GENIC ANALYSIS IN AVENA

A MONOGRAPH[1)]

By

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COLOR INHERITANCE

§ Glume (Grain)

In Avena, color of the grain is located in the glumes. The colors of oats may be grouped into black, brownish red, gray, and white. These colors, however, are easily affected by environmental conditions (such as humidity, degree of maturity, soil conditions). It is nearly impossible to distinguish between yellow and white. A white grain when weathered slightly may have a yellowish tinge.

A detailed study on the inheritance of these colors was made by NILLSSON-EHLE (43). A number of crosses showed monogenic differences between black and white, yellow and white, gray and white. Some crosses between black and yellow gave in F_2 a digenic ratio of 12 black : 3 yellow (or yellowish) : 1 white ; black and white gave likewise a ratio of 12 black : 3 gray : 1 white. In another cross, yellow (Gold Rain) × black (Moss), the F_2 consisted of four types : black, yellow, gray, and white. Some crosses of gray with yellow gave in F_2 gray, yellow, yellowish gray, and white. These results were explained on the assumption of three color genes, S for black, $\underset{\smile}{Gr}$ for gray, and G for yellow. The genic scheme is as follows :

S($\underset{\smile}{Gr}$G) . . . . . black,
s$\underset{\smile}{Gr}$(G) . . . . . gray,
s$\underset{\smile}{gr}$G . . . . . yellow,
s$\underset{\smile}{grg}$. . . . . white.

It was further found that a certain black-white cross gave in F_2 15 black to 1 white, indicating that the black color is produced by duplicate genes, S_1 and S_2. These genes have a cumulative effect. In addition to these main genes, there were found several modifying genes (M_1, M_2, etc.) which dilute the black color.

This genic scheme has been repeatedly confirmed by a number of investigators. WILSON (76, 77), NORTON (51), GAINES (16), ZINN and SURFACE(79), GARBER(22), TSCHEMAK(in 15), QUISENBERRY(57), GARBER and QUISENBERY (26), GARBER, GIDDINGS and HOOVER (24), HAYES, GRIFFEE, STEVENSON and LUNDEN (29), ODLAND (52),—all working with varieties of *A. sativa* found the monogenic difference between black and white ; LOVE and CRAIG (37) obtained a 15 black : 1 white in F_2 from a cross between two black varieties ; SURFACE (65, 66) and LOVE and

CRAIG (36), in crosses of a black *fatua* with a yellow *sativa*, obtained a digenic F_2 segregation of 12 black : 3 gray : 1 yellow. And CAPORN (4) dealing with crosses of three varieties of *sativa* with *sativa nuda* observed the following ratios in F_2. Gray : white=3:1, Black : gray= 3 : 1, or 15 : 1, and black : gray : white=60 : 3 : 1[1]. Similarly MEURMAN (41) from several crosses obtained the mono- and digenic segregations for black and non-black glumes. A cross between two black varieties gave a 15 : 1 ratio which was fully confirmed by F_3 breeding.

The variation within the gray group has been studied by several investigators. NILSSON-EHLE (43) and SURFACE (66) observed that the plants heterozygous for $\underset{\smile}{\mathbf{Gr}}$ are so much lighter in color than those homozygous for $\underset{\smile}{\mathbf{Gr}}$ that the difference can be easily distinguished. They also suggested that there are still other genes which may modify the intensity of the gray color. Later, MEURMAN (41) identified one of these modifying genes. On the basis of the F_3 results of a cross, black × white, the author found that constant deep gray, segregating, and constant light gray strains appeared in a 1 : 2 : 1 ratio. The gene involved was symbolized as **Z** and was considered to be effective only in the presence of $\underset{\smile}{\mathbf{Gr}}$, and heterozygously weakened in its effect.

Another cross was made by FRASER (13) between the Burt variety which belongs to the *A. byzantina* group and produces yellowish red grains, and the Sixty Day variety of *sativa*, which produces yellow grains. The cross gave an intermediate color in F_1 and in F_2 three groups of red, yellow, and white (accurate classification being difficult) in a ratio of 48 : 15 : 1. The results were explained by supposing the Sixty Day variety to carry one gene, **Y′** for yellow (NILSSON-EHLE'S G), and the Burt variety two genes, **R** for red and **Y** for yellow. These two yellow genes are similar in their effect on glume color, but different in the inhibiting effeect on awn production (See p. 84). **R** is considered to be epistatic to both **Y** and **Y′**. The relation between **R** and **S** or $\underset{\smile}{\mathbf{Gr}}$ has not been tested.

§ Stem

In a cross, Algerian × Carter's Royal Cluster, PRIDHAM(55) observed F_2 segregation into plants with the reddish or pinkish tinge (characteristic of Algerian) and those with the green stem. The auther states

1) Actually he obtained : 40 : 2 : 1.

that "Pigment in the straw behaves as a Mendelian character, occurring approximately in the ratio of 1 to 3". But his actual data indicate a ratio close to 1:2 (actually 355:737). The genic situation of stem color needs further experimant.

EAR CHARCTERS

§ Type of Panicles

There are two types of panicle shape in oats, side panicle and open panicle. In the former, the branches all extend upward and out to one side of the rachis. In the latter, the branches spread out on all sides of the rachis, giving an appearance like a tree in shape. Within each type, there are some variations.

According to NILSSON-EHLE (42, 43), the difference between the open-panicled and the side-panicled froms is due to several independent genes, the presence of any one of which produces open panicles, while the absence of all of the genes results in side panicles. The genes were shown to have a cumulative effect. When these genes are homozygous, a variety with a strongly open, lax panicle and drooping branches is obtained. An open-panicled form with obliquely erect branches ('Steifrispentypus') was found to differ by a single gene from the pure recessive side-panicled form. From crossing two 'Steifrispen' forms, he obtained in F_2 9 side forms out of a total of 112 plants. These side-panicled plants bred true, while of the 103 open-panicled forms, 24 again showed segregation, giving both open- and side-panicled plants. Among the open-panicled segregates, some plants were more open than either of the parents.

GARBER (23) identified a single main gene fore open panicles in crosses of Minota or Victory (open) with White Russian (side), and ODLAND (52) reached the same conclusion from crosses of Gothland (open) with Garton 784 (side). QUISENBERY (57), on the other hand, identified two duplicate genes from a cross, Victor (open) × Sparrowbill (side, *sativa orientalis*), the F_2 ratio being close to 15 open : 1 side.

GAINES (16) obtained, however, more complex results from his several crosses of side-panicled with open-panicled oats. Black Tartarian × Swedish Select, Black × Regenerated Swedish Select, Black × Sixty Day, and Black × Palouse Wonder gave in F_2 33 2, 14.4, 1.53, and 5.5 per cent of side oats respectively. Irregular ratios were

also obtained in F_3 from heterozygous tree oats, in which the percentage of side type varied from 51% to 11.4%. It was further recorded that some extracted tree and side plants produced nothing but true intermediates. No explanation was possible on these results.

