

SEEDCOAT COLOR AND DORMANCY IN
WHEAT, TRITICUM AESTIVUM L.

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This is to certify that the

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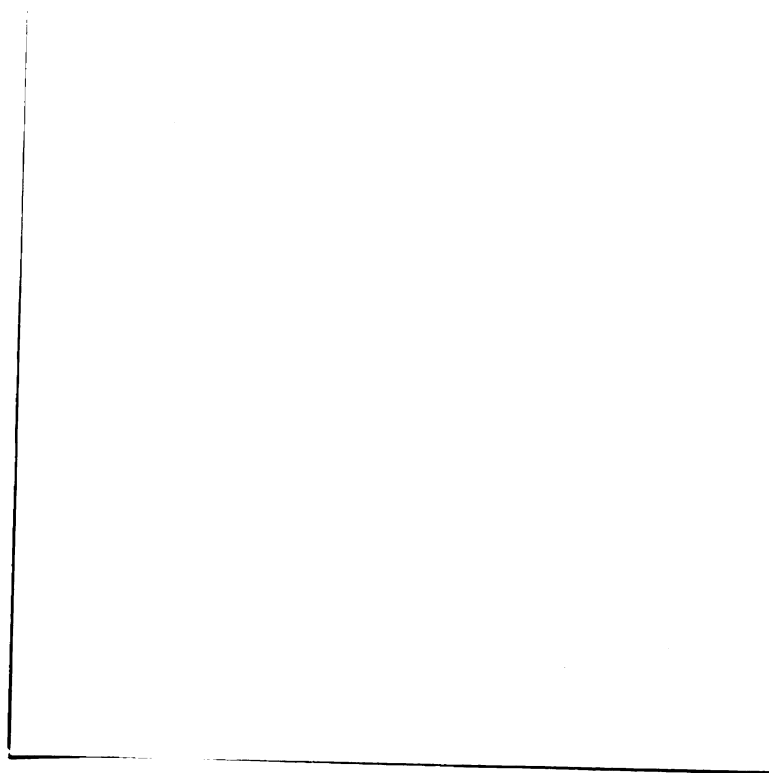
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ABSTRACT

SEEDCOAT COLOR AND DORMANCY IN WHEAT, *TRITICUM AESTIVUM* L.

By

Russell Freed

A study of reciprocal crosses between Genesee, a non-dormant white wheat, and Redcoat, a dormant red wheat, established that seed dormancy was conditioned by the maternal parent. The embryo does not play a significant role in conditioning dormancy.

Reciprocal crosses were made between six red winter wheat cultivars and a white winter cultivar, Genesee, to determine the number of red seedcoat color genes in each cultivar. Monon and Redcoat had two linked color genes while Dual had two independent color genes. Turkey 10016, Seneca and Red Rock each had three independent red seedcoat color genes.

By inter-crossing the six red cultivars six different red seedcoat color genes were established in wheat. Seedcoat color genotypes were given to Monon, Redcoat, Turkey and Dual. By comparing the seedcoat color genotypes of these red cultivars with their dormancy ratings, it was established that different color genes had different degrees of dormancy associated with them. Some wheats with red color genes had a high degree of dormancy while other red genes had only a little effect on dormancy.

Russell Freed

The development of isogenic lines for red seedcoat genes was also outlined.

SEEDCOAT COLOR AND DORMANCY IN WHEAT,
TRITICUM AESTIVUM L.

By
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INTRODUCTION

Sprout damage to wheat in Michigan can be very serious when there is wet weather at harvest. Cultivars with dormancy are not as easily affected by sprouting damage as non-dormant cultivars. All of the soft white wheats grown in Michigan have no dormancy, while the soft red cultivars exhibit varying degrees of dormancy.

Breeding for dormancy in the white cultivars is a major objective of the program at Michigan State University. To place the breeding for this character on a scientific basis, more must be learned about the nature of dormancy and the association between red seedcoat color and dormancy. Is dormancy a pleiotrophic effect conditioned by the red seedcoat color genes, or is it a tight linkage between the color genes and dormancy genes? How much dormancy does the embryo contribute?

The purpose of this study was to (1) determine the number of color genes in six red cultivars which have known differential dormancy, (2) check the association of the different color genes with dormancy, (3) study the association of the seedcoat color and dormancy, and (4) initiate work to establish isogenic lines for each of the color genes. These lines will be used in other studies to associate the amount of dormancy conditioned by each of the color genes.

REVIEW OF LITERATURE

Development of Dormancy

Seeds of many plant species will remain dormant when they are morphologically mature and placed under optimum conditions of light, moisture, and temperature for germination. An after-ripening process is required before such seeds will germinate. The length of dormancy may vary from a few days to a few years, depending upon species, cultivar, and conditions of growth.

Seed dormancy has evolved in nature as an effective means of delaying germination until growing conditions will be optimum for the seedling. Each plant species has evolved its own unique type of dormancy, depending upon the ecosystem under which the plant evolved. Characteristic moisture and temperature patterns are the two most common conditions for dormancy. A single species may have several different types of dormancy.

In 1916 Crocker reported seven different types of dormancy:

- (1) Immature embryo (primary dormancy)
- (2) Impermeability of structures to water
- (3) Mechanical resistance of structures to the growth of the embryo
- (4) Impermeability of seed covers to gases
- (5) Dormancy of embryo
- (6) Secondary dormancy
- (7) Any combination of the above

Mechanisms of Dormancy in Wheat

Mechanisms of dormancy in wheat, *Triticum aestivum* L., have been widely discussed in the literature. The impermeability of the seedcoat

to water and oxygen has been suspect because of studies which show that rupturing the seedcoat breaks dormancy. The impermeability of the seedcoat to water is not the cause of dormancy. Hinton (1955) and Wellington (1956) showed that both dormant and non-dormant cultivars absorbed sufficient water for germination but only the non-dormant cultivars germinated. Miyamoto, Tolbert and Everson (1961) and Wellington and Durham (1961) reported that oxygen impermeability was not involved. No difference was found between the dormant and non-dormant seeds in the initial respiration rate and permeability of the seedcoat to oxygen.

Belderok (1961) showed that rupturing the seedcoat broke dormancy, because it initiated a wound response mechanism which broke the dormancy of the seed. Also Miyamoto and Everson (1958) demonstrated that dormancy factors leach out of broken seedcoats. The leachate inhibited germination of excised embryos.

All excised wheat embryos will germinate readily (26), whereas excised embryos from wild oats, *Avena fatua* L., would not germinate (22).

Chemical inhibitors in the seedcoat have been found by a number of scientists. Miyamoto *et al.* (1961) found four inhibitory fractions in the seedcoat of wheat. They also showed that the addition of gibberellin A₃ would reduce dormancy. Ching and Foote (1961) found water and methanol soluble growth inhibitors in dormant seed. Belderok (1961) reported that disulfide and thio groups in the cell walls of the outer layers of the caryopsis were correlated with dormancy.

It has been reported that unthreshed seeds are more dormant than threshed. Smith (1948) showed that extracts from wheat chaff inhibited seed germination. Wellington and Durham (1958) suggested that the physical properties of the glumes prevented germination, because they

failed to extract inhibitors from the glumes. They suggested that the glumes and the seeds competed for the free moisture, thus reducing the water available for germination.

The association of red seedcoat color and dormancy was first mentioned by Nilsson-Ehle (1914). Cultivars with red seedcoats were dormant, while white cultivars were non-dormant (11,13,21). Miyamoto and Everson (1958) showed a relationship between catechin and catechin tannins in the seedcoats of the grain at the dough stage and the pigmentation of the mature seed. They proposed that catechin and catechin tannins were precursors of phlobaphene, a reddish-brown color in seedcoats. They also postulated that post-harvest dormancy could involve a reversible inhibition of catechin or its precursors.

Wheat Kernel Morphology

The wheat kernel can be divided into three major parts: (1) pericarp, (2) endosperm, and (3) embryo. The pericarp or fruit-coat is maternal tissue from the ovary wall. This maternal tissue is composed of the epidermis, hypodermis, cross cells, tube cells, seedcoat (testa) and nucellar tissue. The endosperm (3N) contains the aleurone layer and the starchy endosperm. The embryo contains the scutellum and root and shoot meristems.

The red kernel color is caused by the red seedcoat (testa) layer in the pericarp. The testa is maternal tissue; therefore, in hybrids the genotype of the testa will be the same as that of the female or seed parent. In a cross between a red and a white wheat the F_1 seed will have the pericarp of the maternal parent, but the seed on the F_1 plant (F_2 seed) will be red because red seedcoat color is dominant over white. The F_2 plants (bearing F_3 seed) will show a segregation ratio for seedcoat color.

