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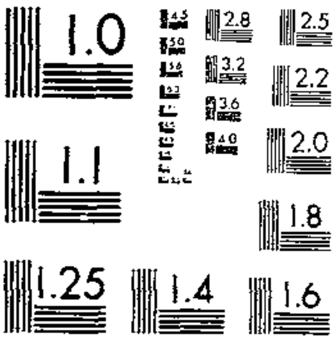

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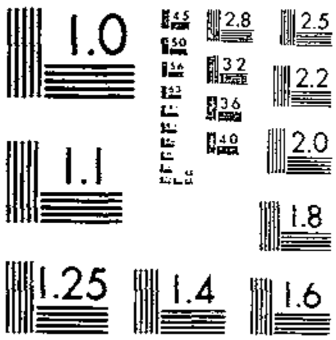

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Some Evolutionary Aspects of Certain Morphologic Characters in a World Collection of Barleys

By David J. Ward

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HIGHLIGHTS OF FINDINGS, REAFFIRMED CONCEPTS, AND GENERAL COMMENTARY

The distribution of characters within the world barley population is not at random.

Barleys from different world areas are different.

Evolution in barley has occurred throughout the world; it has occurred at different rates in different places.

Some characters predominate among world barleys and are widely distributed geographically; others occur in limited proportions of the population and are concentrated in strains from specific world locales.

The predominant characters occur in many combinations; some of the less preponderant ones are restricted to a few combinations.

The predominant characters probably have been involved in a long succession of evolutionary events and have undergone more change than the less preponderant ones; they are less restricted to association with specific characters than the less preponderant ones.

Within Africa and Asia, characters are not derived from any one or two centers of evolutionary activity, but are obtained from different locales over the whole of the barley growing area.

Great phenotypic diversity among barleys from one source does not necessarily imply that the greatest number of genes may be obtained from that source.

Extensive cross-fertilization with attendant recombination may occur in some environments.

Barleys from adjacent world regions may be basically different, but still be similar for a specific character.

Some characters in the same or adjacent regions may remain dissociated from one another.

Man has been influential in the migration, perpetuation, and evolution of barleys.

Genetic recombination has great evolutionary significance.

Only a very small portion of the potential genotypic diversity of barley is represented among 6,200 strains in the World Collection of Barleys.

Basic plant types for modern improved varieties may have come into being within the confines of the germ plasm that was endemic to the locales in which they arose.

Modern breeding has accelerated and expanded evolutionary change.

Information about the world distribution of plant characters may make plant exploration more effective.

SOME QUESTIONS RAISED

Why are some characters predominant?

If predominant characters are superior, have all such characters been recognized and used in plant improvement work?

Why are some characters concentrated among strains from certain areas?

Why is there more diversity of type among strains from some areas than from others?

What will additional data and refinement of existing data reveal?

Are other crops characterized by conditions similar to those found for barley?

How may the world's germ plasm best be obtained and preserved?

What is the significance of obtaining combinations of characters compared to that of individual characters?

What is the potential for evolving new basic highly productive plant types?

CONTENTS

SOME EVOLUTIONARY ASPECTS OF CERTAIN MORPHOLOGIC CHARACTERS IN A WORLD COLLECTION OF BARLEYS

By David J. Ward, *Agricultural Administrator* (formerly *Research Agronomist, Crops Research Division*), *Agricultural Research Service*

Barley, one of the oldest of cultivated plants, has been grown in Africa and Asia since antiquity. The crop has been subjected to evolutionary forces for many centuries, presumably as one or more wild species initially and subsequently as a cultivated annual perpetuated by man. The selective and migratory influences of peoples have been interwoven with forces of nature in determining the makeup of modern-day cultivated barley.

Over the ages mutagenic forces have brought about heritable changes in barley. Within the world population of cultivated barleys are many individual plant characters that distinguish one strain from another. The expression of these characters is governed by genetic factors. Forces of evolution have assembled them into diverse genotypes, as evidenced by widely different combinations of characters. The great diversity among barley genotypes and the versatility of certain ones for interacting favorably with climatic and biologic integrants of local environments have enabled man to cultivate this patriarch of domesticated grains over the vast temperate areas of the earth.

Gains in plant productivity and quality of product have been effected in the past through selection among the diverse types occurring naturally in the world and, in the most recent era, through controlled hybridization. The advent of plant improvement through breeding placed special significance on genes or genotypes that have evolved in barley over the centuries. The principal vehicle for improving plants today is that of combining different germ plasms bearing valuable genetic factors. Breeders of small grain rely almost exclusively on naturally evolved genic materials for developing improved varieties. A strain may have value for as little as a single gene that it carries. Present knowledge indicates that the potential for improving cultivated barley depends in large measure on the availability of useful genes or combinations of genes and on man's ability to bring these together through breeding. In the last analysis, this is but the directing and expediting of evolutionary processes.

None of the small grains is native to the Western Hemisphere. Their culture here was initiated by immigrants from Europe. In recognition of the value of genetic diversity within the world barley population, the U.S. Department of Agriculture has been introducing and perpetuating foreign strains for many years in a World Collection of Barleys. The collection is maintained so that the germ plasm it contains may be used by scientists engaged in plant improvement work or basic research. At present about 8,000 cultivated strains are propagated by the Cereal Crops Research Branch. In addition to foreign introductions acquired by the New Crops Research Branch, selections made in the United States from Old World barleys and superior lines developed in this country through controlled hybridization are included in the collection.

In recent years, collection strains have been evaluated by scientists at many experiment stations in this and other countries. Breeders, pathologists, entomologists, and physiologists have participated in an intensive search for useful germ plasm with which to effect plant improvement—be it the development of varieties with superior agronomic characters; resistance to disease or insects; or tolerance to heat, cold, or drought. Thus, much of this effort has been devoted to factors that may seriously limit the productivity of varieties presently grown by farmers. Often, however, the search among world barleys for useful genic material with which to counteract new deleterious conditions has been little more than a random probing of the collection stocks.

The reliance on the collection for useful germ plasm points up the need for enlarging our acquaintance with the world barley population. We need knowledge of the evolutionary background of the crop. What is the frequency of occurrence and geographic distribution of characters, individually and in combination with one another, in the world barley population? Where and how did the genes for these characters arise? To what extent are the characters associated with one another and how did these associations come about? What has been the role of man in the history of barley? These are but a few of the enigmas that confront us. This study was conducted in an attempt to answer some of these questions, with the particular hope that an increased understanding of evolutionary phenomona may suggest methods by which the development of superior germ plasm can be hastened. Another objective of this study was to develop and evaluate some techniques by which additional studies may be effectively carried out.

LITERATURE REVIEW

Various theories about the origin of cultivated plants have been proposed since the pioneering work of de Candolle (*6*).[1] Willis (*30*) gave a new stimulus to the general fields of plant geography and evolution with his "age and area" hypothesis, which suggested that the area occupied in a country by any given species depends on the age of the species in that country. Vavilov (*26, 27*) attracted widespread attention with his "centers of origin" concepts. He postulated several basic world centers, separated from one another by great deserts or mountain ranges, in which most of the varietal wealth of our major crop plants is located. His theories were largely based on observations of plant materials that indicated areas where there was a maximal diversity of combinations of characters. He initially suggested primary centers of origin for barley in Africa and Asia, but later cited only the African area.

[1] Italic numbers in parentheses refer to Literature Cited, p. 111.

Takahashi (*25*) has summarized several authors' criticisms of Vavilov's theory by indicating that it is questionable whether centers of diversity necessarily coincide with original centers of origin of cultivated plants.

Most recently Brücher and Åberg (*5*) suggested two major gene centers of barley—one in Ethiopia, the other in the highlands of Sikkim and southern Tibet.

Most studies on the nature of world barleys have been devoted to the theoretical question of "origin." Vavilov (*26, 27*), who was keenly aware of the significance of basic germ plasm for plant improvement work, and also Orlov (*15*) observed world barley strains for certain specific plant characters, but they dealt with these characters only in a general way. They considered the strains from the standpoint of the overall diversity of varieties from different world areas or from the standpoint of combinations of characters that might indicate new botanical varieties in the sense of Körnicke (*11*).

Japanese studies of some barley characteristics have a more practical application to plant breeding and genetics. These investigations have been summarized by Takahashi (*25*) under the following headings: (*a*) origin of hereditary variations and their migration, (*b*) geographic distribution of genes or genotypes of barley in relation to selection, and (*c*) geographic regularities in gene distribution in barley. He suggests that mutations and transport by man are key agents for the spread of variant forms of crop plants. He indicates that widespread distribution of certain types may result from the superiority of their genotypes and that their relative evolutionary ages are not necessarily determining factors. Selective forces are suggested as having influenced the nature of the world barley population. A preference for white-kerneled vs. pigmented strains in commerce is noted as being a force for eliminating an unwanted character. Use of the naked types in the Orient is cited as an example of the fixation of a new beneficial character. The semibrachytic barleys used under conditions of heavy manuring in Japan are presented as an example of an adaptive genetic change. A predominance of long hair rachilla types among oriental barleys is considered to be an other-than-adaptive genetic change that has become fixed.

Takahashi concluded from his studies with limited materials that certain barley characters may be prevalent in many areas of the world, whereas others may be found in more or less restricted areas. Although his conclusions may have been based *a priori* on the fact that "some" strains from an area have the characters under study (rather than on information about the comparative frequency with which the characters occur in different areas), his basic concept is worthy of further consideration.

Differences are suggested between barleys of the oriental and occidental regions. These regions are said to be distinguished from one another by a line established by the southern limits of spring barley on the Asiatic Continent.

Harlan (*10*) has stated that "it is well known that the variability of a species is not distributed uniformly over the range of the species." He postulates (*9*) that centers of diversity are largely the result of exceptionally active evolutionary forces operating at present in those areas. His travels as a plant explorer brought to his attention small areas in which concentrated varietal diversities of different crops exist. These are termed "gene microcenters" or "discrete concentration patterns." They were noted on plains and in mountainous areas.

Most biologists agree with Stebbins' (*21*) assertion that mutation is the ultimate source of variation. A fundamental principle of de Vries' (*28*) mutation theory is that specific characters have occurred without any relation to their possible significance in the struggle for life. The implication of the randomness of the nature of mutating characters also carries an implication of randomness of the geographical location of the individuals in which the mutations occur.

Although Lotsy's (*12*) idea that cross-fertilization results in the origin of new types has not been accepted in biology, East (*7*) and Stebbins (*22*) have pointed out that the broadest base within which natural selection can operate is afforded by sexually reproducing organisms in which each new mutation affords a basis for potentially great numbers of new genotypes. Harlan (*8*) referred to the almost incomprehensible number of types that are possible within the world's barley population. Harlan (*10*) stated that "centers of diversity look much like the type of thing found in composite cross populations."

Nearly all modern writings on evolution devote considerable attention to the impact of natural selection on the essentially "blind" variants in livings things. Sheppard (*19*) and Stebbins (*20*) indicate that sound evidence exists that natural selection is a real guiding force in the evolutionary adaptation of plants. Lotsy's concept that selection is the cause for the extinction of many new types seems to be generally accepted. Muller (*13*) has written that "selective elimination gives conditions under which the 'fitter' can really assume their shapes." Suneson (*23*) and Suneson and Stevens (*24*) found that barley genetic characters, like varieties, do not survive equally in mixtures in field plantings, nor similarly at different locations. Two varieties from an initial mixture of equal parts of four varieties were practically missing from the population after 16 years of cropping.

Neatby (*14*) has called attention to the selective effect of man in directing evolution by pointing out that the four varieties of wheat that occupied 95.8 percent of the Manitoba wheat acreage in 1936 were found on only 6.7 percent of the acreage in 1941.

Baker (*4*) recognized the migratory potential of self-fertilized crops by noting that a single propagule is sufficient to start a sexually reproducing colony.

MATERIALS

The records for the 6,200 strains that constituted the U.S. Department of Agriculture World Collection of Barleys in the spring of 1951 include notes classifying the individual strains for a number of plant characters. Data for 37 of these characters within 7 spike categories were used in this study. The characters are listed in table 1, together with the code designations by which they are identified in this publication. Most of them are illustrated in figures 1 and 2. These designations are peculiar to this study and are not intended as substitutes for the accepted gene symbols for the characters. The characters have been described and evaluated as to suitability for classification purposes by Åberg and Wiebe (*1*, *2*, *3*).

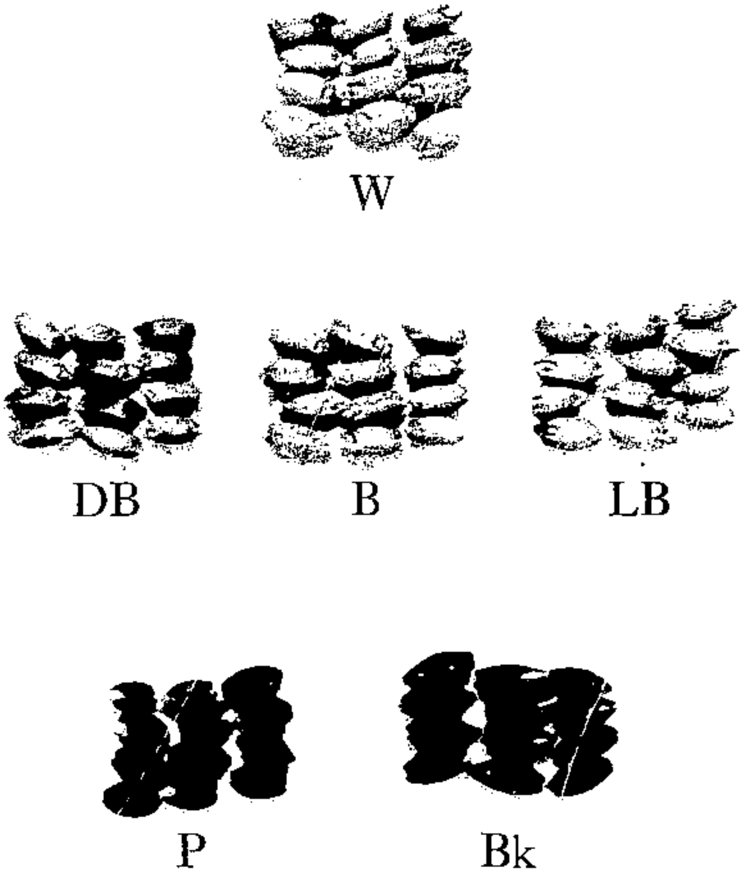

FIGURE 1.—Kernel color.

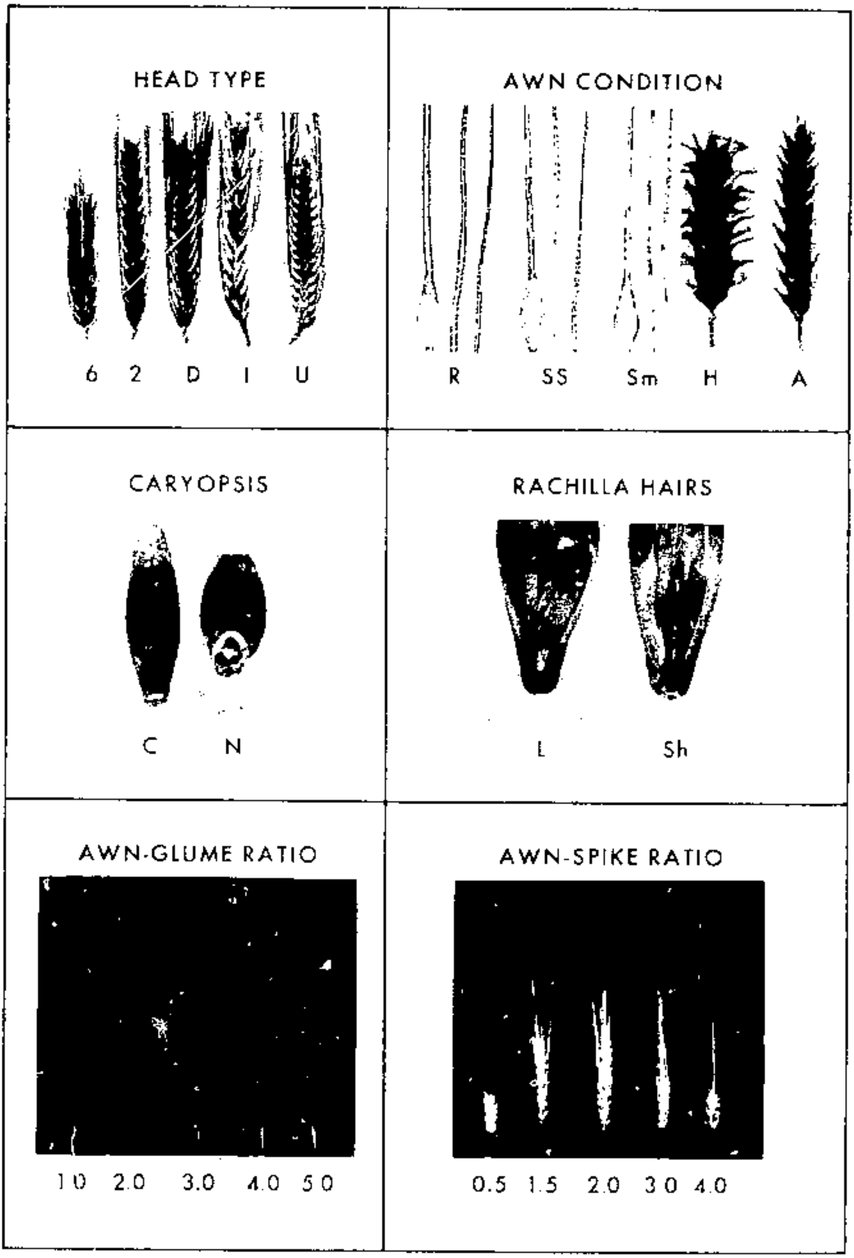

FIGURE 2.—Morphological characters.

Table 1.—*Codes used to designate the 37 characters in 7 spike categories for which 6,200 strains in the World Collection of Barleys are classified*

Spike category and character	Code [1]
I— Head type:	
6-row	6
2-row	2
Deficiens	D
H. irregulare	I
Intermedium	U
II— Kernel color:	
White	W
Light blue	LB
Blue	B
Dark blue	DB
Black	Bk
Purple	P
III— Awn condition:	
Rough	R
Smooth	Sm
Semismooth	SS
Hooded	H
Awnless	A
IV— Caryopsis:	
Covered	C
Naked	N
V— Rachilla hairs:	
Long	L
Short	Sh
VI— Awn-glume ratio:	
Glume awn equal to—	
Length of glume	1.0
1½ times length of glume	1.5
2 times length of glume	2.0
2½ times length of glume	2.5
3 times length of glume	3.0
3½ times length of glume	3.5
4 times length of glume	4.0
4½ times length of glume	4.5
5 times length of glume	5.0
VII—Awn-spike ratio:	
Lemma awns extend beyond tip of spike—	
½ length of spike	0.5
Length of spike	1.0
1½ times length of spike	1.5
2 times length of spike	2.0
2½ times length of spike	2.5
3 times length of spike	3.0
3½ times length of spike	3.5
4 times length of spike	4.0

[1] Code designations relate only to this study.

The notes for the characters in spike categories I to V were recorded from plants grown under the arid environments of Aberdeen, Idaho, and Sacaton, Ariz.[2] The awn-glume and awn-spike ratio notes were recorded at Madison, Wis.; Aberdeen, Idaho; and Sacaton, Ariz.[3] The kernel color notes are based on the gross impression that meets the eye when seed lots of the individual strains are observed. White indicates that the kernels have no blue, black, or purple in the aleurone, pericarp, or hull tissue. Blue indicates color in the aleurone, but not in the pericarp or hulls. Black and purple indicate color in the pericarp or hulls or both, without regard to aleurone color.

Results of studies to determine the genetic factors governing the expression of barley characters and the linkage groups in which they are located have been summarized by Robertson, Wiebe, and Immer (*16*) and Robertson, Wiebe, and Shands (*17, 18*). Current genetic symbols for the factors representing several of the characters included in this publication are given in table 2. These factors are listed according to linkage groups in table 3. None of them are known to be closely linked with one another.

