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Crossing Techniques, Method of Seedling Establishment, and Inheritance Studies of Plant Color and Pubescence Conducted on Pubescent Wheatgrass *Agropyron trichophorum* (Link) Richt

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CROSSING TECHNIQUE, METHOD OF SEEDLING ESTABLISHMENT, AND INHERITANCE STUDIES OF PLANT COLOR AND PUBESCENCE CONDUCTED ON PUBESCENT WHEATGRASS AGROPYRON TRICHOPHORUM (LINK) RICHT.

by

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Introduction

In about half of the angiosperm species the gametic chromosome number is a multiple of that found in some related species. This and the fact that polyploidy has such a pronounced effect on plant physiology and growth, as pointed out by Noggle (30), serve only to emphasize the importance of understanding more about polyploid genetics. The inheritance found in polyploid species is generally considered to be rather complex when compared with ordinary diploid type and for this reason comparatively few critical genetic studies have included species with high chromosome numbers. Nevertheless it is quite necessary that genetics of polyploids be understood before any great advancement can be made in a breeding program involving such species. Pubescent wheatgrass (Agropyron trichophorum) (Link) Richt., an important forage grass, was used in this study. The main objective of the study was to determine the manner of inheritance of color and pubescence. Limited information on how best to obtain progenies of known parentage, and also how best to establish such progenies in the field, led naturally to studies on these phases also. The genetic study is clearly preliminary in nature. The field where the parent plants were growing, and where the controlled populations were produced, is shown in figure 1. From the surrounding area it is clearly a dry-farm section. The location is on the west side of Cache Valley, on the Veibell dry-farm about 1000 feet above the valley floor.

Figure 1. A view of the experimental material and surrounding area. The plots were located on the Veibell dry farm west of Logan, Utah, approximately 1000 feet from the valley floor. The field is in a low saddle separating two valleys where the wind blows almost continually. Careful observations will reveal the blue-green pubescent plants which appear lighter in color.

CROSSING TECHNIQUE

Literature Review

Pope (34) showed that barley (Hordeum vulgare) harvested prior to flowering produced viable seeds following hand emasculation and pollination when detached culms were sustained in distilled water. Keller (19) found that Agropyron ciliare, crested wheatgrass, (A. cristatum), slender wheatgrass, (A. trachycaulum), smooth brome, (Bromus inermis), foxtail barley, (Hordeum jubatum), meadow fescue, (Festuca elatior), and Phalaris tuberosa matured viable seeds on culms detached prior to flowering when cut ends were placed in water. Seed weight was 40 to 80 per cent of those matured on intact culms and germination was fairly high in all species except smooth brome. Earlier work on this subject has been adequately reviewed by Keller (19) and will not be covered at this time. Burton (6) reported that bahiagrass (Paspalum notatum) culms were dug, washed free of soil, placed in cans of water and taken to the laboratory where they were used to produce both single and polycrosses. Battle (5) found that red clover (Trifolium pratense) flowered and produced seeds on stems detached before pollination. It matured seed 18 days after pollination which was the time required for the original plants in the field. The seeds were uniform and plump with production ranging from 0 to 96 per cent, 17 of the 18 plants yielding 50 per cent or better. In the same test alsike (T. Hybridum) and alfalfa (Medicago sativa) yielded

no seed. Fisher (10) reported good seed set on detached spikes of A. trichophorum sustained in top water and suggest that detaching female culms may be a possible method of hybridisation.

Materials and Methods

Fifteen plants with blue-green pubescent glumes and fifteen plants with green glabrous glumes were selected for this study. They were divided into two groups, one with ten plants and the other with twenty plants, each with equal numbers of the two contrasted types. The two groups were handled in the following manner:

In group one, plants one to five, were green glabrous and plants six to ten were blue-green pubescent. Each plant was selfed, using three parchment bags containing ten spikes each. In addition, two detached groups of five spikes each were selfed, one group having the leaves removed with a sharp razor-blade at the time of detaching and the other with leaves intact. Each plant was then crossed with every other plant in reciprocal combinations so that each plant was used as both a female and male with every other plant in the group. When the anthers were turning yellow but before flowering had begun the selected culms were cut from each plant approximately three inches above the ground. These detached culms were immediately placed in quart jars of fresh water and their origin marked with a jewelry tag. They were then moved to the male parent where three intact spikes, which served as pollinators, were included in each bag with five detached spikes used as females. The jars of water, which were kept full until the seeds were harvested, were buried in the ground surrounding the male parent so that the mouth of the jar was approximately level with the surface.

This aided in keeping the water cool and placed the detached spikes of the female parent a few inches below the intact spikes of the male parent, thus facilitating pollination. The arrangement of the jars of water and the manner in which bagging was done is shown in figure 2.

Genetic studies are frequently confronted with the problem of adequate populations. In group one all possible pairings are made, but with a realization that populations obtained may be small. The procedure in group two was designed, therefore, to give larger populations with which to work but at the same time sacrificing some combinations that may be of utmost importance in adapting a genetic explanation to the characters being studied. The number of spikes per plant is a serious limiting factor when so many bulk crosses are made involving a single plant. It was decided therefore that plants 11 to 15, which were blue-green pubescent, would be used as pollen parents on plants 16-20 which were green-glabrous plants. This procedure was then reversed using green-glabrous plants 21 to 25 as pollen parents for blue-green pubescent plants 26 to 30. As in group one each plant was selfed and the same crossing technique, that of detaching the culms of the female parent, was employed. This procedure made it possible to include many more spikes in each cross with the expectation of larger populations. However it limited what could be learned from their progeny because crosses were made between contrasted types only and these were not made in reciprocal. Unfortunately the progenies from this material became contaminated in the field and could not be used to determine genetic relationships.

The plants were bagged June 22nd and 23rd and on the 25th and 26th they began to flower. One plant, which was not used in the study began flowering June 24th. By July 2nd, 90 per cent of the entire field, including the selected plants, was in full flower. At this time a severe wind storm hit the plots and some of the parchment bags were damaged. Most of this damage was detected and corrected where possible with careful notes being taken on these plants. However, some opportunity for contamination may have passed unnoticed. Most of the excised culms remained green and alive as long as necessary to mature seed. However, some culms, which were undoubtedly damaged in some way so that the conductive elements became plugged or damaged, dried up within about a week and in most cases produced no seeds. By July 27th the seed was ripe and well developed but had not begun to shatter. The intact spikes serving as the pollen parent were cut off and the bags were placed inside to dry. Threshing was done by hand and the number and weight of seed was obtained for each spike.

Figure 2. A close-up view of one of the selected plants showing the arrangement of the detached culms in the jars of water. As clearly shown all but a few spikes are included in the parchment bags. The spikes in the foreground are detached open-pollinated spikes. The bags in the center of the plant are the intact selfs while those around the outside are controlled crosses.

Experimental Results

As the data in table 1 indicate seed production was increased 4.4 to 17.4 per cent by removing the leaves on the detached culms. A more detailed presentation of this material is found in the appendix, table 1. Although some variation existed, the general trend of seed size was for smaller seeds on the culms with leaves removed. Under open pollination, intact culms yielded 116 per cent more seed than detached culms while under self-pollination intact culms had a 375 per cent advantage. If cutting the culms had the same effect on both male and female organs the same per cent increase would be expected in both cases. Apparently the shock of detaching the culms was in effect a partial emasculation since it considerably lowered self-pollination. Detaching the culms may cause the anthers to dehisce before the stigmas became receptive although experimental data on this point are lacking. A summary of the data establishing this difference is presented in table 2 (the complete data are presented in the appendix tables 2 and 3). Wind pollination was more effective than controlled pollination under parchment bags. This is in agreement with other studies.

Discussion

One of the important considerations in this investigation was the manner in which the crosses should be made. Hot water emasculation has been successfully used to inactivate the plants own pollen, but subsequent pollination of treated inflorescence under bags has usually given rather low seed yields. Hand emasculation, while possible with pubescent wheatgrass, is obviously much too slow to allow the desired number of crosses. Clonal propagation followed by the isolation of specific pairs would have been preferred, but could not be carried out in the time available for the study. The method used, that of detaching the spikes used as females, was a compromise measure based on some previous observations, and proved quite satisfactory. However, some selfing probably resulted, thus contributing to the difficulty of interpreting the genetic data obtained.

Table 1. Summary of seed production on detached culms as effected by removal of leaves.

	Leaves on					Leaves off					
	Number of Spikes	Number of Seeds	Seed Weight	Seeds Per Spike	Average Seed Weight	Number of Spikes	Number of Seeds	Seed Weight	Seeds Per Spike	Average Seed Weight	% increased seed set on culms with leaves off over culms with leaves on.
elfed:	103	114	0.43	1.12	0.0038	99	116	0.43	1.17	0.0037	4.4%
pen-pollinated:	150	1932	8.01	12.88	0.0042	150	2238	8.41	14.92	0.0038	15.8%
ontrolled crosses:	878	2570	10.47	2.93	0.0041	893	3076	12.42	3.44	0.0040	17.4%
	1128	4616	18.91	4.10	0.0041	1142	5430	21.26	4.75	0.0039	15.8%

Table 2. Summary of seed production on detached vs intact culms.