§ Wax Efflorescence on the Glumes

There is a variation in oats in the amount and in the presence and absence of wax deposit on the lemma. NILSSON-EHLE (42) briefly states that its presence and absence behaves in the ordinary manner of inheritance. MEURMAN (41) found that the formation of wax is due to a single gene, W. The effect of W when heterozygous is weakened, thus the segregation occurring in the 1:2:1 ratio. It was further found that the formation and degree of wax efflorescence is also due to another (possibly one) strengthening gene, the absence of which results in relatively thin deposit, and the plants heterozygous for this gene show weaker formation of wax than the homozygotes.

§ Pubescence on the Glumes

NILSSON-EHLE (42) has studied the inheritance of this character. The basie of the glume of oats is covered by either short or long hairs, or lacks them. Crosses between the long-haired and the short-haired variety gave F_1 plants showing a mixture of both types of hairs and in F_2 a digenic segregation, throwing individuals having no hairs as a new combination. Two genes were assumed, L for long hairs, and K for short hairs. The absence of both the genes results in the absence of hairs.

Later, LOVE and CRAIG (37) mention mono- and digenic (15:1) segregations for pubescent and glabrous glumes in certain crosses. They gave, however, no account concerning the length of hairs.

§ Development of Awns

Oats show a considerable variation in degree of awning. They may be classified into three groups, strong, medium-strong, and weak awns (FRASER, 13). The strong awn is long, stiff, and geniculated. It is twisted at the basal portion and is dark in color on the twisted part. The wild types of oats are characterized by this sort of awns. The

medium-strong awn lacks the geniculation and is less stiff. The weak awn lacks further the tendency to twist, and the dark color as well, and is usually straight from the point of attachment to the tip. The weak awn comprises a large variation in length, thickness, and rigidity.

The inheritance of strong awn of *A. fatua* has been studied by SURFACE(65, 66) in crosses with a cultivated oat, *A. sativa*, var. Kherson which has no or a very few weak awn on the lower grain. The F_1 plants presented an intermediate condition between the parents, awns being present on the lower grain of many spikelets (but never on the upper grain, as in the *sativa* parent). In F_2 a monogenic segregation following a ratio of 1 (no awns) : 2 (intermediate awns) ; 1 (wild awns) was obtained (actually 133 : 215 : 112). The author, however, suggests that modifying genes may be involved which produce awns in various intermediate degrees.

Later, LOVE and FRASER (38) and LOVE and CRAIG (36) likewise reported a 1 : 2 : 1 F_2 ratio in crosses between *A. fatua* and the Sixty Day variety.

Crosses of weak awn × awnless were studied by LOVE and FRASER (38) and FRASER (13). The weak-awned parent was the Burt variety (*A. byzantina*) and the awnless parent was the Sixty Day variety. The F_1 plants were awnless, and the F_2 showed all degrees of awning, from the perfectly awnless condition to those awned like the awned parent. On grouping these forms in the three classes, they obtained a ratio of 1 awnless : 2 partially awned : 1 fully awned (one of the actual results being 172 : 418 : 180 ; FRASER, 12), or 1 fully awned : 3 remaining. The fully awned plants bred true in F_3, nearly all the partially awned plants again segregated, while some of the awnless plants bred true but others were heterozygous as the F_1 plants. The authors consider that some of these variable results are partly due to an influence of environmental conditions on awn development and partly due to an effect of the inhibiting gene possessed by the Sixty Day variety. (See the next page).

Using varieties belonging to the sativa group, QUISENBERRY (38) and HAYES *et al* (29) have studied the inheritance of the strong awn. Their results seemed to indicate a more complex nature of the development of awns. QUISENBERRY, in a cross of Victor (strong-awned) × Sparrowbill (weak-awned, nearly awnless), obtained F_1 plants of an intermediate type, and in F_2 a proportion of 246 plants with strong awns to 752 with other types, of which only 14 plants produced no

awns. In F_3 very few families bred true for awnlessness, and relatively few bred true for strong awns. The data obtained by HAYES *et al* from a cross between a selection (weakly awned) from Minota × White Russian and Black Mesdag (strongly awned) showed a F_2 ratio of 99 plants with strong awns to 270 with weak or no awns, of which 59 produced no awns. F_2 plants with 0 to few awns bred true in F_3 for this character, while strongly awned F_2 types gave segregation for the most part.

Another cross was made by ZINN and SURFACE(79) between a *sativa nuda* and the Victory variety. In this cross, the awn formation, like the pubescence (see p. 85), was found to be affected by the nature of the glumes. All naked grains of the naked forms or the naked spikelets of the heterozygotes bear only a thin, weak awn. Owing to this relation between the kind of awn and the character of the hull, plants with naked or almost naked grains were disregarded in studying the inheritance of the awns, and thus considering only the hulled and intermediate types of grain, the authors obtained a 3 : 1 ratio in F_2 between plants with medium-strong to strong awns and those with weak awns (actually 245 : 77).

NILSSON-EHLE (48) appears to be the first investigator to have made an observation on the relation of the production of awns to glume color. From crossing an awnless yellow Probsteier strain with an awned black cultivated oat, he found that the yellow oats segregated from the cross contained fewer awns than did the blacks, whites, and grays. This negative correlation between awning and yellow color was explained on the assumption that the yellow gene acts as an inhibitor upon the production of awns. Analogous cases were reported by LOVE and CRAIG (36) and TSCHERMAK (71) in the *fatua-sativa* cross. The yellow types possessed very few or no awns, making a sharp contrast to the blacks or grays which showed varying degrees of the awned condition from awnless to fully awned.

SURFACE (65, 66) states, on the other hand, from his experiments with a black *fatua* and a yellow *sativa* (var. Kherson) that "while there is a slightly greater proportion of the yellow plants which are awnless than the other color, yet the difference can not be regarded as significant." But the number obtained was too small to make a final decision whether the Kherson variety possesses an inhibiting gene or not.

Later, LOVE and FRASER (38) and FRASER (13) reported on a variety,

Burt, containing a gene for yellow which does not inhibit awning. This gene was designated as Y.[1] Y has a similar effect on glume color as the other yellow gene, Y′, but differs from the latter in having no power of inhibiting the production of awns.

The existence of such a yellow gene, independent of awn development has been demonstrated by frequent occurrence of yellow fatuoids (which are essentially awned) in yellow-grained varieties, as reported by several workers such as CREPIN (8, 9), GARBER (22), STANTON, COFFMAN and WIEBE (64), and STANTON and COFFMAN (63).

JONES (35), on the other hand, in a cross between a fatuoid plant bearing white grains which was found in yellow-grained Golden Rain oats and the parental variety, obtained segregation in F_2 into non-fatuoid plants which were all yellow-grained and fatuoid plants which were all white-grained, although the fatuoid plants when less mature showed grains which were distinctly greenish yellow in color.