The collection records include information about the source of the seed of each strain. The individual sources in the collection records are listed in table 4, together with the number of strains obtained from each source. Most of the source designations relate to geographic places or areas. Some, such as Engledow, Dickson, Pissarev, and Vavilov, relate to scientists who collected materials from different parts of the world. Strains from some of the sources are endemic to the areas from which they were obtained. Those from other areas have been moved from place to place by man. The barley collection includes materials ranging from stocks that have been perpetuated by primitive peoples living in a wide range of latitudes and elevations to improved lines developed in advanced societies through the application of modern plant breeding techniques.

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[2] The 4,360 strains that comprised the barley collection in 1946 were classified for characters in spike categories I to V by G. A. Wiebe and M. N. Pope from a field planting made at Aberdeen, Idaho, in that year. The remainder of the strains were classified by G. A. Wiebe and D. J. Ward in 1951 and by D. J. Ward in 1952. All of the spring barley classifications were checked in the field at Aberdeen, Idaho, in 1951 by J. G. Moseman and D. A. Reid.

[3] Most of the nearly 4,100 strains that comprised the barley collection in 1942 were classified for awn-glume ratios by Ewert Aberg from a field planting made in Madison, Wis., in that year. The remainder of the strains were classified for this spike category by D. J. Ward in field plantings at Aberdeen, Idaho, in 1951 and Sacaton, Ariz., in 1952. Awn-spike ratio classifications for all of the strains were made by D. J. Ward at Aberdeen and Sacaton in the same years. All of the spring barley awn-glume and awn-spike ratio classifications were checked in the Aberdeen nursery by D. A. Reid and J. G. Moseman.

TABLE 2.—*Gene symbols for genetic factors for a number of barley spike characters* [1]

Spike category and character	Gene symbol	Code [2]
Head type:		
6-row	v	6
2-row	V	2
Deficiens	V^t	D
H. irregulare	Ir	I
Intermedium	I^h	U
Kernel color:		
White lemma, pericarp, and aleurone	b–bl–re–J	W
Blue aleurone	Bl	LB, B, or DB
Black lemma and pericarp	B	Bk
Purple lemma and pericarp	Re	P
Awn condition:		
Rough	R	R
Smooth	r	Sm
Semismooth	----------	SS
Hooded	K	H
Awnless	lk	A
Caryopsis:		
Covered	N	C
Naked	n	N
Rachilla hairs:		
Long	S	L
Short	s	Sh
Awn-spike ratio:		
Spike density	L	----------
Rachis internode number	Rin	----------
Awn length	Lk	----------

[1] Symbols are presented in a general sense only; e.g., the genetic backgrounds for the different intensities of blue aleurone have not been identified. A more detailed listing would include multiple alleles in some instances and complementary factors in some others.

[2] For explanation of codes, see table 1.

TABLE 3.—*Linkage groups in which genetic factors for certain barley spike characters are located* [1]

Linkage group and character	Gene symbol	Code [2]	Spike category
I:			
6-row	v	6	Head type.
2-row	V	2	Do.
Deficiens	V^t	D	Do.
Purple lemma and pericarp	Re2	P	Kernel color.
Rachis internode number	Rin		Awn-spike ratio.
Awn length	Lk		Awn condition or Awn-spike ratio.
II:			
Black lemma and caryopsis	B	Bk	Kernel color.
Do	B^g	Bk	Do.
Do	B^{mb}	Bk	Do.
Purple lemma and pericarp	Re	P	Do.
III and VII: [3]			
Blue aleurone	Bl2	LB, B, or DB	Kernel color.
Rough awns	R4	R	Awn condition.
Smooth awns	r4	Sm	Do.
Covered caryopsis	N	C	Caryopsis.
Naked caryopsis	n	N	Do.
IV:			
Intermedium	I^h	U	Head type.
Blue aleurone	Bl	LB, B, or DB	Kernel color.
Hooded	K	H	Awn condition.
Awn length	Lk5		Awn condition or Awn-spike ratio.
V:			
Rough awns	R	R	Awn condition.
Smooth awns	r	Sm	Do.
Long rachilla hairs	S	L	Rachilla hairs.
Short rachilla hairs	s	Sh	Do.
VI: Spike density	Lc		Awn-spike ratio.

[1] The connection between the genetic factors cited and the classifications used in this study is only general in some cases; e.g., it is known that R4 gene relates to the expression of barbing on awns, but the strains in this study have not been classified for the presence of this particular gene.

[2] For explanation of codes, see table 1.

[3] For explanation of this group, see ROBERTSON, WIEBE, and SHANDS (*18*).

TABLE 4.—*Sources of seed for the World Collection of Barleys, and number of strains obtained from each source*

Source	Strains
EUROPE:	
BRITISH ISLES:	*Number*
England	52
Engledow [1]	15
Orkney Islands	1
Scotland	8
Total	76
NORTH EUROPE:	
Denmark	23
Finland	13
Germany	100
Bavaria	4
Thuringia	1
Silesia	1
Holland	17
North Europe	1
Norway	10
Poland	86
Sweden	69
Svalof [1]	4
Total	329
CENTRAL EUROPE:	
Austria	53
Belgium	5
Czechoslovakia	13
Bohemia	5
Moravia	8
France	82
Vilmorin [1]	1
Hungary	7
Romania	4
Switzerland	15
Total	193
SOUTH EUROPE:	
Bulgaria	2
Greece	1
Italy	19
Portugal	7
Spain	42
Yugoslavia	62
Total	133
OTHER:	
Eurasia	1
Europe	19
Total	20
Subdivision total	751
AFRICA:	
NORTH AFRICA:	*Number*
Algeria	45
Egypt	51
Mariout [1]	69
Minia [1]	12
Delta	28
Sinai	1
Morocco	8
North Africa	56
Sahara	2
Tunisia	-------
Tunis	23
Total	295
CENTRAL AFRICA:	
Ethiopia	367
Total	367
SOUTH AFRICA:	
Rhodesia	2
Union of South Africa	4
Transvaal	5
Total	11
Subdivision total	673
ASIA:	
WEST U.S.S.R.:	
Ukraine	-------
Kharkov	28
Odessa	1
Valki [1]	125
Crimea	3
Total	157
SOUTH U.S.S.R.:	
Armenia	-------
Gonzah [1]	2
Yerevan	1
Azerbaidzhan	-------
Baku	3
Ciscaucasia	40
Otrada Kubanska [1]	31
Kasafute [1]	8
Dagestan	2
Derbent	1
Georgia	5
Mount Kazbek [1]	2
Tiflis	4
South Russia	5
Transcaucasia	61
Dickson [1]	6
Total	171

See footnote at end of table.

TABLE 4.—*Sources of seed for the World Collection of Barleys, and number of strains obtained from each source*—Continued

Source	Strains
ASIA—Continued	
CENTRAL U.S.S.R.:	*Number*
Uzbek	------
Bukhara	4
Total	4
EAST U.S.S.R:	
Siberia	32
Total	32
OTHER:	
Russia	223
Pissarev [1]	47
Vavilov [1]	86
Total	356
NEAR EAST:	
Arabia	3
Iran	102
Persia	11
Iraq	25
Mesopotamia	22
Palestine	5
Syria	28
Turkey	804
Smyrna	2
Anatolia	1
Asia Minor	6
Northeast Turkey	49
Total	1, 058
MIDEAST:	
Afghanistan	168
Baluchistan	1
Chinese Turkistan	5
Kashgar	2
India	489
Kashmir	57
Punjab	1
Nepal	2
Mount Everest	3
Tibet	24
Turkistan	12
Total	764
FAR EAST:	
China	199
North China	1
Northwest China	2
Japan	269
Korea	134
Manchuria	434
Mongolia	3
Total	1, 042
ASIA—Continued	
OTHER:	*Number*
Asia	23
Central Asia	4
Orient	1
Total	28
Subdivision total	3, 612
SOUTH PACIFIC:	
Australia	52
New South Wales	1
Java	2
Total	55
Subdivision total	55
SOUTH AMERICA:	
Argentina	26
Brazil	1
Chile	7
Paraguay	2
Peru	5
Uruguay	1
Venezuela	15
Total	57
Subdivision total	57
CENTRAL AMERICA:	
Guatemala	3
Total	3
Subdivision total	3
NORTH AMERICA:	
U.S. DOMESTIC SELECTIONS:	
Alaska	30
Canada	49
Saskatchewan	1
Mexico	21
United States:	
Arizona	4
Arkansas	1
California	60
Colorado	12
Georgia	1
Idaho	7
Indiana	5
Iowa	1
Kansas	9
Kentucky	4

See footnote at end of table.

TABLE 4.—*Sources of seed for the World Collection of Barleys, and number of strains obtained from each source*—Continued

Source	Strains
NORTH AMERICA—Con.	
U.S. DOMESTIC SELECTIONS—Con.	
United States—Con.	*Number*
Michigan	2
Minnesota	22
Missouri	1
Montana	4
Nebraska	5
New Mexico	4
New York	2
North Carolina	5
North Dakota	13
Ohio	3
Oklahoma	7
Oregon	2
Pennsylvania	1
South Carolina	5
South Dakota	5
Tennessee	7
Texas	10
Utah	8
Virginia	5
Washington	6
West Virginia	3
Wisconsin	39
U.S. Department of Agriculture	5
Total	369
U.S. BREEDING LINES:	
Alaska	6
Canada	35
United States:	
Arizona	2
California	7
Colorado	9
Georgia	1
Idaho	2
Indiana	2
Iowa	2
U.S. BREEDING LINES—Continued	
United States—Con.	*Number*
Kansas	4
Kentucky	4
Maryland	8
Michigan	2
Minnesota	88
Missouri	9
Montana	3
Nebraska	8
New Jersey	2
New York	7
North Carolina	6
North Dakota	8
Ohio	4
Oklahoma	2
Oregon	14
Pennsylvania	1
South Carolina	1
South Dakota	20
Tennessee	7
Texas	6
Utah	16
Washington	4
West Virginia	1
Wisconsin	19
Wyoming	1
U.S. Department of Agriculture	328
Total	680
Subdivision total	1, 049
SOURCE UNKNOWN	41
Subdivision total	41
Grand total	6, 200

[1] Dickson—J. G. Dickson, American pathologist who made a plant exploration trip to southern Russia in 1930.

Engledow—F. L. Engledow, British scientist who collected seeds from diverse world areas.

Gonzah—Village in Armenia, U.S.S.R.

Kasafute—Area on northern slopes of Transcaucasian Mountains.

Mariout—District along Mediterranean coast of Egypt.

Minia—City on Nile River in Egypt.

Mount Kazbek—Mountain in central Transcaucasian range.

Otrada Kubanska—Site of experiment station near city of Armavir, South Soviet Russia.

Pissarev—V. E. Pissarev, Russian plant explorer.

Svalof—Site of experiment station in Sweden.

Valki—Site of experiment station, southwest of Kharkov, Ukraine, U.S.S.R.

Vavilov—N. I. Vavilov, Russian plant breeder.

Vilmorin—Vilmorin-Andrieux & Co., French seed firm.

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METHODS

Spike character code designations and source records for each of the 6,200 barley collection strains were punched in cards for use with electronic data processing equipment. The data from the cards were organized for tabulation to yield information about the frequency of occurrence of the spike characters, individually and in combination with one another, together with information about the source of seed of the strains considered. These data were analyzed for each of the individual characters and for the existing two-, five-, and seven-character combinations.

The designation "character combination" is used to describe the joint occurrence of individual characters from the indicated number of spike categories; e.g., 6–W=two-character combination (all possible two-way conjunctions of the spike categories), 6–W–R–C–L=five-character combination (spike categories I to V only), and 6–W–R–C–L–1.0a–g–1.5a–s=seven-character combination (spike categories I to VII).

The individual character and two-character combination analyses were conducted because they afforded the most direct approach to acquiring information about the world barleys. The five- and seven-character combination analyses were carried out as much for practical reasons as for any thought that they would be more informative than, say, studies of three-, four-, or six-character combinations. The seven-character combinations were analyzed in order to use all the data in the study. The five-character combination assay was conducted after the seven-character combinations had been tabulated, when it became evident that the awn-glume and awn-spike ratios were serving to subdivide the five-character combinations into many component parts.

For the most part, this study is concerned with different approaches to making comparisons between, and drawing inferences from, values for the proportions of the strains having each of the characters and their combinations. Comparisons were made within the scope of the entire collection and within segments of the collection or component parts of these segments, selected on the basis of geographic factors or a combination of plant characters and geographic origin. This procedure was followed because of the limited numbers of strains from some sources, some imprecise source listings, and the complexity of the task of dealing with the many sources that are represented in the barley collection.

Five major subdivisions of the collection sources are utilized in interpreting data in parts of this study. They are listed below with brief comments about the nature of the barley strains involved:

EUROPE: Includes materials that probably trace back to seeds carried by migrating Asians; these materials have since been subjected to some intensive selection and improvement.

AFRICA-ASIA: Source of the most profuse assemblage of diverse genetic stocks, including many true endemic strains representing the end-products of centuries of evolutionary change—the source of strains that best reveal the intrinsic nature of cultivated barley.

U.S. DOMESTIC SELECTIONS: Includes materials introduced into North America by early settlers and succeeding generations up to the early 1900's and selections therefrom; materials that afford a unique opportunity for evaluating the impact of the migration and advancement of peoples on the world barley picture.

U.S. BREEDING LINES: Includes a large proportion of the best strains and varieties developed through hybridization since 1900—germ plasm that affords a basis for measuring the impact of controlled hybridization, using superior genotypes, on the barley picture.

SOUTH PACIFIC AND SOUTH-CENTRAL AMERICA: Source of materials introduced from the Old World plus some strains developed through hybridization.

The most difficult and time-consuming parts of the data processing for this study were accomplished through the punch card medium. However, numerous manual calculations were made after the machine tabulations had been completed.

Several footnotes throughout the text refer to an appendix. Many data computed for this study were too voluminous to be included in this publication. However, reproductions of these data in an appendix to a 1961 University of Minnesota dissertation of the same title can be obtained from University Microfilms Inc., 313 North First Street, Ann Arbor, Mich. (Order No. 61–4615).

INDIVIDUAL CHARACTERS

RESULTS

Proportions of Strains in Which Characters Occur

Entire Collection

The proportions of the 6,200 World Barleys in which the individua spike characters occur are given in table 5. Some characters occur in only a limited proportion of strains while others are found in a large proportion, the range being from 0.05 percent to 88.3 percent.

The characters that occur in the greatest proportion of the strains within the respective spike categories are as follows:

Spike category:	*Character*
I	6 rows of keels.
II	White kernels.
III	Rough awns.
IV	Covered kernels.
V	Long rachilla hairs.
VI	Glume-awn-equal-to-length-of-glume, (1.0a–g).
VII	Lemma-awns-extend-beyond-tip-of-spike-to-a-distance-equal-to-1½-times-the-length-of-the-spike, (1.5a–s).

These will be referred to as the *predominant* characters. Six of these characters occur in more than 55 percent of the strains within their respective spike categories; the seventh occurs in more than 40 percent.

TABLE 5.—*Proportion of 6,200 strains in the World Collection of Barleys that have each of 37 characters within 7 spike categories*

Spike category and character (code)[1]	Percent	Spike category and character (code)[1]	Percent
Head type:		Rachilla hairs:	
6	71.0	L	60.9
2	25.1	Sh	39.1
D	2.0	Awn-glume ratio:	
I	1.2	1.0	55.2
U	.7	2.0	16.8
Kernel color:		2.5	11.2
W	55.1	1.5	9.0
B	16.5	3.0	6.0
DB	13.1	3.5	1.1
LB	7.1	4.0	.5
Bk	5.7	4.5	.1
P	2.5	5.0	.05
Awn condition:		Awn-spike ratio:	
R	88.3	1.5	42.2
Sm	6.0	1.0	29.3
SS	2.7	2.0	17.0
H	2.6	0.5	3.7
A	.4	2.5	2.6
Caryopsis:		3.0	1.7
C	87.5	3.5	.4
N	12.5	4.0	.2

[1] For explanation of codes, see table 1.

The disparate backgrounds for the predominant characters may be noted in the following summary drawn from information presented in tables 2 and 3.

6 (6-row)	Recessive condition at a single locus in linkage group I.
W (White)	Recessive condition at several loci, some of which are in linkage groups I, II, and IV; dominant condition at 1 or 2 loci of unknown linkage relationships.
R (Rough)	Dominant conditions at from 1 to 4 loci, some of which are in linkage groups III–VII and V.
C (Covered)	Dominant condition at a single locus in linkage groups III–VII.
L (Long)	Dominant condition at a single locus in linkage group V.
1.0a–g (glume-awn-equal-to-length-of-glume).	Unknown.
1.5a–s (lemma-awn-1½-times-length-of-spike).	Determined by the interaction of an unknown number of complementary factors governing spike density, rachis internode number, and awn length; the greatest number of these factors being presumed to be dominant.

In contrast to the large proportions of the strains in which the predominant characters occur, 25 of the 37 characters occur in less than one-sixth of the strains in their respective categories. Sixteen of these occur in less than one-twentieth of the strains in their respective categories.

Of the other-than-predominant characters in spike categories I to V, all of the known factors controlling them are dominant except those for smooth awns, awnless, naked caryopsis, and short rachilla hairs; the genetic background for *H. irregulare* is unknown. Little is known about the genetic background for the awn-glume ratios. Strains with high awn-spike ratios are usually characterized by long awns and short, lax spikes, a condition that probably represents the interaction of the "Lk," "rin," and "l" genes. Strains with very short awns (0.5a–s) often have dense spikes, a situation in which the actions of the "lk" and "l" genes are probably being expressed. Many of the strains with lemma awns extending beyond the tip of the spike to a distance ranging from equal to the length of the spike to one and one-half times the length of the spike (1.0a–s to 1.5a–s) are characterized by long awns and lax spikes, situations in which the actions of the "Lk," "Rin," and "L" genes probably are expressed.

Subdivisions

Data on the proportions of the strains from each of five subdivisions of the collection that have each of the spike characters are included in table 6. Although the general pattern of the predominance of certain characters remains evident, exceptions to the pattern cited for the entire collection may be noted—the 2-row head type occurs in the greatest number of the strains obtained from Europe; more strains exist with short rachilla hairs than with long ones in barleys from the Americas; and a strikingly greater proportion of smooth awn types occur among the strains developed through hybridization in North America than among any other group.

Geographic Distribution of the Characters

Proportions of Strains Having Each Character Obtained From Each Subdivision

Information about (1) the proportions of the collection constituted by strains from each of the subdivisions and (2) the proportions of the strains with each character that have been obtained from these subdivisions is presented in table 7. African and Asian sources have yielded the greatest proportions of the strains. Although some of the characters were not found among barleys from some of the subdivisions, all were found among the African-Asian strains. In a general way, the proportions of the sort listed under (1) and (2) above tend to correspond to one another within the respective subdivisions. There are several notable exceptions to this. More than one-fourth of the 2-row strains are included among the 12.1 percent of the strains obtained from Europe. More than one-half of the intermedium and smooth awn types are included in the 11.0 percent of the strains developed through breeding in North America, etc.

TABLE 6.—*Proportion of strains in the World Collection of Barleys from each of 5 source subdivisions that have each of 37 characters in 7 spike categories*

Spike category and character (code) [1]	Europe	Africa-Asia	South Pacific-South and Central America	U.S. Domestic Selections	U.S. Breeding Lines
Head type:	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
6	43.8	73.3	78.7	85.1	78.1
2	55.0	22.5	19.9	12.6	16.3
D	1.1	2.4	0	.9	2.1
I	0	1.7	0	0	0
U	.1	.3	.7	1.4	3.5
Kernel color:					
W	67.4	53.4	35.3	56.3	55.3
LB	11.1	5.1	11.0	14.4	10.6
B	13.0	16.3	27.2	19.5	17.9
DB	6.5	14.7	24.3	6.9	11.5
Bk	1.6	7.2	.7	2.6	3.5
P	.4	3.3	1.5	.3	1.2
Awn condition:					
R	94.8	92.9	93.4	82.5	54.4
Sm	1.5	3.4	1.5	3.2	29.6
SS	2.3	2.6	.7	1.1	5.0
H	.5	.9	4.4	12.1	10.4
A	.9	.2	0	1.1	.6
Caryopsis:					
C	95.6	83.9	91.9	94.8	96.0
N	4.4	16.1	8.1	5.2	4.0
Rachilla hairs:					
L	67.0	66.4	26.5	28.2	42.6
Sh	33.0	33.6	73.5	71.8	57.4
Awn-glume ratio:					
1.0	63.5	53.2	77.9	35.9	64.1
1.5	7.2	9.3	7.4	12.9	7.5
2.0	12.4	17.5	11.8	24.4	14.1
2.5	7.9	12.4	2.2	14.1	7.5
3.0	6.4	6.0	0	7.8	5.3
3.5	1.6	1.0	.7	2.3	1.0
4.0	.8	.4	0	1.4	.4
4.5	0	.1	0	.3	0
5.0	.1	.1	0	0	0
Awn-spike ratio:					
0.5	1.1	4.6	2.2	.3	3.4
1.0	46.7	28.2	6.6	28.7	21.6
1.5	42.2	42.9	25.0	34.2	45.7
2.0	7.6	18.4	42.7	20.1	14.0
2.5	.3	2.6	11.8	2.9	2.5
3.0	.1	2.0	5.1	.3	1.6
3.5	.2	.5	1.4	.3	.1
4.0	.1	.2	.7	0	0

[1] For explanation of codes, see table 1.