The texture of the endosperm and the nature of the pericarp will also have a minor influence on kernel color (32). Kernels with vitreous endosperm appear darker. Therefore it is sometimes difficult to separate vitreous white kernels from light red kernels.

Genetics of Seedcoat Color

In 1914 Nilsson-Ehle showed that red seedcoat color in wheat is controlled by three independent loci. Hayes and Robertson (1924) found two color genes in 'Marquis' (CI 3641) and a third factor in 'Minturki' (CI 6155). Ibrahim (1966) reported one color locus in 'Redcoat' (CI 13170).

Red seedcoat color was dominant to white in each case. Each allele has an accumulative effect for seedcoat color, with the light red grain having only a few genes and a dark red having many.

Sears (1944) reported that the locus causing red seedcoat color in the cultivar 'Chinese Spring' (CI 6223) is located on chromosome 3D. Allan and Vogel (1965) reported another locus on chromosome 3A in CI 13253, and Metzger and Silbaugh (1970) placed one of the two loci in the cultivar 'Kharkof' (CI 1442) on chromosome 3B.

Inheritance of Dormancy

Deming and Robertson (1933) studied the inheritance of dormancy in wheat. They crossed Marquis (CI 3641), a dormant red cultivar, with 'Federation' (CI 4734), a non-dormant white. They found the F_1 to be dormant like Marquis, thus concluding that dormancy was dominant. Harrington and Knowles (1940) concluded that there were many genes for dormancy. They found transgressive segregation in some of their populations. They also concluded that selection for good agronomic types had no effect on dormancy. Gfeller and Svejda (1960) reported a 73 percent heritability for dormancy in wheat.

Mueller (1963) found that in the F_1 's of the spring wheat 'Koga', crossed with 'Bernburg 38626', sprouting occurred as rapidly as in Koga. The correlation between the F_2 plant selections for dormancy and their descendants was only 0.12. The F_3 generation selections showed that $r = 0.38$. He concluded that dormancy is a polygenic trait and that selection in the F_2 generation is meaningless.

Gfeller and Svejda (1960) suggested a pleiotrophic effect of seedcoat color and dormancy because of the complete association of red seedcoat color and dormancy.

Everson and Hart (1961) tested dormancy in 289 wheat cultivars and placed them into three major groups. The red cultivars 'Turkey' (CI 10016) and Redcoat (CI 13170) were placed in the first group which had a high degree of dormancy. 'Dual' (CI 13083) and 'Red Rock' (CI 5579) had an intermediate degree of dormancy while 'Monon' (CI 13278) and all the white wheats were in the last group with little or no post-harvest dormancy. They found that red cultivars were present in all three groups while white cultivars were found only in the last group.

Ibrahim (1966) reported that F_2 plants heterozygous for red seedcoat color (Rr) sprouted more than homozygous (RR) seeds. He suggested that the red alleles had an additive effect for dormancy.

Everson and Hart (1961) proposed two explanations for the association between seedcoat color and dormancy. The first explanation was a very close linkage between seedcoat color and dormancy. The dormancy gene(s) could be linked with any of the color genes. The other explanation was pleiotrophic gene action where the genes which condition red seedcoat color also condition dormancy.

Ibrahim (1966) proposed two hypotheses to explain the inheritance of dormancy. The complementary gene hypothesis assumed that there were minor dormancy genes to complement the dormancy given by the red seedcoat genes. The second hypothesis suggested quantitative genes that promote germination and counteract the dormancy imposed by seedcoat pigmentation.

Factors Affecting Dormancy

Growing seasons which are hot and dry followed by wet periods when the grain is ripe produce the most sprout damage. Over the years the amount of sprout damage was the least when the growing season was cool or the harvest seasons dry (3,4,14).

Belderok (1961) used the temperature sum index (days during wax ripeness x the mean daily environmental temperature minus 12.5 C) to forecast the degree of dormancy present in certain crops. He found that the duration of dormancy was inversely related to the temperature sum index. The critical temperature sums to insure a ten-day dormant period vary from cultivar to cultivar, e.g., 'Felix'-70, 'Apollo'-100, and 'Peko'-140. When the sum exceeds these values, sprouting is likely to occur in less than ten days under unfavorable environmental conditions.

The Netherlands Grain Center has issued regional sprout forecasts for the principal wheat cultivars from 1964 through 1967 using the critical temperature as a basis for predictions, and the warning system has been useful (5).

Belderok (1961) showed that the development of dormancy was temperature dependent. When the spring wheat Peko was grown at 18 C during the day and 12 C during the night, dormancy lasted sixty days.

When plants were grown at the same temperatures, but subjected to six days at 25 C at or before the milk stage, no reduction in dormancy was noted. However, when plants were subjected to six days at 25 C after the transition to the milk stage, dormancy was reduced to twenty-five days. This indicated that the temperature during the milk stage was critical for development of dormancy. This helps explain the yearly variation in the degree of dormancy present in certain cultivars.

Temperatures of stored grain have also been shown to be very important in the expression of dormancy. Belderok (1961) showed that high storage temperatures (25 C) reduced dormancy while cool storage temperatures tended to maintain dormancy. Ching and Foote (1961) reported that wheat stored at 38 C lost its dormancy, while wheat stored at 3 C retained dormancy.

Germination temperatures are important when testing cultivars for dormancy. George (1967) noted that the dormancy response was different when germination temperatures varied. At 10 C none of the twelve cultivars was dormant, but dormancy was expressed at 20 C and 30 C. Soaking seeds in cold water is commonly used to break dormancy in many species, including wheat.

Essery, Kirsop and Pollock (1954) demonstrated that the germination of barley was dependent on the amount of water available. When excessive amounts of water were present, the barley seeds failed to germinate because of water-sensitivity. This phenomenon also occurs in wheat. Belderok (1961) also showed that water-sensitivity decreased as dormancy decreased. Cultivars allowed to after-ripen showed no water-sensitivity.

Hardesty and Elliot (1956) reported differences in germination caused by the position of the floret in the spikelet. The outside

florets which reach anthesis first had the slowest germination rate. Seeds from the middle florets germinated quicker than seeds from the outside florets.

Sprouting Damage

Dormancy in wheat has been a very important factor to growers and processors. Many wheat growing regions have frequent rains during harvest which cause seeds to start germinating in the head.

The process of seed germination has been investigated by many workers. The steps of this process are still only partially understood. MacLeod, Duffus, and Johnston (1964) reported that alpha-amylase activation starts thirty hours after water imbibition. Naylor (1966) showed that the time required for alpha-amylase production varied from twenty to fifty-five hours depending on the cultivars tested. Gibberellic acid secreted by the embryo activates the aleurone layer to produce alpha-amylase. The alpha-amylase then reacts with the endosperm starch to supply energy for the embryo to develop.

Seeds which sprout in the head reduce the quality and value of the crop. Baking quality is adversely affected by excessive amounts of alpha- and beta-amylase present in the flour. The amylases convert starch to sugar with excessive amounts causing the flour to have a sticky crumb texture and also an undesirable bread crust color. However, a small amount of alpha-amylase is desired to prevent the flour from becoming too dry because of its low water-binding capacity (31).

Sprouted grain is also less valuable as a seed stock because of its low germination. Damage to the grain quality may occur even in the absence of visual sprouting (9).

It is a common recommendation that in regions where sprout damage is prevalent, wheat cultivars with dormancy should be planted. Planting cultivars with differing maturity dates may help to insure against a total loss from sprouting, since the harvest demands will be spread over a longer period of time (3).

Tests for Dormancy

Laboratory tests for dormancy have been conducted in several ways. The first method, the Ear Germination Test, has been described by Schmidt (1934) and Wellington (1953). In this test, wheat heads are placed in flats containing sand and then covered with another layer of sand. The sand is moistened and the heads are considered sprouted when three sprouts are seen.

The Grain Germination Test is performed on threshed seeds which are placed in petri dishes with moist filter paper on the bottom, or the seeds may be placed between two layers of moist blotter paper (11,17,20).

Both tests are conducted at 20 C and run from three to twenty days depending on the amount of dormancy in the selections being tested. Germination counts are recorded daily. A seed is considered germinated when the coleorhiza ruptures the seedcoat. Hutchinson *et al.* (1948) and Everson and Hart (1961) showed that the results of both tests were similar.

Another method used to check dormancy is the falling number test. This test is a quick method to determine the amount of alpha-amylase present in the grain. Cultivars with low alpha-amylase would exhibit dormancy, while those with high alpha-amylase readings would lack dormancy (31).