§ Fatuoid Type

In the sowing of cultivated oats, *A. sativa* or *A. sativa orientalis*, individuals are sometimes found that differ from the common type in the production of strong awns on all grains in heavy pubescence and in the marked basal articulation,[2] resembling the wild oats, *A. fatua*. Apart from these characters, the entire plant is indistinguishable from the cultivated variety in which it arises. These aberrant forms are known under the name of 'fatuoids' or 'false wild oats.' The fatuoids usually differ monogenically from the normal plants, the heterozygotes segregating into normal, heterozygous, and fatuoid forms in a 1:2:1 ratio. Heterozygotes have the geniculate awn and the fatua type of callus only on the lower grain. This situation was first reported by

1) FRASER, however, assuming an inhibiting gene I, tends toward an alternative hypothesis that Y for yellow color is closely linked with I. Since no data have been obtained to determine whether the result is due to linkage between the two genes or to the pleiotropic effect of one gene, the latter hypothesis may be adopted in the present discussion.

2) A type which was found in Kanota oats, a variety of *A byzantina* (described in 54) is 'false wild' with respect to awns and pubescence, but differs from the fatuoid type in its nonarticulate character.

NILSSON-EHLE (44, 49), and repeatedly confirmed by several other investigators, e.g., ÅKERMAN (1), GARBER (22), GARBER and QUISENBERRY (25), GOULDEN (27), HUSKINS (30), RAUM and HUBER (58), JONES (35) &c[1].

In addition to this normal fatuoid type, HUSKINS (32, 33) found still other segregation types of fatuoids which are analogous to the A, B, C series of Speltoids of NILSSON-EHLE. Their cytology is also similar.

Another peculiar type of fatuoids has been described by GOULDEN (27), in which fatuoid dwarfs and heterozygous fatuoids occur in a 1 : 1 ratio, the normal type being practically eliminated.

§ Hulled versus Hull-less Grains

The hull-less or naked oats (*A. sativa nuda*) are distinguished from the other species of *Avena* by the following four characteristics: (1) The lemma and paleae do not clasp the grain, the latter remaing loose or free within the chaff and readily separating in threshing; (2) The rachillae of the spikelets are much elongated so that the uppermost grains are borne well above the empty glumes; (3) The empty glumes and lemmas are similar in structure, being thin and membranous; (4) The spikelets of the panicle are multiflowered varying from 4 to 9.

Crosses involving naked oats have been investigated by a number of workers, viz., NORTON (51), NILSSON-EHLE (44, 48), GAINES (16), ZINN and SURFACE (79), CAPORN (4), LOVE and CRAIG (37), LOVE and MCROSTIE (39), TSCHERMAK in 15), etc. All these investigators have obtained intermediate conditions in F_1, with both kinds of grains, hulled and hull-less, borne in the same panicle. As a rule, the basal portions of the panicle contain many more hulled grains than the terminal portions. The F_2 segregation suggests a monogenic difference between

1) STANTON, COFFMAN and WIEBE (64), however, are of another opinion different from other investigatior's conclusions in the following two points: (1) the heterozygotes are not phenotypically distinguishable from the homozygous fatuoids, (2) several fatuoid forms found in *A. byzabtina* (Fulghum and Burt) may be heterozygous. According to their designation, there are therefore four genotypes to be distinguished: (1) homozygous-fatuoid, (2) heterozygous fatuoid, (3) heterozygous-cultivated (heterozygous-fatuoid of other writers), and (4) homozygous cultivated. Though the complete genic analysis had not yet been given, they obtained evidence showing that fatuoids found in *A. byzantina* may differ from the cultivated form by several, at least, two genes, making a contrast with fatuoids in *A. sativa* differing by a single gene.

the hulled and hull-less conditions.[1)2)] The hulled and hull-less grains from heterozygous plants give similar results, viz., the 1 : 2 : 1 ratio.

LOVE and MCROSTIE have further studied the nature of great variability in the percentage of hulled or hull-less grains which was shown in the different heterozygous individuals of the F_2 generation. The variation ranged from less than 5 per cent to 95 per cent or more. They observed a close agreement in regard to the hulled percentage between the F_2 intermediate plants and their heterozygous offspring giving high or low percentage respectively. These results seem to indicate the presence of some modifying gene or genes which affect the heterozygous forms in such a way as to modify the amount of hulled or hull-less grains present. But this explanation did not appear to hold true in all cases tested. In certain cases, the degree of hull-lessness seemed to influence the segregation type in the following generations, the plants having a low percentage of hulled grains tending to produce a relatively higher number of hull-less plants than the expected 1 : 2 : 1 ratio.

CAPORN, on the other hand, made observations on variations in the structure of paleae. Heterozygous F_2 plants from crosses of *A. nuda* with Thousand Dollar and Ligowa gave several intermediate forms in addition to the parental forms. They were grouped into: (1) 'Pure tight' in which all the grains on the plant are tight; (2) 'Tight-containers' in which some of the grains are pure tight; (3) 'Hard-backs' in which paleae are partly membranous, partly hardened, but no pure tight paleae were found; (4) 'Penultilooses' which resemble the former type, but the hardening is never found above the lowest palea in any of the spikelets; and (5) 'Pure looses' in which all paleae are absolutely membranous. It was further found that most tight-containers throw pure tight plants among their offspring, but some of them do not throw any. Actual results indicated a 1 : 2 : 1 ratio for pure tights, heterozygous tight-containers, and other *nuda* forms.

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1) Some actual F_2 data may be given:

		Hulled	Interm.	Hull-less
ZINN and SURFACE:	*A. sativa nuda* var. *inermis* × *A. sativa patula*	221	404	229
LOVE and MCROSTIE:	Hullesss × Black Tartarian	37	85	38
	Danish Island × Hulless	115	216	114
	Hulless × *A. fatua*	68	111	78
	Hulless × Swdish Select	41	90	31
	Hulless × Sixty Day	75	193	53

2) REED (58), on the contrary, reports that the F_1 plants from his cross of Hulless with Black Mesdag did not show the intermediate type of spikelets, the few-flowered hulled type being completely recessive.

The appearance of these several forms in the *nuda* group led the author to the tentative assumption of the following genes:

X: a gene capable of rendering all the paleae on the plant pure tight,

Y: a gene capable of rendering some of the paleae on the plant pure tight,

Z: a gene capable of rendering some of the paleae on the plant more or less sclerotised but never wholly tight.

The pure tight are homozygous for X, and the heterozygous tight-containers are Xx. Several different combinations of Y and Z are responsible for several forms present in the *nuda* group (xx). Some evidence favoring this hypothesis was further obtained by breeding behaviors of *nuda* forms. Five distinct breeding behaviors have been recognized, indicating the segregation involving either Y or Z or both. They are:

1) Forms throwing 1 tight-containers to 3 three other forms (hardbacks, penulti-looses, and pure looses).