	Detached Culms					Intact Culms					
	Number of Spikes	Number of Seeds	Seeds Per Spike	Seed Weight	Average Seed Weight	Number of Spikes	Number of Seeds	Seeds Per Spike	Seed Weight	Average Seed Weight	% seed increase on culms intact over culms detached.
elfed plants:	201	226	21.70	0.76	0.0034	630	3354	119.70	18.15	0.0064	375%
pen-pollinated lants:	300	4151	283.29	17.42	0.0042	205	6210	611.50	34.01	0.0055	116%

SEEDLING ESTABLISHMENT STUDIES

Literature Review

Parkey (32) found that freshly harvested seeds of reed canary grass (Phalaris arundinaceae), smooth brome, orchard (Dactylis glamerata), tall oat (Arrhenatherum elatuis), crested wheat and alta fescue (Festuca elatior arumdenaceae) when planted directly in the field not later than September 15th flowered at the normal time the following summer. Good seedling emergence and winter survival resulted when seeds were planted August 15th to October 3rd.

Materials and Methods

In order to learn more about what could be expected from seeding pubescent wheatgrass directly in the field a test was set up in two locations using seven methods of establishment as listed in table 5. The method of placing the sprouting seeds in an atmosphere of high humidity was included because of difficulty encountered earlier when seeds were sprouted under these conditions. In order to maintain high humidity the saucers were placed in a shallow pan of water with a five gallon bucket placed over them with only a small opening around the bottom to allow air passage. Remaining seeds were placed on saucers and covered only with another saucer to keep out the light. To see what effect chilling would have on breaking the dormancy period one lot of seed was soaked for 12 hours, placed in the refrigerator for 24 hours at 35° F, and then placed on saucers in the greenhouse to germinate. One lot of seed was planted in sand on the greenhouse bench with the remaining seed planted directly in the field. This planting and the later plantings of sprouted seeds were kept moist with frequent irrigations. A small pair of twizers proved quite efficient in picking out and planting the sprouted seeds which were placed in a small hole made in moist soil. Three replications of 100 seeds each were used for the seven methods using both new and old seed.

Experimental Results

The data are presented in table 3. In all cases except where the bucket was placed over the sprouting seeds in the greenhouse more seeds sprouted on the saucers and more plants emerged in the field than when the unsprouted seed was planted directly in the field. However, placing the bucket over the sprouting seeds tended to reduce the number that germinated in both locations. Direct seeding of the new seed was believed more practical because of the extra labor involved in sprouting the seeds and planting them in the field which required several plantings before all the sprouted seeds were in the ground and because this practice did not increase the seedling emergence sufficiently to justify the extra labor. These plantings were completed August 17th and the later plantings of the genetic material were begun August 31 and completed September 3. The early fall plantings were superior in vegetative growth and produced considerably more spikes per plant than the later plantings. However, little difference in heading time was observed.

Table 3. Per cent seedling emergence when using various methods of seeding both new and old Agropyron trichophorum seed.

Greenhouse where temperature was high during day		Per cent seedling emergen	
		New Seed	Old Seed
1. Seed placed on saucers and covered so that humidity was maintained at high level.		40	40
		31	42
		40	37
	Average	37.0	39.7
2. Seeds on saucers with lower humidity.		60	55
		60	56
		59	61
	Average	59.7	57.3
3. Planted directly in sand on greenhouse bench.		56	79
		60	68
		50	73
	Average	55.3	73.3
4. Seeds soaked for 12 hours, place in refrigerator for 24 hours at 35° F and then placed on saucers in the greenhouse.		61	65
		51	57
		63	49
	Average	58.3	57.0
In laboratory where temperature remained fairly constant and much cooler.			
5. Seeds on saucer and covered so that humidity was maintained at high level.		52	43
		63	49
		55	61
	Average	59.7	51.0
6. Seeds on saucers with lower humidity.		60	63
		65	57
		59	68
	Average	61.3	62.7
7. Seeds planted directly in field.		61	65
		51	57
		63	49
	Average	58.3	57.0

L.S.D. P.05= 3.5
L.S.D. P.01= 4.8

Discussion

Very little difference was obtained using old and new seed. There was, however, a sizable increase in the germination of old seed when it was planted in sand on the greenhouse bench. It appears from this test that the dormancy period in pubescent wheatgrass is very short because the new seed was gathered from the field and the test was immediately begun. It was observed however, that the new seed was about two days slower germinating than the old seed.

An explanation for the decreased amount of germination where the humidity was kept high is not clear. It is possibly the interaction of humidity with temperature and possibly CO_2.

INHERITANCE OF PLANT COLOR AND PUBESCENCE

Review of Literature

Pubescent wheatgrass has many distinct, easily classified morphological characters which should lend themselves readily to genetic classification and study which is vital and necessary for understanding of polyploid genetics. The species has the same chromosome number as wheat (n - 21), Peto (33), Nielsen (30) and Hartung (16), but is naturally cross pollinated and exhibits extreme variability in outward appearance. According to the work of Smith (44) and Keller (20), the species has low self fertility. However, individual plants will range from quite fertile to totally self sterile.

Lindstrom (22) emphasized that in general the genetic evidence obtained from polyploids harmonizes very well with the modern concept of heredity as developed largely from diploids but that little critical genetic research exists with polyploids above the tetraploid level. Considerable work has been done with hexaploid wheat (Triticum aestivum), however, which behaves largely as a diploid, but this does not compare in scope or magnitude with the work accomplished in corn (Zea mays) and barley (Hordeum jubatum), Emerson, Beadle and Fraser (8), and Robertson, Wiebe and Immer (38), where the linkage groups are identified and in many cases associated with the proper chromosome through cytological investigation. Much less is known about the majority of forage grasses with practically no genetic or cytological information on many of the species.

Cytological aspects of polyploidy are dealt with in detail by Sansome and Philip (39), Darlington (7), Sharp (41) and Riley (37).

According to Newton and Darlington (29), pairing in triploids is between two of the three threads at a time at any one point and never all three at any one point although it may appear that way at times. In tetraploids only two of the four associate at any one point. The same procedure holds for higher polyploids. The complexity of polyploid genetics, according to Myers (27), is increased because of the difficulty of distinguishing between disomic and polysomic inheritance. Critical evidence can only be obtained when marker genes are available for all or most of the chromosomes for a given organism. Sansome and Philip (39) comment as follows: "In all allopolyploids where all the sets of chromosomes are of different kinds, the possibilities and complexity of types of pairing are greatly increased. It is not surprising, therefore, that interspecific polyploid hybrids normally give complex segregation. To recognise the particular type of segregation is often well nigh impossible."

It is generally recognized that random chromatid segregation occurs only when the factors concerned are more than 50 cross-over units from the spindle-fiber attachment, Sinnot and Dunn (42) and Hays and Immer (17), and that the ratios obtained in ordinary diploids are the same with chromosome and chromatid segregation. However, Lindstrom (22) points out that entirely different ratios are obtained in the case of polyploids. Random chromosome assortment in a 4N hybrid, AAaa, results in a 1AA:4Aa:1aa diploid gametic ratio while random assortment of the eight chromatids of the same organism

result in a 3AA:8Aa:3aa diploid gametic ratio. Chromosome segregation in a 6N hybrid, AAAaaa, results in a $1A^3:9A^2a:9Aa^2:1a^3$ triploid gametic ratio, while chromatid segregation of this individual results in a $2A^3:9A^2a:9Aa^2:2a^3$ triploid gametic ratio. In other words, the number of recessive gametes increase as the distance from the spindle-fiber attachment increases up to the maximum point of crossingover, or approximately 50 cross-over units. Randolph (35) states that the genetics of autotetraploids has been studied sufficiently to indicate that tetrasomic inheritance, rather than the disomic inheritance of diploids, prevails quite generally in tetraploids as would be expected since four sets of homologous chromosomes instead of two are normally present. This may apply generally to the higher autopolyploids and is of far-reaching importance to the plant breeder.