MATERIALS AND METHODS

Dormancy and Seedcoat Color Study

To establish the number of seedcoat color genes in six red winter wheats which were previously studied (11) at Michigan State University, reciprocal crosses were made between the six red wheats and a non-dormant white winter wheat, 'Genesee' (CI 12653), in the greenhouse in 1966. The red cultivars included the highly dormant cultivars, Turkey (CI 10016) and Redcoat (CI 13170); the moderately dormant cultivars, 'Seneca' (CI 12529), Dual (CI 13083), and Red Rock (CI 5597); and the slightly dormant cultivar Monon (CI 13278) (11). Reciprocal crosses were also made between each of the red cultivars to see which cultivars had color genes in common.

The F_1 seeds were space planted in the field in the fall of 1966. The F_2 seed was bulk harvested and 180 seeds from each cross were space planted in the field in the fall of 1967. All the plants were individually threshed in the summer of 1968 when the moisture content was about 14%. The seed was stored at 3 C until color readings and germination tests were performed.

Color ratings using a scale from zero through three (0=white, 1=light red, 2=medium red, 3=dark red) were made on seed from each plant. Fifty seeds from each F_2 plant were then tested for dormancy.

Sand was placed to a depth of five centimeters in wooden flats (55 cm. x 37 cm. x 10 cm.). Blotter paper (6 cm. x 14 cm.) was folded in half and placed on the sand. Fifty seeds from each selection were

placed between the folds of the blotter paper. Each paper was identified with a selection number. A Genesee check was included in each flat.

The papers and sand were dampened with a 1:60,000 solution of Panogen : water (v/v). The Panogen was added to the water to inhibit microbial growth which could affect the dormancy of the samples. To maintain high humidity the flats were covered with polyethylene sheets. The tests were conducted in growth chambers at 20 C with incandescent lights.

The germinated seeds were removed and their numbers recorded after three, five, and seven days, and the percent germination calculated. A seed was considered germinated when the seedcoat was split by the coleorhiza.

Reciprocal Crosses with Genesee and Redcoat to Study the
Contribution to Dormancy by the Maternal Seedcoat
Tissue vs. the Nucleus

In the spring of 1971 reciprocal crosses were made in the field between Genesee, a non-dormant white winter wheat, and Redcoat, a dormant red winter wheat. To make a cross, the middle row of secondary florets was removed leaving only the two primary florets. The lemma and palea were then clipped removing the upper halves. The anthers were removed and the inflorescence was covered with white onion-skin paper to prevent unwanted pollination. Two days after emasculation the paper was removed and controlled pollinations were made. The paper was replaced over the spike until harvest.

Twenty heads of Genesee and Redcoat were prepared in the same way, except the anthers were not removed. These plants served as controls for the experiment.

When mature (about 14 percent moisture), the crosses were harvested and stored at 3 C until germination tests were conducted. These tests were conducted in controlled environment chambers and the germination readings were made each day.

Three tests were conducted, each three weeks apart. The experimental design was a randomized block with two replications. Each replication contained fifty seeds of each cross and the two parents.

Development of Isogenic Lines for Seedcoat
Color Genes in Dual, Redcoat and Monon

To isolate the red seedcoat color genes from Dual, Redcoat, and Monon, seven seeds from each of forty red F_2 selections (Dual x Genesee, Redcoat x Genesee, Monon x Genesee) were planted. Two hundred seeds of Genesee were germinated at 20 C, vernalized for eight weeks at 3 C, and then grown in the greenhouse at 20 C in 15 cm. pots. Test crosses were made onto as many plants as possible using Genesee as the male parent.

When the crosses were harvested, selfed seed from each plant was also harvested and cross numbers were given to the plants and test crosses. Seven seeds of each test cross were planted, vernalized, grown to maturity, harvested and classified as either red or white wheat. The selfed seed was placed into storage.

Twenty to forty seeds from test crosses containing only red seeds were planted, vernalized, and matured in the greenhouse. Each back-cross one (BC_1) F_2 plant was harvested and classified as either red or white seed.

To check the probability of segregation ratios in the F_3BC_1 seeds, tables in Bulletin No. 463 by B. L. Warwich from the Texas Agricultural Experiment Station were used (36).

RESULTS AND DISCUSSION

Section I

Inheritance of Red Seedcoat Color in Six Red Wheat Cultivars

The progenies of crosses with Dual x Genesee gave segregation ratios indicating two independent red color genes (Table 1). The progenies from crosses involving Monon x Genesee and Redcoat x Genesee indicated two linked gene pairs. The data suggest that there are two gene pairs in Monon separated by thirty-four crossover units, and the two gene pairs in Redcoat separated by thirty-two crossover units (Table 1). Progenies from Seneca, Turkey, and Red Rock crosses with Genesee each segregated 63:1 indicating three independent gene pairs for red seedcoat color (Table 1). The segregation ratios obtained in 1968 and 1971 were very similar (Appendix A).

Crosses between different red wheat cultivars were used to identify those cultivars which had red color genes in common. The data in Tables 1 and 2 indicate that at least six different loci are involved in red seedcoat color. It has been shown above that Turkey had three independent color genes. Because the two color genes in Redcoat are linked, and since none of the three genes in Turkey demonstrate linkage, Turkey can possess only one, if any, of the Redcoat genes. Turkey has neither of the two Monon genes because of the two white segregates in the cross Turkey x Monon (Table 2). Therefore, there are at least six different loci controlling red seedcoat color.

Table 1. Segregation ratios for seedcoat color in F₂ plants involving a white and red wheat parent in 1968 and 1971

Hybrid	<u>Seedcoat Color Ratios (red:white)</u>		χ^2	Probability
	Observed	Expected Ratio		
Genesee(w) x Monon(R)*	284 35	15:1(305:14) 8:1**(284:35) 3:1(239:80)	32.90	0.01 0.01
Genesee(w) x Redcoat(R)*	369 48	15:1(391:26) 8:1***(369:48) 3:1(313:104)	19.86 41.02	0.01 0.01
Genesee(w) x Dual(R)*	249 19	15:1(251:17)	0.60	0.45
Brevor(w) x Dual(R)	195 10	15:1(192:13)	0.75	0.35
Genesee(w) x Seneca(R)*	215 5	63:1(217:3)	0.25	0.57
Genesee(w) x Turkey(R)*	816 11	63:1(814:13)	0.31	0.51
Genesee(w) x Red Rock(R)	415 6	63:1(414:7)	0.14	0.70

* Reciprocal crosses pooled.

** Linkage between two genes with 34% crossover rate.

*** Linkage between two genes with 32% crossover rate.

Table 2. Segregation ratios for seedcoat color in F₂ plants involving red parents

Hybrid	No. of Plants		Expected Ratio (red:white) if cultivars have no color genes in common
	Red	White	
Redcoat x Monon	121	1	80:1
Dual x Monon*	243	1	143:1
Turkey x Monon*	315	2	575:1
Redcoat x Dual*	312	0	143:1
Turkey x Seneca*	179**	0	4095:1
Turkey x Red Rock*	329**	0	4095:1
Redcoat x Seneca*	302**	0	575:1
Redcoat x Red Rock*	293**	0	575:1
Dual x Seneca*	150**	0	1033:1
Dual x Turkey	178**	0	1023:1
Monon x Red Rock*	219**	0	1575:1

* Reciprocal crosses pooled to obtain presented data.

** Population sizes too small.

Crosses between Monon (two linked genes) x Redcoat (two linked genes) and Monon x Dual (two independent genes) both gave white segregates (Table 2). Each cross indicates that there are four different loci involved. Since the color genes in Redcoat are linked and the two genes in Dual are independent, this would indicate at least five different loci for seedcoat color among the soft red cultivars Redcoat, Monon and Dual.

In this study six red cultivars were tested for their seedcoat genes. Since there are thousands of other red cultivars, the

possibility of finding other loci is highly probable. This study could only detect the number of loci involved, and not the total number of alleles involved.

From Tables 1 and 2 tentative genotypes can be derived for the cultivars Redcoat, Monon, Dual and Turkey with respect to seedcoat color. Redcoat had two linked color genes, R_a and R_b . The white segregate observed from intercrossing Redcoat and Monon demonstrated no genes for seedcoat color in common (Table 2). Therefore, the two color genes in Monon were assigned R_c and R_d . Dual had two independent genes with one locus (R_a) in common with Redcoat (Table 2). Since Dual had no genes in common with Monon (Table 2), it must have the R_e locus as a second color gene. The color genes in Dual and Redcoat which occupy the R_a locus are iso-alleles. At the present time the only way to separate the different alleles is by color studies and all the alleles are red. There is a possibility, however, that with isogenic lines they may be separated by dormancy tests.