2) Forms throwing 1 tight-containers to 3 two other forms (hardbacks and penulti-looses).

3) Forms throwing 3 tight-containers to 1 hardback.

4) Forms throwing 3 hardbacks to 1 two other forms (penulti-looses and pure looses).

5) Forms throwing 1 penulti-looses to 3 pure looses.

Grain Characters

§ Pubescence on the Back of the Grain

A. fatua is characterized by having heavy pubescence on the back of each (upper and lower) grain. This pubescence is longer and heavier in ther case of the lower grain.

Surface (65, 66) made a cross of *fatua* with the Kherson variety of *A. sativa*, the latter lacking this pubescence entirely. The F_1 plants were pubescent on the lower grain, but smooth on the upper. As regards the lower grain, the F_2 segregation occurred in a 3:1 ratio, indicating that a single gene—which was symbolized as P—was concerned. The gene P was found to be closely linked with the color gene B (for black). (See under Linkage Relations). As for the upper grain,

the F_2 consisted of smooth and pubescent plants in a 13 : 3 ratio. This suggests that the gene for pubescence on the back of the upper grain—which was designated as s—is unable to act in the absence of **P**. Thus we get :

PS . . . . .lower grains pubescent, upper grains smooth,
Ps . . . . .lower grains pubescent, upper grains pubescent,
p(S). . . . .lower grains smooth, upper grains smooth.

These three types appeared in a 9 : 3 : 4 ratio, or pubescent and smooth in 3 : 1.[1]

On the other hand, LOVE and CRAIG (36) in the *fatua* × Sixty Day cross obtained another segregation ratio in F_2, viz., pubescent : smooth =57 : 7.[2] They observed in this case, that all of the black oats are pubescent, the gray oats are pubescent or smooth (the ratio of pubescent : smooth=3 : 1), while the yellow oats have smooth grains. From these results they assumed that there are two genes for pubescence, one of which, **P**,[3] is linked with black and the other, **P′**,[4] is independent of any color gene, and further that the yellow gene **Y′** inhibits the production of pubescence in the absence of **B** (for black) and **G** (for gray). Thus the cross, *fatua* (**BPGP′Y′**) × Sixty Day (**bpgp′Y′**), gives in F_2 :

BP(GP′)Y′. . . . . .black, pubescent (48),
bpGP′Y′. . . . . .gray, pubescent (9),
bpGp′Y′. . . . . .gray, smooth (3),
bpg(P′)Y′ . . . . . .yellow, smooth (4).

The actual results obtained were found to accord well with the theoretical ratio. In other crosses, *fatua* × Tartar King, they obtained in F_2 a 15 (pubescent) : 1 (smooth) ratio in one strain and 3 : 1 in another. From these results where no inhibiting effect was produced by the yellow gene, the presence of two kinds of genes for pubescence in *fatua* was fully confirmed.

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1) Actually he obtained : 87 (both grains pubescent), 258 (one grain pubescent), and 120 (smooth).

2) Actually they obtained : 138 (both grains pubescent), 240 (one grain pubescent), and 42 (smooth) in F_2 ; and 110 (both grains pubescent), 156 (one grain pubescent), and 42 (smooth) in F_3 from the heterozygous F_2 plants.

3) **B** of LOVE and CRAIG.

4) **P** of LOVE and CRAIG.

§ Pubescence at the Base of the Grain

SURFACE (65, 66) made some observations on the inheritance of pubescence at the base of the lower grain in his *fatua-sativa* crosses. On the grain of the wild parent the callus is surrounded on the dorsal and lateral sides with a ring of short stiff hair. On the grain of the cultivated parent (the Kherson variety) this pubescence is entirely absent. The F_1 plants showed an intermediate condition, showing medium-heavy tuft of hairs at the side of the base, but the dominance of no pubescene on the base of the upper grain. There was no pubescence on the base of the upper grain of any plants except those with a typical wild base. In F_2 a 1:2:1 ratio was obtained for lower grains and 3:1 for upper grains.

ZINN and SURFACE (79) worked on a *sativa-sativa nuda* cross, the former (the Victory variety) having a long but rather sparse pubescence at the sides of the base of the lower grain, while the latter lacked it. The character proved to be controlled by two independent genes, since a clear 15:1 ratio was obtained (actually 578:47). They also found that in this pubescence two lengths of hair are involved, the longer hairs being monogenically dominant to the short (also NILSSON-EHLE, 42). Among pubescent plants, some (81) were characterized by pubesence at the base of the upper grain only. This fact is interesting, for no single case has been reported of an oat with a smooth lower grain and pubescent upper grain. These fooms were found to appear only on spikelets where the lower grain is naked or semi-naked, and so the authors consider that the presence of this pubescence at the base of the upper grain is due to physiological disturbances caused by the presence of the naked lower grain.

Another observation was made by FRASER (13) in a *sativa-byzantina* cross. The variety Burt of the latter species has a dense tuft of hairs at each side of the basal callus of the grain. The *sativa* parent, Sixty Day, is practically devoid of hairs or occassionaly has a few short hairs. The F_1 plants inclined toward the condition found in the Sixty Day in length and density. The results in F_2 and F_3 seemed to indicate a monogenic difference between these two characters, the Burt type being recessive.

§ Type of the Base of the Grain

The base of the grain of the wild oat, *A. fatua*, is expanded into a broad sucker-like ring which permits the grain to shatter very easily,

while the cultivated races possess a narrow base which does not separate from the axis readily.

This difference was found to be monogenic by SURFACE (65, 66), TSCHERMAK (71), LOVE and CRAIG (36), and GARBER and QUISENBERRY (24). SURFACE obtained in F_2 the 3 (cultivated) : 1 (wild) ratio for the base of the upper grain and 1 (cultinated) : 2 (intermediate) : 1 (wild) for the base of the lower grain (actually 117 : 236 : 112). The F_3 breeding verified this situation. (See also under Linkage Relations).

Cultivated forms of *A. byzantina* differ from other oat species in having the upper grain adherent to the rachilla. The base of the lower grain resembles *A. fatua* in its articulation. In crosses between Burt belonging to *A. byzantina* and the Sixty Day variety, FRASER (13) obtained an intermediate F_1 and a ratio of 1 articulated base to 3 intermediate and sativa types in F_2.

As to the relation of the base to the grain color, SURFACE (65, 66) in the cross, *fauta* × *sativa* var. Kherson found that the gene for the 'cultivated base' of the grain is inherited independently of the glume color genes. On the other hand, LOVE and CRAIG (36) working with *fatua* × *sativa* var. Sixty Day[1] found that the black oats show segregation into the wild and cultivated forms as also do the grays, while the yellow oats exhibits no wild type of base but are all of the cultivated class. It seems that the yellow gene Y' inhibits the production of the wild type of base in the absence of **B** (for black) and **G** (for gray).