Comparatively little genetic research has been undertaken with the higher polyploids but the groundwork has been laid by such investigators as Haldane (15), Fisher (9) and Geiringer (11) in their development of the theoretical genetics of autopolyploids, linkage of polyploids and polysomic inheritance. Such time-saving formulas as the following taken from Haldane's (15) paper prove very useful when dealing in autopolyploids: "From a zygote $A^r a^{2m-r}$ a gamete $A^s a^{m-s}$ can be chosen in $\frac{r!}{(r-s)!\,s!} \cdot \frac{(2m-r)!}{(m-r\,s)!\,(m-s)!}$ ways. The probability of such a zygote producing a gamete of that constitution is $\frac{(m!)^2\,(2m-r)!\,r!}{(2m)!\,(m-s)!\,(m-r\,s)!\,s!\,(r-s)!}$". In a recent paper by Geiringer

(12) it was pointed out that while chromosome segregation might be assumed, as an approximation theory, the study of polyploids should actually be based on the consideration of chromatid segregation. In her paper, formulas are given for theoritical chromatid segregation of polyploids in the Nth generation.

According to Kostoff (21), as the degree of polyploidy increases the variability of the plant increases. The degree to which polyploidy can advance before the species becomes so variable that sterility and extinction results varies with the species in question. The genera Oxycoccus and Deschampsia as reported by Hagerup (14) reaches a plateau or optimum at the tetraploid level above which sexual reproduction ceases.

Polyploids are most generally classified into autopolyploids or allopolyploids depending on their origin and method of chromosome pairing. True autopolyploids are, according to Sharp (41), those in which heteroploidy is due to the multiplication of a single kind of genome, whereas true allopolyploids are those in which heteroploidy is due to the combination and subsequent multiplication of specifically different genomes. Stebbins (46) considers this classification entirely inadequate since intermediate types exist so that the species may be autopolyploid for some genomes and allopolyploid for the remainder. He points out that many natural autopolyploids reported in the literature are actually allopolyploids are that the "raw allopolyploid becomes progressively 'diploidized' until its behavior resembles that of a diploid species." Segmental allopolyploids are defined as "an allopolyploid of which the component genomes bear the

majority of their chromosomal segments in common, so that the diploid hybrid from which it is derived has good pairing at meiosis, but in which these genomes differ from each other by a large enough number of chromosomal segments or gene combinations so that free interchange between them is barred by partial or complete sterility on the diploid level." Myers and Hill (26) and Smith, Huskins and Sanders (45) also suggest that because of the continual process of crossingover, mutations, new recombinations and selections, some species which now behave cytologically as allopolyploids may have been derived from autopolyploids.

When autopolyploids are inbred the rate of approach to homozygosity is expected to be very low. Bartlett and Haldane (4) give the number of generations needed to half heterozygosis in diploid and polyploid species. If self fertilized, diploids require one, tetraploids 3.8 and hexaploids 6.58 generations. Brother-sister mating of diploids require a somewhat shorter time than selfing tetraploid species. Myers (27) points out that to reach the same degree of homozygosity, more generations of inbreeding are required with autopolyploids than with allopolyploids. Under certain conditions, such as the production of commercial hybrids involving inbred lines, a characteristic of this nature may be a distinct advantage since reduction in vigor in advanced generations should be less rapid than with diploids or allopolyploids. Gustafsson (13) lists other advantages of polyploids such as their ability to cover up recessive lethals more easily than diploids or at least cause these genes to lose most of their destructive effect.

The genome theory has been used extensively by Aase (1,2) in studies of the cereals. It is generally believed that the genome homology found in Triticum extends over into the Agropyrons with one genome in A. intermedium and A. trichophorum and two in A. elongatum being the same or very similar to the A and/or B genomes in the genus Triticum. Considerable chromosome pairing, particularly where A. elongatum is involved, has been reported from Triticum - Agropyron hybrids. Vakar (50) reported up to 28 bivalents in T. vulgare x A. intermedium hybrids. He postulated that A. elongatum had three genomes homologous to the three in T. vulgare plus two other genomes homologous with each other and that A. intermedium had two genomes in common with T. vulgare plus an additional genome. He gave these two species the genome constitution of $A_1B_1D_1X_1X_2$ and $A_aD_aX_1$ respectively. Peto (34) questioned this much pairing because he observed only 21 bivalents in T. vulgare x A. elongatum and only 7 bivalents in T. vulgare x A. intermedium hybrids. He believed A. intermedium to have the genome constitution A X Y and that A. elongatum may have arisen through chromosome doubling in a hybrid of A. intermedium with some other tetraploid Agropyron species. Armstrong (3) reports approximately the same results. At present, Peto's theory is considered more acceptable. Excellent reviews of this work are given by Johnson (16), Smith (45), White (52), Love and Suneson (24), McFadden and Sears (25) and Sears (40).

In recent publications by Love (23) and Smith, Huskins and Sanders (45) it was pointed out that more and more caution should

be exercised in placing too much reliance on "genome" analysis. Because of the continual process of crossing over, gene mutation and the production of new recombinations these genomes are in a constant state of change. However, the true picture of this relationship is still not understood.

It was found by Thompson and Grafius (48) that after two backcrosses to the wheat parent Triticum vulgare x Agropyron trichophorum hybrids still maintained the perennial habit and pubescent characters. Previous crosses involving wheat and pubescent wheatgrass have been reported by Love and Suneson (24), Smith (43), Suneson and Pope (47), White (52) and Verushkine and Sheshurdine (51).

Materials and Methods

The plants were crossed in the manner described in materials and methods for crossing technique. By June 25th most of the material was headed out sufficiently for classification which was completed by the first of July. The four classifications used in this study are shown in figure 3. Blue-green was not clearly differentiated from green by black and white photography but was as distinct as pubescence upon visual examination. Although the four types (Blue-green pubescent, blue-green glabrous, green pubescent and green glabrous plants) were distinct and easily classified, considerable variation was observed in degree of color and pubescence. The color as well as pubescence was not limited to the spikes but extended into the stems and leaves. However, their presence was more pronounced on the spikes. An attempt was made to classify these plants as to degree of color and pubescence but no logical basis for such a classification could be found.

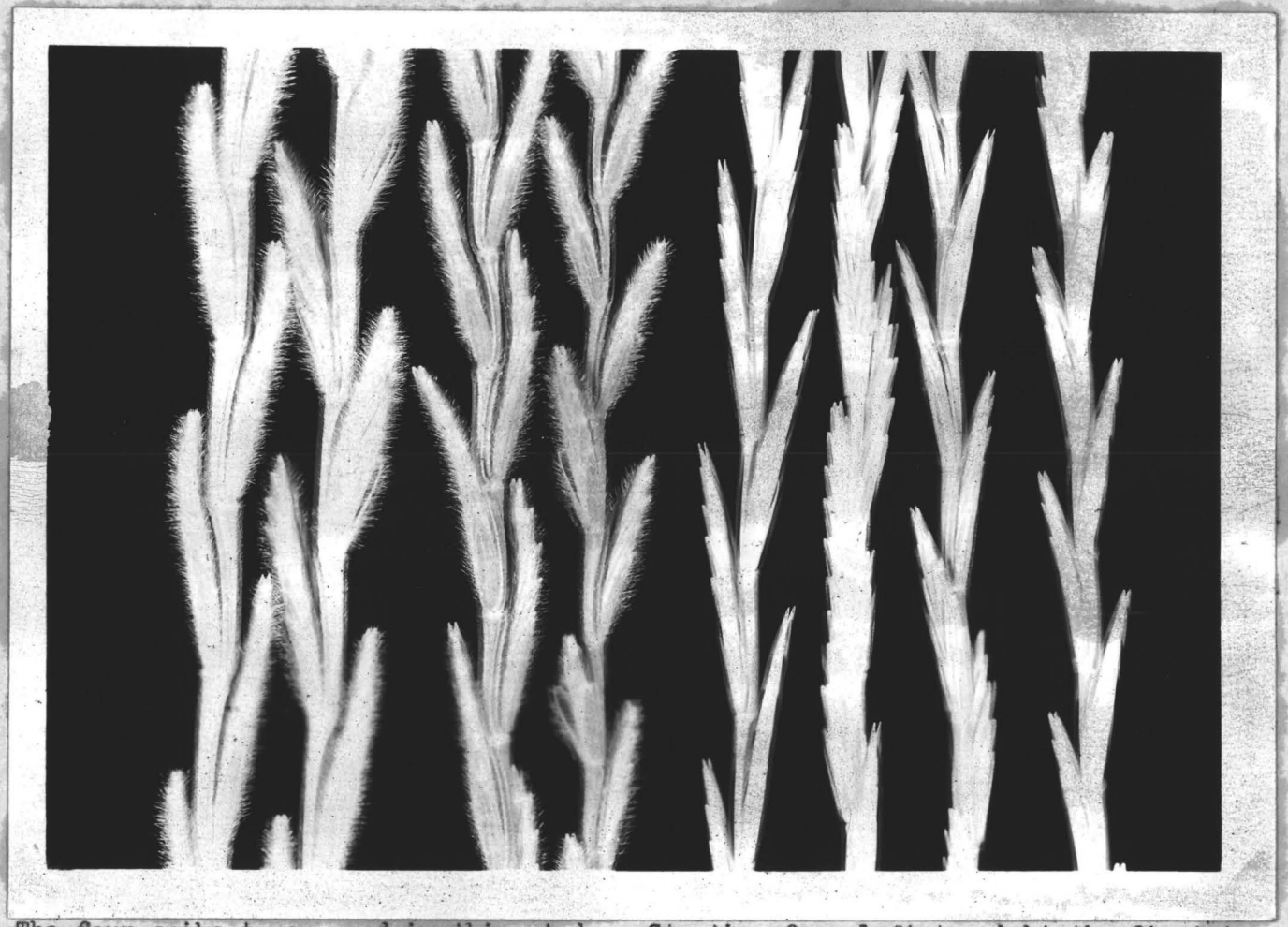

Figure 3. The four spike types used in this study. Starting from left to right the first two spikes are blue-green pubescent, the next two are green pubescent, the next two are blue-green glabrous and the last two are green glabrous. The pubescent plants, as shown in this photograph, are very distinct. The blue-green color is just as distinct but does not show up in black and white photography.