The cross between Turkey and Monon indicated they had no genes for red seedcoat color in common (Table 2). Therefore, Turkey had recessive genes at the R_c and R_d loci. There are six different genotype possibilities for Turkey (Table 3). It has one color gene at the R_f locus not present in Monon, Dual or Redcoat. Since the cross between Redcoat and Turkey winter-killed in the field, the genotype at the R_a and R_b loci could not be determined. Turkey can have only one (if any at all) of these two Redcoat loci, because the R_a and R_b loci are linked and Turkey has three independent genes. If it had the R_a locus, it could either have the R_e locus present in Dual (b) or the R_g locus (a). If Turkey had the R_b locus instead of the R_a locus the two options would also be the same as seen in (c) and (d) in Table 3. If Turkey

Table 3. Seedcoat color genotypes for five wheat cultivars

Cultivar	Genotype
Genesee(w)	$r_a r_b r_c r_d r_e r_f \cdots r_n$
Redcoat(R)	$\overset{32\%}{R_a} R_b r_c r_d r_e r_f \cdots r_n$
1. Genesee x Redcoat =	2 linked red loci
Monon(R)	$r_a r_b \overset{34\%}{R_c} R_d r_e r_f \cdots r_n$
1. Genesee x Monon =	2 linked red loci
2. Redcoat x Monon =	white segregate $\therefore$ no loci in common
Dual(R)	$R_a r_b r_c r_d R_e r_f \cdots r_n$
1. Genesee x Dual =	2 independent red loci
2. Dual x Redcoat =	no white segregate $\therefore$ one loci in common
3. Dual x Monon =	white segregates $\therefore$ no loci in common
4. Dual x Turkey	(population too small)
Turkey(R)	$r_c r_d - R_f$
1. Genesee x Turkey =	3 independent red loci
2. Turkey x Monon =	white segregate $\therefore$ no loci in common
(a).	$R_a -r_b -r_c -r_d -r_e -R_f R_g r_h$
(b).	$R_a r_b r_c r_d R_e R_f r_g r_h$
(c).	$r_a R_b r_c r_d R_e R_f r_g r_h$

Table 3 (cont'd.)

Cultivar	Genotype
	(d). $r_a R_b r_c r_d r_e R_f R_g r_h$
	(e). $r_a r_b r_c r_d r_e R_f R_g R_h$
	(f). $r_a r_b r_c r_d R_e R_f R_g r_h$

did not have the R_a or R_b locus two options exist. Either it has the R_e locus (f) or does not have the R_e locus (e) and has the R_h locus.

Genotypes were not assigned to Red Rock and Seneca because the population size from the intercrossing of the red cultivars was too small. Only three different color genes had been anticipated: progeny sizes were planned with that in mind.

The Association of Dormancy and Seedcoat Color

The role of the seedcoat and the nucleus regarding dormancy in wheat is not fully understood. To find the importance of the seedcoat, crosses which had the same nuclear complement, but had different seedcoats were tested for dormancy (Table 4).

The factors responsible for seed dormancy in the cross between the dormant soft red cultivar Redcoat, and the non-dormant soft white wheat cultivar Genesee, are contributed by the female parent. Dormancy of F_1 seeds resulting from the reciprocal crosses between Genesee and Redcoat is the same as in the female parent in the cross (Table 4). The Redcoat (female parent) x Genesee (male parent) F_1 seeds had dormancy whereas the Genesee (female parent) x Redcoat (male parent) were non-dormant.

Table 4. Percent ungerminated seed of parent and F_1 seeds (100 possible) after 10 days

	Redcoat	$\frac{\text{Redcoat (F)}}{\text{Genesee (M)}}$	$\frac{\text{Genesee (F)}}{\text{Redcoat (M)}}$	Genesee
Test 1	81	79	17	2
Test 2	87	76	26	4
Test 3	44	56	0	0
$\bar{x}$ of 3 tests	71	70	14	2

This would indicate that the embryo does not contribute significantly to dormancy. By using reciprocal crosses instead of excised embryos to check for embryo dormancy, wound response factors did not interfere with the results.

The difference between the first two tests and the third test was due to the seed losing a degree of its dormancy in storage before the third test was initiated. The seed was stored at 3 C, but still lost some dormancy after six weeks of storage. Dormant seeds can usually be stored for months before they lose dormancy, but that was not the case in 1971. The loss of dormancy was probably due to the unusually hot and dry weather during seed maturation.

The F_3 seeds from the reciprocal crosses in the 1968 study show the same degree of dormancy; thus, the dormancy is not contributed by cytoplasmic factors, but is conditioned by the seedcoat, a maternal characteristic. The seedcoat of the Redcoat (female parent) x Genesee (male parent) F_1 is the same as Redcoat, and the seedcoat of the Genesee (female parent) x Redcoat (male parent) F_1 is the same as Genesee.

Dormancy Studies Involving Red Cultivars

Dormancy and color readings from F_2 plants from crosses between Genesee and the red cultivars are shown in Table 5. The seeds from the Genesee x Turkey cross shows the most dormancy, followed by crosses to Seneca, Red Rock, Dual, Redcoat, with Monon exhibiting the least amount of dormancy. These data are very similar to the dormancy data reported by Everson and Hart (1961). They showed Turkey as the most dormant cultivar and Monon as the least dormant red cultivar.

Because of the very hot and dry weather in Michigan in June of 1971, very little dormancy developed. Even the Genesee x Turkey populations showed very little dormancy. Therefore, dormancy readings from the F_2 plants grown in 1971 were not reported.

No white segregates from any of the populations examined exhibited dormancy (Table 5). The dormancy values of the white segregates vary from 1.2 percent to 16.1 percent. The white segregates have no red color genes; therefore, if color genes are related to dormancy the differences exhibited are due to other genetic systems or reflect some type of environmental influence. Progeny from the cross with Monon had the highest tendency to germinate while progeny of crosses with Turkey, Seneca, Red Rock, Dual and Redcoat did not germinate as easily. This indicates that it may be possible to increase the dormancy in white cultivars. However, this increase in dormancy is not very large.

The dormancy values between the light red selections (number 1's) and the dark red selections (number 3's) do not vary significantly (Table 5). This may be because of misclassification in part of seed-coat color since it is very difficult to assess differences between a number 1 and a number 2 or between a number 2 and a number 3. The

Table 5. Percent of ungerminated F₃ wheat seeds after seven days in each of four color classes

Hybrid Population	No. of Seedcoat Color Genes*	No. of Plants in Population	0**	Seed Color, Dormancy			$\bar{x}$ of red lines
				1	2	3	
Genesee x Turkey	(3)	469	15.0***	77.6	76.9	77.8	76.7
Genesee x Seneca	(3)	113	16.1	60.0	71.0	61.9	66.5
Genesee x Red Rock	(3)	271	10.5	59.1	57.2	53.8	56.4
Genesee x Dual	(2)	268	11.1	53.5	60.5	57.5	55.2
Genesee x Redcoat	(2)	248	13.1	36.7	57.6	63.0	49.3
Genesee x Monon	(2)	272	1.2	30.9	40.0	44.6	34.0
Genesee	(0)	---	0				

* Reciprocal crosses pooled.

** 0=white seed, 1=light red seed, 2=medium red seed, 3=dark red seed.

*** Percent ungerminated F₃ wheat seed after seven days in each of four color classes.

small amount of variation in dormancy between the number 1's and number 3's indicates that the dormancy genes exhibit dominance.

The three cultivars with the highest dormancy ratings are Turkey, Seneca, and Red Rock. Each of these cultivars has three color genes, yet there is a twenty percent difference in dormancy. On the basis of this, one could speculate that Turkey, Seneca and Red Rock each have at least one different color gene: the three color genes in Turkey giving the highest dormancy, the three color genes in Red Rock giving a lower dormancy rating.

The cultivars Dual, Redcoat and Monon each have two color genes. The dormancy ratings for Redcoat and Dual are similar, while the dormancy for Monon is very low. This also is an indication that the different color genes have different effects on dormancy.

Since dormancy appears to be conditioned by the red seedcoat color genes, different levels of dormancy may be assigned to each of the different color genes. The R_c and R_d loci in Monon both have low dormancy values because of the low dormancy rating for Monon (Table 5).

The high dormancy rating for Redcoat and Dual may be due to one locus having a much greater effect than the other or both having a moderately high activity and acting additively.

In the process of developing isogenic lines with single color genes from Redcoat, two F_2 selections were separated each being homozygous for a single color gene. Selection 1565-1-12 had a good dormancy rating (50 percent), while selection 1567-1-33 had a very low dormancy rating (20 percent) (Appendix D). This indicates that the homozygous color genes from the two populations are different. One gene has a high degree of dormancy while the other gene has only a little dormancy.