§ Pubescence on the Rachilla

A. fatua has a very strong pubescence on the rachilla which bears the upper grain. This character has been found by SURFACE (65, 65) to behave as a monogenic recessive to the absence of pubescence in crosses with the Kherson variety.

Using several cultivated varieties, HAYES *et al* (29) studied the inheritance of the number of hairs on the rachilla bearing the upper grain. Three selected strains from crosses of White Russian with Victory or Minota, which produced few or no hair, were crossed with Black Mesdag which produced many hairs. Two of the crosses gave a 3 : 1 ratio in F_2 of few to many hairs on the spikelet, while the other cross produced a greater proportion of few-haired segregates than the expected 3 : 1 ratio (actually 513 : 76).

1) LOVE and CRAIG state that "this Sixty Day variety is identical with the Kherson as used by Surface so far as general varietal characters are concerned."

ODLAND (52) made another observation based on the rachilla of the lower grain. A clear monogenic difference was obtained between Early Gothland (*sativa*, pubescent) and Garton 784 (*sativa orientalis*, smooth), with the dominance of smoothness.

§ Length of the Rachilla

With respect to the inheritance of rachilla length, ODLAND (52) showed that it can be explained on the multiple genic basis. The Early Gothland parent has a rachilla approximately 2.7 mm. long on its lower grain, while in the Garton 784 parent the rachilla is extremely short, being only approximately 1.6 mm. long. The F_1 plants were intermediate and the F_2 plants ranged from one parent to the other for this character. The frequency curve in F_2 suggested that the multiple genes are apparently not equal in value. In F_3, homozygous lines were obtained, both parental as well as for intermediate lengths. (See also under Linkage Relations.)

§ Length of the Grain

QUISENBERRY (57) has studied the inheritance of length of the grain (flowering glume) in a cross between Victor (*A. sativa*) and Sparrowbill (*A. sativa orientalis*). The Victor had a length of primary grain averaging 16.4 mm, while Sparrowbill had a mean length of 11.5 mm. The F_1 was intermediate in grain length, although tending to approach that of Victor. In F_2 a wide variability was obtained, ranging from the length of one parent to the length of the other. Among a total of 150 F_3 strains, 4 were recovered with a mean length as great as Victor, and 2 with a mean length as short as Sparrowbill. Between these two extremes were found lines apparently homozygous for grain of intermediate length. For explanation, the author assumed three main genes or gene complexes for grain length.

OTHER MORPHOLOGICAL CHARACTERS

§ Dwarfishness

WARBUTON (75) describes a dwarf found in the Victory variety. The dwarf plants measured not over 9 inches in height. This character proved to be a monogenic recessive.

Later, STANTON (62) reports two cases of dwarf plants appearing in F_4 and F_6 of his two crosses. In one instance the dwarfishness proved to be heterozygous giving a 3 (dwarf) : 1 (tall) ratio, and in the other case it proved to be homozygous.

§ Presence and Absence of Ligules

NILSSON-EHLE (43) appears to be the first to have observed that the presence of ligules is dominant to their absence. The crosses were made between 'Jaune géante à grappes' (liguleless) and several other normal varieties. Segregation was 3 : 1, but further segregation ratios were found, which suggested the presence of, at least, four duplicate genes.[1] Similarly LOVE and CRAIG (37) obtained results showing that "the presence of ligule was represented by one or two factors in different sorts," Using Garton 784 as the liguleless parent, GARBER (22) observed di- and trigenic segregations in F_2, and ODLAND (52) obtained digenic segregation. The result by the latter author was practically identical with the calculated 15 : 1 ratio, actually being 1176 : 79.

MEURMAN (41) working on several crosses between Jaune géante à grappes and other liguled varieties fully confirmed the results of NILSSON-EHLE. The four crosses proved to be monogenic, the seven crosses digenic, and one cross trigenic.[2] An interesting result was obtained from a cross between Sapeli and Abend 306, both having ligules. In F_2 of this cross, a liguleless plant appeared in the ratio of 63 : 1 (actually 67 : 1). Crosses with Jaune géante à grappes, showed that Sapeli has one gene and Abend 306 has two genes for ligule formation. Consequently the gene of Sapeli is not the same as either of the genes of Abend 306.

A close association was found by NILSSON-EHLE between panicle type and ligule. The absence of ligule was always associated with the side-panicled form, no open liguleless forms being found in any of the crosses made. In a cross, open-liguled × side-liguleless (Ligowo II × Jaune géante à grappes) where the digenic segregation was shown in F_2 for the ligule character, the results indicated that both of the two duplicate genes, L_1 and L_2, involved in the liguled parent had a certain influence on the panicle type. Each of them, when present alone, produced intermediate panicle types (although one of them L_2, is

1) Actually he obtained : 125 : 8; 220 : 5; 213 : 3; 547 : 2.
2) Actually he obtained : 663 : 229; 1513 : 108; 368 : 4

weaker in its effect than the other, L_1), and the absence of both resulted in a side panicle. This association of ligulelessness with side panicle was also observed by MEURMAN.

NILSSON-EHLE suggests from other crosses, however, that there are apparently genes for panicle type which have no effect on the development of ligules. ODLAND in a cross involving such a gene for panicle type obtained a F_2 ratio of 45:15:4 for open-liguled, side-liguled, and side-liguless individuals. It was therefore concluded that the absence of both the genes for ligule inhibit the effect of the gene for open panicles.

§ Chlorophyll Deficiencies

CHRISTIE (6) has studied the inheritance of the yellow striped leaf and found that this is inherited in a non-Mendelian manner. The green type (Moistard Grenadier) only exceptionally shows the segregation into green and striped descendants and in very variable and indefinite proportions. As a rule the striped individuals out-number the green. Some of the green plants resulting from segregation are fixed, while the others are liable to segregate and the green type in turn can produce the striped.

ÅKERMAN (2) found seedlings which appeared a normal green at first, but gradually yellowed and perished in a short time when grown in the bright sunshine. In subdued light (1/4–1/5 sunlight) defective plants retain their green color and mature grains. This form was called lutescens. Some green plants showed segregation in a ratio of about 1 yellow to 70 green. By analysis of F_4 this was found to be in the ratio of 63:1 indicating the existence of three independent homomeric genes, all recessive to the genes for the normal green.

§ Height of Plants and Other Size Characters

In a cross between two *sativa* varieties which differed in height, NILSSON-EHLE (42) obtained transgressive segregation in F_2. A similar result was obtained SURFACE (65, 66) in the cross between *A. fatua* (tall) and *A. sativa* var. Kherson (low). The results may be explained by the assumption of multiple genes.

NILSSON-EHLE (42) also made crosses involving leaf breadth, grain size, and number of florets in the spikelet. In these cases occurred

also transgressive segregation, indicating that the character owed their expression to several genes.