Experimental Results

The progenies obtained are presented in tables 4 to 7. Table 4 contains the progenies from plants 1-10 when random open-pollination is allowed to take place. Although the location of the plant in the field in relation to other plants as well as time of flowering may somewhat alter the proportions obtained it seems reasonable to expect that any genetic difference would still show up. The progenies obtained from plants 1 and 3 are very similar but behave different than the remaining green glabrous plants. Plants 4 and 5 behave very much alike. However, plant 4 does show an excessive amount of blue-green pubescent plants in its progeny. Plant number 2 appears to behave different than any of the other plants. The behavior of these plants when they are selfed and crossed with plants of the same phenotype is presented in table 5. There is a consistent relationship between plants 1 and 3. Both plants give essentially the same ratio upon selfing, 3 green glabrous to 1 blue-green glabrous. The same relationship was found when 3 was pollinated by 1 as well as when 1 and 3 were involved in any cross except with plant 4. The behavior of plant 4 on selfing is strikingly different than the other plants and when used as a pollen parent on 3 and 5 the number of green glabrous plants obtained is large, as would be expected, since 4 produced an excess of these plants when selfed. When 4 was used as the female parent only two plants were obtained, both of which were green glabrous. These could possibly have been selfs. Plant 2 when selfed and when

crossed with the remaining plants behaved very much like numbers 1 and 3. However, most of the crosses involving 2 produced very few plants. Although the selfed progeny of 3 deviated somewhat all of the crosses gave a 1:3 ratio except with plant 4 where again the ratio was widened. It could be assumed, therefore, that plants 1 and 3 are very similar genetically with respect to the characters green and glabrous and that 2 and 5 may have only minor differences with 1 and 3 but that plant 4 has a much different behavior from all the other green glabrous plants.

Blue-green pubescent plants in table 4 can be grouped so that plants 6 and 10, 8 and 9, and 7 divided themselves into three groups. Possibly 7 could be in the same group as 6 and 10. The interesting thing is that plants 8 and 9 produced no blue-green glabrous plants which indicates that they must have a large number of genes necessary for the expression of pubescence. By observing the numbers in the separate classes it seems quite evident that blue-green and pubescence are the dominant characters. If we now follow these blue-green pubescent plants through their selfs and controlled crosses in table 6 it is found that here as well as in the open-pollinated material plants 6 and 10 behave very much alike producing approximately 25 blue-green pubescent plants to 1 blue-green glabrous plant. When used as male or female these plants behaved alike with only one exception when 7 was pollinated by 10. In this cross one green glabrous plant was produced. The appearance of this one plant is not out of line because upon selfing plant 7 produced both glabrous and green plants. The other pair of blue-green pubescent plants that

behaved alike when open-pollinated were 8 and 9. However, upon selfing their behavior was quite different, but so few plants were obtained from 8 selfed that very little can be said about it. Although some irregularities occur the crosses involving these two plants are consistent with each other. It has already been pointed out that plant 7 behaved differently when selfed. One irregularity is evident when 7 is pollinated by 6 and by 10. However, such an inconsistency could be explained by assuming selfing on the part of 7. The over all picture still holds, therefore, that perhaps plants 6 and 10, 8 and 9, and 7 represent three genotypic classes.

If these plants, both green glabrous and blue-green pubescent, are followed on through the reciprocal crosses between types as presented in table 7 a more complicated picture is found. Plants 8 and 9 which produced no blue-green glabrous plants under open-pollination, or when selfed and crossed within their type still produced no blue-green glabrous plants except in crosses with plants 1 and 3. Some of the plants obtained when 3 was used as the female parent in this case could be the result of self-fertilization. In any event it appears quite evident that the combination necessary for the production of blue-green glabrous plants occurs very infrequently in plants 8 and 9. No other pronounced similarity can be pointed out except that the preponderence of genes necessary for the expression of the green glabrous condition in plant 4 is again emphasized in the cross where 4 is pollinated by 8. The largest advantage that can be obtained from the information in table 7 is that the data there can be used to

check the plant behavior presented in tables 4, 5, and 6.

Although in general the plants behave in a consistent manner the numbers obtained are so small that an accurate working genetic explanation is rather difficult to obtain. The problem would be greatly simplified with larger populations and/or data from more than one generation. The possibility of obtaining large populations was comparatively high in this study since each reciprocal cross comprised ten spikes with an average of 25 spiklets per spike and six florits in each spiklet. If only half of the florits produced seed it would amount to 750 which is a fair population. In group number two where plants were only crossed between types approximately twice this number could be obtained.

After exploring some of the possibilities offered by assuming ordinary diploid, autopolyploid and allopolyploid types of inheritance it appeared that allopolyploid segregation offered the best explanation for the characters being studied. The proposed genotypes for plants 1-10 are listed in table 7 along with observed and calculated ratios. Plants showing satisfactory agreement of the observed with the calculated ratios, as determined by chi-square, are indicated with an asterix (*). In determining chi-square values the computations were carried to four decimal places and rounded to two figures so that all of the data could be placed in one table which would make evaluation of the reciprocal crosses much easier for the reader. The assumptions necessary for this hypothesis are that two dominant genes (BB) are necessary for the expression of blue-green color and that the complementary action of dominant genes

(P) and (T) are necessary for the expression of pubescence. This explanation was decided upon after exploring some of the possibilities offered by diploid, autopolyploid and allopolyploid types of segregation. It is realized that some of the populations reported in tables 5-7 are small and that even though satisfactory agreement was found with a sizable portion of the data other genetic explanations may be given which are more accurate.

When this hypothesis is applied to selfs and reciprocal crosses involving plant 1-5 (table 5) good agreement is found on all of the selfed material except plant 4. In order for plant 4 to fit this hypothesis it would be necessary to assume some contamination. Such a thing may have occurred but the records had no mention of possible contamination. All of the crosses where sufficient numbers were obtained were in good agreement except where 4 pollinated 3.

When plants 6-10 (table 6) are subjected to this hypothesis, all of the plants except number 8 give satisfactory agreement of the observed with the calculated ratios. All of the crosses with sufficient populations give satisfactory agreement except with the reciprocal crosses with 7 and 10 and when 9 pollinates 6 and 7. The irregularity found when 7 pollinates 10 can be explained if selfing is assumed for number 10 which did show considerable self-fertility. The same thing can be applied to 6 pollinated by 9 and possibly 7 pollinated by 9. With 7 pollinated by 10 it is a different story and larger numbers are needed before much can be said.

When the green glabrous plants 1-5 and the blue-green pubescent plants 6-10 are reciprocally crossed (table 7) the agreement

of observed with calculated is not as great as when the plants are crossed within their type. However, as pointed out earlier plants 1 and 3 behave alike and 8 and 10 behave alike. By looking at the progeny received from the reciprocal crosses involving these four plants it is found that satisfactory agreement is obtained in all cases where any plants have been obtained except where 3 in pollinated by 8 and some of this irregularity can be explained if selfing on the part of 3 is assumed. This is not unlikely because plant 3 does show considerable self-fertility (table 5). In reciprocal crosses involving 2 with 8 and 10 good agreement is found and in the crosses of 5 with 8 and 10 good agreement is found in all cases except where 5 is pollinated by 10 but here the populations are quite small and selfing of 5 would produce an excess of green glabrous plants as observed values show. Plant number 4, which did not give a satisfactory fit when selfed, does not give satisfactory agreement of observed with calculated in any of the crosses with the blue-green pubescent plants except when it was used as a pollen parent in a cross with plant 10. Small populations on some crosses make it impossible to follow all of the plants through this procedure.

Table 4. Progeny obtained from random wind pollination of plants 1-10.