With this information, we can assign the R_a locus in Redcoat as a major dormancy gene and the R_b locus as a minor gene. Since Redcoat and Dual have one gene in common (Table 2) and the same dormancy (Table 5), the R_a locus contributes the major effect of dormancy in Dual while the R_e locus contributes only a small degree of dormancy.

The R_a gene possibly gives Turkey, Seneca and Red Rock their major amounts of dormancy while the other two color genes add minor increments.

Since the R_a locus gives a major degree of dormancy and the R_b , R_c , R_d , and R_e loci only give a small degree of dormancy, an interesting speculation arises. Either the R_a gene has a unique pathway involved

in seedcoat pigmentation which gives the drastic difference in dormancy when compared to the other color genes, or there is a tight linkage between the R_a locus and a dormancy gene. The only way to clarify this would be to break the linkage between the two genes. Although hundreds of lines have been tested, such a recombination has not yet been recovered.

If there is a linkage between the color gene (R_a) and the dormancy gene, the production of a white dormant wheat should be possible. However, if the R_a gene for seedcoat color also conditions dormancy (pleiotrophy), the means of producing a dormant white wheat are not evident.

The actual mechanism of dormancy is still uncertain. Miyamoto and Everson (1958) have shown that inhibitors are very important in conditioning dormancy. From the findings discussed in this paper a scheme for dormancy can be proposed. In the development of the wheat seed, certain red seedcoat color genes or factors closely linked to them produce different amounts of germination inhibitors. Certain color genes (e.g., R_a) produce a large quantity of inhibitors while others (e.g., R_b , R_c , R_d , and R_e) produce lesser amounts. The inhibitors are produced by the female plant in the seedcoat or stored there. The embryo of the seed plays no part in the production of the inhibitors.

The action of the dormancy factors appears to be additive. There could also be epistatic interactions which would affect the amount of inhibitors produced. Different promotor and inhibitor genes could also interact with the color genes to vary the production of inhibitors.

Different cultivars may have the same color genes, but have a different dormancy rating. This may be the case since seed germination

involves the interaction of many genetic systems. Germination is affected by the rate and amount of gibberellic acid produced by the scutellum which in turn affects the release of alpha-amylase from the aleurone layer (23). The amount or rate of release of alpha-amylase regulates the amount of sugars available for the embryo. The production of proteinases is also important, as are the mechanisms which influence oxygen and water permeability.

Each genetic system involved in germination may have many genes affecting them. Some genes promote germination, while other genes inhibit germination. The interaction of promoters and inhibitors within each system will further complicate the germination process.

Near isogenic lines for the different seedcoat color genes in Redcoat, Dual, Monon, Turkey, Seneca and Red Rock are being developed. These lines have Genesee as the recurrent parent. When these lines are developed the exact amount of dormancy for each color gene can be established. The major difference between these lines will be the color genes and closely associated chromosome segments. Therefore, any difference in dormancy should be associated with the color genes. The interactions of the different systems involved in seed germination will be removed by the isogenic lines.

Tester stocks having different combinations of the color genes should also be established. These stocks would test the interaction of the different color genes for dormancy.

The development of isogenic lines for seedcoat color should also be developed in another background besides Genesee. Some cultivars may have genes which affect the action of a color gene differently than Genesee. It would be impractical to develop isogenic lines for

all the color genes with another background, but it would be interesting to check a few genes in another background.

Section II

Procedure for Developing Isogenic Lines for Seedcoat Color Genes in Dual, Redcoat and Monon

The development of isogenic seedcoat color lines should make it possible to establish dormancy values for each color gene. In Section I color genes were found to possess different dormancy values. However, because of the complex nature of germination only high and low dormancy values were given. With isogenic lines a more precise dormancy rating can be assigned to each color gene. Also iso-alleles may be separated by different dormancy ratings.

After the isogenic lines for one color gene are established, combinations with one, two, three, four, five, etc., color genes should be made. All the possible combinations of the color genes should be made. The interaction of the different color genes may also help to distinguish iso-alleles. The R_a allele from Redcoat combined with the R_c allele from Monon may have a low dormancy value, while the R_a allele from Dual combined with the R_c allele from Monon may have a high dormancy value. This would show that there are at least two different alleles at the R_a locus.

The color genes in Seneca, Turkey, and Red Rock are also being isolated in isogenic lines, but at a slower rate, because three color genes are involved with each of these cultivars.

Development of Isogenic Lines for the Color Genes in Dual

Seven F_3 seeds from forty red F_2 Genesee x Dual red-seeded plants were planted. Backcrosses with Genesee as a recurrent parent were made

to as many F_3 plants as possible. The crosses by Genesee also served as test crosses since Genesee has no red color genes.

When the crosses (BC_1F_1) were harvested, selfed seed (F_4) from the secondary tillers was also harvested. Each cross was given a number from 501 through 627. Seven BC_1F_1 seeds from each cross were planted. The BC_1F_1 plants were harvested and color readings taken on BC_1F_2 seed (Appendix B).

White BC_1F_2 seeds indicate that the F_3 plant to which the cross was made produced some homozygous recessive gametes ($r_a r_b$). Those F_3 populations which contained white BC_1F_2 seeds were discarded (e.g., 1625-1-01, 1625-1-02, 1625-1-05). Crosses 501 through 506 from population 1625-1-01 were discarded. This eliminated all materials resulting from F_3 plants not homozygous for at least one color gene.

Crosses from the seven F_3 populations which produced all red BC_1F_2 seeds were saved (e.g., 510-514, 550-554, etc.) (Appendix B). Each BC_1F_1 plant from the saved material was given a selection number and twenty to forty BC_1F_2 seeds from each selection were planted.

The BC_1F_2 plants were harvested and color readings made (Appendix C). Selections 510-1, 510-2, 510-3, and 510-5 segregated 15:1, while selection 510-4 segregated 3:1 (Table 5). This shows that plant 510 was homozygous for one red color gene and heterozygous for the other. Similarly, crosses 511, 513, and 514 also had both 3:1 and 15:1 ratios in their selections. However, the five selections from cross 512 all segregated 3:1, indicating one homozygous red color gene.

Table 7 lists the other BC_1F_2 families which segregated 3:1 indicating one homozygous red gene. The probability of obtaining five 3:1 ratios from a heterozygous plant is about three percent.

These seven plants (512, 579, 580, 587, 588, 600 and 614) were homozygous for either the R_a locus or the R_e locus. To check which loci are involved, crosses should be made between the different plants on which the crosses were made. If the F_2 plants segregate 15:1 for white seed, the two plants contain different color genes. If all the F_2 plants are red, then they have the same gene. Crosses should also be made to Red Bobs (3A), Chinese Spring (3D) and Kharkof (3B) to see if any genes are identical to those known to be located on chromosome 3A, 3B, or 3D.

Three red plants from each BC_1F_2 selection containing one homozygous red gene should be backcrossed to Genesee producing BC_2F_1 's to produce isogenic lines with only one color gene. The red BC_2F_1 selections should be again crossed with Genesee. The red BC_3F_1 selections should be again crossed with Genesee. The BC_4F_1 seed should be planted and allowed to self-pollinate. Progeny tests should be conducted to identify plants which are homozygous for one color gene.

The tester stocks for the two different red color genes in Dual will then be established when six backcross generations have been completed.

Table 6. Segregation ratios from testcrosses to one F_3 population of Genesee x Dual hybrid

F_3 Selection	BC_1F_2	<u>No. of F_2 Plants</u>		<u>Probability of Fit</u>	
		Red	White	3:1	15:1
1625-1-03	510-1	30	3	.02	.19
	-2	26	1	<.01	.32
	-3	27	3	.03	.17
	-4	25	4	.12	.02
	-5	31	0	<.01	.14

Table 6 (cont'd.)

F ₃ Selection	BC ₁ F ₂	No. of F ₂ Plants		Probability of Fit	
		Red	White	3:1	15:1
	511-1	15	1	.05	.38
	-2	26	8	.16	<.01
	-3	21	1	<.01	.35
	-4	30	0	.01	.14
	-5	21	8	.16	<.01
	512-1	20	7	.17	<.01
	-2	20	5	.16	.01
	-3	20	3	.09	.12
	-4	18	5	.19	.01
	-5	17	5	.19	<.01
	513-1	17	6	.19	<.01
	-2	8	13	<.01	<.01
	-3	20	2	.05	.25
	-4	20	3	.09	.12
	-5	23	6	.16	<.01
	514-1	21	3	.08	.13
	-2	22	7	.17	<.01
	-3	28	0	.01	.17

Table 7. BC₁F₂ plant segregation ratios which show one homozygous red color gene

BC ₁ F ₂	<u>No. of F₂ Plants</u>		<u>Probability of Fit</u>	
	Red	White	3:1	15:1
512-1	20	7	.17	<.01
-2	20	5	.16	.01
-3	20	3	.09	.12
-4	18	5	.19	.01
-5	17	5	.19	<.01
579-1	23	12	.07	<.01
-2	29	8	.14	<.01
-3	24	9	.14	<.01
-4	25	7	.15	<.01
-5	20	3	.19	.12
580-1	33	6	.06	.02
-2	25	2	.02	.27
-3	22	7	.16	<.01
-4	23	6	.15	<.01
-5	29	8	.14	<.01
-6	25	8	.15	<.01
-7	28	9	.15	<.01
587-1	22	7	.17	<.01
-2	29	4	.04	.10
-3	19	7	.17	<.01
-4	15	9	.06	<.01
588-1	13	9	.05	<.01
-2	22	7	.17	<.01
-3	25	3	.04	.16
-4	20	8	.15	<.01
-5	23	4	.09	.06

Table 7 (cont'd.)