GARBER and QUISENBERRY (26; also GARBER *et al*, 24) treated with F_1, F_2, and F_3 of a *sativa* cross as to the inheritance of leaf width. Although the mode of its inheritance was not exactly determined, owing to its variable nature by environmental influences, the results showed the existence of multiple genes for leaf width, as NILSSON-EHLE had suggested. The same authors made also some observation on number of culm. This character, like leaf width, is greatly influenced by environal conditions. A high number of culms appeared to be dominant.

PHYSIOLOGICAL CHARACTERS

§ Resistance to Disease

Resistance to Crown Rust. PARKER (53) made a cross between Burt (*A. byzantina*) and Sixty Day (*A. sativa*) and studied the inheritance of resistance to crown rust, *Puccinia cornata* Corda, under greenhouse conditions. The results showed that susceptibility behaves as a partial dominant and the F_2 comprised of susceptible and resistant plants as well as several intermediate plants. He concluded that susceptibility and resistance did not depend on a single gene.

DAVIES and JONES (10, 11), on the other hand, reached a different conclusion in crosses between selections of Red Rustproof (*A. byzantina*) and Scotch Potato (*A. sativa*), the former being resistant and the latter susceptible. The F_1 plants showed a high degree of resistance. Of a large number of F_2 seedlings inoculated and studied under greenhouse condition, 258 were recorded as susceptible and 777 as resistant, the ratio being very close to 1:3. This monogenic relation was further confirmed by F_3 breeding.

Resistance to Stem Rust. The inheritance of resistance to stem rust, *Puccinia graminis avenae* Erikss. and Henn., was studied by GARBER (21, 23) and GRIFFEE (28) in crosses between White Russian oat which is resistant and other susceptible varieties (Minota and Victory). They found that resistance apparently behaves as a monogenically dominant character. The same genic situation was recently demonstrated by HAYES *et al* (29) in crosses between Black Mesdag (susceptible) and three selected lines (resistant) originated from White Russian × Minota or Victory.

DIETZ (12) observed also the monogenic dominance of resistance in crosses, Green Russian × Early Ripe, White Tartar × National and White Tartar × Lincoln, in which the first given varieties in each cross are resistant to stem rust and the latters susceptible to the same. Crosses involving Burt (susceptible) revealed some interesting results. A Burt —White Russian cross gave susceptible F_1's and in F_2 a ratio of 3 resistant to 13 susceptible plants (actually 58 : 251). In another White Russian—Burt cross the F_1 plants were resistant and a ratio of 3 resistant to 1 susceptible were resistant and a ratio of 3 resistant to 1 susceptible was obtained in F_2. Still another White Russian—Burt cross gave susceptible F_1 plants and in F_2 a ratio of 3 susceptible to 1 resistant. It is clear from these results that there are three genically different strains of Burt which breed true to susceptibility. These different strains were represented as Si, sI and si were S stands for resistance and I for resistance-inhibitor, Similar results were also recorded in Green Russian—Burt crosses. DIETZ also made crosses between different resistant varieties, such as Green Russian × Richland and White Russian × Ruakura. The F_1 plants of these crosses were resistant and in F_2 some plants appeared which were more resistant than either parent, indicating that other genes than the above-mentioned genes are probably involved in the inheritance of resistance to stem rust.

Resistance to Covered Smut and Loose Smut. Several workers have studied the inheritance of resistance to covered smut, *Ustilago levis* (K. and S.) Magn. WAKABAYASHI (74) has represented some data of the behavior or the progeny of a cross between Red Rustproof (*A. byzantina*, immune) and Black Tartarian (*A. sativa orientalis*, susceptible). He observed no smut among the F_1 and F_2 plants. In F_3, however, a few infected individuals were found. Immunity was thus dominant and several genes were considered to be involved.

The immunity of Red Rustproof to *U. levis* was also investigated by GAINES (17, 18) in crosses with four susceptible oats (Black Tartarian, Abundance, Large Hulless, and Chinese Hulless). The last two varieties (belonging to *A. sativa nuda*) are much more susceptible than the first two varieties (belonging to *A. sativa orientalis*). In all these crosses the author found the large number of immune segregates, and concluded that "The crosses with Black Tartarian and Abundance indicate that Red Rustproof carries three dominant factors for immunity, any one of which prevents the production of covered smut spores. In crosses with Large and Chinese Hulless, one factor ap-

parently does not give complete dominance in hulless segregates, but otherwise the prepotency of the factors for immunity is similar in all four crosses."

BARNEY (3) has studied the reaction to loose smut, *Ustilago avenae* (Pers.) Jens., in three different crosses, resistant (Fulghum) × resistant (Black Mesdag), resistant (Burt) × susceptible (Swedish Select), and susceptible (Turkish Rustproof) × susceptible (Golden Rain). He interpreted his results on the basis that in the first cross three different genes are concerned with resistance in the second two genes, and in the third only one gene. The data obtained, however, were not sufficient to prove the hypothesis.

REED and STANTON (61) worked with a cross between Fulghum and Swedish Select, the former being very resistant to both loose smut and covered smut, while the latter is susceptible to the both. The behavior of the F_2 plants was not recorded but that of the F_3 progeny was studied; some showed a degree of susceptibility corresponding to that of Swedish Select, a few of the progeny showed a much greater susceptibility, while still others a resistance corresponding to that of Fulghum.

HAYES *et al* (29) obtained several grades of susceptibility to both the smuts in F_2 of a cross between Black Mesdag (immune) and a selected line from White Russian × Minota (susceptible). Out of a total of 378 F_2 lines which were classified on the basis of F_3 to F_5 breeding behaviors, 86 were as susceptible as the susceptible parent, 47 were pure-immune, 36 appeared highly resistant, and the remainder, 209, produced some smut infection, less than the susceptible parent and more than the lines classed as resistant. Presumably two genes, **I** for immunity and **R** for resistance, were assumed as a possible explanation. **I** was considered to be epistatic to **R**. Blacd Mesdag has the constitution of **RRII**.

GARBER *et al* (24), from data based on the F_3 and F_4 of a cross of Black Mesdag-Gopher (moderately susceptible), found that the reaction to the smuts seems to be governed by a single dominant gene for resistance. Segregates were obtained in this cross, however, which were more susceptible than the susceptible parents. This was considered to be due to, at least, one supplementary gene, presumably carried by the Black Mesdag parent. Some evidence showed that this supplementary gene is linked with the gene for black glume color. That HAYES *et al* did not treat with this gene is suggested from the

fact that no linkage was found between smut reaction and glume color in their case.

The resistance of Black Mesdag was likewise found by REED (59, 60) to be due to a single gene in the cross with Hulless (A. sativa nuda var. inermis). He obtained in F_2 358 resistant to 107 susceptible plants as to loose smut and 156 resistant to 40 susceptible plants as to covered smut. This monogenic relation was confirmed by F_3 breeding. The dominance of this variety was also manifested in another cross with Silvermine.[1] REED also made crosses between certain susceptible varieties (Canadian Victor, and Silvermine Hulless). These crosses gave in F_2 only progeny as susceptible as the original parental varieties.