TABLE 7.—*Proportion of all strains in the World Collection of Barleys from 5 source subdivisions, and proportion of strains having each of 37 characters in 7 spike categories that came from each source*

Spike category and character (code) [1]	Europe	Africa-Asia	South Pacific-South and Central America	U.S. Domestic Selections	U.S. Breeding Lines
	Percent	*Percent*	*Percent*	*Percent*	*Percent*
All strains	12. 1	69. 1	2. 2	5. 6	11. 0
Head type:					
6	7. 5	71. 3	2. 4	6. 7	12. 1
2	26. 5	61. 8	1. 7	2. 8	7. 2
D	6. 0	80. 3	0	2. 5	11. 2
I	0	100. 0	0	0	0
U	2. 3	27. 9	2. 3	11. 7	55. 8
Kernel color:					
W	14. 8	67. 0	1. 4	5. 8	11. 0
LB	18. 9	49. 9	3. 4	11. 4	16. 4
B	9. 6	68. 3	3. 6	6. 6	11. 9
DB	6. 0	77. 4	4. 1	2. 9	9. 6
Bk	3. 4	87. 0	. 3	2. 5	6. 8
P	1. 9	90. 9	1. 3	. 6	5. 3
Awn condition:					
R	13. 0	72. 7	2. 3	5. 2	6. 8
Sm	3. 0	39. 5	. 5	3. 0	54. 0
SS	10. 1	66. 9	. 6	2. 4	20. 0
H	2. 5	23. 6	3. 7	26. 1	44. 1
A	30. 4	34. 8	0	17. 4	17. 4
Caryopsis:					
C	13. 3	66. 3	2. 3	6. 1	12. 0
N	4. 2	88. 6	1. 4	2. 3	3. 5
Rachilla hairs:					
L	13. 3	75. 4	1. 0	2. 6	7. 7
Sh	10. 2	59. 3	4. 1	10. 3	16. 1
Awn-glume ratio:					
1.0	13. 9	66. 6	3. 1	3. 7	2. 7
1.5	9. 7	71. 3	1. 8	8. 1	9. 1
2.0	9. 0	72. 1	1. 5	8. 2	9. 2
2.5	8. 5	76. 6	. 4	7. 1	7. 4
3.0	13. 0	70. 0	0	7. 3	9. 7
3.5	17. 4	59. 4	1. 4	11. 7	10. 1
4.0	19. 4	54. 8	0	16. 1	9. 7
4.5	0	80. 0	0	20. 0	0
5.0	33. 3	66. 7	0	0	0
Awn-spike ratio:					
0.5	3. 6	84. 7	1. 3	. 4	10. 0
1.0	19. 4	66. 5	. 5	5. 5	8. 1
1.5	12. 1	70. 2	1. 3	4. 5	11. 9
2.0	5. 4	73. 5	5. 5	6. 6	9. 0
2.5	1. 3	71. 9	10. 0	6. 3	10. 5
3.0	1. 0	80. 7	6. 7	1. 0	10. 6
3.5	8. 0	76. 0	8. 0	4. 0	4. 0
4.0	11. 1	77. 8	11. 1	0	0

[1] For explanation of codes, see table 1.

Analysis of Character Distribution Patterns

A listing of the proportions of the strains from an individual source that have each of the characters in each spike category constitutes a "character distribution pattern" for the strains in the collection from that source. Data from individual sources were brought together to determine the possibility of consolidating the sources into logical world barley regions. They were analyzed to determine the degree of similarity of distribution patterns for the different sources. Comparable patterns were frequently in evidence when the spike character data were alined according to the geographic proximity of the sources. When the patterns for adjacent sources were comparable, the data were pooled to yield a regional distribution pattern. Clear-cut differences were noted between these regional patterns, although the actual lines of demarcation between the areas with different character patterns were often indistinct. Certain sources lying geographically within a distinct spike character region gave patterns contrary to the general pattern for the region. The geographic factor was accorded first importance in these cases and the data were incorporated with those for the region as a whole.

Regions Postulated

Thirty-one geographic regions within the five subdivisions of the collection were postulated from the combined plant character and geographic information.

The sources comprising the regions are listed in table 8. In pages that follow, these regions are identified by the code numbers shown in this table. In general, the regions in the Eastern Hemisphere were established because the barleys obtained from those areas have certain characters in a greater proportion of the strains than do the barleys from other areas. However, regions 2 and 9 were established because the barleys from those areas, although lacking distinguishing characters, were different from those of the adjoining regions. There were insufficient strains from the South Pacific and from South and Central America areas to justify an attempt to establish specific geographic regions. Geographic and ecologic factors and the current varietal distribution pattern, as revealed by uniform yield and hardiness nurseries conducted by the U.S. Department of Agriculture in cooperation with the State experiment stations, were used to establish the source groupings for the United States. The States were organized into seven regions. These regional alinements were used for both the U.S. Domestic Selections and the U.S. Breeding Lines. Region 18 corresponds to region 25, 19 to 26, etc.

TABLE 8.—*Sources of strains in the World Collection of Barleys grouped by regions* [1]

Region	Source	Region No.
Northwest Europe	England	1
	Scotland	
	Orkney Islands	
	Denmark	
North and Central Europe	Europe	2
	North Europe	
	Holland	
	Germany	
	Bavaria	
	Thuringia	
	Silesia	
	Poland	
	Norway	
	Sweden	
	Svalof	
	Finland	
Southeast Europe	Belgium	3
	France	
	Vilmorin	
	Portugal	
	Spain	
	Switzerland	
	Italy	
Southwest Europe	Czechoslovakia	4
	Bohemia	
	Moravia	
	Austria	
	Hungary	
	Rumania	
	Yugoslavia	
	Bulgaria	
	Greece	
Ethiopia	Ethiopia	5
North Africa	North Africa	6
	Sahara	
	Algeria	
	Morocco	
	(Tunisia)	
	Tunis	
	Egypt	
	Delta	
	Mariout	
	Minia	
	Sinai	
	Palestine	
Black Sea area	Syria	7
	Turkey	
	Anatolia	
	Asia Minor	
	(Ukraine)	
	Crimea	
	Odessa	
	Kharkov	
	Valkie	

See footnote at end of table.

TABLE 8.—*Sources of strains in the World Collection of Barleys grouped by regions* [1]—Continued

Region	Source	Region No.
Caucasus area	South Russia	8
	Ciscaucasia	
	Otrada Kubanska	
	Kasafute	
	Dagestan	
	Derbent	
	Georgia	
	Mount Kazbek	
	Tiflis	
	(Armenia)	
	Gonzah	
	Yerevan	
	(Azerbaidzhan)	
	Baku	
	Transcaucasia	
	Dickson	
	(Turkey)	
	Northeast Turkey	
Near East, Mideast, and Russia	Arabia	9
	Iraq	
	Mesopotamia	
	Iran	
	Persia	
	Baluchistan	
	Afghanistan	
	Turkistan	
	Bukhara	
	Russia	
India	India	10
	Kashmir	
	Punjab	
Central Asia	Nepal	11
	Mount Everest	
	Tibet	
	Chinese Turkistan	
	Kashgar	
	(China)	
	Northwest China	
	Mongolia	
	Siberia (2-row naked)	
	Central Asia	
	Pissarev	
	Vavilov	
	Asia	
Manchuria	Manchuria	12
	Siberia (6-row covered)	
Korea	Korea	13
China	China	14
	North China	
	Orient	
Japan	Japan	15
South Pacific	Australia	16
	New South Wales	
	Java	

See footnote at end of table.

TABLE 8.—*Sources of strains in the World Collection of Barleys grouped by regions* [1]—Continued

Region	Source	Region No.
South and Central America	Argentina	17
	Chile	
	Uruguay	
	Paraguay	
	Peru	
	Brazil	
	Venezuela	
	Guatemala	
	Mexico	
United States:		
	U.S. Domestic Selections	
Far West	California	18
	Arizona	
	New Mexico	
	Utah	
	Idaho	
	Montana	
	Washington	
	Oregon	
West North Central	North Dakota	19
	South Dakota	
	Nebraska	
	Colorado	
North Central	Minnesota	20
	Wisconsin	
	Iowa	
East North Central	Indiana	21
	Ohio	
	Michigan	
Northeast	New York	22
	Pennsylvania	
	West Virginia	
South Central	Kansas	23
	Missouri	
	Arkansas	
	Oklahoma	
	Texas	
Southeast	Virginia	24
	Kentucky	
	North Carolina	
	South Carolina	
	Tennessee	
	Georgia	
	U.S. Breeding Lines	
Far West	California	25
	Arizona	
	Utah	
	Idaho	
	Montana	
	Washington	
	Oregon	
West North Central	North Dakota	26
	South Dakota	
	Nebraska	
	Wyoming	
	Colorado	

See footnote at end of table.

TABLE 8.—*Sources of Strains in the World Collection of Barleys grouped by regions*[1]—Continued

Region	Source	Region No.
United States—Continued		
U.S. Breeding Lines—Continued		
North Central	Minnesota Wisconsin Iowa	27
East North Central	Indiana Ohio Michigan	28
Northeast	New York New Jersey Pennsylvania Maryland West Virginia	29
South Central	Kansas Missouri Oklahoma Texas	30
Southeast	Kentucky North Carolina South Carolina Tennessee Georgia	31

[1] Based on geographic factors, plant characters that distinguish strains of one region from those of the others, and known varietal distribution patterns.

Regional Character Distribution Patterns

The character distribution patterns for each of the regions are illustrated in figure 3.[4]

EUROPE.—Among the European regions, the strains from Northwest Europe (region 1) and from Southwest Europe (region 4) are distinguished by a large proportion of 2-row head types. The strains from North and Central Europe (region 2) are fairly evenly divided between 6-row and 2-row head types, whereas the barleys from Southeast Europe (region 3) are preponderantly 6-rowed. Region 3 includes more blue kernel strains than does region 2. The character distribution patterns for regions 1 and 4 are very similar except for a preponderance of strains with a 1.5 awn-spike ratio in region 1 compared to a preponderance of strains with a 1.0 ratio in region 4.

SOUTH PACIFIC-SOUTH AND CENTRAL AMERICA.—The strains from the South Pacific area have proportionately more strains with dark blue kernels, hoods, short rachilla hairs, and awn-spike ratios of 2.0 than do those comprising the remainder of the collection. The pattern for the South and Central American strains also deviates from the remainder of the collection in similar ways. The proportions of strains with blue kernel types and short rachilla hairs are somewhat

[4] Spike character proportions for the individual sources and for the regions are included in tables I and II of the appendix referred to on p. 13.

greater among the barleys obtained from South and Central America than among those from the South Pacific. The hooded character was not observed in strains from the southern part of the Western Hemisphere.

U.S. Domestic Selections.—The U.S. Domestic Selections do not include as great a proportion of head types other than 6-row as the remainder of the collection. Only the Far West (region 18), West North Central (region 19), and East North Central (region 20) regions are comprised by any appreciable proportions of strains with a head type other than 6-row; i.e., 2-row. The hooded character is markedly present among the Domestic Selections, particularly in the regions from the East (regions 22 and 24). The preponderance of short hair rachilla types among the U.S. Domestic Selections is in direct contrast to the picture for the remainder of the collection. Only the Far West and West North Central regions include any marked proportions of strains with long rachilla hairs. Also only these regions have significant numbers of strains with an awn-glume ratio of 1.0. The other regions in the U.S. Domestic Selections subdivision have greater proportions of strains with high awn-glume ratios than is the case with the remainder of the collection. The awn-glume ratio patterns for regions 20 to 24 are marked by their dissimilarity. Although numerous differences exist between the patterns for the individual regions, the different awn-spike characters occur in proportions of the domestic selections that correspond quite closely with those for the remainder of the collection.

U.S. Breeding Lines.—With the exception of characters in the head type and caryopsis spike categories, the spike character distribution patterns for the regions constituting the U.S. Breeding Lines subdivision are marked by their dissimilarity. Of special interest is the comparatively large proportion of blue kernel types among the strains from regions 29 to 31 as compared with those from regions 25 to 28—a reflection of a demand for white kernel types among the malting barleys grown in the North Central States. The disparities between the proportions of rough or smooth awn strains from the same groups of regions also reflect different objectives in the breeding programs. The data in table 6 indicate that only slightly more than one-half of the breeding line strains have short hair rachillas. It is evident from figure 3 that the different rachilla hair types are not uniformly distributed among the U.S. Breeding Lines, but that each type is concentrated in strains from certain regions. The greatest proportion of the strains, except those from region 30, have an awn-glume ratio of 1.0. No general trend is evident among the awn-spike ratio patterns for the different regions.

Africa and Asia.—The areas in Africa and Asia where the individual characters appear to be concentrated or occur in a large proportion of the strains are summarized in table 9. Strains from all the regions except the Near East, Mideast, and Russia (region 9) are distinguished by one or more characters that are concentrated in the region in question. Some characters, such as 6-row, occur in a large proportion of the strains from most of the regions, whereas others, such as 2-row, occur in only a few regions or a single region. The characters among the African and Asian barleys that distinguish the strains of one region from those of other regions are noted in table 10.

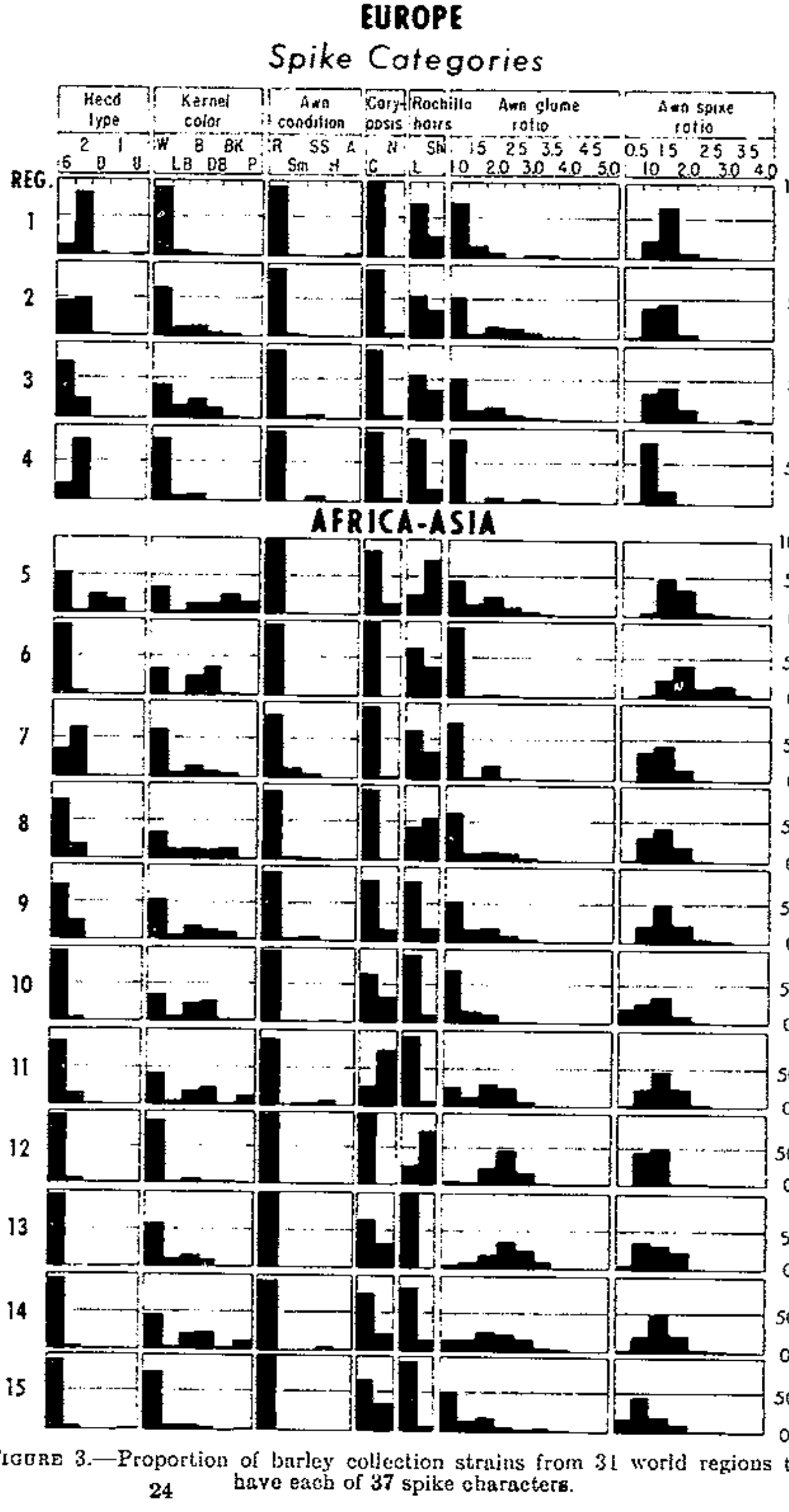

FIGURE 3.—Proportion of barley collection strains from 31 world regions that have each of 37 spike characters.

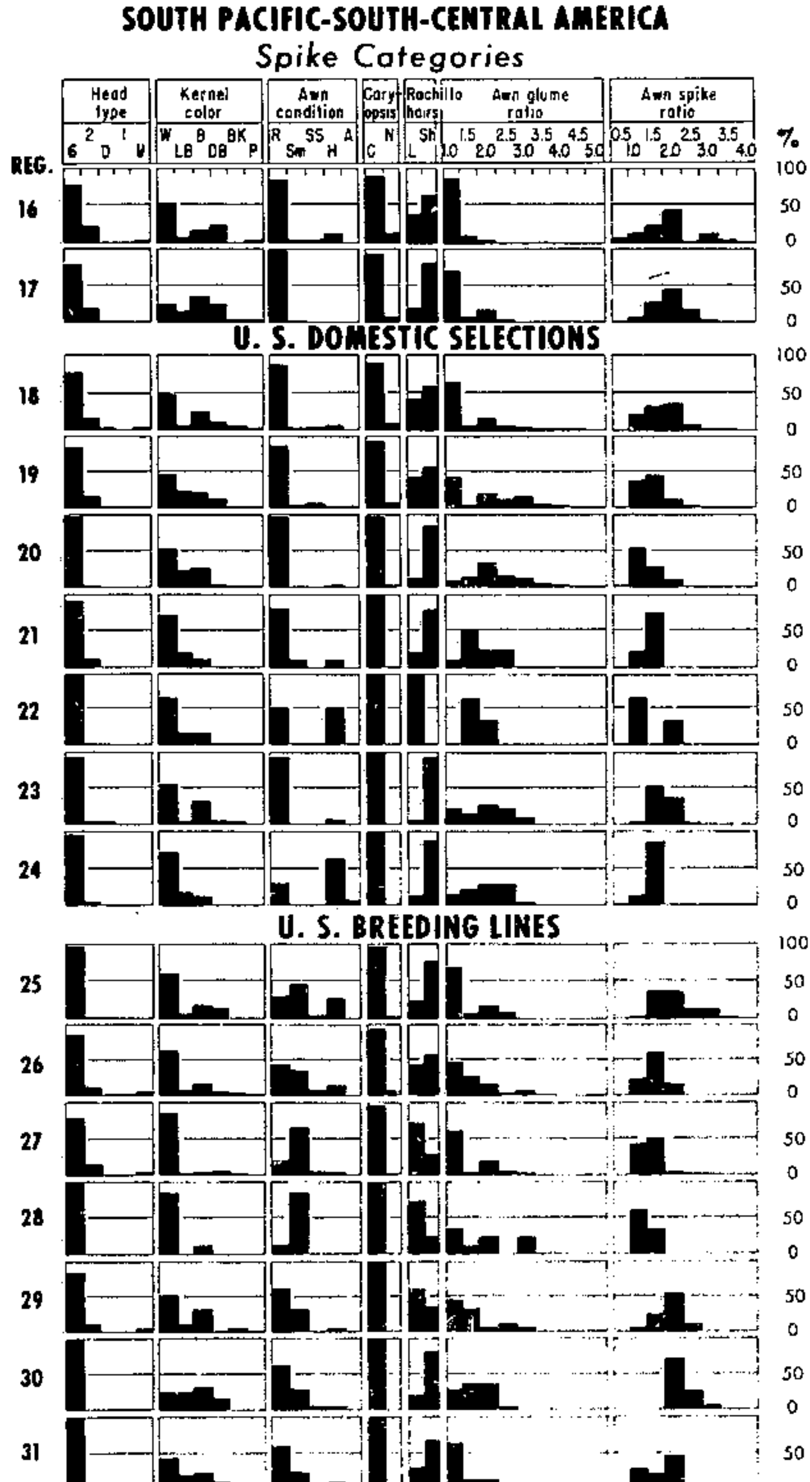

FIGURE 3.—Continued.