BC ₁ F ₂	No. of F ₂ Plants		Probability of Fit	
	Red	White	3:1	15:1
600-1	22	4	.10	.06
-2	13	4	.22	.02
-3	14	5	.20	.01
-4	14	5	.20	.01
-5	15	3	.17	.08
-6	22	9	.14	.01
-7	10	4	.22	.01
614-1	11	4	.23	.01
-2	14	3	.19	.07
-3	12	4	.23	.01
-4	11	4	.23	.01
-5	16	4	.19	.03
-6	19	4	.14	.04

Development of Isogenic Lines for the Color Genes in Redcoat (R R_a b)

Seven seeds from forty F₂ Genesee x Redcoat selections were planted. Genesee test crosses were made.

The crosses were harvested along with selfed seed from each plant. The crosses were numbered from 1 through 107. Seven BC₁F₁ seeds from each cross were planted. They were then harvested and color readings taken (Appendix D).

Those F₃ populations which contained white BC₁F₂ seed were discarded. Crosses which produced all red BC₁F₂ seed were selected and forty seeds were planted from each cross.

These plants were harvested and color readings were taken (Appendix E). Crosses number 19, 21, 91 and 93 segregated 3:1 indicating one homozygous color gene (Table 8).

Table 8. Segregation ratios for BC_1F_2 plants which show one homozygous red color gene

Selection No.	No. of Plants		Probability of Fit	
	Red	White	3:1	15:1
19-1	31	8	.12	<.01
-2	23	6	.15	<.01
-3	18	6	.19	<.01
-4	20	2	.05	.25
-5	32	7	.09	<.01
-6	18	5	.18	.01
21-1	27	8	.15	<.01
-2	34	18	.04	<.01
-3	21	4	.12	.05
-4	13	3	.21	.06
-5	5	0	.24	.72
-6	9	0	.08	.56
-7	46	11	.09	<.01
91-1	14	2	.13	.18
-2	24	5	.12	.02
-3	17	4	.17	.03
-4	12	3	.23	.05
-5	21	4	.12	.05
-6	6	2	.31	.07
-7	22	7	.17	<.01

Table 8 (cont'd.)

Selection No.	No. of Plants		Probability of Fit	
	Red	White	3:1	15:1
93-1	24	8	.16	<.01
-2	17	3	.13	.09
-3	23	3	.05	.14
-4	28	4	.04	.09
-5	13	8	.07	<.01
-6	29	9	.15	<.01

Crosses 19 and 21 originated from the F_3 population 1625-1-12 which had a high degree of dormancy (Appendix D). Crosses 91 and 93 were made to the F_3 population 1625-1-33 which had a very low dormancy reading. This suggests that the two color genes are different, one (R_a) associated with a high degree of dormancy and the other (R_b) associated with a low degree of dormancy.

This will be clarified when the backcrossing program is completed. The backcrossing should be done by the same procedure as the Genesee x Dual program.

Development of Isogenic Lines for the Color Genes in Monon

Sixty-four Genesee crosses were made to the F_3 population of Genesee x Monon. Seven seeds from each cross were planted. The plants were harvested and color readings taken (Appendix F). Six different crosses were selected for further study. Twenty to forty seeds of each F_1 were planted. The plants were harvested and classified according to color (Appendix G). None of the populations had good 3:1 ratios.

However, certain selections within each cross had good 3:1 ratios and these selections should be used in the backcross program.

SUMMARY AND CONCLUSIONS

The number of red seedcoat color genes were established for six different wheat cultivars. Monon and Redcoat had two linked color genes while Dual had two independent color genes. Turkey, Seneca and Red Rock each exhibited three independent red seedcoat color genes.

By using reciprocal crosses between Genesee, a white non-dormant wheat, and Redcoat, a red dormant wheat, it was established that seed dormancy was conditioned by the maternal parent. The embryo does not play a major role in conditioning dormancy.

This study also suggested that there are at least six different red seedcoat color genes in wheat. Red seedcoat color genotypes were given to the red cultivars, Monon, Redcoat, Dual and Turkey. By associating the seedcoat color genotypes of these red cultivars with their dormancy ratings, it was established that different color genes gave different dormancy ratings. Some red color genes give a high degree of dormancy while other genes give only a little dormancy.

Finally, the development of isogenic lines for red seedcoat genes was begun. What has been done to date was discussed and what has to be done was outlined.

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APPENDICES

APPENDIX A

Table 1A. Segregation ratios for seedcoat color in F₂ plants involving a white and a red parent in 1968 and 1971

Hybrid	Percent of White Plants**	
	1968	1971
Genesee(w) x Monon(R)*	31/272=11.4%	4/47=8.5%
Genesee(w) x Redcoat(R)*	29/248=11.7%	19/169=11.2%
Genesee(w) x Dual(R)*	19/268=7.1%	
Brevor(w) x Dual(R)	10/205=4.9%	
Genesee(w) x Seneca(R)*	3/113=2.7	2/107=1.9%
Genesee(w) x Turkey(R)*	6/469=1.3%	5/358=1.4%
Genesee(w) x Red Rock(R)*	3/271=1.1%	3/150=2.0%

* Reciprocal crosses pooled.

** 1 gene=25%; 2 genes=6.3%; 3 genes=1.6%; 4 genes=0.4%.

APPENDIX B

Table 2B. Segregation ratios from F₁BC₁ plants along with dormancy reading from F₃ selection of a Genesee x Dual hybrid

F ₃ Population to Which Cross was Made	Dormancy of F ₃ Selection (% un- germinated seed)	Cross No. (BC ₁)	No. of F ₁ Plants	
			Red	White
1625-1-01 (Dual/Ge)	60	501	1	1
		502	7	0
		503	0	2
		504	0	6
		505	4	1
		506	0	5
1625-1-02	76	507	2	1
		508	2	1
		509	3	0
1625-1-03	76	510	5	0
		511	6	0
		512	5	0
		513	5	0
		514	3	0
1625-1-05	78	515	4	0
		516	1	1
		517	6	0
		518	2	1
		519	5	0
		520	0	5
1625-1-06	32	521	3	3
		522	1	1
		523	5	0
		524	6	0
		525	6	0
1625-0-07	74	526	0	5
		527	0	4
		528	2	1
		529	3	1

Table 2B (cont'd.)

F ₃ Population to Which Cross was Made	Dormancy of F ₃ Selection (% un- germinated seed)	Cross No.	No. of F ₁ Plants	
		(BC ₁)	Red	White
		530	6	0
		531	2	1
		532	4	2
1625-1-08	64	533	7	0
		534	5	1
		535	5	0
		536	4	0
		537	5	1
1625-1-09	72	538	2	2
		539	4	1
		540	1	5
		541	4	0
		542	1	1
1625-1-10	68	543	2	2
		544	3	3
		545	4	1
		546	0	1
		547	2	1
		548	2	0
		549	1	1
1625-1-11	58	550	2	0
		551	2	0
		552	1	0
		553	4	0
		554	4	0
1625-1-12	2	555	0	5
		556	-	-
		557	1	3
		558	3	2
1625-1-13	68	559	2	1
		560	3	0
		561	6	1
		562	6	0
		563	4	0
1625-1-14	78	564	2	0
		565	0	6
		566	3	0
		567	3	3

Table 2B (cont'd.)