With respect to the relation between reactions to loose smut on one hand and to covered smut on the other hand, REED observed a distinct parallelism. In the earlier paper (61), he suggests that resistance to both smuts appears to be governed by the same gene. Some extensive work in the cross between Hulless and Black Mesdag (60), however, showed that the situation may be more complicated. Of the total of 590 F_3 families grown from this cross and inoculated with each of the smuts, 541 gave a similar reaction to both smuts, the remaining 49 manifesting a dissimilar behavior. The elucidation of this problem needs further experiments.

On the other hand, we have oat varieties which are dissimilar in their reaction to these smuts. REED (50) also worked with these varieties. Early Gothland is susceptible to loose smut, but highly resistant to covered smut. In crosses with Hulless or Victory, this variety was found to possess a dominant gene for resistance to covered smut.[1] No clear segregation was obtained as to reaction to loose smut. The Monarch variety, on the other hand, is susceptible to covered smut, but resistant to loose smut. Crosses with Hulless gave in F_2 a segregation as to reaction to loose smut only, resistance being similarly dominant.[2]

§ Maturing Time

Earliness and lateness are sharply defined characters for varieties of oats. From a cross between medium early and late varieties,

1) Actual F^2 data: 78 : 17 as to *U. avenae*; 74 : 15 as to *U. levis*.
2) Actual data: 36 : 8 from Early Gothland Victor; 57 : 37 from Early Gothland Hulless.
3) Actual data: 155 : 41.

NILSSON-EHLE (42) observed transgressive segregation in F_2 in which homozygous forms earlier than the early parent and also those later than the late parent were obtained. Of 112 F_2 plants, 98 proved to be heterozygous for maturity and 14 seemed to be homozygous.

CAPORN (5), in a cross between an early variety (Mesdag) and a late one (Hopetown), obtained F_1 individuals with a more or less intermediate condition. The F_2 plants were all harvested together and 106 plants tested in F_3. Two were considered to be homozygous for early maturity equivalent to the early parent. The lateness of the late parent was not recovered. He interpreted these results on the assumption that earliness is possibly a function of three genes. He also noted that a type which is comparatively early, in that its period never extends into the period of the late parent, appeared in a monogenic basis in this generation.

NOLL (50), working with a number of crosses involving 13 varieties of *A. sativa* and 2 varieties of *A. byzantina*, presented data on this subject. Some crosses gave F_1 plants which headed with the early parents, while others gave those earlier than the early parents. In some crosses in which the parents headed together, the F_1 plants were distinctly earlier than the parents. Usually, in the crosses of which the F_1 plants headed at the same time as the early parents, the F_2 plants began heading with the early parents, and in the crosses in which the F_1 plants headed earlier than the early parents, the F_2 plants began heading earlier than the early parents. From these results it was concluded that earliness is dominant to lateness, depending on a series of genes which have a cumulative effect. The data in the later generations supported this multiple genic hypothesis. Homozygous lines were obtained which are earlier than the early parents, similar to the early parents. intermediate, and later than the late parents.

The dominance of earliness was also observed by GARBER and QUISENBERRY (26; also GARBER, GIDDINGS and HOOVER, (24) in a cross with two sativa varieties (Gopher × Black Mesdag or early × late). The date of heading of the F_1 was approximately the same as the early parent. Segregation occurred in F_2, and 9 of 150 F_3 lines bred like the late parent. It was suggested that two genes are probably involved in earliness.

§ Germinating Percentage

The grain of *A. fatua* is characterized by delayed germination owing to having a heavy seed coat which is supposed to prevent oxygen

from reaching the germinating embryo. *A. sativa* has no such a character. According to GARBER & QUISENBERRY (25), Garton 784 and Victory oats germinate 95 per cent or above. A yellow wild oat ranged from 0 to 55 per cent germination and a Brown Hairy wild oat ranged from 0 to 25 per cent germination. Crosses between these *sativa* and *fatua* forms gave in F_2 a wide range of variations in per centage of germination. The range was in most cases from 31 or below to 100 per cent. The frequency distribution showed that the character, delayed germination, is recessive.[1)]

§ Pollen Abortion

According to GARBER (23), Victory, Minota, and White Russian produced averages of 12.4, 1.0, and 0.9 per cent, respectively, of abortive pollen grains. Crosses were made between White Russian and the other varieties. Segregation was observed in F_2 of the Victory-White Russian cross. Of a total of 250 F_2 plants, 7 produced percentages of aborted pollen with the range exhibited by the Victory parent. The author considers that the abortive pollen as found in Victory was inherited as a recesssive character involving at least two genes.

LIST OF CHARACTERS GENICALLY ANALYZED

The following list is prepared with an aim of summarizing the results hitherto obtained on genic analysis in *Avena*. The character pairs studied may be grouped into five classes according to their genetical behaviors: (1) monogenic, (2) digenic, (3) trigenic, (4) tetragenic, and (5) multigenic. The last class concerns with cases in which the exact number of genes involved are not known. It must be remembered, however, that some of these characters are based on rather meagre data.

§ Monogenic

The 3 : 1 type

1) Black—non-black grain. 4, 15, 16, 22, 24, 26, 29, 36, 41, 43, 51, 52, 57, 65, 66, 76, 77, 79.

1) Although the false wild oats are very similar to the true wild oats the former does not show delayed germination (GARBER and QUISENBERRY). This is an interesting fact when one considers the problem on the origin of false wild oats.

2) Gray—white grain. 4, 36, 41, 43, 65, 66.
3) Yellow—white grain. 43.
4) Red—non-red (yellow, white) grain. 13.
5) Open—side panicle. 23, 42, 43, 52.
6) Long-haired—grabrous glumes. 42.
7) Short-haired—glabrous glumes. 42.
8) Non-stongly—strongly awned types (data much somplicated). 29, 57.
9) Presence—absence of ligules. 37, 41, 43.
10) Pubescent—glabrous back of the lower grain. 36, 65, 66.
11) Glabrous—pubescent base of the upper grain. 65, 66.
12) Long—short hairs at the base of the lower grain. 42, 79.
13) Short—no hairs at the base of the lower grain. 79.
14) Glabrous (or nearly glabrous)—medium-haired *Burt* type of the grain. 13.
15) Non-articulated—articulated *fatua* type of the upper grain. 25, 36, 65, 66, 71.
16) Glabrous—pubscent rachilla. 65, 66.
17) Normal—dwarf type. 75.
18) Dwarf—normal type. 62.
19) Few or smooth—pubescent (*sativa*) rachilla. 29, 52.
20) Resistance—susceptibility to crown rust. 10, 11.
21) Resistance—susceptibility to stem rust. 12, 21, 23, 28, 29.
22) Susceptibility—resistance to stem rust. 12.
23) Resistance—susceptibility to loose smut. 3, 24, 29, 59, 60.
24) Resistance—susceptibility to covered smut. 17, 18, 24, 29, 60.