Regions in Which Individual Characters Occur in Comparatively Large Proportions of Strains

Table 11 indicates regions in which each character is concentrated or where it occurs in a comparatively large proportion of the strains. This table was developed by designating regions in which the propor-

TABLE 9.—*Regions in Africa and Asia in which each of 37 characters in 7 spike categories among 6,200 strains in the World Collection of Barleys appears to be concentrated*

Spike category and character (code) [1]	Region [2]
Head type:	
6	Widely distributed.
2	Black Sea area (7).
D	Ethiopia (5).
I	Do.
U	Korea (13), Japan (15).
Kernel color:	
W	Widely distributed.
LB	Caucasus area (8), Korea (13).
B	North Africa (6), India (10).
DB	Do.
Bk	Ethiopia (5), Caucasus area (8).
P	Ethiopia (5), Central Asia (11), China (14)
Awn condition:	
R	Widely distributed.
Sm	Black Sea area (7).
SS	Do.
H	Central Asia (11).
A	China (14).
Caryopsis:	
C	Widely distributed.
N	Central Asia (11).
Rachilla hairs:	
L	Widely distributed.
Sh	Ethiopia (5), Manchuria (12).
Awn-glume ratio:	
1.0	Widely distributed.
1.5	Do.
2.0	Do.
2.5	Central Asia (11), Manchuria (12), Korea (13), China (14).
3.0	Manchuria (12), Korea (13), China (14).
3.5	Korea (13), Japan (15).
4.0	Korea (13), China (14), Japan (15).
4.5	Korea (13), Japan (15).
5.0	Japan (15).
Awn-spike ratio:	
0.5	India (10), Japan (15).
1.0	Widely distributed.
1.5	Do.
2.0	Ethiopia (5), North Africa (6).
2.5	North Africa (6).
3.0	Do.
3.5	Do.
4.0	Do.

[1] For explanation of codes, see table 1.
[2] Region numbers, in parentheses, refer to listing in table 8.

TABLE 10.—*Characters of strains from Africa and Asia in the World Collection of Barleys that distinguish strains of one geographic region from those of other regions*

Spike category and character (code) [1]	Region No. [2]										
	5	6	7	8	9	10	11	12	13	14	15
Head type:											
6	----	----	----	----	----	----	----	----	----	----	----
2	----	----	√	----	----	----	----	----	----	----	----
D	√	----	----	----	----	----	----	----	----	----	----
I	√	----	----	----	----	----	----	----	----	----	----
U	----	----	----	----	----	----	----	----	√	----	√
Kernel color:											
W	----	----	----	----	----	----	----	√	----	----	----
LB	----	----	----	√	----	----	----	----	√	----	----
B	----	----	----	----	----	----	----	----	----	----	----
DB	----	√	----	----	----	----	----	----	----	----	----
Bk	√	----	----	√	----	----	----	----	----	----	----
P	√	----	----	----	----	----	√	----	----	√	----
Awn condition:											
R	----	----	----	----	----	----	----	----	----	----	----
Sm	----	----	√	----	----	----	----	----	----	----	----
SS	----	----	√	----	----	----	----	----	----	----	----
H	----	----	----	----	----	----	√	----	----	----	----
A	----	----	----	√	----	----	----	----	----	√	----
Caryopsis:											
C	----	----	----	----	----	----	----	----	----	----	----
N	----	----	----	----	----	----	√	----	----	----	----
Rachilla hairs:											
L	----	----	----	----	----	----	----	----	----	----	----
Sh	√	----	----	√	----	----	----	√	----	----	----
Awn-glume ratio:											
1.0	----	√	----	----	----	----	----	----	----	----	----
1.5	----	----	----	----	----	----	----	----	----	----	----
2.0	----	----	----	----	----	----	----	----	----	----	----
2.5	----	----	----	----	----	----	----	√	----	----	----
3.0	----	----	----	----	----	----	----	√	√	√	----
3.5	----	----	----	----	----	----	----	----	√	----	----
4.0	----	----	----	----	----	----	----	----	----	----	----
4.5	----	----	----	----	----	----	----	----	√	----	√
5.0	----	----	----	----	----	----	----	----	----	----	√
Awn-spike ratio:											
0.5	----	----	----	----	----	√	----	----	----	----	√
1.0	----	----	----	----	----	----	----	----	----	----	----
1.5	----	----	----	----	----	----	----	----	----	----	----
2.0	----	----	----	----	----	----	----	----	----	----	----
2.5	----	√	----	----	----	----	----	----	----	----	----
3.0	----	√	----	----	----	----	----	----	----	----	----
3.5	----	√	----	----	----	----	----	----	----	----	----
4.0	----	√	----	----	----	----	----	----	----	----	----

[1] For explanation of codes, see table 1.
[2] For list of regions, see table 8.

tions of the strains having each character equal or exceed arbitrarily selected proportions of all strains from these regions. These base proportions are given for the characters, together with ranges to indicate the smallest and largest proportions of the strains with those characters from any regions.

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TABLE 11.—*World regions in which the proportion of strains equals or exceeds arbitrarily selected base values for each of 37 characters in 7 spike categories among 6,200 strains in the World Collection of Barleys* [1]

Spike category and character (code)[2]	Range among regions		Base for this table	Region No.[3]																														
	Minimum	Maximum		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Head type:	*Percent*	*Percent*	*Percent*																															
6	11.9	100.0	73.2			x			x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
2	0	85.7	51.4	x			x			xx																								
D	0	24.3	24.3					xx																										
L	0	10.3	10.3					xx																										
U	0	5.3	2.2													xx		xx			x								x	x		x		
Kernel color.																																		
W	23.8	91.7	50.9	x	x		x			x		x			x	x		x	x				x	x	x	x	x	x	x	x	x	x	x	
LB	0	23.8	11.2		x	x					xx					xx				x		x	x	x	x		x						x	x
B	2.4	38.1	15.5			x			xx		x	x	xx	x		x	x		x	x	x	x	x		x	x		x	x			x	x	x
DB	0	27.4	10.5			x		x	xx		x	x	xx	x		x	x		x	x	x	x						x					x	x
Bk	0	24.8	8.5					xx		x	xx	x																						
P	0	16.1	10.5					xx						xx			xx																	
Awn condition:																																		
R	12.5	100.0	50.0	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x						x	x	x
Sm	0	87.5	10.0							xx														x				x	x	x	x	x	x	x
SS	0	8.7	4.2			x	x			xx												x						x	x	x			x	
H	0	63.0	8.7											xx							x			x	x		x	x	x					x
A	0	7.4	.9	x							x						xx					x					x							

Caryopsis:																																		
C	27.4	100.0	66.0	x	x	x	x	x	x	x	x	x	x	----	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
N	0	33.1	21.5	----	----	----	----	----	----	----	----	----	x	xx	----	x	x	x	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Rachilla hairs:																																		
L	0	100.0	60.2	x	x	x	x	----	x	x	----	x	x	x	----	x	x	x	---	---	---	---	---	---	---	---	---	---	---	x	x	x	---	---
Sh	0	100.0	58.1	----	----	----	----	xx	----	----	x	----	----	----	xx	----	----	----	x	x	x	x	x	x	x	x	x	x	x	---	---	---	x	x
Awn-glume ratio:																																		
1.0	0	85.5	50.6	x	x	x	x	----	x	x	x	x	x	----	----	----	----	x	x	x	x	---	---	---	---	---	---	x	---	x	---	---	---	x
1.5	.6	66.7	10.6	x	----	x	----	x	----	----	x	x	x	x	----	----	x	x	---	---	---	---	x	x	x	x	x	---	x	---	x	x	x	x
2.0	2.7	33.3	14.7	----	x	x	----	x	----	x	----	x	----	x	x	x	x	x	---	x	x	x	x	x	x	x	x	x	x	x	x	---	x	x
2.5	0	48.8	9.8	----	----	x	----	----	----	----	x	----	----	xx	xx	xx	xx	----	---	---	---	x	x	x	---	x	x	---	---	---	---	x	---	---
3.0	0	25.0	10.7	----	----	----	----	----	----	----	----	----	----	----	xx	xx	xx	----	---	---	---	x	x	---	---	x	---	---	---	---	x	---	---	---
3.5	0	9.0	3.0	----	----	x	----	----	----	----	----	----	----	----	----	xx	x	xx	---	---	---	x	x	---	---	---	---	---	---	---	---	---	---	---
4.0	0	4.9	.7	----	x	----	----	----	----	----	----	----	----	----	----	xx	xx	xx	---	---	x	x	x	---	---	---	---	---	---	---	---	---	---	---
4.5	0	1.1	.7	----	----	----	----	----	----	----	----	----	----	----	----	xx	----	xx	---	---	x	---	---	---	---	---	---	---	---	---	---	---	---	---
5.0	0	.7	.7	----	----	----	----	----	----	----	----	----	----	----	----	----	----	xx	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Awn-spike ratio:																																		
0.5	0	19.7	6.2	----	----	----	----	----	----	----	----	----	xx	----	----	x	----	xx	x	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
1.0	0	81.9	20.5	x	x	x	x	----	----	x	x	x	x	x	x	x	x	x	---	---	x	x	x	x	x	---	---	---	x	x	x	---	---	x
1.5	0	87.5	43.8	x	x	x	----	x	----	x	x	x	----	x	x	----	x	----	---	---	---	x	---	---	---	x	---	---	x	x	---	---	---	---
2.0	0	70.0	21.2	----	----	----	----	xx	xx	----	x	x	----	x	----	x	x	----	x	x	x	---	---	---	x	x	---	x	---	---	---	x	x	x
2.5	0	25.0	3.5	----	----	----	----	x	xx	----	----	x	----	----	----	----	x	----	---	x	x	x	---	---	---	x	---	x	---	---	---	x	x	---
3.0	0	15.0	11.1	----	----	----	----	----	xx	----	----	----	----	----	----	----	----	----	x	---	---	---	---	---	---	---	---	x	---	---	---	---	---	---
3.5	0	4.1	2.8	----	----	----	----	----	xx	----	----	----	----	----	----	----	----	----	x	---	---	---	---	---	---	---	---	x	---	---	---	---	---	---
4.0	0	2.0	1.7	----	----	----	----	----	xx	----	----	----	----	----	----	----	----	----	x	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---

[1] xx=proportions greatly exceed those for the other regions, or the only region from which the character has been obtained.
[2] For explanation of codes, see table 1.
[3] For list of sources comprising the regions, see table 8.

The predominant characters from the head type, awn characteristic, and caryopsis spike categories are preponderant in the strains from most of the regions. The other characters in these spike categories occur in a limited number of regions. In only a few of these regions do these characters occur in a markedly higher proportion of strains than the others. The remaining spike categories are marked by distribution patterns in which several of the characters occur in comparatively large proportions of the strains from several regions. However, the differences between the proportions of strains with each character are not so sizable.

Patterns indicating the concentration of certain characters in certain geographic areas are most striking in the awn-glume and awn-spike ratio categories.

Examples of Concentration of Characters in Certain African or Asian Regions

Certain characters are concentrated among strains from specific regions. A few examples are cited in the following paragraphs.

2-ROW.—Sources from whence a high proportion of 2-row types have been obtained are given in table 12. Only five regions are represented. Four out of five of the Asian sources are in the Black Sea area. Only three regions, all European, are represented in addition to the Asian areas. More than 85 percent of the 2-row barleys in the collection are from Europe and Asia. About 71 percent of the 2-row barleys from Europe and Asia are from the sources listed in table 12. The 2-row character occurs in 64.5 percent of the strains obtained from the Asian sources listed.

HOODED.—Table 13 cites the Asian sources for the hooded character. These relate primarily to the general area of the Himalayan Mountains and affiliated ranges in Central Asia. The hooded character comprises only 2.4 percent of the barleys from regions 9, 10, 11, and 14. However, 97 percent of the hooded barleys from Africa and Asia were obtained from these regions.

TABLE 12.—*Asian and European sources from which more than half the strains acquired for the World Collection of Barleys are 2-row head types*[1]

Source	Region No.	Source	Region No.
Asia:		Europe (continued):	
Syria	7	**Bavaria**	2
Turkey	7	Poland	2
Kharkof	7	**Svalof** (Sweden)	2
Valkie	7	**Czechoslovakia**	4
Asia	11	**Bohemia**	4
Europe:		**Moravia**	4
England	1	Austria	4
Scotland	1	**Hungary**	4
Denmark	1	**Yugoslavia**	4
Germany	2		

[1] 68 percent of all strains in the collection with the 2-row character were obtained from these sources. Boldface type indicates that more than 75 percent of the barleys obtained from these sources are 2-row types.

TABLE. 13—*Asian sources of hooded strains included in the World Collections of Barleys* [1]

Source	Region No.	Source	Region No.
Otrada Kubanska	8	Pissarev	11
Russia	9	Vavilov	11
India	10	China	14
Nepal	11	North China	14
Tibet	11		

[1] Of the 38 hooded strains from Asian sources, not more than 10 were from any one source.

AWN-SPIKE RATIOS.—The proportions of the Egyptian strains and the remainder of the collection that have each of the awn-spike ratios in covered kernel types are illustrated in figure 4. It is evident that the Egyptian barley spikes are distinct from those obtained from the remainder of the world. The Egyptian barleys have short rachises and lemma awns of a normal length. The net result is a high awn-spike ratio.

RACHILLA HAIRS.—Rachilla hair proportions for strains from some major African and Asian sources are given in table 14. Barleys from Ethiopia and Manchuria are distinct from those of other areas because of the striking preponderance of short rachilla hair types among them. It does not follow, however, that the strains from these two sources are similar in other ways. Figure 3 indicates that whereas there is a striking uniformity of morphologic type among the Manchurian strains, the Ethiopian strains are characterized by a diversity of types. Also, nearly all the Manchurian barleys are 6-row, white kernel types, but the Ethiopian barleys include numerous deficiens and *H. irregulares* in addition to the 6-row head types and a fairly even distribution of white, blue, black, and purple kernel

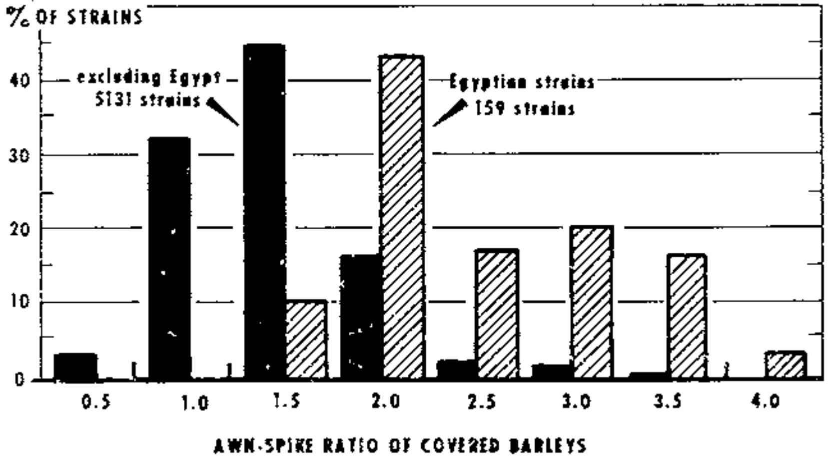

FIGURE 4.—Proportion of barley collection strains (covered kernels) from Egypt and from the rest of the world that have each of 8 awn-spike ratios.

types. It is of interest to note the contrast between the rachilla hair proportions for the Ethiopian and Manchurian barleys and the proportions for barleys from adjacent countries.

TABLE 14.—*Proportion of strains from several African and Asian sources in the World Collection of Barleys that have long and short rachilla hairs.*

Source	Strains	Rachilla hairs	
		Long	Short
	Number	*Percent*	*Percent*
Ethiopia	367	27. 8	72. 2
North Africa [1]	300	60. 7	39. 3
Turkey	804	64. 3	34. 7
Afghanistan	168	95. 2	4. 8
India	489	89. 8	10. 2
Russia	223	71. 3	28. 7
China	198	85. 4	14. 6
Manchuria	434	26. 7	73. 3
Korea	134	100. 0	0
Japan	269	93. 7	6. 3
Turkey	804	64. 3	34. 7
Northeast Turkey	49	28. 6	71. 4
Caucasus area	40	70. 0	30. 0

[1] Represents sources comprising region 6.

Differences Among Strains Within a Region

The results of the character distribution pattern analyses for the individual sources permit some broad generalizations about barley types from a region. The data at the bottom of table 14 indicate that these generalizations may not always afford a sound basis for drawing precise conclusions about the nature of all barleys within a country or a region. The distribution of rachilla hair types among strains from Northeast Turkey is unlike that for strains listed under the Caucasus or Turkey source designations. The basic data for this study reveal that the greatest number of strains from Northeast Turkey are 6-rowed. This is contrary to the general pattern for Turkey, from whence mostly 2-row strains have been obtained, but it is similar to the pattern for the Caucasus area.

The Northeast Turkey strains were incorporated into region 8 because a large proportion of the strains from the Caucasus area, as distinct from the specific Caucasus source, are 6-row, short hair rachilla types. This is not to say that there are no strains with this makeup among the general group from Turkey.

Some Changes in Spike Characters Through Breeding

Figure 5 presents for comparison the proportions of strains with each character among the Domestic Selections and Breeding Lines from the seven U.S. regions. The character distribution patterns for regions 18 and 25, etc., are shown side by side.