F ₃ Population to Which Cross was Made	Dormancy of F ₃ Selection (% un- germinated seed)	Cross No. (BC ₁)	No. of F ₁ Plants	
			Red	White
1625-1-15	60	568	4	0
		569	5	0
		570	0	4
		571	6	0
		572	5	0
1625-1-16	48	573	5	2
		574	3	0
		575	0	6
		576	2	3
		577	0	2
		578	3	1
1625-1-17	82	579	5	0
		580	7	0
		581	6	0
		582	4	0
1625-1-18	72	585	1	0
1625-1-19	74	587	5	0
		588	5	0
		589	1	0
		590	1	0
1625-1-20	60	591	6	0
		592	6	0
		593	7	0
1625-1-22	72	594	6	0
		595	7	0
1625-1-23	74	596	6	0
		597	6	0
		598	6	0
		599	6	0
		600	7	0
		601	7	0
1625-1-24	48	602	2	5
		603	7	0
		604	6	0
		605	4	2
		606	6	0
		607	2	4

Table 2B (cont'd.)

F ₃ Population to Which Cross was Made	Dormancy of F ₃ Selection (% un- germinated seed)	Cross No. (BC ₁)	No. of F ₁ Plants	
			Red	White
1625-1-25	76	608	-	-
		609	5	0
		610	1	1
		611	2	1
1625-1-26	38	612	7	0
		613	6	0
		614	6	0
		615	7	0
1625-1-28	68	616	3	2
		617	4	2
		618	3	2
		619	3	0
		620	3	2
1625-1-29	70	621	-	-
		622	1	1
		623	2	0
		624	3	0
		625	1	0
1625-1-30	48	626	3	3
		627	5	0

APPENDIX C

Table 3C. Segregation ratios from test crosses to populations of the Genesee x Dual hybrid

BC ₁ F ₂	No. of F ₂ Plants		Probability of Fit	
	Red	White	3:1	15:1
510-1	30	3	.02	.19
-2	26	1	<.01	.32
-3	27	3	.03	.17
-4	25	4	.12	.02
-5	31	0	<.01	.14
511-1	15	1	.05	.38
-2	26	8	.16	<.01
-3	21	1	.01	.35
-4	30	0	.01	.14
-5	21	8	.16	<.01
512-1	20	7	.17	<.01
-2	20	5	.16	.01
-3	20	3	.09	.12
-4	18	5	.19	.01
-5	17	5	.19	<.01
513-1	17	6	.19	<.01
-2	8	13	<.01	<.01
-3	20	2	.05	.25
-4	20	3	.09	.12
-5	23	6	.16	<.01
514-1	21	3	.08	.13
-2	22	7	.17	<.01
-3	28	0	<.01	.17
579-1	23	12	.07	<.01
-2	29	8	.14	<.01
-3	24	9	.14	<.01
-4	25	7	.15	<.01
-5	20	3	.09	.12

Table 3C (cont'd.)

BC ₁ F ₂	<u>No. of F₂ Plants</u>		<u>Probability of Fit</u>	
	<u>Red</u>	<u>White</u>	<u>3:1</u>	<u>15:1</u>
580-1	33	6	.06	.02
-2	25	2	.02	.27
-3	22	7	.16	<.01
-4	23	6	.15	<.01
-5	29	8	.14	<.01
-6	25	8	.15	<.01
-7	28	9	.15	<.01
581-1	55	3	<.01	.22
-2	36	1	<.01	.23
-3	12	2	.18	.16
-4	24	2	.02	.27
-5	31	2	<.01	.28
582-1	24	2	.02	.27
-2	24	9	.15	<.01
-3	17	1	.03	.38
-4	12	1	.10	.37
587-1	22	7	.17	<.01
-2	29	4	.04	.10
-3	19	7	.17	<.01
-4	15	9	.06	<.01
588-1	13	9	.05	<.01
-2	22	7	.17	<.01
-3	25	3	.04	.16
-4	20	8	.15	<.01
-5	23	4	.09	.06
591-1	17	1	.03	.38
-2	19	0	<.01	.29
-3	19	0	<.01	.29
-4	15	4	.20	.02
-5	17	1	.03	.38
-6	23	0		
592-1	19	1	.02	.37
-2	6	3	.23	.01
-3	17	5	.19	.01
-4	8	6	.07	<.01
-5	21	3		
-6	18	3	.12	.10

Table 3C (cont'd.)

BC ₁ F ₂	No. of F ₂ Plants		Probability of Fit	
	Red	White	3:1	15:1
593-1	18	2	.07	.23
-2	22	1	<.01	.35
-3	17	4	.18	.03
-4	14	2	.13	.19
-5	20	0	<.01	.28
-6	22	3	.06	.14
-7	22	2	.03	.26
594-1	24	0	<.01	.21
-2	24	0	<.01	.21
-3	20	1	.02	.36
-4	28	1	<.01	.30
-5	31	1	<.01	.27
595-1	20	1	.02	.36
-2	16	1	.04	.38
-3	18	2	.07	.23
-4	20	1	.02	.36
-5	20	0	<.01	.28
-6	27	1	<.01	.31
596-1	15	1	.05	.38
-2	11	1	.13	.37
-3	17	4	.18	.04
-4	22	0	<.01	.24
-5	16	1	.04	.38
-6	16	2	.10	.21
597-1	12	8	.06	<.01
-2	20	9	.12	<.01
-3	18	2	.07	.23
-4	15	2	.11	.20
-5	14	1	.07	.37
-6	8	1	.23	.34
598-1	19	3	.10	.11
-2	18	4	.16	.03
-3	19	5	.18	.01
-4	16	7	.15	<.01
-5	16	2	.10	.21
-6	13	5	.20	<.01
599-1	14	4	.21	.02
-2	19	1	.02	.37
-3	18	4	.21	.02
-4	21	1	.01	.35
-5	23	2	.03	.27
-6	19	0	<.01	.30

Table 3C (cont'd.)

BC ₁ F ₂	<u>No. of F₂ Plants</u>		<u>Probability of Fit</u>	
	Red	White	3:1	15:1
600-1	22	4	.10	.06
-2	13	4	.22	.02
-3	14	5	.20	<.01
-4	14	5	.20	<.01
-5	15	3	.17	.08
-6	22	9	.14	<.01
-7	10	4	.22	<.01
601-1	25	2	.02	.27
-2	21	0	<.01	.26
-3	22	1	.01	.35
-4	10	5	.16	<.01
-5	17	0	<.01	.33
-6	24	8	.16	<.01
-7	19	0	<.01	.30
612-1	10	1	.15	.36
-2	14	2	.13	.19
-3	18	5	.19	.01
-4	14	1	.07	.38
-5	18	2	.07	.23
-6	19	4	.15	.04
-7	12	3	.23	.05
613-1	15	3	.17	.08
-2	31	4	.03	.11
-3	18	5	.19	.01
-4	15	2	.11	.20
-5	12	1	.10	.37
-6	16	1	.04	.38
614-1	11	4	.23	.01
-2	14	3	.19	.07
-3	12	4	.23	.01
-4	11	4	.23	.01
-5	16	4	.19	.03
-6	19	4	.14	.04
615-1	11	0	.04	.49
-2	19	4	.15	.04
-3	17	3	.17	.09
-4	18	1	.03	.37
-5	9	0	.08	.56
-6	24	1	<.01	.33
-7	19	2	.06	.24

APPENDIX D

Table 4D. Segregation ratios from F₁BC₁ plants along with dormancy reading from F₃ selection of Genesee x Redcoat hybrid

F ₃ Selection of Ge x Rct Hybrid	Dormancy (% un- germinated seed) of F ₃ Selection	BC ₁ Cross Number	No. of F ₁ Plants	
			Red	White
1565-1-01	36	1	1	0
		2	2	0
1565-1-10	48	5	2	1
		6	1	0
		7	2	0
		8	3	3
1565-1-11	76	9	4	1
		10	2	3
		11	4	0
		12	2	1
		13	3	0
		14	5	0
		15	7	0
1565-1-12	50	16	5	0
		17	4	0
		18	4	0
		19	6	0
		20	3	0
		21	7	0
		22	3	0
1565-1-13	62	23	2	0
		24	3	0
		25	4	0
		26	2	0
		27	5	0
		28	4	0
		29	2	0
1565-1-14	50	30	4	3

Table 4D (cont'd.)

F ₃ Selection of Ge x Rct Hybrid	Dormancy (% un- germinated seed) of F ₃ Selection	BC ₁ Cross Number	No. of F ₁ Plants	
			Red	White
1566-1-16	68	31	5	0
		32	2	3
		33	1	0
		34	4	1
		35	2	2
		36	1	6
		37	2	3
		38	3	3
		39	6	0
1566-1-17	54	42	2	0
		43	5	0
		44	2	2
		45	1	4
		46	0	5
		47	0	3
1566-1-19	48	48	2	5
1566-1-18	16	49	3	3
		50	7	0
		51	3	2
1566-1-20	50	52	3	0
		53	1	2
		54	7	0
		55	7	0
1566-1-21	72	56	1	0
		57	5	0
		58	7	1
		59	5	0
1566-1-22	70	60	5	0
		61	1	3
1566-1-23	68	62	7	0
		63	6	0
		64	5	1
1566-1-25	48	65	4	2
		66	2	4
		67	6	0
		68	5	0
		69	6	0
		70	4	3

Table 4D (cont'd.)