W- Blue-green pubescent
X- Blue-green glabrous
Y- Green pubescent
Z- Green glabrous

Green glabrous plants				Blue-green pubescent plants			
W	X	Y	Z	W	X	Y	Z
31	38	34	57	128	17	12	1
9	17	14	10	209	36	43	5
27	41	39	73	53	0	23	2
19	14	69	64	207	0	51	0
33	51	116	157	225	40	33	4

Table 5. Progeny obtained from plants 1-5 when selfed and crossed reciprocally in all combinations.

O = Observed ratio. C = Calculated ratio; *observed ratio satisfactory as tested by chi-square. W = Blue-green pubescent plants. X = Blue-green glabrous plants. Y = Green pubescent plants. Z = Green glabrous plants.

Female Plants		Male Plants 1				2				3				4				5			
		W	X	Y	Z	W	X	Y	Z	W	X	Y	Z	W	X	Y	Z	W	X	Y	Z
1	O	0	29	0	113	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2
	*C	36	0	107														*0	.8	0	2.2
2	O	0	0	0	3	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0
	*C	0	1	0	3	*0	.8	0	2.2												
3	O	0	5	0	13	0	0	0	3	0	10	0	37	0	3	0	25	0	1	0	2
	*C	0	4	0	14					*0	12	0	35	0	7	0	21	*0	.8	0	2.2
4	O	0	0	0	0	0	0	0	1	0	0	0	0	1/ 1	1	0	57	0	0	0	1
	*C													0	15	0	45	*0	.3	0	.7
5	O	0	3	0	10	0	1	0	3	0	0	0	4	0	1	0	16	2/ 0	0	1	11
	*C	0	3	0	10	*0	1	0	3	*0	1	0	3	*0	4	0	15	*0	1	0	3

1/ Class W assumed to be result of contamination.

2/ Good fit assuming class X derived by selfing.

Table 6. Progeny obtained from blue-green pubescent plants 6-10 when selfed and crossed reciprocally in all possible combinations.

O = Observed ratio. C = Calculated ratio. * = Observed ratio satisfactory as tested by chi-square. W = Blue-green pubescent. X = Blue-green glabrous. Y = Green pubescent. Z = Green glabrous plants.

		Male Plants																			
		1				2				3				4				5			
		W	X	Y	Z	W	X	Y	Z	W	X	Y	Z	W	X	Y	Z	W	X	Y	Z
1	O	34	1	0	0	6	0	0	0	6	0	0	0	9	0	0	0	2	0	0	0
	*C	34	1	0	0	*5	.2	.7	.1	*5.9	.1	0	0	*8.9	.1	0	0	*1.9	0	.1	0
2	O	27	2	0	0	40	4	4	0	6	0	0	0	66	0	0	0	13	0	0	1
	*C	24	1	3.9	.1	*38	3	6	1	*5.2	.1	.7	0	57	.9	8	.1	12	.3	1.6	.1
3	O	5	0	0	0	1	0	0	0	0	0	2	0	4	0	1	0	6	0	0	0
	*C	4.9	.1	0	0					1.9	0	.1	0	*4.9	0	.1	0	*5.9	0	.1	0
Female Plants																					
4	O	0	0	0	0	2	0	0	0	10	0	1	0	125	0	0	0	32	0	0	0
	*C					*.7	.1	.2	0	*10.8	0	.2	0	*125	0	2	0	*28	.4	3.5	.1
5	O	15	0	0	0	2	0	0	0	16	0	0	0	8	0	0	0	247	10	0	0
	*C	14	0	1	0	1.7	.1	.2	0	*15.8	0	.2	0	*6.9	.2	.9	0	*249	8	0	0

Table 7. Progenies obtained from reciprocal crosses between green glabrous plants 1-5 and blue-green pubescent plants 6-10, together with expected ratios assuming that BB is necessary for the expression of blue-green color and pubescence results from the complimentary action of P and T. In the table O represents observed populations, C is for calculated ratios, and an asterix (*) denotes satisfactory agreement between the two. Types are (W) blue-green pubescent, (X) blue-green glabrous, (Y) green pubescent, and (Z) green glabrous. The assumed genotypes are as follows:
(1) BbbbbbPpPpppttttttt (2) BbbbbbPpppppttttttt (3) Bbbbbbpppppptttttt (4) BbbbbbPPPpppttttttt (5) BbbbbbPpPpPpttttttt
(6) BBbbbbPpPpPpTtTttt (7) BbBbBbPpPpPpTtTttt (8) BBbbbbPpPpPpTTTtTt (9) BBbbbbPpPpPpTTTtTt(10) BBbbbbPpPpPpTtTtTt

	TYPE					TYPE					TYPE					TYPE					TYPE			
	W	X	Y	Z		W	X	Y	Z		W	X	Y	Z		W	X	Y	Z		W	X	Y	Z
1x6	O	4	4	3	0	1x7					1x8					1x9					1x10				
	*C	3.2	2.3	3.2	2.3																				
6x1						7x1					8x1					9x1	O	2	0	5	0	10x1	O	8	3	3	2
																	*C	3.4	.1	3.4	.1		*C	6.8	1.2	6.8	1.2
2x6	O	1	1	2	0	2x7					2x8	O	2	0	0	0	2x9	O	0	0	1	0	2x10				
	*C	1.6	.4	1.6	.4																					
6x2						7x2	O	15	0	5	1	8x2					9x2						10x2	O	9	2	5	3
							C	8	4	10	4													*C	7.8	1.7	7.8	1.7
3x6	O	4	5	8	9	3x7	O	1	1	1	4	3x8	O	1	2	6	9	3x9	O	2	1	0	1	3x10	O	2	0	4	0
	C	10	3	10	3		*C	2.0	1.0	2.5	1.5		C	7	1	7	1		*C	1.8	.2	1.8	.2		*C	2.3	.7	2.3	.7
6x3	O	3	1	0	0	7x3	O	16	1	10	4	8x3						9x3	O	14	0	3	0	10x3	O	4	0	2	0
	*C	1.5	.5	1.5	.5		C	9	5	11	6								C	7.4	1.1	7.4	1.1		*C	2.3	.7	2.3	.7
4x6						4x7						4x8	O	4	0	3	21 1/	4x9	O	3	0	3	3	4x10					
													C	1	0	1	0		C	1	0	1	0 1/					
6x4	O	3	0	4	3	7x4					8x4						9x4	O	10	0	1	0	10x4	O	3	1	4	1
	C	4.3	.7	4.3	.7													C	5.5	0	5.5	0		*C	3.9	.6	3.9	.6
5x6	O	29	6	36	7	5x7	O	1	2	6	2	5x8	O	3	0	9	0	5x9	O	13	0	44	0	5x10	O	2	1	2	3
	*C	34	5	34	5		C	6	.6	4	.4		*C	63	1	63	1		C	28	.5	28	.5		C	4.5	.5	4.5	.5
6x5	O	1	0	0	0	7x5	O	1	0	2	1	8x5						9x5	O	1	0	1	0	10x5	O	0	0	1	0
							*C	2.3	.2	1.4	.1								*C	.98	.02	.98	.02		*C	.4	.1	.4	.1

1/ A good fit assuming class Z derived by selfing.

Discussion

The genetic explanation for the expression of pubescence and plant color as reported in tables 5-7 is in agreement with some of the observed data and fails to agree with other. The hypothesis is based on the assumption that (BB) is necessary for the expression of blue-green color and that the complementary action of (P) and (T) is necessary for the expression of pubescence. As written out in table 7 each genetic factor pair is assumed to be in a different genome. This appears logical, but the same results can be obtained if these genes are assumed to be carried on different chromosomes within one genome. Any pair of them could even lie widely removed from one another on the same chromosome. Allopolyploid type of segregation is assumed so that if the species has the genetic constitution $B_1B_1B_2b_2b_3b_3$ the resulting gametes will be $B_1B_2b_3$ and $B_1b_2b_3$ and not $B_1B_1B_2$, $B_1B_1b_2$, $B_1B_1b_3$, $B_1B_2b_3$, $B_2b_2b_3$, and $b_2b_3b_3$ as is the case with autopolyploids. Under such conditions a plant that has a pair of homozygous dominant genes, necessary for the expression of blue-green color, will breed true for that character regardless of the genetic constitution of the remaining genomes.

Classification of the plants in several rows of a large spaced nursery yielded the following: 1248 blue-green pubescent, 441 blue-green glabrous, 501 green pubescent, and 208 green glabrous plants with 260 plants not easily classified. This approximates a 9:3:3:1 ratio suggesting that possibly two independent genetic factors could

be involved in the expression of blue-green color and pubescence. This is based on the assumption that a cross pollinated species tends to maintain itself with all of the genotypes in their proportionate numbers providing no differential mortality exists. In other words a plant with the genetic constitution A_a would produce a 1:2:1 ratio in the F_1 and if all of the progeny resulting from random pollination in the F_2 or later generations were available the 1:2:1 ratio would still be maintained. It does not seem unreasonable therefore, that this could be applied to additional factors with the same results. This is quite different from the situation found in self-pollinated species where heterozygosity is halved with each succeeding generation.