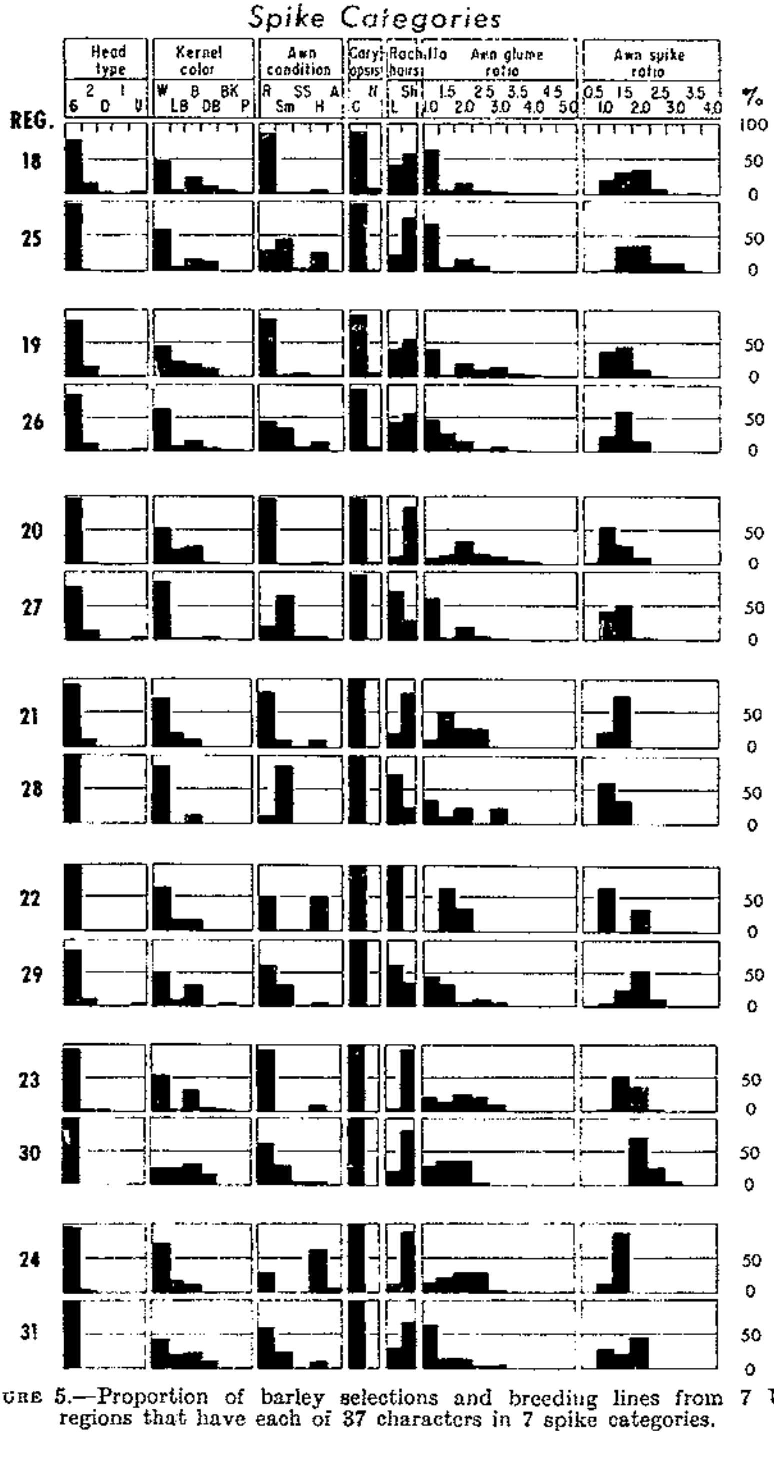

FIGURE 5.—Proportion of barley selections and breeding lines from 7 U.S. regions that have each of 37 characters in 7 spike categories.

TABLE 15.—*Summary: Direction of changes in spike characteristics of breeding lines of barley developed in 7 U.S. regions as compared with introduced selections initially grown in these regions*

Spike category and character (code)[1]	Area and region No.[2]						
	Far West, 25	West North Central, 26	North Central, 27	East North Central, 28	Northeast, 29	South Central, 30	Southeast, 31
Head type:							
6	+	----	−	----	−	----	----
2	−	----	+	----	+	----	----
D	----	----	----	----	----	----	----
I	----	----	----	----	----	----	----
U	−	−	+	----	+	----	----
Kernel color:							
W	----	----	+	----	----	−	−
LB	----	−	−	−	----	+	----
B	----	----	−	----	+	----	+
DB	----	−	----	----	----	+	+
Bk	−	+	+	----	+	----	----
P	----	----	----	----	----	----	----
Awn condition:							
R	−	−	−	−	----	−	+
Sm	+	+	+	+	+	+	+
SS	----	+	----	----	----	+	----
H	+	----	+	−	−	----	−
A	----	----	----	----	----	----	−
Caryopsis:							
C	+	----	----	----	----	----	----
N	−	----	----	----	----	----	----
Rachilla hairs:							
L	−	----	+	+	+	+	+
Sh	+	----	−	−	−	−	−
Awn-glume ratio:							
1.0	----	----	+	+	+	----	+
1.5	----	+	−	−	−	+	----
2.0	----	----	−	----	−	----	−
2.5	----	−	−	−	+	−	−
3.0	−	−	−	+	+	−	----
3.5	----	----	−	----	----	----	----
4.0	----	----	−	----	----	----	----
4.5	----	----	----	----	----	----	----
5.0	----	----	----	----	----	----	----
Awn-spike ratio:							
0.5	----	----	----	----	----	----	----
1.0	−	----	----	+	−	----	+
1.5	----	----	+	−	+	−	----
2.0	----	----	−	----	+	+	−
2.5	----	----	----	----	+	+	+
3.0	+	----	----	----	----	+	----
3.5	----	----	----	----	----	----	----
4.0	----	----	----	----	----	----	----

[1] For explanation of codes, see table 1.
[2] For list of regions, see table 8.

Several changes in the morphology of the heads of American varieties have been effected since the advent of controlled hybridization. These are summarized in table 15. The smooth awn and long hair rachilla characters that were incorporated into varieties through hybridization constitute the most striking examples of such changes. The use of the smooth awn character in barley improvement work in the United States has represented a considered action on the part of breeders. There seems reason to doubt that this was true for the long hair rachilla trait; rather it would seem to have been a side result of breeding to change some other characteristics of the plants.

Comments

Certain characters are predominant among world barleys. Some occur in a very limited way.

The predominant characters are very widely distributed geographically. With the exception of the 2-row character among European barleys, short hair rachillas in selections from barleys introduced into North America, and a 2.0 awn-spike ratio among strains from the South Pacific and South American areas, the predominant characters among all the collection strains occupy the same position among the strains from the five component subdivisions. It might be reasoned that these characters are the oldest evolutionwise, that they have best met the challenge of natural competition and hazards, and that they best suit the needs of man.

The characters that occur in but a limited proportion of the collection are generally restricted in their geographic distribution. Some insight into evolutionary activity in barley may perhaps be achieved from a study of these characters. The African-Asian portion of the collection revealed that the characters studied are not concentrated in any one or two centers of evolutionary activity, but that they occur in different specific geographic (ecological) locales over the whole of the barley-growing area. The occurrence of the 2-row types among strains from the Black Sea area; the deficiens, *H. irregulare*, and short hair rachilla types from Ethiopia; the types with high awn-spike ratios from North Africa; the types with low awn-spike ratios from India; and the hooded and naked types from the Central Asia areas, point to a concentration of certain characters among strains from certain regions. These regions may be considered to be "centers of concentration" for specific characters.

Information about the frequency of occurrence and geographic distribution of characters (character distribution patterns) in world plant populations may be of value in determining methods to use in selection and breeding to obtain superior genotypes. Available strains from sources indicated as being "centers of concentration" for specific characters, e.g., resistance to rust, might be evaluated first in a search for a gene or genes with which to combat a new problem. Breeding programs using methods involving the interpollination of many varieties or strains might be strengthened by taking character distribution patterns into account in determining the size and scope of the parental group and the number of progeny needed to obtain desired recombinations. Deficiencies in programs involving narrow germ plasm bases may be highlighted by data giving some indication of the prospects for obtaining diverse genotypes within the scope of the parental materials used.

Since many of our crops were derived from the Old World, plant introduction work is fundamental to an effective national plant improvement program. Character distribution data, particularly those relating to "centers of concentration," hold a special significance for planning and conducting effective plant exploration work. Search for a specific character, such as resistance to rust, might be directed to one or more world locales from whence similar characters had been obtained with greatest regularity in the past.

The "centers of concentration" concept implies that evolutionary change in barley has occurred in the many parts of the world where the crop is grown. One may hypothesize that it was in these centers that the specific characters arose. Lacking proof of this, it may be stated that these centers are areas in which the characters became established and have been perpetuated in reproducible plant types. This points up the fact that it is not enough just to have a precursor to evolutionary change, e.g., mutagenic agent; the right genetic background and environment must be available for the new character to become established. It might be that the 2-row character, for example, has arisen in barleys in many areas in Africa and Asia over the centuries, but found its true niche in the Black Sea area.

The character distribution analysis of world barleys calls attention to areas in which certain characters are conspicuous because they occur in either large or small proportions of the strains from general or specific world areas. The extent to which the true picture among the world barley population is reflected by such an analysis is determined in part by the number and type of characters studied. The regions postulated in this study might be revised, refined, or subdivided by the inclusion of additional characters.

This study provides new information about relationships, or the lack of them, between barleys from different sources. Certain misconceptions that have arisen in barley literature may be corrected. For example, Weaver (*29*) concluded that it was fair to assume that ancient Egyptian barleys were derived from Ethiopia. The results of this study indicate that there is very little relationship between the strains from these sources. Marked differences between barleys from Ethiopia (region 5) and Egypt, as represented by North Africa (region 6), are shown in figure 3 for characters in five of the seven spike categories. As was noted in figure 4, Egyptian strains are particularly distinctive because of their high awn-spike ratios. Other data not included in this study indicate that, on the average, Egyptian barleys are several inches shorter and mature several days earlier than those from Ethiopia.

The results of this study suggest that man has carried many of the different characters out of their African and Asian habitats into Europe and the Western Hemisphere. The distribution patterns for the regions indicate that he has been selective in determining which characters to utilize. They may also indicate restrictions of new environments as to which introduced types are adapted. The large proportion of 2-row types among the European strains might be attributed to the conquests of the Western Goths and the westward migrations of peoples of the Ottoman Empire since it is likely that seed carried from the Black Sea area would include a goodly proportion of 2-row types. Central Europe yielded a preponderance of 6-row types. This may reflect the influence of a different human migration picture, but it may also be that these types are better adapted in this area.

The broad representation of the different characters among the foreign-derived U.S. Domestic Selections is further evidence that man has been a dynamic force in the migration, perpetuation, and evolution of barley types. Apparently the early settlers grew barleys from many world areas, among which certain types were found to be best adapted to this country. There seems reason to assume that many 2-row types were brought to America by immigrants from Europe, yet a large proportion of the strains grown in the United States through the early 1900's are characterized by having six rows of kernels. The striking preponderance of short hair rachilla types among Western Hemisphere barleys is further evidence that man has applied selection pressures on the world barley population in acquiring plants adapted to the environments where he grows his crops, even though probably unknowingly for characters such as this one.

Marked changes were effected in the characteristics of the U.S. barleys following the advent of controlled hybridization. Man had a new tool for directing and expediting evolutionary change. In the changes in the characteristics of the U.S. varieties through breeding, we find evidence of conscious change and of other changes that may have been effected without their having been recognized or deemed to be important. The comparative preponderance of hooded types among the U.S. strains, as compared to other subdivisions, reflects a preference by farmers for a plant type devoid of the discomforts that are associated with the harvesting or eating (by animals) of rough awn types. The concentration of the smooth awn character among U.S. Breeding Lines reflects a different course of action that was followed to serve the same objective.

TWO-CHARACTER COMBINATIONS

Results

Combinations Present

The characters in this study may occur in 549[5] possible two-character combinations; i.e., the joint occurrence of individual characters from two spike categories. Among the 6,200 world barleys, 451 combinations exist, about 82.1 percent of the potential.

Proportions of Possible Combinations in Which Individual Characters Occur

If we assume a condition in which the individual characters occur in equal numbers of strains and are associated with one another in a completely random way, we find that the characters within each spike category might occur in equal numbers of two-character combinations; for example, head type characters, each 32; kernel color characters, each 31; caryopsis characters, each 35. These constitute the maximum possible numbers of combinations in which the individual characters may occur. The proportions of the possible two-

[5] There are no awn-spike ratios for hooded or awnless strains.

character combinations in which each of the individual characters occur, within the scope of the 6,200 collection strains, are cited in table 16. The following characters from the respective spike categories occur in all possible two-character combinations:

Spike Category	*Character*
I	6 rows of kernels.
II	White kernels.
III	Rough awns.
IV	Covered kernels
V	Long rachilla hairs.
VI	Glume-awns-equal-to-length-of-the-glume (1.0a–g). Glume-awns-twice-the-length-of-the-glume (2.0a–g).
VII	Lemma-awns-extend-beyond-tip-of-spike-to-a-distance-twice-the-length-of-the-spike (2.0a–s).

TABLE 16.—*Proportion of possible 2-character combinations in which each of 37 characters in 7 spike categories occur among 6,200 strains in the World Collection of Barleys*

Spike category and character (code)[1]	Percent	Spike category and character (code)[1]	Percent
Head type:		Rachilla hairs:	
6	100.0	L	100.0
2	91.9	Sh	94.3
D	71.9	Awn-glume ratio:	
U	71.9	1.0	100.0
I	62.5	2.0	100.0
Kernel color:		1.5	92.9
W	100.0	2.5	92.9
B	96.8	3.0	89.3
DB	93.6	3.5	67.9
LB	93.6	4.0	60.7
Bk	87.1	4.5	39.3
P	67.8	5.0	28.6
Awn condition:		Awn-spike ratio:	
R	100.0	2.0	100.0
H	87.5	1.5	96.6
Sm	78.1	1.0	93.1
SS	75.0	0.5	89.7
A	68.8	2.5	82.8
Caryopsis:		3.0	82.8
C	100.0	3.5	51.7
N	94.3	4.0	48.3

[1] For explanation of codes, see table 1.

The characters from spike categories I to V and the 1.0 awn-glume ratio from category VI are predominant within their respective categories. Although the predominant character in category VII, an awn-spike ratio of 1.5, does not appear in the above list, it occurs in all but one of the possible combinations. With the exception of the intermedium head type, hooded awn condition, and 2.0 awn-spike ratio, the order of preponderance of the characters in table 16 is the same as that shown for the individual characters in table 5.

Data in table 7 indicate that 55.8 percent of the intermedium types and 44.1 percent of the hooded types in the collection occur among the U.S. Breeding Lines. This would seem to explain the occurrence of these characters in more two-character combinations than is the case with some other characters that occur in greater proportions of the collection strains. There does not seem to be any ready explanation for the preponderance of the 2.0 awn-spike ratio character among the two-character combinations.

Proportions of Existing Combinations in Which Individual Characters Occur

The proportions of the existing two-character combinations in which the individual characters occur are shown in table 17. If the characters occurred in equal numbers of strains and were associated with one another in a random way, they might occur in equal proportions of the combinations that involve the characters within their respective spike categories; for example, head type characters, each 20.0 percent; kernel color characters, each 16.7 percent; caryopsis characters, each 50.0 percent. The proportions of the existing combinations in which the individual characters occur do not agree with these values. Some of the characters do not occur in all possible combinations. The values for the most preponderant characters are weighted by the deficiencies among the less preponderant ones. Thus, the proportion of the existing combinations in which the 2-row character occurs is larger than the theoretical value in spite of the fact that this character was found in only 91.9 percent of the combinations in which it might have occurred.

TABLE 17.—*Proportion of existing 2-character combinations in which each of 37 characters in 7 spike categories occur among 6,200 strains in the World Collection of Barleys*

Spike category and character (code)[1]	Percent	Spike category and character (code)[1]	Percent
Head type:		Rachilla hairs:	
6	25.2	L	51.5
2	22.8	Sh	48.5
D	18.1	Awn-glume ratio:	
U	18.1	1.0	14.9
I	15.7	2.0	14.9
Kernel color:		1.5	13.8
W	18.3	2.5	13.8
B	17.8	3.0	13.3
DB	17.2	3.5	10.1
LB	17.2	4.0	9.0
Bk	16.6	4.5	5.9
P	13.0	5.0	4.3
Awn condition:		Awn-spike ratio:	
R	24.4	2.0	15.5
H	21.4	1.5	15.0
Sm	19.1	1.0	14.4
SS	18.3	0.5	13.9
A	16.8	2.5	12.8
Caryopsis:		3.0	12.8
C	52.2	3.5	8.0
N	47.8	4.0	7.5

[1] For explanation of codes, see table 1.

PROPORTIONS OF COMBINATIONS VS. PROPORTIONS OF STRAINS.—Data in table 18 indicate that the proportions of the two-character combinations in which the individual characters occur are not of the same magnitude as the proportions of the strains in which they occur. It is striking to note that some individual characters occur in relatively large proportions of the existing two-character combinations as compared to the proportions of the strains in which they occur.

Proportions of Strains in Which Existing Combinations Occur

ENTIRE COLLECTION.—The proportions of the 6,200 strains in which the existing two-character combinations occur are presented in table 19.[6] These values range from 0.02 to 76.7 percent.

In a fixed population, the values for the proportions of the strains that have the respective two-character combinations are in part a function of the product of the proportions of the strains in which the component characters occur. No two-character combination may occur in a greater proportion of the strains than does the least preponderant character in the combination. Therefore, the proportions of the strains having each of the combinations within each two-spike category combination are successively smaller as the less and less preponderant characters are involved in the combinations. The association of a character in one spike category with a particular character in another category, to the general exclusion of its companion characters, results in the proportion of the strains having this combination closely approximating its maximum theoretical value. On the other hand, certain characters occur with one another in considerably fewer than the maximum possible number of strains, giving proportions that are markedly less than the theoretical values.

The *principal* (most preponderant) two-character combination within each conjunction of two spike categories is comprised of the predominant individual characters from the categories involved.

SUBDIVISIONS.—The proportions of the strains in the subdivisions and the entire collection that are constituted by some of the two-character combinations are presented in table 20.[7] Data of the sort presented in table 19 are assembled for the head type characters in combination with the characters from the remaining spike categories. Th proportions of the strains with these combinations corroborate the previous evidence that different character patterns prevail in barleys from different world areas. Whereas more than half of the barleys from Europe are 2-row types with white kernels, less than one-fifth of the strains from the other subdivisions have this makeup. A much larger proportion of the African-Asian 6-row types have long rachilla hairs than do the strains from any other subdivision.

[6] Additional data for combinations occurring among strains from each of the subdivisions are included in table III of the appendix referred to on p. 13.

[7] Additional data for all existing two-character combinations are included in table IV of the appendix referred to on p. 13.

TABLE 18.—*Proportion of all strains in the World Collection of Barleys that bear each character and proportion of all 2-character combinations in which these characters occur*

Spike category and character (code) [1]	All strains	Strains having each character that occur in each 2-character combination (average)	2-character combinations
Head type:	*Percent*	*Percent*	*Percent*
6	71.0	3.1	25.2
2	25.1	3.4	22.8
D	2.0	4.3	18.1
I	1.2	5.0	15.7
U	.7	4.3	18.1
Kernel color:			
W	55.1	3.2	18.3
B	16.5	3.3	17.8
DB	12.1	3.4	17.2
LB	7.1	3.4	17.2
Bk	5.7	3.7	16.6
P	2.5	4.8	13.0
Awn condition:			
R	88.3	3.1	24.4
Sm	6.0	4.0	19.1
SS	2.7	4.2	18.3
H	2.6	3.6	21.4
A	.4	4.5	16.8
Caryopsis:			
C	87.5	2.9	52.2
N	12.5	3.1	47.8
Rachilla hairs:			
L	60.9	2.9	51.5
Sh	39.1	3.0	48.5
Awn-glume ratio:			
1.0	55.2	3.6	14.9
2.0	16.8	3.6	14.9
2.5	11.2	3.8	13.8
1.5	9.0	3.8	13.8
3.0	6.0	4.0	13.3
3.5	1.1	5.3	10.1
4.0	.5	5.9	9.0
4.5	.1	9.1	5.9
5.0	.05	12.5	4.3
Awn-spike ratio:			
1.5	42.2	3.6	15.0
1.0	29.3	3.7	14.4
2.0	17.0	3.4	15.5
0.5	3.7	3.9	13.9
2.5	2.6	4.2	12.8
3.0	1.7	4.2	12.8
3.5	.4	6.7	8.0
4.0	.2	7.1	7.5

[1] For explanation of codes, see table 1.