F ₃ Selection of Ge x Rct Hybrid	Dormancy (% un- germinated seed) of F ₃ Selection	BC ₁ Cross Number	No. of F ₁ Plants	
			Red	White
1566-1-26	36	71	1	0
1566-1-27	82	77	5	0
		78	1	0
		79	2	0
		80	4	0
		81	5	0
		82	3	0
1566-1-28	4	83	0	4
1567-1-31	64	84	0	5
		85	1	2
		86	5	0
		87	2	2
1567-1-32	70	88	2	1
		89	4	2
1567-1-33	20	90	6	0
		91	7	0
		92	4	0
		93	6	0
1567-1-34	12	94	0	5
		95	1	4
		96	3	2
		97	0	5
		98	2	0
		99	4	2
1567-1-35	66	100	2	0
		101	2	0
		102	1	0
		103	2	0
		104	1	0
		105	1	0
		106	2	0
		107	2	0

APPENDIX E

Table 5E. Segregation ratios from test crosses to populations of a
Genesee x Redcoat hybrid

BC ₁ F ₂	No. of Plants		Probability of Fit	
	Red	White	3:1	15:1
16-1	43	0	<.01	.06
-2	16	4	.19	.03
-3	23	3	.05	.14
-4	23	7	.17	<.01
-5	41	0	<.01	.07
17-1	28	6	.10	.01
-2	46	3	<.01	.23
-3	21	4	.18	.05
-4	40	2	<.01	.25
18-1	46	8	.04	.02
-2	41	6	.02	.05
-3	25	0	<.01	.20
-4	28	7	.13	<.01
19-1	31	8	.13	<.01
-2	23	6	.16	<.01
-3	18	6	.19	<.01
-4	20	2	.05	.25
-5	32	7	.09	<.01
-6	18	5	.18	.01
20-1	31	13	.10	<.01
-2	20	6	.18	<.01
-3	30	6	.08	<.02
21-1	27	8	.15	<.01
-2	34	18	.04	<.01
-3	21	4	.12	.05
-4	13	3	.21	.06
-5	5	0	.24	.72
-6	9	0	.08	.56
-7	46	11	.09	<.01

Table 5E (cont'd.)

BC ₁ F ₂	<u>No. of Plants</u>		<u>Probability of Fit</u>	
	Red	White	3:1	15:1
22-1	33	6	<.06	.02
-2	35	8	.09	<.01
-3	38	2	<.01	.26
23-1	39	8	.06	<.01
-2	31	7	.10	<.01
24-1	22	0	<.01	.24
-2	23	2	.03	.27
-3	19	1	.02	.37
25-1	19	4	.15	.04
-2	21	3	.08	.13
-3	15	3	.17	.08
-4	39	3	<.01	.23
27-1	42	4	<.01	.16
-2	17	7	.16	<.01
-3	13	2	.16	.18
-4	28	2	<.01	.28
-5	33	6	.06	.02
54-1	31	2	<.01	.28
-2	18	5	.19	.01
-3	22	7	.17	<.01
-4	21	9	.13	<.01
-5	13	4	.22	.02
-6	18	3	.12	.10
-7	18	3	.12	.10
55-1	15	3	.17	.08
-2	22	3	.06	.14
-3	32	6	.07	.02
-4	11	4	.23	.01
-5	19	0	<.01	.29
-6	26	5	.09	.03
-7	14	3	.19	.07
58-1	12	4	.23	.01
-2	0	18	.01	.31
-3	16	4	.19	.03
-4	15	4	.20	.02
-5	15	3	.17	.08
-6	23	8	.16	.01
-7	17	5	.19	.01

Table 5E (cont'd.)

BC ₁ F ₂	No. of Plants		Probability of Fit	
	Red	White	3:1	15:1
77-1	16	2	.10	.21
-2	23	7	.17	<.01
-3	14	5	.20	<.01
-4	22	5	.14	.01
-5	28	3	.02	.18
81-1	11	2	.21	.15
-2	11	4	.22	.01
-3	19	1	.02	.36
-4	12	5	.19	<.01
-5	18	1	.03	.22
91-1	14	2	.13	.18
-2	24	5	.12	.02
-3	17	4	.17	.03
-4	12	3	.23	.05
-5	21	4	.12	.05
-6	6	2	.31	.01
-7	22	7	.17	<.01
93-1	24	8	.16	<.01
-2	17	3	.13	.09
-3	23	3	.05	.14
-4	28	4	.04	.09
-5	13	8	.07	<.01
-6	29	9	.15	<.01

APPENDIX F

Table 6F. Segregation ratios from F₁BC₁ plants along with dormancy readings from F₃ selection of Genesee x Monon hybrid

F ₃ Selection of Ge x Monon Hybrid	BC ₁ Cross Number	No. of F ₁ Plants		Dormancy of F ₃ Selection (% ungermin- ated seed)
		Red	White	
1709-1-02	201	3	0	
	202	2	1	
	203	3	0	
	204	7	0	
	205	6	0	
	206	5	1	
1709-1-03	208	4	1	52
	209	4	0	
	210	2	0	
	211	5	1	
	212	3	3	
	213	6	0	
1709-1-04	214	2	0	52
	215	2	0	
	216	7	0	
	217	5	0	
	218	3	0	
1709-1-05	219	4	0	36
	220	3	0	
	221	5	0	
	222	6	0	
1709-1-06	223	4	0	68
	224	5	0	
	225	4	1	
	226	3	0	
1709-1-07	227	6	0	48
	228	6	0	

Table 6F (cont'd.)

F ₃ Selection of Ge x Monon Hybrid	BC ₁ Cross Number	No. of F ₁ Plants		Dormancy of F ₃ Selection (% ungermin- ated seed)
		Red	White	
1709-1-08	229	0	5	40
	230	1	0	
	231	1	0	
	232	1	0	
	235	2	0	
	236	2	0	
1709-1-09	237	4	0	72
	238	3	2	
	239	5	0	
	240	4	0	
	241	4	2	
	242	7	0	
1709-1-10	243	2	1	64
	245	4	0	
	246	3	0	
	247	1	0	
1709-1-15	248	7	0	26
	249	5	0	
	250	4	0	
1709-1-18	251	1	1	40
1709-1-19	252	4	0	30
	253	2	0	
1709-1-29	256	1	0	80
1709-1-32	257	2	2	26
1709-1-04	258	6	0	16
	259	1	0	
1829-1-10	260	1	0	10
1829-1-15	262	3	2	34
1829-1-17	263	1	0	26
	264	3	0	

Table 6F (cont'd.)

F ₃ Selection of Ge x Monon Hybrid	BC ₁ Cross Number	No. of F ₁ Plants		Dormancy of F ₃ Selection (% ungermin- ated seed)
		Red	White	
1829-1-18	265	2	0	8
1829-1-22	267	2	0	22
	268	1	0	
1829-1-31	269	3	1	34

APPENDIX G

Table 7G. Segregation ratios from test crosses to populations of a Genesee x Monon hybrid

BC ₁ F ₂	No. of Plants		Probability of Fit	
	Red	White	3:1	15:1
216-1	13	0	.02	.43
-2	13	3	.21	.06
-3	7	3	.25	.02
-4	16	4	.19	.03
-5	20	4	.13	.04
-6	22	1	.01	.35
-7	33	7	.09	<.01
217-1	20	9	.12	<.01
-2	19	2	.06	.24
-3	12	6	.14	<.01
-4	13	0	.02	.43
-5	20	5	.16	.01
221-1	20	2	.05	.25
-2	21	2	.04	.25
-3	11	5	.11	<.01
-4	23	3	.05	.14
-5	15	0	.01	.38
222-1	15	0	.01	.38
-2	17	0	.01	.33
-3	8	0	.10	.60
-4	15	0	.01	.38
-5	9	1	.19	.35
-6	14	4	.21	.02
248-1	17	5	.19	.01
-2	17	1	.03	.38
-3	21	0	<.01	.26
-4	29	1	<.01	.29
-5	36	2	<.01	.27
-6	23	0	<.01	.23
-7	31	0	<.01	.14

Table 7G (cont'd.)

BC ₁ F ₂	<u>No. of Plants</u>		<u>Probability of Fit</u>	
	Red	White	3:1	15:1
249-1	32	0	<.01	.13
-2	18	0	.01	.31
-3	14	1	.07	.38
-4	18	4	.16	.04
-5	19	11	.06	<.01

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