Because pubescent wheatgrass is quite closely related to wheat and because wheat behaves largely as a diploid the logical starting point appeared to be with diploid ratios. Tingey (49) reported that an inhibiting factor operated in the expression of dwarfing in wheat. He found that when certain wheat plants of normal height were crossed dwarf plants were obtained. It is quite evident from the data obtained in this study that the expression of blue plant color may behave in much the same manner. When the selected green glabrous plants were selfed they gave a clear-cut segregation of 3 green glabrous to 1 blue-green glabrous plant. This 1:3 ratio was also obtained when the plants were crossed among themselves. This type of segregation can also be explained by assuming two homozygous dominant genes to be necessary for the expression of blue-green color. Wider ratios than this 1:3 are needed for plant number 4 and additional factors must be

used or allo- or autopolyploid segregation. It is not difficult, therefore, to find a considerable number of genetic explanations for individual plants or groups of plants. However, when the observed ratios of crosses between these plants are compared to the theoretical ratios many of them are very quickly eliminated. This is especially true when the two contrasted types are crossed. Heatby (28) found two factors involved in the expression of pubescence in H-44-24 x Marquis cross, and it appears that two factors may be involved in the expression of pubescence in pubescent wheatgrass. It is possible to fit some of the blue-green pubescent plants to such a hypothesis. After studying these and some of the many other possibilities offered by ordinary diploid inheritance auto- and allopolyploid ratios were investigated. Cytological investigation would have been very helpful by determining the type of pairing and chromosome association in pubescent wheatgrass but time did not permit such a study to be conducted.

Autopolyploid segregation was found to be quite flexible and for this reason is very useful. With autopolyploid segregation the position of the gene in relation to the spindle-fiber attachment becomes increasingly important. When complete linkage between the gene in question and the spindle attachment exists segregation is reduced to random chromosome assortment. However, if the gene is 50 or more crossover units from the spindle-fiber attachment random chromatid segregation results. In ordinary diploids this makes no difference but in autopolyploids, for instance, altogether different ratios are obtained. Thus the location of the gene in question in relation to

the spindle-fiber attachment determines the ratio, which may range from random chromatid segregation (50% crossing over) to random chromosome segregation (no crossing over). For instance, upon selfing a hexaploid with the genetic constitution AaAaAa it is possible to obtain a 63:1 ratio with diploid chromosome type inheritance, 120:1 ratio with random chromatid segregation, and 399:1 with random chromosome assortment. Chromatid segregation of closely linked genes also gives a 399:1 ratio. This is mentioned to emphasize the complicated relationship that exists when dealing with polyploid species. It appears from the literature that allopolyploidy is more common than autopolyploidy in natural hybrid species. However, species which behave largely as allopolyploids often exhibit varying degrees of autopolyploid segregation. Therefore, in addition to true auto- and allopolyploids intermediate types occur. Such a situation as this may account for some of the irregularities found. If only a single factor difference exists the ratios obtained using diploid and polyploid segregation are very much alike for both chromosome and chromatid segregation.

Because pubescence is rather uncommon in most grass species it seems quite likely that perhaps only one or two genomes may carry genes for expression of this character. On the other hand, however, blue-green color is comparatively common in grass species and genes responsible for this character may be found in all of the genomes.

A few of the possibilities, limitations, and complications involved in a genetic study of polyploids have been emphasized by this study. However, if it has laid some of the groundwork for further

studies on pubescent wheatgrass and related polyploid species it has served its purpose.

Summary

Results of this study support earlier findings that viable seed can be produced on grass culms detached prior to flowering and sustained in water until seeds have fully developed. Detaching the culms just prior to flowering produces, in effect, a certain degree of emasculation. The removal of leaves at this time results in a small increase in seed production but the seed weight is somewhat smaller.

Freshly harvested seed planted directly in the field at or near the first of September produced plants that flowered at the normal time the following summer. Freshly harvested seed was slightly slower to germinate but per cent germination was approximately the same as for old seed.

Sprouting seeds before planting gave only small increased seedling emergence over plots where ungerminated seeds were placed in dry soil and immediately irrigated. A sizable decrease in germination was obtained when high humidity was maintained.

Progenies obtained from selfed, controlled crosses and open-pollinated plants permitted classifying the parents into groups that behaved very much alike genetically, for the characters being observed. Moderate success was obtained by assuming a genetic explanation where (BB) produces blue-green plant color and the complementary action of (P) and (T) results in the expression of pubescence. Although a sizable portion of the data gave satisfactory agreement a great deal more information must be obtained. The species appears to behave as an allopolyploid.

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Table 1. Number and weight of seeds obtained when detached grass culms had leaves removed and when leaves were left intact.

Parental Plants		Culms With Leaves Intact					Culms With Leaves Removed				
		Number of Spikes	Number of Seeds	Seeds Per Spike	Total Seed Weight	Average Seed Weight (mg.)	Number of Spikes	Number of Seeds	Seeds Per Spike	Total Seed Weight	Average Seed Weight (mg.)
2	1	5	10	2.00	0.03	3.0	4	5	1.25	0.02	4.0
3	1	5	36	7.20	0.13	3.6	5	32	6.40	0.10	3.1
4	1	5	0	0.00	0.00	0.0	5	0	0.00	0.00	0.0
5	1	5	67	13.40	0.34	5.1	5	5	1.00	0.02	4.0
6	1	5	2	0.40	0.01	5.0	5	2	0.40	0.01	5.0
7	1	5	1	0.20	0.00	0.0	5	1	0.20	0.00	0.0
8	1	5	1	0.20	0.00	0.0	5	3	0.60	0.02	6.7
9	1	5	50	10.00	0.20	4.0	5	5	1.00	0.02	4.0
10	1	5	71	14.20	0.35	4.9	5	1	0.20	0.00	0.0
1	2	5	0	0.00	0.00	0.0	5	0	0.00	0.00	0.0
3	2	5	13	2.60	0.05	3.8	5	39	7.80	0.11	2.8
4	2	4	00	0.00	0.00	0.0	4	9	2.25	0.02	2.2
5	2	5	0	0.00	0.00	0.0	5	42	8.40	0.17	4.0
6	2	5	0	0.00	0.00	0.0	5	7	1.40	0.02	2.9
7	2	3	12	4.00	0.05	4.2	5	40	8.00	0.20	5.0
8	2	4	0	0.00	0.00	0.0	5	5	1.00	0.02	4.0
9	2	5	1	0.20	0.00	0.0	5	5	1.00	0.02	4.0
10	2	5	12	2.40	0.06	5.0	5	45	9.00	0.23	5.1
1	3	5	10	2.00	0.04	4.0	5	0	0.00	0.00	0.0
2	3	5	1	0.20	0.00	0.0	5	0	0.00	0.00	0.0
4	3	5	0	0.00	0.00	0.0	5	0	0.00	0.00	0.0
5	3	5	19	3.80	0.06	3.2	5	5	1.00	0.02	4.0
6	3	5	10	2.00	0.04	4.0	5	0	0.00	0.00	0.0
7	3	5	62	12.40	0.26	4.2	5	2	0.40	0.01	5.0
8	3	5	0	0.00	0.00	0.0	5	1	0.20	0.00	0.0
9	3	5	11	2.20	0.05	4.5	5	24	4.80	0.10	4.2
10	3	5	16	3.20	0.06	3.8	5	26	5.20	0.13	5.0
1	4	5	1	0.20	0.00	0.0	5	0	0.00	0.00	0.0
2	4	5	0	0.00	0.00	0.0	5	0	0.00	0.00	0.0
3	4	5	53	10.60	0.28	5.3	3	68	22.66	0.24	3.5
5	4	5	8	1.60	0.04	5.0	5	55	17.60	0.33	3.7
6	4	5	11	2.20	0.09	8.2	5	35	7.00	0.16	4.6
7	4	5	5	1.00	0.01	2.0	5	11	2.20	0.06	5.5
8	4	5	6	1.20	0.02	3.3	5	0	0.00	0.00	0.0
9	4	5	38	7.60	0.10	2.6	5	25	5.00	0.09	3.6
10	4	5	80	16.00	0.44	5.5	5	4	0.80	0.01	2.5

Table 1. (continued)