TABLE 19.—*Proportion of strains in the World Collection of Barleys that have each combination of 2 characters possible among 37 characters in 7 spike categories*

Spike category and character (code) [1]	Head Type						Kernel Color					Awn Condition				
	6	2	D	I	U	W	LB	B	DB	Bk	P	R	Sm	SS	H	A
Kernel color:	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*
W	33.9	19.8	0.7	0.2	0.5											
LB	6.2	.8	.03	.03	.02											
B	14.5	1.4	.3	.2	.1											
DB	11.8	.9	.1	.2	.02											
BK	2.9	1.9	.6	.2	.08											
P	1.7	.3	.2	.3	0											
Awn condition:																
R	64.0	20.7	1.9	1.2	.5	48.0	6.2	15.0	12.1	4.7	2.4					
Sm	3.8	2.2	.03	0	.02	3.9	.4	.8	.5	.5	0					
SS	.7	2.0	.02	0	.02	1.6	.2	.3	.2	.4	0					
H	2.3	.1	.1	0	.1	1.5	.2	.4	.3	.2	.08					
A	.2	.1	0	0	0	.1	.08	.1	.02	.02	0					
Caryopsis:																
C	60.2	23.7	1.9	1.2	.5	47.7	6.2	14.6	12.2	5.2	1.6	76.7	5.9	2.7	1.8	0.4
N	10.8	1.4	.2	0	.1	7.3	.9	1.9	1.0	.5	.9	11.6	.1	.02	.8	.02

Rachilla hairs:																
L	37.8	21.3	1.0	.3	.4	35.8	3.5	8.5	8.1	3.4	1.6	53.5	3.9	2.2	.9	.3
Sh	33.2	3.8	1.0	.9	.3	19.3	3.6	8.0	5.0	2.4	.9	34.8	2.1	.5	1.7	.03
Awn-glume ratio:																
1.0	29.8	23.0	1.7	.3	.4	31.7	3.3	8.0	7.4	3.9	.9	46.8	4.2	2.4	1.5	.3
1.5	7.7	.9	.08	.2	.08	4.4	.8	1.8	1.3	.4	.2	8.3	.3	.05	.4	0
2.0	15.5	.6	.2	.5	.06	8.3	1.2	3.5	2.5	.6	.7	15.5	.9	.1	.3	.02
2.5	10.6	.3	.06	.2	.06	6.4	.9	1.9	1.2	.4	.5	10.5	.3	.06	.3	.02
3.0	5.7	.1	.05	.03	.02	3.4	.6	1.0	.4	.3	.2	5.5	.2	.08	.09	0
3.5	1.0	.08	0	0	.03	.5	.2	.2	.2	.1	0	1.1	0	0	.02	0
4.0	.5	.02	0	0	0	.2	.08	.08	.05	.05	0	.5	.02	0	0	0
4.5	.08	0	0	0	0	.05	0	.02	0	0	.02	.08	0	0	0	0
5.0	.05	0	0	0	0	.03	.02	0	0	0	0	.05	0	0	0	0
Awn-spike ratio:																
0.5	3.2	.2	.02	0	.2	1.9	.4	.4	.6	.2	.05	3.6	.06	.02		
1.0	15.9	12.9	.4	.05	.08	20.3	1.7	3.2	2.4	1.3	.4	25.1	2.6	1.5		
1.5	29.7	10.6	1.2	.6	.2	22.0	3.3	7.4	5.8	2.6	1.2	38.9	2.5	.9		
2.0	15.1	1.1	.3	.4	.08	6.9	1.2	3.8	3.2	1.2	.7	16.1	.7	.2		
2.5	2.5	.06	0	.06	0	1.1	.08	.8	.5	.2	.02	2.4	.08	.06		
3.0	1.6	.02	0	.03	0	.9	.08	.3	.3	.08	0	1.6	.05	.03		
3.5	.4	.02	0	0	0	.2	0	.1	.08	0	0	.4	0	0		
4.0	.1	0	0	0	0	.06	.03	.03	.02	0	0	.1	0	0		

See footnote at end of table.

TABLE 19.—*Proportion of strains in the World Collection of Barleys that have each combination of 2 characters possible among 37 characters in 7 spike categories*—Continued

Spike category and character (code) [1]	Caryopsis		Rachilla Hairs		Awn-Glume Ratio								
	C	N	L	Sh	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0
Kernel color:	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*
W													
LB													
B													
DB													
BK													
P													
Awn condition:													
R													
Sm													
SS													
H													
A													
Caryopsis:													
C													
N													

Rachilla hairs:													
L	50.3	10.6											
Sh	37.2	1.9											
Awn-glume ratio:													
1.0	49.3	5.9	38.8	16.4									
1.5	7.3	1.7	6.0	3.0									
2.0	14.3	2.5	7.4	9.4									
2.5	9.8	1.4	4.8	6.4									
3.0	5.1	.9	2.9	3.1									
3.5	1.0	.1	.6	.5									
4.0	.5	.05	.3	.2									
4.5	.06	.02	.08	0									
5.0	.05	0	.05	0									
Awn-spike ratio:													
0.5	2.5	1.2	3.3	.4	2.9	0.3	0.1	0.2	0.08	0.02	0	0.02	0
1.0	26.7	2.6	20.8	8.5	18.3	1.7	3.4	3.4	1.8	.4	.2	0	0
1.5	37.4	4.9	24.5	17.7	20.4	4.6	8.5	5.4	2.7	.5	.2	0	.02
2.0	14.4	2.6	8.3	10.3	8.3	1.6	4.0	1.6	1.2	.2	.1	.03	.03
2.5	2.3	.3	1.3	1.3	1.6	.3	.3	.2	.1	0	.03	0	0
3.0	1.6	.06	1.0	.7	1.3	.05	.2	.03	.03	.02	0	.03	0
3.5	.4	0	.3	.1	.3	.02	.03	0	0	0	0	0	0
4.0	.1	.02	.1	.05	.1	0	.02	0	0	0	0	0	0

[1] For explanation of codes, see table 1.

TABLE 20.—SUMMARY: *Proportion of all strains in the World Collection of Barleys and proportion of strains from 5 source subdivisions that have each combination of 2 characters possible between 5 head type characters and 32 other characters in 6 spike categories*

Head type character and subdivision [1]	Spike category and code [2]														
	Kernel color						Awn condition					Caryopsis		Rachilla hairs	
	W	LB	B	DB	Bk	P	R	Sm	SS	H	A	C	N	L	Sh
6:															
E	15. 2	9. 5	12. 0	6. 1	0. 8	0. 3	41. 9	0. 9	0. 5	0. 4	0	41. 0	2. 8	19. 1	24. 7
A	36. 1	4. 3	13. 9	13. 0	3. 7	2. 3	71. 5	. 5	. 3	. 9	. 1	58. 9	14. 4	44. 9	28. 4
S	18. 4	8. 8	25. 7	23. 5	. 7	1. 5	72. 1	1. 5	. 7	4. 4	0	72. 8	5. 9	17. 6	61. 1
D	42. 8	14. 4	19. 2	6. 9	1. 4	. 3	69. 0	3. 1	. 3	11. 5	1. 2	81. 4	3. 7	16. 7	68. 4
B	39. 6	9. 7	16. 5	10. 9	1. 0	. 5	37. 6	28. 3	3. 7	8. 0	. 6	76. 5	1. 6	28. 7	49. 4
T	33. 9	6. 2	14. 5	11. 8	2. 9	1. 7	64. 0	3. 8	. 7	2. 3	. 2	60. 2	10. 8	37. 8	33. 2
2:															
E	51. 6	1. 6	1. 0	. 3	. 3	. 1	51. 8	. 6	1. 7	0	. 9	53. 4	1. 6	47. 7	7. 3
A	16. 1	. 7	1. 7	1. 1	2. 5	. 3	17. 2	2. 9	2. 3	0	. 05	21. 0	1. 5	19. 8	2. 7
S	16. 2	2. 2	. 7	. 7	0	0	19. 9	0	0	0	0	18. 4	1. 5	8. 1	11. 8
D	11. 7	0	. 3	0	. 6	0	11. 4	0	. 9	. 3	0	12. 0	. 6	10. 0	2. 6
B	13. 1	. 9	. 6	. 6	. 9	. 3	13. 1	1. 2	1. 2	. 9	0	15. 3	1. 0	10. 7	5. 6
T	19. 8	. 8	1. 4	. 9	1. 9	. 3	20. 7	2. 2	2. 0	. 1	. 1	23. 7	1. 4	21. 3	3. 8

D:															
E	.4	0	0	.1	.6	0	1.0	0	0	.1	0	1.1	0	.3	.8
A	.8	.05	.4	.2	.7	.3	2.3	.05	.02	0	0	2.3	.1	1.1	1.3
S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D	.3	0	0	0	.6	0	.9	0	0	0	0	.6	.3	.9	0
B	.7	0	0	0	.9	.4	1.4	0	0	.7	0	1.5	.6	1.5	.6
T	.7	.03	.3	.1	.6	.2	1.9	.03	.02	.1	0	1.9	.2	1.0	1.0
I:															
E	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A	.3	.05	.3	.3	.3	.4	1.7	0	0	0	0	1.7	0	.4	1.3
S	0	0	.7	0	0	0	.7	0	0	0	0	.7	0	0	.7
D	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T	.2	.03	.2	.2	.2	.3	1.2	0	0	0	0	1.2	0	.3	.9
U:															
E	.1	0	0	0	0	0	.1	0	0	0	0	.1	0	0	.1
A	.2	.02	.05	.02	0	0	.3	0	0	0	0	.3	.02	.3	0
S	.7	0	0	0	0	0	.7	0	0	0	0	0	.7	.7	0
D	1.4	0	0	0	0	0	1.1	0	0	.3	0	.8	.6	.6	.8
B	1.9	0	.9	0	.7	0	2.3	.1	.1	.9	0	2.8	.7	1.8	1.8
T	.5	.02	.1	.02	.08	0	.5	.02	.02	.1	0	.5	.1	.4	.3

See footnotes at end of table.

TABLE 20.—SUMMARY: *Proportion of all strains in the World Collection of Barleys and proportion of strains from 5 source subdivisions that have each combination of 2 characters possible between 5 head type characters and 32 other characters in 6 spike categories*—Continued

Head type character and subdivision [1]	Spike category and code [2]																
	Awn-glume ratio									Awn-spike ratio							
	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	0.5	1.0	1.5	2.0	.25	3.0	3.5	4.0
6:																	
E	11.9	4.6	11.0	7.6	6.1	1.4	0.8	0	0.1	0.4	11.6	24.1	6.7	0.1	0.1	0.3	0.1
A	29.9	8.2	16.1	11.7	5.9	1.0	.4	.07	.07	4.3	16.7	30.3	16.3	2.6	1.9	.4	.1
S	61.8	3.7	11.0	2.2	0	0	0	0	0	2.2	1.5	18.4	33.1	11.8	5.1	1.5	.7
D	23.3	12.7	23.3	13.8	7.7	1.7	1.4	.3	0	.3	23.0	27.3	18.4	2.9	.3	.3	0
B	46.2	6.5	12.8	6.8	4.7	.7	.5	0	0	1.6	14.8	35.8	13.1	2.3	1.6	.2	0
T	29.8	7.7	15.5	10.6	5.7	1.0	.5	.08	.05	3.2	15.9	29.7	15.1	2.5	1.6	.4	.1
2:																	
E	50.6	2.5	1.2	.3	.3	.1	0	0	0	.7	35.0	17.4	.8	.1	0	0	0
A	20.9	.6	.5	.3	.07	.02	.02	0	0	.09	10.9	10.4	1.0	.05	.02	.02	0
S	15.5	3.7	0	0	0	.7	0	0	0	0	5.2	6.6	8.1	0	0	0	0
D	10.9	.3	.9	.3	0	.3	0	0	0	0	5.2	5.7	1.4	0	0	0	0
B	13.7	.4	1.2	.4	.4	.02	0	0	0	.6	6.2	7.8	.7	.02	0	0	0
T	23.0	.9	.6	.3	.1	.08	.02	0	0	.2	12.9	10.6	1.1	.06	.02	.02	0

D:																	
E	1.0	0	.1	0	0	0	0	0	0	0	.3	.7	0	0	0	0	0
A	1.9	.1	.2	.1	.07	0	0	0	0	0	.5	1.5	.5	0	0	0	0
S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D	.6	0	.3	0	0	0	0	0	0	0	0	.6	.3	0	0	0	0
B	2.1	0	0	0	0	0	0	0	0	.1	.3	.9	0	0	0	0	0
T	1.7	.08	.2	.06	.05	0	0	0	0	.02	.4	1.2	.3	0	0	0	0
I:																	
E	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A	.4	.3	.6	.2	.05	0	0	0	0	0	.07	.9	.6	.1	.05	0	0
S	0	0	.7	0	0	0	0	0	0	0	0	0	.7	0	0	0	0
D	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T	.3	.2	.5	.2	.03	0	0	0	0	0	.05	.6	.4	.06	.03	0	0
U:																	
E	.1	0	0	0	0	0	0	0	0	0	0	0	.1	0	0	0	0
A	.2	.02	.08	.05	0	0	0	0	0	.2	.02	.02	.05	0	0	0	0
S	.7	0	0	0	0	0	0	0	0	0	0	0	.7	0	0	0	0
D	1.1	0	0	0	0	.3	0	0	0	0	.6	.6	0	0	0	0	0
B	2.2	.6	.1	.3	.1	.1	0	0	0	1.0	.3	1.2	.1	0	0	0	0
T	.4	.08	.06	.06	.02	.03	0	0	0	.2	.08	.2	.08	0	0	0	0

[1] E=Europe; A=Africa-Asia; S=South Pacific-South and Central America; D=U.S. Domestic Selections; B=U.S. Breeding Lines; T=total collection.

[2] For explanation of codes, see table 1.

Proportions of Strains With the Respective Characters That Have Each of the Other Characters

Entire collection.—It has been noted that 33.9 percent of the barleys in the collection are characterized by the 6-row, white kernel combination. This does not give us any inkling as to what proportion of the 6-row types are white, and vice versa. Table 21[8] includes this information for all two-character combinations that occur in the collection. We note, for example, that a considerably larger proportion of the 2-row strains have white kernels than is the case with any other head type character. This is not to say, however, that most white kernel types are 2-rowed. Nearly 85 percent of all 2-row types have long rachilla hairs, but only 35 percent of all long hair rachilla types are 2-rowed.

In contrast to the data in table 19, the proportions in table 21 are independent of and do not in any way reflect the magnitude of the proportions of the 6,200 strains in which the individual characters occur. They range from 0 to 100 percent. Nevertheless, the largest proportions cited opposite each of the characters listed within each spike category on the left-hand side of the table usually relate to the predominant individual characters from the other spike categories. Following are instances in which characters other than the most predominant ones in the respective spike categories occur in the greatest proportion of the strains with the key character:

Key character		*Key character*	
2	1.0a–s.	LB	Sh.
I	P.	Sm	1.0a–s.
I	Sh.	SS	2.
I	2.0a–g.	SS	1.0a–s.
U	0.5a–s.	H	Sh.
		A	B.

These and other combinations involving the less predominant characters are evidence that factors in addition to that of the function of numbers influence the extent to which the individual characters occur in combination with one another.

Subdivisions.—Information about the proportions of the strains with each of the head type characters, from the five subdivisions and the entire collection, that have each of the characters in the other spike categories is presented in table 22.[9] It was noted in table 20 that a large proportion of the strains obtained from Europe are 2-row, white kernel types. We now see that the European strains do not have a monopoly on the white character among 2-row types. The greatest proportion of 2-row strains from *all* the regions is white. On the other hand, the large proportion of smooth awn, 6-row strains among the U.S. Breeding Lines noted in table 20 is confirmed as a condition peculiar to these strains.

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[8] Additional data for all existing two-character combinations are included in Table V of the appendix referred to on p. 13.

[9] Additional data for all existing two-character combinations are included in table VI of the appendix referred to on p. 13.

TABLE 21.—*For each of 37 characters in 7 spike categories, proportion of strains in the World Collection of Barleys having each character that occurs in each possible combination of that character with other individual characters*

Spike category and character (code)[1]	Kernel color						Awn condition					Caryopsis		Rachilla hairs	
	W	LB	B	DB	Bk	P	R	Sm	SS	H	A	C	N	L	Sh
Head type:															
6	47.8	8.7	20.4	16.7	4.1	2.4	90.2	5.3	1.0	3.2	0.3	84.8	15.2	53.2	46.8
2	78.9	3.3	5.6	3.6	7.5	1.1	82.3	8.7	7.9	.4	.6	94.4	5.6	84.9	15.1
D	33.3	1.6	14.3	7.1	31.7	11.9	92.9	1.6	.8	4.8	0	92.1	7.9	50.0	50.0
I	16.7	2.8	18.1	19.4	18.1	25.0	100.0	0	0	0	0	100.0	0	23.6	76.4
U	65.1	2.3	18.6	2.3	11.6	0	79.1	2.3	2.3	16.3	0	79.1	20.9	62.8	37.2

Spike category and character (code)[1]	Awn-glume ratio									Awn-spike ratio							
	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0
6	42.0	10.9	21.8	14.9	8.1	1.4	0.7	0.1	0.1	4.5	22.4	41.8	21.2	3.5	2.3	0.6	0.2
2	91.5	3.5	2.5	1.3	.5	.3	.1	0	0	.8	51.2	42.1	4.4	.3	.1	.1	0
D	82.5	4.0	7.9	3.2	2.4	0	0	0	0	.8	18.3	59.5	16.7	0	0	0	0
I	25.0	19.4	38.9	13.8	2.8	0	0	0	0	0	4.2	51.4	36.1	5.6	2.8	0	0
U	62.8	11.6	9.3	9.3	2.3	4.7	0	0	0	34.9	11.6	25.6	11.6	0	0	0	0

[1] For explanation of codes, see table 1.

TABLE 21.—*For each of 37 characters in 7 spike categories, proportion of strains in the World Collection of Barleys having each character that occurs in each possible combination of that character with other individual characters*—Con.

Spike category and character (code)[1]	Head type					Awn condition					Caryopsis		Rachilla hairs	
	6	2	D	I	U	R	Sm	SS	H	A	C	N	L	Sh
Kernel color:														
W	61.6	36.0	1.2	0.4	0.8	87.1	7.1	2.9	2.6	0.2	86.7	13.3	65.0	35.0
LB	87.2	11.6	.5	.5	.2	87.0	5.5	3.4	3.0	1.1	87.5	12.5	48.7	51.3
B	87.7	8.5	1.8	1.3	.8	90.5	4.7	1.8	2.1	.9	88.3	11.7	51.6	48.4
DB	90.1	6.9	1.1	1.7	.6	92.5	3.4	1.7	2.2	.1	92.6	7.4	61.7	38.3
BK	50.7	33.0	11.3	3.7	1.4	81.4	8.2	6.5	3.7	.3	90.7	9.3	58.9	41.1
P	67.5	11.0	9.7	11.7	0	96.8	0	0	3.2	0	64.3	35.7	65.6	34.4

Spike category and character (code)[1]	Awn-glume ratio									Awn-spike ratio							
	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0
W	57.5	8.0	15.1	11.6	6.1	1.0	0.4	0.1	0.1	3.5	36.9	40.1	12.6	2.0	1.6	0.4	0.1
LB	46.2	11.6	17.1	12.3	8.9	2.3	1.1	0	.2	6.2	23.7	46.0	17.3	1.1	1.1	0	.5
B	48.7	10.7	21.0	11.7	6.2	1.0	.5	.1	0	2.6	19.2	44.7	22.7	4.6	2.1	.8	.2
DB	56.5	10.1	19.3	9.1	3.2	1.2	.4	0	0	4.9	18.2	43.9	24.1	3.4	2.5	.6	.1
Bk	67.6	7.3	10.1	6.2	5.9	1.7	.8	0	0	3.4	22.5	44.8	21.1	2.8	1.4	0	0
P	37.0	9.7	26.6	18.2	7.8	0	0	.6	0	1.9	15.6	49.4	29.2	.6	0	0	0

	Head type					Kernel color						Caryopsis		Rachilla hairs	
	6	2	D	I	U	W	LB	B	DB	Bk	P	C	N	L	Sh
Awn condition:															
R	72. 5	23. 4	2. 1	1. 3	0. 6	54. 3	7. 0	16. 9	13. 8	5. 3	2. 7	86. 8	13. 2	60. 6	39. 4
Sm	62. 6	36. 6	. 5	0	. 3	65. 3	6. 5	12. 9	7. 5	7. 8	0	98. 9	1. 1	64. 8	35. 2
SS	26. 0	72. 8	. 6	0	. 6	58. 6	8. 9	10. 7	8. 3	13. 6	0	99. 4	. 6	79. 9	20. 1
H	87. 6	4. 4	3. 7	0	4. 3	55. 9	8. 1	13. 7	11. 2	8. 1	3. 1	68. 3	31. 7	36. 0	64. 0
A	60. 9	39. 1	0	0	0	30. 4	21. 7	39. 1	4. 3	4. 3	0	95. 7	4. 3	91. 3	8. 7

	Awn-glume ratio									Awn-spike ratio						
	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0
R	52. 9	9. 4	17. 5	11. 8	6. 3	1. 2	0. 5	0. 1	0. 1	4. 1	28. 4	44. 0	18. 2	2. 8	1. 8	0. 5	0. 2
Sm	70. 7	4. 6	14. 2	5. 6	4. 0	0	. 3	0	0	1. 1	44. 1	41. 1	11. 6	1. 3	. 8	0	0
SS	87. 6	1. 8	4. 7	2. 4	3. 0	0	0	0	0	. 6	55. 0	33. 1	7. 7	2. 4	1. 2	0	0
H	57. 1	14. 9	11. 8	11. 8	3. 7	. 6	0	0	0	-----	-----	-----	-----	-----	-----	-----	-----
A	91. 3	0	4. 3	4. 3	0	0	0	0	0	-----	-----	-----	-----	-----	-----	-----	-----

[1] For explanation of codes, see table 1.