The 1 : 2 : 1 type

25) Deep—light gray grain. 41.
26) Waxy—non-waxy lemma. 41.
27) Awnless—strong-awned type. 36, 38, 51, 65, 66.
28) Awnless—weak-awned type. 13, 38.
29) Normal—fatuoid type. 1, 22, 25, 27, 30, 32, 33, 35, 44, 49, 58, 64, 78.
30) Hulled—hull-less grain. 4, 16, 37, 39, 44, 48, 51, 79.
31) Glabrous—pubesc nt base of the lower grain. 65, 66.
32) Non-articulated—articulated (*fatua* and Burt) base of the lower grain. 12, 25, 36, 65, 66, 71.

§ Digenic

The 15 : 1 type

33) Black—non-black grain. 4, 37, 41, 43.
34) Yellow—white grain. 13.
35) Open—side panicle. 42, 43, 57.
36) Pubescent—brabrous glumes. 37.
37) Pubescent—glabrous back of the lower grain. 36.
38) Pubescent—glabrous base of the lower grain. 79.
39) Presence—absence of ligules. 22, 37, 41, 43, 52.
40) Resistance—susceptibility to loos smut (data incomplete). 3.
41) Early—late heading period (data incomplete). 24, 26.
42) Many—few percentage of aborted pollen grains (data incomplete). 23.

The 13 : 3 type

43) Glabrous—pubescent back of the upper grain. 65, 66.
44) Susceptibility—resistance to stem rust. 12.

§ Trigenic

The 63 : 1 type

45) Long—short grain (data incomplete). 57.
46) Presence—absence of ligules. 22, 41, 43.
47) Green—'lutescens' seedlings. 2.
48) Resistance—susceptibility to covered smut (no data). 17, 18.
49) Resistance—susceptibility to loose smut. (data incomplete). 3.
50) Early—late ripening period (the homozygous early plants appearing in 1/64). 5.

The other types

51) Open—side panicle (45 : 19). 52.
52) Pubescent—blabrous back of the lower grain (57 : 7). 36.

§ Tetragenic

The 254 : 1 type

53) Presence—absence of ligules. 43.

§ Multigenic

54) Height of plants. 42, 65, 66.
55) Breadth of leaves. 24, 26, 42.
56) Number of florets per spikelet. 42.
57) Number of culm. 24, 26.
58) Length of rachilla. 52.
59) Heading period. 50.
60) Resistance to stem rust. 12.

LINKAGE RELATIONS

Although several investigators have treated with linkage relations in *Avena*, their works are mostly fragmentary. In the following summary, the discussion is made, for convenience, under the different crosses made, viz., *fatua* × *sativa*, *byzantina* × *sativa*, and *sativa* × *sativa*. We have no available data on the genic relation between *A. byzantina* and *A. fatua*. These species are members of the 21-haploid chromosome group of *Avena*.

The fatua-sativa cross

Some extensive work carried out by SURFACE (65, 66) showed two linkage groups in his *fatua-sativa* cross. The wild base type of the lower grain was found to be always associated with the following seven characters:

1) Heavy awn on the lower grain,
2) Awns on the upper grain,
3) Wild base on the upper grain,
4) Pubescence on the pedicel on the lower grain,
5) Pubescence on the pedicel on the upper grain,
6) Pubescence on all sides of the base of the lower grain,
7) Pubescence on the base of the upper grain.

These characters seemed to be governed by the same single gene pair, C–c for cultivated vs. wild grain base, and therefore they may be considered as the *fatua* complex. On this point, however, he states that "Evidence from certain other crosses, as yet not completely analyzed, indicates the existence of separate genes for some of these characters."

A gene pair Ss (smooth vs. pubescent back of the upper grain) was found to be another member of this group. In this case, the association was not complete. The F_1 plants, CS. cr, gave in F_2 a phenotypic ratio of 257 CS : 2 Cs : 3 cS : 85 cs (based on black plants only), indicating 1.52 per cent of crossovers between C and S.

The other linkage group identified by SURFACE comprises two genes, P for pubescence of the back of the lower grain, and B for black glume color. The F_1 plants, BP. bp, gave in F_2 257 BP : 2 Bp : 0 bP : 118 bp. The number is too small to determine the exact degree of linkage, but indicates that there are about 0.7 per cent of cross overs.

LOVE and CRAIG (36) likewise obtained results showing linkage between B and P, but in their case no crossavers appeared.[1)]

GARBER and QUISENBERRY (25) found that delayed germination, a characteristic of *A. fatua*, is somewhat loosely linked with the *fatua* type of grain base. This character, as yet not completely analyzed, seems therefore to belong to the C group of SURFACE.

The byzantina-sativa cross

In this cross, FRASER (13; also LOVE and FRASER, 38) identified a linkage group containing three genes. These genes may be designated here as A, H and U. A concerns with the formation of awn, a producing full awns; H is a gene for short or no basal hairs, h originating medium strong hairs; U governs the non-Burt base of the lower grain, u being responsible for the Burt (articulated) base. The F_2 results obtained may be summarized as:

AH . ah gave 1647 AH : 53 aH : 64 Ah : 577 ah.
UA . ua gave 1668 UA : 54 Ua : 43 uA : 576 ua.
HU . hu gave 1690 HU : 32 hU : 10 Hu : 609 hu.

It was calculated from these results that there is 5 per cent of crossovers between A and H, 4.14 per cent between U and A, and 1.79 per cent between H and U. The order of these genes is represented as: A–U–H.

The sativa-sativa cross

QUISNEBERRY (57) studing the relation between color, length, and awning of grain, and type of panicle in a Victor-Sparrowbill cross, has

1) As already stated, there is another pubescent genes P', which behaves independently of P. (see p. 88).

identified the following three linkage groups:

I. A gene for color (B)+a gene for awns;

II. A gene for open panicle type+a gene or gene complex for length of grain and awns, respectively.

III. Another gene for panicle type+a gene or genes for grain length.

Other possibilities of linkage of **B** for black color with other genes has been reported by several investigators. GARBER, GIDDINGS and HOOVER (23) suggest a possibility of linkage between **B** and a supplementary gene for smut susceptibility carried by the Black Mesdog parent. HAYES *et al* (29) suggest a loose linkage of **B** with a gene for pubescence on the rachilla of the upper spikelet in their cross between Black Mesdag and some selected lines. The data presented by ODLAND (52), however, showed that **B** behaves independently of a gene for smooth rachilla (of the lower grain) in the Early Gothland-Garton 784 cross. He points out, on the other hand, a possible loose linkage between **B** and length of rachilla, and a close linkage between length of rachilla and its pubescence.

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