor is some unit character within the germ cell. That is, it is a character which is latent, and under certain environmental conditions may be entirely suppressed, but under other conditions may become very noticeable. The conditions which seem to favor the suppression of yellow-berry are dry, short growing seasons, (Lyon and Keyser, Neb. Sta. Bul. 89.) and an excess of nitrogen in the soil, (Headon, Col. Sta. Bul. 205.), while the environmental influences which bring about the opposite condition are long moist growing seasons and an excess of potassium fertilizer. Just how these factors exert their influence in regulating the perceptible amount of yellow berry is a problem for the plant physiologist.

At the present stage of this investigation no final statement can be made of the proportions into which the different types or classes of yellow-berry segregate. A summation of all of the segregating populations shows the healthy berries and yellow-berries to be in the proportion of 28.62% to 71.38% which is very nearly a Mendelian ratio of one to three, but on account of the erratic behavior of some of the individual populations the significance of this is questionable. It is probable that yellow-berry is not a simple Mendelian character or if it is, there are certain influences which may obscure the condition and make the results difficult of interpretation. Coupled with these outside influences are other considerations such as the exceptions to the general rule of dominance, illustrated by imperfect dominance, blending inheritance, reversed dominance, the necessity for more than one factor for the production of yellow-berry or absence of yellow-berry and so forth which would confuse our results with the available data. Only the data of succeeding generations can, with any certainty, establish the establish the exact proportions in which yellow-berry is transmitted. The present work is, at best merely a contribution to our knowlege of the phenomena attending the inheritance of yellow-berry, which is as yet an unsolved problem. The object of this paper is to show that there is something more than environmental factors concerned in its prevalence,and the evidence points strongly to the fact that yellow-berry is due fundamentally to some innate character in the germ cell,and is heritable.

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