TABLE 21.—*For each of 37 characters in 7 spike categories, proportion of strains in the World Collection of Barleys having each character that occurs in each possible combination of that character with other individual characters*—Con.

Spike category and character (code)[1]	Head type					Kernel color						Awn condition				
	6	2	D	I	U	W	LB	B	DB	Bk	P	R	Sm	SS	H	A
Caryopsis:																
C	68. 8	27. 1	2. 1	1. 3	0. 6	54. 6	7. 1	16. 7	13. 9	5. 9	1. 8	87. 7	6. 8	3. 1	2. 0	0. 4
N	86. 4	11. 2	1. 3	0	1. 2	58. 4	7. 1	15. 4	7. 7	4. 2	7. 1	92. 7	. 5	. 1	6. 6	. 1

Spike category and character (code)[1]	Rachilla hairs		Awn-glume ratio									Awn-spike ratio							
	L	Sh	1. 0	1. 5	2. 0	2. 5	3. 0	3. 5	4. 0	4. 5	5. 0	0. 5	1. 0	1. 5	2. 0	2. 5	3. 0	3. 5	4. 0
C	57. 5	42. 5	56. 4	8. 4	16. 3	11. 2	5. 8	1. 1	0. 5	0. 1	0. 1	2. 8	30. 5	42. 7	16. 4	2. 6	1. 8	0. 5	0. 2
N	84. 6	15. 4	46. 8	13. 4	19. 7	11. 3	7. 2	1. 0	. 4	. 1	0	9. 8	20. 5	39. 0	21. 0	2. 3	. 5	0	. 1

Rachilla hairs:	Head type					Kernel color						Awn condition				
	6	2	D	I	U	W	LB	B	DB	Bk	P	R	Sm	SS	H	A
L	62. 1	35. 0	1. 7	0. 5	0. 7	58. 8	5. 7	14. 0	13. 3	5. 5	2. 7	87. 9	6. 4	3. 6	1. 5	0. 6
Sh	84. 8	9. 7	2. 6	2. 3	. 7	49. 2	9. 3	20. 4	12. 9	6. 0	2. 2	88. 9	5. 4	1. 4	4. 2	. 1

	Caryopsis		Awn-glume ratio									Awn-spike ratio							
	C	N	1. 0	1. 5	2. 0	2. 5	3. 0	3. 5	4. 0	4. 5	5. 0	0. 5	1. 0	1. 5	2. 0	2. 5	3. 0	3. 5	4. 0
L	82. 6	17. 4	63. 8	9. 8	12. 1	7. 8	4. 7	1. 0	0. 4	0. 1	0. 1	5. 5	34. 1	40. 3	13. 6	2. 1	1. 7	0. 5	0. 2
Sh	95. 1	4. 9	41. 9	7. 8	23. 9	16. 4	8. 0	1. 3	. 6	0	0	. 9	21. 7	45. 2	22. 3	3. 4	1. 7	. 3	. 1

[1] For explanation of codes, see table 1.

TABLE 21.—*For each of 37 characters in 7 spike categories, proportion of strains in the World Collection of Barleys having each character that occurs in each possible combination of that character with other individual characters*—Con.

Spike category and character (code)[1]	Head type					Kernel color						Awn condition				
	6	2	D	I	U	W	LB	B	DB	Bk	P	R	Sm	SS	H	A
Awn-glume ratio:																
1.0	54.0	41.6	3.0	0.5	0.8	57.4	5.9	14.6	13.4	7.5	1.7	84.7	7.7	4.3	2.7	0.6
1.5	85.8	9.8	.9	2.5	.9	49.1	9.1	19.7	14.7	4.7	2.7	92.1	3.0	.5	4.3	0
2.0	92.2	3.8	1.0	2.7	.4	49.6	7.2	20.7	15.1	3.5	3.9	92.2	5.1	.8	1.8	.1
2.5	94.5	2.9	.6	1.4	.6	57.0	7.8	17.3	10.7	3.2	4.0	93.5	3.0	.6	2.7	.1
3.0	96.2	2.2	.8	.5	.3	56.2	10.5	17.3	7.0	5.7	3.2	93.0	4.1	1.4	1.6	0
3.5	89.9	7.2	0	0	2.9	47.8	14.5	14.5	14.5	8.7	0	98.6	0	0	1.4	0
4.0	96.8	3.2	0	0	0	48.4	16.1	16.1	9.7	9.7	0	96.8	3.2	0	0	0
4.5	100.0	0	0	0	0	60.0	0	20.0	0	0	20.0	100.0	0	0	0	0
5.0	100.0	0	0	0	0	66.7	33.3	0	0	0	0	100.0	0	0	0	0

Spike category and character (code)[1]	Caryopsis		Rachilla hairs		Awn-spike ratio							
	C	N	L	Sh	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0
1.0	89.4	10.6	70.3	29.7	5.3	33.2	36.9	15.0	3.0	2.4	0.6	0.2
1.5	81.4	18.6	66.1	33.9	3.6	18.6	51.4	17.7	3.6	.5	.2	0
2.0	85.3	14.7	44.1	55.9	.6	20.1	50.6	23.6	1.8	1.1	.2	.1
2.5	87.3	12.7	42.7	57.3	2.0	30.7	48.2	14.3	1.6	.3	0	0
3.0	84.9	15.1	47.8	52.2	1.4	30.3	44.6	19.7	1.9	.5	0	0
3.5	88.4	11.6	55.1	44.9	1.4	34.8	44.9	15.9	0	1.4	0	0
4.0	90.3	9.7	51.6	48.4	0	32.3	35.5	25.8	6.5	0	0	0
4.5	80.0	20.0	100.0	0	20.0	0	0	40.0	0	40.0	0	0
5.0	100.0	0	100.0	0	0	0	33.3	66.7	0	0	0	0

Awn-spike ratio:	Head type					Kernel color						Awn condition				
	6	2	D	I	U	W	LB	B	DB	Bk	P	R	Sm	SS	H	A
0.5	87.3	5.7	0.4	0	6.6	52.4	11.8	11.8	17.5	5.2	1.3	97.8	1.7	0.4	------	------
1.0	54.4	43.9	1.3	.2	.3	69.5	5.7	10.9	8.2	4.4	1.3	85.8	9.0	5.1	------	------
1.5	70.3	25.0	2.9	1.4	.4	52.2	7.7	17.5	13.6	6.1	2.9	92.0	5.8	2.1	------	------
2.0	88.6	6.4	2.0	2.5	.5	40.8	7.2	22.1	18.6	7.1	4.3	94.7	4.1	1.2	------	------
2.5	95.0	2.5	0	2.5	0	43.1	3.1	29.4	17.5	6.3	.6	94.4	3.1	2.5	------	------
3.0	97.1	1.0	0	1.9	0	51.0	4.8	20.2	19.2	4.8	0	95.2	2.9	1.9	------	------
3.5	96.0	4.0	0	0	0	48.0	0	32.0	20.0	0	0	100.0	0	0	------	------
4.0	100.0	0	0	0	0	44.4	22.2	22.2	11.1	0	0	100.0	0	0	------	------

Awn-spike ratio:	Caryopsis		Rachilla hairs		Awn-glume ratio								
	C	N	L	Sh	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0
0.5	66.8	33.2	90.0	10.1	79.5	8.7	2.6	6.1	2.2	0.4	0	0.4	0
1.0	91.2	8.8	70.9	29.1	62.6	5.7	11.5	11.7	6.2	1.3	.6	0	0
1.5	88.4	11.6	58.1	41.9	48.2	11.0	20.1	12.8	6.3	1.2	.4	0	.1
2.0	84.5	15.5	48.7	51.3	48.8	9.4	23.2	9.4	6.9	1.0	.8	.2	.2
2.5	88.8	11.2	48.8	51.2	63.1	12.5	11.9	6.9	4.4	0	1.3	0	0
3.0	96.2	3.8	60.6	39.4	79.8	2.9	10.6	1.9	1.9	1.0	0	1.9	0
3.5	100.0	0	68.0	32.0	84.0	4.0	8.0	0	0	0	0	0	0
4.0	88.9	11.1	66.7	33.3	88.9	0	11.1	0	0	0	0	0	0

[1] For explanation of codes, see table 1.

TABLE 22.—*Proportion of strains from 5 source subdivisions and all of the World Collection of Barleys that have each head type character, and the proportion of these strains that have each character in the other 6 spike categories*

Head type character and subdivision [1]	Proportion of all entries	Spike category and character (code), percent [2]															
		Kernel color						Awn condition					Caryopsis		Rachilla hairs	
		W	LB	B	DB	Bk	P	R	Sm	SS	H	A	C	N	L	Sh
6:																
E	43.8	34.7	21.6	27.4	14.0	1.8	0.6	95.7	2.1	1.2	0.9	0	93.6	6.4	43.5	56.5
A	73.3	49.2	5.9	19.0	17.8	5.1	3.1	97.5	.7	.4	1.2	.2	80.3	19.7	61.3	38.7
S	78.7	23.4	11.2	32.7	20.9	.9	1.9	91.6	1.9	.9	5.6	0	92.5	7.5	22.4	77.6
D	85.1	50.3	16.9	22.6	8.1	1.7	.3	81.1	3.7	.3	13.5	1.4	95.6	4.4	19.6	80.4
B	78.1	50.7	12.4	21.1	13.9	1.3	.6	48.2	36.2	4.7	10.2	.8	97.9	2.1	36.7	63.3
T	71.0	47.8	8.7	20.4	16.7	4.1	2.4	90.2	5.3	1.0	3.2	.3	84.8	15.2	53.2	46.8
2:																
E	55.0	93.9	2.9	1.9	.5	.5	.2	94.2	1.0	3.1	0	1.7	97.1	2.9	86.7	13.3
A	22.5	71.6	3.1	7.6	5.1	11.1	1.5	76.6	12.6	10.3	0	.2	93.3	6.7	87.8	12.2
S	19.9	81.5	11.1	3.7	3.7	0	0	100.0	0	0	0	0	92.6	7.4	40.7	59.3
D	12.6	93.2	0	2.3	0	4.5	0	90.9	0	6.8	2.3	0	95.5	4.5	79.5	20.5
B	16.3	80.2	5.4	3.6	3.6	5.4	1.8	80.2	7.2	7.2	5.4	0	93.7	6.3	65.8	34.2
T	25.1	78.9	3.3	5.6	3.6	7.5	1.1	82.3	8.7	7.9	.4	.6	94.4	5.6	84.9	15.1

646718—62——5

D:																
E	1. 1	37. 5	0	0	12. 5	50. 0	0	87. 5	0	0	12. 5	0	100. 0	0	25. 0	75. 0
A	2. 4	32. 7	2. 0	17. 8	7. 9	27. 7	11. 9	97. 0	2. 0	1. 0	0	0	95. 0	5. 0	47. 5	52. 5
S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D	. 9	33. 3	0	0	0	66. 7	0	100. 0	0	0	0	0	66. 7	33. 3	100. 0	0
B	2. 1	35. 7	0	0	0	42. 9	21. 4	64. 3	0	0	35. 7	0	71. 4	28. 6	71. 4	28. 6
T	2. 0	33. 3	1. 6	14. 3	7. 1	31. 7	11. 9	92. 9	1. 6	. 8	4. 8	0	92. 1	7. 9	50. 0	50. 0
I:																
E	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A	1. 7	16. 9	2. 8	16. 9	19. 7	18. 3	25. 4	100. 0	0	0	0	0	100. 0	0	23. 9	76. 1
S	. 7	0	0	100. 0	0	0	0	100. 0	0	0	0	0	100. 0	0	0	100. 0
D	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T	1. 2	16. 7	2. 8	18. 1	19. 4	18. 1	25. 0	100. 0	0	0	0	0	100. 0	0	23. 6	76. 4
U:																
E	. 1	100. 0	0	0	0	0	0	100. 0	0	0	0	0	100. 0	0	0	100. 0
A	. 3	66. 7	8. 3	16. 7	8. 3	0	0	100. 0	0	0	0	0	91. 7	8. 3	100. 0	0
S	. 7	100. 0	0	0	0	0	0	100. 0	0	0	0	0	0	100. 0	100. 0	0
D	1. 4	100. 0	0	0	0	0	0	80. 0	0	0	20. 0	0	60. 0	40. 0	40. 0	60. 0
B	3. 5	54. 2	0	25. 0	0	20. 8	0	66. 7	4. 2	4. 2	25. 0	0	79. 2	20. 8	50. 0	50. 0
T	. 7	65. 1	2. 3	18. 6	2. 3	11. 6	0	79. 1	2. 3	2. 3	16. 3	0	79. 1	20. 9	62. 8	37. 2

See footnotes at end of table.

TABLE 22.—*Proportion of strains from 5 source subdivisions and all of the World Collection of Barleys that have each head type character, and the proportion of these strains that have each character in the other 6 spike categories*—Continued

Head type character and subdivision [1]	Proportion of all entries	Awn-glume ratio									Awn-spike ratio						
		1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0
6:																		
E	43.8	27.1	10.6	25.2	17.3	14.0	3.3	1.8	0	0.3	0.9	26.4	55.0	15.2	0.3	0.3	0.6	0.3
A	73.3	40.8	11.2	22.0	16.0	8.0	1.3	.5	.1	.1	5.8	22.8	41.3	21.9	3.5	2.6	.6	.2
S	78.7	78.5	4.7	14.0	2.8	0	0	0	0	0	2.8	1.9	23.4	42.1	15.0	6.5	1.9	.9
D	85.1	27.4	14.9	27.4	16.2	9.1	2.0	1.7	.3	0	.3	27.0	32.1	21.6	3.4	.3	.3	0
B	78.1	59.1	8.3	16.4	8.7	6.0	.9	.6	0	0	2.1	19.0	45.9	16.8	3.0	2.1	.2	0
T	71.0	42.0	10.9	21.8	14.9	8.1	1.4	.7	.1	.1	4.5	22.4	41.8	21.2	3.5	2.3	.6	.2
2:																		
E	55.0	92.0	4.6	2.2	.5	.5	.2	0	0	0	1.2	63.7	31.7	1.5	.2	0	0	0
A	22.5	92.8	2.8	2.0	1.5	.3	.1	.1	0	0	.4	48.5	46.0	4.3	.2	.1	.1	0
S	19.9	77.8	18.5	0	0	0	3.7	0	0	0	0	25.9	33.3	40.7	0	0	0	0
D	12.6	86.4	2.3	6.8	2.3	0	2.3	0	0	0	0	40.9	45.5	11.4	0	0	0	0
B	16.3	83.8	2.7	7.2	2.7	2.7	.1	0	0	0	3.6	37.8	47.7	4.5	.1	0	0	0
T	25.1	91.5	3.5	2.5	1.3	.5	.3	.1	0	0	.8	51.2	42.1	4.4	.3	.1	.1	0

D:																		
E	1.1	87.5	0	12.5	0	0	0	0	0	0	0	25.0	62.5	0	0	0	0	0
A	2.4	80.2	5.0	7.9	4.0	3.0	0	0	0	0	0	18.8	61.4	19.8	0	0	0	0
S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D	.9	66.7	0	33.3	0	0	0	0	0	0	0	0	66.7	33.3	0	0	0	0
B	2.1	100.0	0	0	0	0	0	0	0	0	7.1	14.3	42.9	0	0	0	0	0
T	2.0	82.5	4.0	7.9	3.2	2.4	0	0	0	0	.8	18.3	59.5	16.7	0	0	0	0
I:																		
E	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A	1.7	25.4	19.7	38.0	14.1	2.8	0	0	0	0	0	4.2	52.1	35.2	5.6	2.8	0	0
S	.7	0	0	100.0	0	0	0	0	0	0	0	0	0	100.0	0	0	0	0
D	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T	1.2	25.0	19.4	38.9	13.9	2.8	0	0	0	0	0	4.2	51.4	36.1	5.6	2.8	0	0
U:																		
E	.1	100.0	0	0	0	0	0	0	0	0	0	0	0	100.0	0	0	0	0
A	.3	50.0	8.3	25.0	16.7	0	0	0	0	0	66.7	8.3	8.3	16.7	0	0	0	0
S	.7	100.0	0	0	0	0	0	0	0	0	0	0	0	100.0	0	0	0	0
D	1.4	80.0	0	0	0	0	20.0	0	0	0	0	40.0	40.0	0	0	0	0	0
B	3.5	62.5	16.7	4.2	8.3	4.2	4.2	0	0	0	29.2	8.3	33.3	4.2	0	0	0	0
T	.7	52.8	11.6	9.3	9.3	2.3	4.7	0	0	0	34.9	11.6	25.6	11.6	0	0	0	0

[1] E=Europe; A=Africa-Asia; S=South Pacific-South and Central America; D=U.S. Domestic Selections; B=U.S. Breeding Lines; T=total collection.

[2] For explanation of codes, see table 1.

Comparisons Between Proportions of Strains From Each Subdivision That Have Each of the Combinations and Proportions of Strains in Entire Collection That Have the Same Combinations

Numerous differences between the proportions of strains with given two-character combinations have been noted among the several subdivisions. A statistical analysis was conducted to determine if they were real or were only due to chance. The deviations of the subdivision proportions from the proportions for the entire collection, plus or minus, and standard errors were calculated for the two-character combinations. This technique sacrificed some precision because the comparison of, say, the 6–W proportion for the European subdivision with that for the entire collection embodies in part a comparison of the European subdivision with itself. This is particularly true for the African-Asian subdivision that represents a major portion of the collection strains. However, additional precision is not needed to arrive at the proper conclusion relative to most of the combinations.

Proportions of strains in which combinations occur.—Calculations based on the data in table 20 are summarized in table 23 in terms of significant differences between subdivision proportions for two-character combinations involving the 6-row character. These findings give added credence to previous observations on the character distribution patterns. Combinations involving other characters exhibit similar differences.

Proportions of strains with the respective characters that have each of the other characters.—Differences among the subdivisions for the proportion of the 6-row strains that have each of the characters in the other spike categories are summarized in table 24. The findings are based on data in table 22. Many of the differences noted in this table are confirmed as real distinctions that exist between 6-row types grown in different world areas. Comparable distinctions exist for other characters.

Frequency-of-Occurrence-of-Characters and Association-of-Characters Analyses

We have learned that 19.8 percent of the strains in the collection are 2-row, white kernel types (table 19); that 78.9 percent of the 2-row types are white (table 21); and 36.0 percent of the white barleys are 2-rowed (table 21). The first percentage value affords us an understanding of the frequency of occurrence of strains with two rows of white kernels. The second and third percentages reveal the extent to which the characters are associated—coexist. For example, barleys with the 2-row head type are preponderantly white-kerneled; however, white kernels are not limited to occurrence in 2-row heads. The data in tables 20 and 22 afford a basis for conducting "frequency" and "association" analyses, respectively, among the two-character combinations.

TABLE 23.—*Two-character combinations involving 6-row head type for which the proportion of strains from each of 5 source subdivisions in the World Collection of Barleys differs significantly, plus or minus, from the proportion from the other subdivisions*

6-row head type combined with [1]—	Europe (E)		Africa-Asia (A)		South Pacific-South and Central America (S)		U.S. Domestic Selections (D)		U.S. Breeding Lines (B)	
	+	−	+	−	+	−	+	−	+	−
Kernel color:										
W		A, D, B	E, S			D, B	E, S		E, S	
LB	A			E, D, B			A		A	
B		S, D		S, D						
DB		A, S, B	E, D	S	E, A, D, B			A, S		
Bk		A	E, S, D, B			A		A		A
P		A	E, D, B					A		A
Awn condition:										
R		A, S, D	E, B		E, B		E, B			A, S, D
Sm		B		B		B		B	E, A, S, D	
SS		B		B				B	E, A, D	
H		D, B		D, B		D	E, A, S		E, A	
Caryopsis:										
C		A, S, D, B	E	S, D, B	E, A		E, A		E, A	
N		A	E, S, D, B			A		A		A

[1] For explanation of codes, see table 1.