Parental Plants		Number of Spikes	Number of Seeds	Seeds Per Spike	Total Seed Weight	Average Seed Weight (mg.)	Number of Spikes	Number of Seeds	Seeds Per Spike	Total Seed Weight	Average Seed Weight (mg.)
1	5	4	2	0.50	0.01	5.0	5	22	4.40	0.05	2.3
2	5	5	0	0.00	0.00	0.0	5	2	0.40	0.01	5.0
3	5	5	25	5.00	0.11	4.4	5	23	4.60	0.07	3.0
4	5	5	3	0.60	0.01	3.3	5	3	0.60	0.01	3.3
6	5	5	5	1.00	0.03	6.0	5	4	0.80	0.01	2.5
7	5	4	12	3.00	0.04	3.3	5	7	1.40	0.02	2.9
8	5	5	0	0.00	0.00	0.0	5	0	0.00	0.00	0.0
9	5	5	0	0.00	0.00	0.0	5	110	2.00	0.05	3.0
10	5	5	5	1.00	0.01	2.0	5	17	3.40	0.08	4.7
1	6	5	4	0.80	0.01	2.5	5	53	10.60	0.21	4.0
2	6	5	8	1.60	0.04	5.0	5	1	0.20	0.00	0.0
3	6	5	26	5.20	0.12	4.6	5	41	8.20	0.15	3.7
4	6	5	6	1.20	0.02	3.3	5	8	1.60	0.01	1.3
5	6	5	80	16.00	0.39	4.9	5	99	19.80	0.41	4.1
7	6	5	63	12.60	0.26	4.1	5	57	11.40	0.27	4.7
8	6	5	14	2.80	0.05	3.6	5	13	2.60	0.06	4.6
9	6	5	2	0.50	0.01	5.0	5	4	0.80	0.01	2.5
10	6	5	9	1.80	0.04	4.4	5	65	13.00	0.31	4.8
1	7	5	0	0.00	0.00	0.0	5	0	0.00	0.00	0.0
2	7	4	0	0.00	0.00	0.0	5	0	0.00	0.00	0.0
3	7	5	38	7.60	0.10	2.6	5	0	0.00	0.00	0.0
4	7	5	5	1.00	0.01	2.0	5	6	1.20	0.03	5.0
5	7	5	1	0.20	0.00	0.0	5	42	8.40	0.14	3.3
6	7	4	27	6.75	0.13	4.8	5	1	0.20	0.00	0.0
8	7	5	0	0.00	0.00	0.0	5	0	0.00	0.00	0.0
9	7	5	20	4.00	0.05	2.5	5	109	21.80	0.34	3.1
10	7	5	11	2.20	0.02	1.8	5	38	7.60	0.10	2.6
1	8	5	0	0.00	0.00	0.0	5	23	4.60	0.07	3.0
2	8	4	2	0.50	0.01	0.5	5	4	0.80	0.02	5.0
3	8	6	33	5.50	0.13	3.9	5	6	1.20	0.02	3.3
4	8	5	53	10.60	0.18	3.4	5	51	10.20	0.19	3.7
5	8	5	61	12.20	0.22	3.6	5	25	5.00	0.14	5.6
6	8	5	43	8.60	9.19	4.4	5	0	0.00	0.00	0.0
7	8	5	5	1.00	0.02	4.0	4	20	5.00	0.09	4.5
9	8	4	10	2.50	0.04	4.0	5	46	9.20	0.18	3.9
10	8	5	35	7.00	0.19	5.4	5	26	5.20	0.13	5.0
1	9	5	0	0.00	0.00	0.0	5	0	0.00	0.00	0.0
2	9	5	8	1.60	0.05	6.0	5	5	1.00	0.04	8.0
3	9	5	18	3.60	0.06	3.3	5	0	0.00	0.00	0.0
4	9	3	16	8.00	0.08	5.0	3	5	1.67	0.02	4.0
5	9	3	45	15.00	0.22	4.9	5	83	16.60	0.45	5.4
6	9	5	26	5.20	0.10	3.8	5	9	1.80	0.04	4.4
7	9	5	92	18.40	0.47	5.1	5	85	17.00	0.45	5.3
8	9	4	11	2.75	0.05	4.5	5	28	5.60	0.11	3.9
10	9	5	14	2.80	0.08	5.7	5	32	6.40	0.15	4.7

Table 1. (continued)

Parental Plants		Number of Spikes	Number of Seeds	Seeds Per Spike	Total Seed Weight	Average Seed Weight (mg.)	Number of Spikes	Number of Seeds	Seeds Per Spike	Total Seed Weight	Average Seed Weight (mg.)
1	10	4	0	0.00	0.00	0.0	5	0	0.00	0.00	0.0
2	10	5	0	0.00	0.00	0.0	5	7	1.40	0.02	2.9
3	10	5	31	6.20	0.10	3.2	5	32	6.40	0.10	3.1
4	10	5	2	0.40	0.01	5.0	5	2	0.40	0.01	5.0
5	10	4	40	10.00	0.16	4.0	5	12	2.40	0.05	4.2
6	10	5	17	3.40	0.08	4.7	5	11	2.20	0.04	3.6
7	10	5	72	14.40	0.29	4.0	5	19	3.80	0.10	5.3
8	10	5	23	4.60	0.10	4.3	5	28	5.60	0.16	5.7
9	10	5	46	9.20	0.22	4.8	4	41	8.20	0.18	4.4
11	16	9	6	0.76	0.01	1.6	10	60	6.00	0.25	4.2
11	17	11	32	2.91	0.10	3.1	8	40	5.00	0.15	3.8
11	18	10	4	0.40	0.02	5.0	9	6	0.67	0.02	3.3
11	19	10	3	0.30	0.01	3.3	9	6	0.67	0.05	5.0
11	20	11	20	1.82	0.05	2.5	9	54	5.00	0.15	2.8
12	16	10	0	0.00	0.00	0.0	9	82	9.11	0.42	5.1
12	17	10	117	11.70	0.40	3.4	8	22	2.75	0.11	5.0
12	18	11	0	0.00	0.00	0.0	10	10	1.00	0.05	5.0
12	19	10	2	0.20	0.00	0.0	10	4	0.40	0.02	5.0
12	20	11	14	1.27	0.04	2.8	10	40	4.00	0.17	4.3
13	16	10	64	6.40	0.24	3.8	9	21	2.33	0.09	4.3
13	17	10	61	6.10	0.29	4.8	9	42	4.66	0.19	4.5
13	18	10	9	0.90	0.03	3.3	8	4	0.50	0.02	5.0
13	19	10	2	0.20	0.01	5.0	9	18	2.00	0.09	5.0
13	20	9	23	2.55	0.09	3.9	10	72	7.20	0.28	3.9
14	16	9	0	0.00	0.00	0.0	9	19	2.11	0.05	2.6
14	17	7	25	3.57	0.07	2.8	7	4	5.71	0.01	2.5
14	18	10	14	1.40	0.00	0.0	9	1	0.11	0.00	0.0
14	19	10	0	0.00	0.00	0.0	10	0	0.00	0.00	0.0
14	20	9	13	1.44	0.04	3.1	10	44	4.40	0.17	3.9
15	16	9	4	4.44	0.01	2.5	9	6	0.67	0.03	5.0
15	17	10	0	0.00	0.00	0.0	10	3	0.30	0.01	3.3
15	18	10	0	0.00	0.00	0.0	10	0	0.00	0.00	0.0
15	19	10	26	2.60	0.11	4.2	10	0	0.00	0.00	0.0
15	20	10	4	0.40	0.02	5.0	10	1	0.10	0.00	0.0
21	26	9	1	0.11	0.00	0.0	10	11	1.10	0.03	2.7
21	27	10	9	0.90	0.00	0.0	8	38	4.75	0.11	2.9
21	28										
21	29	8	5	0.62	0.01	2.0	10	31	3.10	0.11	3.5
21	30	10	11	1.10	0.02	1.8	10	6	0.60	0.00	0.0

Parental Plants		Number of Spikes	Number of Seeds	Seeds Per Spike	Total Seed Weight	Average Seed Weight (mg.)	Number of Spikes	Number of Seeds	Seeds Per Spike	Total Seed Weight	Average Seed Weight (mg.)
22	26	9	3	3.33	0.01	3.3	10	26	2.60	0.10	3.8
22	27	9	0	0.00	0.00	0.0	10	0	0.00	0.00	0.0
22	28	10	1	0.10	0.00	0.0	11	1	0.09	0.00	0.0
22	29	10	0	0.00	0.00	0.0	12	8	0.67	0.03	3.8
22	30	10	24	2.40	0.08	3.3	10	25	2.50	0.08	3.2
23	26	10	7	0.70	0.01	1.4	10	37	3.70	0.16	4.3
23	27	11	17	1.54	0.04	2.3	9	0	0.00	0.00	0.0
23	28	10	2	0.20	0.00	0.0	8	4	0.50	0.02	5.0
23	29	10	0	0.00	0.00	0.0	11	2	0.18	0.01	5.0
23	30	11	0	0.00	0.00	0.0	10	3	0.30	0.00	0.0
24	26	10	123	12.30	0.52	4.2	12	236	19.66	1.05	4.4
24	27	10	115	11.50	0.42	3.6	10	165	16.50	0.63	3.8
24	28										
24	29	5	26	5.20	0.11	4.2	10	20	1.20	0.05	2.5
24	30	10	136	13.60	0.54	4.0	10	100	10.00	0.39	3.9

Table 2. Seed production on detached vs intact culm with plants being selfed.

	Detached Culms					Intact Culms				
Plant Number	Number of Spikes	Number of Seeds	Seed Weight	Seeds Per Spike	Average Seed Weight (mg.)	Number of Spikes	Number of Seeds	Seed Weight	Seeds Per Spike	Average Seed Weight (mg.)
1	10	36	0.15	3.60	4.2	23	382	2.32	16.61	6.1
2	9	1	0.00	0.11	0.0	28	48	0.21	1.64	4.6
3	10	38	0.18	3.80	4.7	27	160	0.70	5.93	4.4
4	10	0	0.00	0.00	0.0	28	167	0.73	5.96	4.4
5	10	5	0.00	0.00	0.0	29	23	0.10	[illegible]	4.4
6	10	6	0.01	0.60	0.2	34	103	0.62	3.03	6.0
7	10	29	0.11	2.90	3.8	31	233	1.07	7.52	4.6
8	10	0	0.00	0.00	0.0	27	6	0.04	0.22	6.7
9	13	25	0.10	1.92	4.0	28	407	2.00	14.53	4.9
10	9	19	0.10	2.11	5.4	28	522	3.63	19.[illegible]	7.0
11	10	47	0.15	4.70	3.2	19	215	1.01	11.21	4.7
12	10	0	0.00	0.00	0.0	16	161	0.88	10.06	5.5
13	10	4	0.01	0.40	2.5	20	84	0.39	4.20	4.6
14	10	0	0.00	0.00	0.0	20	27	0.18	1.35	6.7
15	10	0	0.00	0.00	0.0	20	32	0.13	1.60	4.1
21	10	0	0.00	0.00	0.0	50	0	0.00	0.00	0.0
22	10	0	0.00	0.00	0.0	37	76	0.42	2.05	5.5
23	10	16	0.05	1.60	3.1	46	456	2.54	9.91	5.7
24	10	0	0.00	0.00	0.0	57	256	1.18	4.49	4.6
25	10	0	0.00	0.00	0.0	62	0	0.00	0.00	0.0
Total	201	226	0.76	21.74	8.7	630	3354	18.15	119.74	4.8

Table 3. Seed production on detached vs intact culms with open-pollination.

	Detached Culms					Intact Culms				
Plant Number	Number of Spikes	Number of Seeds	Seed Weight	Seeds Per Spike	Average Seed Weight (mg.)	Number of Spikes	Number of Seeds	Seed Weight	Seeds Per Spike	Average Seed Weight (mg.)
1	10	17	0.06	1.70	3.5	10	388	1.86	34.80	5.3
2	10	17	0.07	1.70	4.1	10	122	0.60	12.20	4.9
3	10	270	1.20	27.00	4.4	10	207	0.91	20.70	4.4
4	11	197	0.87	17.91	4.4	10	310	1.61	31.00	5.2
5	10	345	2.07	34.50	6.0	10	395	2.16	39.30	5.5
6	10	93	0.43	9.30	4.6	10	252	1.45	25.20	5.8
7	10	294	1.44	29.40	4.9	10	360	2.01	36.00	5.6
8	10	70	0.42	7.00	6.0	10	168	1.13	16.80	6.7
9	10	196	0.85	19.60	4.3	6	241	1.25	40.17	5.2
10	10	179	0.78	17.90	4.4	10	511	3.19	51.10	6.2
11	20	674	2.62	33.70	3.9	10	487	2.36	48.70	4.8
12	20	179	0.59	8.95	3.3	10	361	1.91	36.10	5.3
13	20	390	1.04	19.50	2.7	11	452	2.54	39.27	5.9
14	21	126	0.31	6.00	2.5	10	454	2.69	45.40	5.9
15	19	46	0.13	2.42	2.8	10	327	1.80	32.70	5.5
21	20	262	0.87	13.10	3.3	11	277	1.44	25.18	5.2
22	20	150	0.68	7.50	4.5	12	146	0.80	12.17	5.5
23	19	136	0.51	7.16	3.8	10	247	1.58	24.70	6.4
24	20	465	2.26	23.25	4.9	15	473	2.28	31.53	4.8
25	20	54	0.22	2.70	4.1	10	94	0.46	9.40	4.9
Total	300	4151	17.42	283.29	2.4	205	6210	34.01	611.52	9.2

Table 4. Seed production from selfed and crossed detached female culms showing fall seedling emergence and winter survival of their progeny.

Crosses Female	Crosses Male	No. of Seeds Planted	No. of Fall Seedlings	Per Cent Emergence	No. of Spring Plants	Per Cent Winter Survival
1	1	418	146	35	142	34
1	2	0	0	0	0	0
1	3	12	0	0	0	0
1	4	1	1	100	1	100
1	5	24	5	21	3	12
1	6	57	14	24	11	19
1	7	0	0	0	0	0
1	8	23	1	4	0	0
1	9	0	0	0	0	0
1	10	0	0	0	0	0
2	1	15	5	33	3	20
2	2	47	20	42	16	34
2	3	1	0	0	0	0
2	4	0	0	0	0	0
2	5	2	0	0	0	0
2	6	9	5	56	4	44
2	7	0	0	0	0	0
2	8	6	2	33	2	33
2	9	13	1	8	1	8
2	10	7	1	14	0	0
3	1	68	21	31	18	26
3	2	52	9	17	3	6
3	3	198	66	33	47	24
3	4	121	36	30	28	23
3	5	48	4	8	3	6
3	6	67	28	42	26	39
3	7	38	12	32	7	18
3	8	39	24	62	18	46
3	9	18	5	28	4	22
3	10	65	11	17	6	10
4	1	0	0	0	0	0
4	2	22	5	23	1	4
4	3	0	0	0	0	0
4	4	167	77	46	59	35
4	5	6	1	17	1	17
4	6	14	1	7	0	0
4	7	11	1	9	0	0
4	8	104	37	36	28	27
4	9	21	11	52	9	43
4	10	4	1	25	1	25

Table 4. (continued)

Crosses Female	Crosses Male	No. of Seeds Planted	No. of Fall Seedlings	Per Cent Emergence	No. of Spring Plants	Per Cent Winter Survival
5	1	72	14	19	13	18
5	2	42	4	10	4	10
5	3	24	4	17	4	17
5	4	96	24	25	17	18
5	5	77	39	51	38	49
5	6	179	84	47	78	44
5	7	43	13	30	11	26
5	8	86	15	17	12	14
5	9	128	59	46	57	44
5	10	52	11	21	8	15
6	1	4	0	0	0	0
6	2	7	1	14	0	0
6	3	10	4	40	4	40
6	4	57	11	19	10	18
6	5	9	2	22	1	11
6	6	109	41	38	35	32
6	7	28	7	25	6	21
6	8	43	9	21	6	14
6	9	35	9	26	9	26
6	10	28	2	7	2	7
7	1	0	0	0	0	0
7	2	52	24	46	21	40
7	3	64	55	55	31	48
7	4	16	1	6	1	6
7	5	19	4	21	4	21
7	6	120	38	32	29	24
7	7	262	85	32	48	18
7	8	25	9	36	6	24
7	9	177	70	40	66	37
7	10	91	16	18	14	15
8	1	4	1	25	1	25
8	2	5	0	0	0	0
8	3	1	0	0	0	0
8	4	6	0	0	0	0
8	5	0	0	0	0	0
8	6	27	5	18	5	18
8	7	1	1	100	1	100
8	8	6	3	50	2	33
8	9	39	9	23	5	13
8	10	51	9	18	6	12

Table 4. (continued)

Crosses Female	Crosses Male	No. of Seeds Planted	No. of Fall Seedlings	Per Cent Emergence	No. of Spring Plants	Per Cent Winter Survival
9	1	55	16	29	7	13
9	2	3	0	0	0	0
9	3	35	17	48	17	48
9	4	63	11	17	11	17
9	5	10	2	20	2	20
9	6	6	1	17	0	0
9	7	129	50	39	41	32
9	8	56	19	34	11	20
9	9	432	153	35	125	30
9	10	87	34	39	32	37
10	1	71	21	30	16	22
10	2	57	24	42	19	33
10	3	42	8	19	6	14
10	4	84	10	12	9	11
10	5	22	1	4	1	4
10	6	74	17	23	15	20
10	7	49	3	6	2	4
10	8	61	19	31	16	26
10	9	46	8	17	8	17
10	10	541	266	50	257	48