TABLE 23.—*Two-character combinations involving 6-row head type for which the proportion of strains from each of 5 source subdivisions in the World Collection of Barleys differs significantly, plus or minus, from the proportion from the other subdivisions*—Continued

6-row head type combined with [1]—	Europe (E)		Africa-Asia (A)		South Pacific-South and Central America (S)		U.S. Domestic Selections (D)		U.S. Breeding Lines (B)	
	+	−	+	−	+	−	+	−	+	−
Rachilla hairs:										
L		A B	E S D B			A B		A B	E S D	A
Sh		S D B		S D B	E A B		E A B		E A	S D
Awn-glume ratio:										
1.0		A S D B	E D	S B	E A D B		E	A S B	E A D	S
1.5		A D	E S			A D	E S B		S	D
2.0		A D	E	D		D	E A S B			D
2.5	S	A D	E S B			E A D	E S B			A D
Awn-spike ratio:										
0.5		A	E S D B			A		A		A
1.0	S	A D	E S	D		E A S B	E A S B		S	D
1.5		A B	E S			A B			E S	
2.0		A S D B	E	S	E A D B		E	S	E	S
2.5		A S D B	E	S	E A D B		E	S	E	S
3.0		A B	E D		E D			A S	E	

[1] For explanation of codes, see table 1.

TABLE 24.—*Six-row head type strains having characters in the other spike categories for which the proportion from each of 5 source subdivisions in the World Collection of Barleys differs significantly, plus or minus, from the proportion for each of the other subdivisions*

6-row head type combined with [1]—	Europe (E)		Africa-Asia (A)		South Pacific-South and Central America (S)		U.S. Domestic Selections (D)		U.S. Breeding Lines (B)	
	+	−	+	−	+	−	+	−	+	−
Kernel color:										
W	S	A D B	E S			E A D B	E S		E S	
LB	A S B			E D B	A	E	A		A	E
B	A			E S	A B					S
DB	D	S	D	S	E A D B			E A S B	S	D
Bk		A	E S D B			A		A		A
P		A	E D B					A		A
Awn condition:										
R	D B		S D B		D B	A	B	E A S		A E S D
Sm		B		D B		B	A	B	A E S D	
SS		B		B		B		B	A E S D	
H		D B		D B		D B	E A S		E A	
Caryopsis:										
C		B		E S D B	A		A		E A	
N	B	A	E S D B			A		A	B	A

[1] For explanation of codes, see table 1.

TABLE 24.—*Six-row head type strains having characters in the other spike categories for which the proportion from each of 5 source subdivisions in the World Collection of Barleys differs significantly, plus or minus, from the proportion for each of the other subdivisions*—Continued

6-row head type combined with [1]—	Europe (E)		Africa-Asia (A)		South Pacific-South and Central America (S)		U.S. Domestic Selections (D)		U.S. Breeding Lines (B)	
	+	−	+	−	+	−	+	−	+	−
Rachilla hairs:										
L	S D	A	E S D B	—	—	E A B	—	E A B	S D	A
Sh	A	S D	—	E S D B	E A B	—	E A B	—	A	S D
Awn-glume ratio:										
1.0	—	A S B	E D	S B	E A D B	—	—	A S B	E A D	S
1.5	—	D	S	—	—	A D	S B	—	—	D
2.0	S B	—	S B	—	—	E A D	S B	—	—	E A D
2.5	S B	—	S B	—	—	E A D B	S B	—	S	E A D
3.0	A S D B	—	—	E	—	—	—	E	—	E
3.5	A B	—	—	E	—	—	—	—	—	E
Awn-spike ratio:										
0.5	—	A	E D B	—	—	—	—	A	—	A
1.0	S B	—	S	—	—	E A D B	S B	—	S	E D
1.5	A S D B	—	S D	E	—	E A B	—	E A B	S D	E
2.0	—	A S	E	S B	E A D B	—	—	S	—	A S
2.5	—	A S D B	E	—	E A D B	—	E	S	E	S
3.0		A S B	E D	—	E D	—	—	A S B	E D	S

[1] For explanation of codes, see table 1.

Frequency.—Table 25 [10] affords rankings of the head type two-character combination frequency data based on the horizontal rows of figures within each individual character block in table 20. Rankings based on frequency of occurrence are fairly comparable for all subdivisions; therefore, patterns within most of the character blocks are quite uniform.

Association.—Rankings of the head type two-character combination association data represented by figures within the vertical columns beneath each character in the manner shown in table 21 are given in table 26.[11] An example follows:

Example:

Entire collection		
6-row	Association ranking	
W 61. 6	5	Interpretation: Within the kernel color category, dark blue is more restricted to association with the 6-row character than is any other color.
LB 87. 2	3	
B 87. 7	2	
DB 90. 1	1	
Bk 50. 7	6	
P 67. 5	4	

The rankings in table 21 reveal marked differences among the subdivisions.

In many instances, the character within a spike category that ranks highest for association with another character occurs in the fewest strains.

Frequency vs. association.—Table 27 includes a listing of characters that occur most frequently with each individual character and of characters that are most closely associated with the individual characters. In the "frequency" portion of the table the predominant characters from the spike categories are cited almost to the exclusion of all other characters. On the other hand, there is no consistent pattern within the "association" segment. Nearly every character is listed. It is evident, though, that the predominant characters from the respective spike categories are not restricted to association with given characters to the extent that the less preponderant ones are.

[10] Complete frequency rankings for all two-character combinations in the entire collection and the five subdivisions are included in table VIII of the appendix referred to on p. 13.

[11] Complete association rankings for all existing two-character combinations are included in table IX of the appendix referred to on p. 13.

TABLE 25.—*For strains from 5 source subdivisions and for all strains in the World Collection of Barleys, a ranking of the frequency with which characters in 6 spike categories occur in combination with each character in the head-type category*

Spike category and character (code) [1]	Head type and source subdivision [2]																													
	6						2						D						I						U					
	E	A	S	D	B	T	E	A	S	D	B	T	E	A	S	D	B	T	E	A	S	D	B	T	E	A	S	D	B	T
Kernel color:																														
W	1	1	3	1	1	1	1	1	1	1	1	1	2	1	---	2	2	1	---	4	---	---	---	5	1	1	1	1	1	1
LB	3	4	4	3	4	4	2	5	2	---	2	5	---	6	---	---	---	6	---	6	---	---	---	6	---	3	---	---	---	4
B	2	2	1	2	2	2	3	3	3	3	4	3	---	3	---	---	---	3	---	4	1	---	---	3	---	2	---	---	2	2
DB	4	3	2	4	3	3	4	4	3	---	4	4	3	5	---	---	---	5	---	2	---	---	---	2	---	3	---	---	---	4
Bk	5	5	6	5	5	5	4	2	---	2	2	2	1	2	---	1	1	2	---	3	---	---	---	3	---	---	---	---	3	3
P	6	6	5	6	6	6	6	6	---	---	5	6	---	4	---	---	3	4	---	1	---	---	---	1	---	---	---	---	---	---
Awn condition:																														
R	1	1	1	1	1	1	1	1	1	1	1	1	1	1	---	1	1	1	---	1	1	---	---	1	1	1	1	1	1	1
Sm	2	3	3	3	2	2	4	2	---	---	2	2	---	2	---	---	---	3	---	---	---	---	---	---	---	---	---	---	3	3
SS	3	4	4	5	4	4	2	3	---	2	2	3	---	3	---	---	---	4	---	---	---	---	---	---	---	---	---	---	3	3
H	4	2	2	2	3	3	---	---	---	3	4	5	2	---	---	---	2	2	---	---	---	---	---	---	---	---	---	2	2	2
A	---	5	---	4	5	5	3	4	---	---	---	4	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	1
Caryopsis:																														
C	1	1	1	1	1	1	1	1	1	1	1	1	1	1	---	1	1	1	---	1	1	---	---	1	1	1	---	1	1	1
N	2	2	2	2	2	2	2	2	2	2	2	2	---	2	---	2	2	2	---	---	---	---	---	---	---	2	1	2	2	2
Rachilla hairs:																														
L	2	1	2	2	2	1	1	1	2	1	1	1	2	2	---	1	1	1	---	2	---	---	---	2	---	1	1	2	1	1
Sh	1	2	1	1	1	2	2	2	1	2	2	2	1	1	---	---	2	1	---	1	1	---	---	1	1	---	---	1	1	2

Awn-glume ratio:																														
1.0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	---	1	1	1	---	2	---	---	---	2	1	1	1	1	1	1
1.5	5	4	3	4	4	4	2	2	2	3	3	2	---	3	---	---	---	3	---	3	---	---	---	3	---	4	---	---	2	2
2.0	2	2	2	1	2	2	3	3	---	2	2	3	2	2	---	2	---	2	---	1	1	---	---	1	---	2	---	---	4	2
2.5	3	3	4	3	3	3	4	4	---	3	3	4	---	4	---	---	---	4	---	4	---	---	---	4	---	3	---	---	3	2
3.0	4	5	---	5	5	5	4	5	---	---	3	5	---	5	---	---	---	5	---	5	---	---	---	5	---	---	---	---	4	6
3.5	6	6	---	6	6	6	6	6	---	3	6	6	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	2	4	5
4.0	7	7	---	7	7	7	---	6	---	---	---	7	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
4.5	---	8	---	8	---	8	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
5.0	8	9	---	---	---	8	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Awn-spike ratio:																														
0.5	4	4	5	5	5	4	4	4	---	---	4	4	---	---	---	---	3	4	---	---	---	---	---	---	---	1	---	---	2	1
1.0	2	2	6	2	2	2	1	1	3	2	2	1	1	3	---	---	2	2	---	4	---	---	---	4	---	3	---	1	3	3
1.5	1	1	2	1	1	1	2	2	2	1	1	2	2	1	---	1	1	1	---	1	---	---	---	1	---	3	---	1	1	2
2.0	3	3	1	3	3	3	3	3	1	3	3	3	---	2	---	2	---	3	---	2	1	---	---	2	1	2	1	---	4	3
2.5	6	5	3	4	4	5	5	5	---	---	5	5	---	---	---	---	---	---	---	3	---	---	---	3	---	---	---	---	---	---
3.0	6	6	4	5	5	6	---	6	---	---	---	6	---	---	---	---	---	---	---	5	---	---	---	5	---	---	---	---	---	---
3.5	5	7	6	5	7	7	---	6	---	---	---	6	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
4.0	6	8	8	---	---	8	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---

[1] For explanation of codes, see table 1.

[2] E=Europe; A=Africa-Asia; S=South Pacific-South and Central America; D=U.S. Domestic Selections; B=U.S. Breeding Lines; T=Total collection.

TABLE 26.—*For strains from 5 source subdivisions and for all strains in the World Collection of Barleys, a ranking within each of 6 spike categories of the extent to which each of its characters tends to be associated with each character in the head type category*

Spike category and character (code) [1]	Head type and source subdivision [2]																													
	6						2						D						I						U					
	E	A	S	D	B	T	E	A	S	D	B	T	E	A	S	D	B	T	E	A	S	D	B	T	E	A	S	D	B	T
Kernel color:																														
W	6	5	6	5	4	5	1	2	1	2	3	1	3	4	---	2	3	4	---	6	---	---	---	6	1	2	1	1	3	2
LB	3	3	5	1	3	3	4	3	2	---	4	3	---	6	---	---	---	6	---	5	---	---	---	5	---	1	---	---	---	4
B	2	2	4	4	2	2	5	4	4	3	6	5	---	3	---	---	---	3	---	4	1	---	---	4	---	2	---	---	2	2
DB	1	1	3	1	1	1	6	6	3	---	5	6	2	5	---	---	---	5	---	3	---	---	---	3	---	4	---	---	---	5
Bk	5	6	1	6	6	6	3	1	---	1	1	2	1	1	---	1	2	1	---	2	---	---	---	2	---	---	---	---	1	1
P	4	4	1	1	5	4	2	5	---	---	1	4	---	2	---	---	1	2	---	1	---	---	---	1	---	---	---	---	---	---
Awn condition:																														
R	3	2	4	3	5	2	3	4	1	2	1	4	2	1	---	1	2	2	---	1	1	---	---	1	1	1	1	2	2	2
Sm	2	4	1	1	2	3	4	2	---	---	4	3	---	2	---	---	---	4	---	---	---	---	---	---	---	---	---	---	4	4
SS	4	5	1	4	4	5	2	1	---	1	2	1	---	3	---	---	---	3	---	---	---	---	---	---	---	---	---	---	3	2
H	1	1	1	2	3	1	---	---	---	3	3	5	1	---	---	---	1	1	---	---	---	---	---	---	---	---	---	1	1	1
A	---	3	---	1	1	4	1	3	---	---	---	2	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Caryopsis:																														
C	2	2	1	1	1	2	1	1	1	1	2	1	2	1	---	2	2	1	---	1	1	---	---	1	1	1	---	2	2	2
N	1	1	2	2	2	1	2	2	2	2	1	2	1	2	---	1	1	2	---	---	---	---	---	---	---	2	1	1	1	1
Rachilla hairs:																														
L	2	2	2	2	2	2	1	1	1	1	1	1	2	2	---	1	1	2	---	2	---	---	---	2	---	1	1	1	1	1
Sh	1	1	1	1	1	1	2	2	2	2	2	2	1	1	---	---	2	1	---	1	1	---	---	1	1	---	---	2	2	2

Awn-glume ratio:																														
1.0	8	9	3	8	6	9	1	1	3	1	1	1	1	1		1	1	1		4				4		3	1	2	4	3
1.5	7	8	4	5	5	8	2	2	2	4	5	2		2				2		2				2	1	3			2	2
2.0	6	7	2	6	2	6	3	5		3	3	4	2	4		2		5		1				1		1			6	5
2.5	3	5	1	4	3	5	6	4		5	5	6		5				4		3	1			3		1			3	4
3.0	4	4		1	4	4	5	7			3	7		3				3		4				4					5	6
3.5	5	3		7	7	7	4	6	1	2	2	3																1	1	1
4.0	1	6		1	1	3		3				5																		
4.5		1		1		1																								
5.0	1	1				1																								
Awn-spike ratio:																														
0.5	7	5	1	1	7	6	2	5			2	4					1	4								1			1	1
1.0	8	8	8	6	6	8	1	1	1	1	1	1	2	3			3	3		5				5		3			3	4
1.5	5	7	7	7	5	7	4	2	2	2	3	2	1	1		1	2	1		4				4		3		1	2	3
2.0	4	6	6	5	4	5	5	3	3	3	5	3		2		2		2		2	1			1	1	2	1	2	4	2
2.5	6	3	1	1	3	1	3	6			4	6								1				1						
3.0	1	2	1	1	1	2		7				7								3				3						
3.5	1	4	1	1	1	3		3				5																		
4.0	1	1	1			1																								

[1] For explanation of codes, see table 1.
[2] E=Europe; A=Africa-Asia; S=South Pacific-South and Central America; D=U.S. Domestic Selections; B=U.S. Breeding Lines; T=Total collection.

TABLE 27.—*Individual characters that occur most frequently and are most closely associated with each of the other characters in 7 spike categories among the 6,200 strains in the World Collection of Barleys*

Spike category and character (code)[1]	Frequency							Association[2]						
	Head type	Kernel color	Awns	Caryopsis	Rachilla hairs	Awn-glume ratio	Awn-spike ratio	Head type	Kernel color	Awns	Caryopsis	Rachilla hairs	Awn-glume ratio	Awn-spike ratio
Head type:														
6	----	W	R	C	L	1.0	1.5	------	DB	H	N	Sh	4.5/5.0	4.0
2	----	W	R	C	L	1.0	1.0	------	W	SS	C	L	1.0	1.0
D	----	W	R	C	L/Sh	1.0	1.5	------	Bk	H	C	Sh	1.0	1.5
I	----	P	R	C	Sh	2.0	1.5	------	P	R	C	Sh	2.0	2.0/2.5
U	----	W	R	C	L	1.0	0.5	------	Bk	H	N	Sh/L	3.5	0.5
Kernel color:														
W	6	------	R	C	L	1.0	1.5	2	------	Sm	N	L	5.0	1.0
LB	6	------	R	C	Sh	1.0	1.5	6	------	A	C/N	Sh	5.0	4.0
B	6	------	R	C	L	1.0	1.5	6	------	A	C	Sh	2.0	3.5
DB	6	------	R	C	L	1.0	1.5	I	------	R	C	L	2.0	3.5
Bk	6	------	R	C	L	1.0	1.5	D	------	SS	C	Sh	4.0	2.0
P	6	------	R	C	L	1.0	1.5	I	------	H	N	L	4.5	2.0
Awn condition:														
R	6	W	------	C	L	1.0	1.5	I	P	------	N	Sh	4.5/5.0	3.5/4.0
Sm	6	W	------	C	L	1.0	1.0	2	Bk	------	C	L	1.0	1.0
SS	2	W	------	C	L	1.0	1.0	2	Bk	------	C	L	1.0	1.0
H	6	W	------	C	Sh	1.0	------	U	Bk	------	N	Sh	1.5	------
A	6	B	------	C	L	1.0	------	2	LB	------	C	L	1.0	------

Caryopsis:														
C	6	W	R	------	L	1. 0	1. 5	I	DB	Sm	------	Sh	5. 0	3. 5
N	6	W	R	------	L	1. 0	1. 5	U	P	H	------	L	4. 5	0. 5
Rachilla hairs:														
L	6	W	R	C	------	1. 0	1. 5	2	P	A	N	------	4. 5/5. 0	0. 5
Sh	6	W	R	C	------	1. 0	1. 5	I	LB	H	C	------	2. 5	2. 0
Awn-glume ratio:														
1.0	6	W	R	C	L	------	1. 5	2	Bk	A	C	L	------	4. 0
1.5	6	W	R	C	L	------	1. 5	I	LB	H	N	L	------	2. 5
2.0	6	W	R	C	Sh	------	1. 5	I	P	R	N	Sh	------	2. 0
2.5	6	W	R	C	Sh	------	1. 5	6	P	R/H	N	Sh	------	1. 5
3.0	6	W	R	C	Sh	------	1. 5	6	LB	R	N	Sh	------	2. 0
3.5	6	W	R	C	L	------	1. 5	U	LB	R	C	Sh	------	1. 0
4.0	6	W	R	C	L	------	1. 5	6	LB	R	C	Sh	------	2. 5
4.5	6	W	R	C	L	------	2. 0/3. 0	6	P	R	C/N	L	------	3. 0
5.0	6	W	R	C	L	------	2. 0	6	LB	R	C	L	------	2. 0
Awn-spike ratio:														
0.5	6	W	R	C	L	1. 0	------	U	LB	R	N	L	4. 5	------
1.0	6	W	R	C	L	1. 0	------	2	W	SS	C	L	3. 5	------
1.5	6	W	R	C	L	1. 0	------	D	P	R	C	Sh	1. 5	------
2.0	6	W	R	C	Sh	1. 0	------	I	P	R	N	Sh	5. 0	------
2.5	6	W	R	C	Sh	1. 0	------	I	B	R	C	Sh	4. 0	------
3.0	6	W	R	C	L	1. 0	------	I	DB	R	C	L/Sh	4. 5	------
3.5	6	W	R	C	L	1. 0	------	6	B	R	C	L	1. 0	------
4.0	6	W	R	C	L	1. 0	------	6	LB	R	C	L	1. 0	------

[1] For explanation of codes, see table 1.
[2] Not intended to imply genetic linkage.

Theoretical Proportion of Strains That Might Be Constituted by Each Combination

Computations were made to determine the theoretical proportions of the strains that might have each two-character combination if the distribution of characters had been at random within the limits of the proportions of all the strains in which each character occurs. These figures were obtained by multiplying together the actual proportions of the strains in which each of the components of the combinations occur; e.g., character "a" (50%)×character "b" (50%)=theoretical proportion of 25 percent for the two-character combination "ab."

The computed theoretical values were paired with the figures for the actual proportions of the strains that have the respective two-character combinations.

CHI-SQUARES.—Chi-squares were computed using the actual and theoretical data for the two-character combinations within each possible conjunction of two spike categories. The chi-square values were all large, reflecting the fact that certain combinations of the characters in each spike category occur in greater or lesser proportions of the strains than would be expected if the characters occurred together in a random way. The chi-square values for all possible two spike category conjunctions are listed in table 28.

TABLE 28.—*Chi-square values for each possible 2 spike category combination among 6,200 strains in the World Collection of Barleys*[1]

Combination	Chi-square value	Combination	Chi-square value
Caryopsis and—		Head type and—	
Head type	107.98	Kernel color	837.40
Kernel color	107.19	Awn condition	291.54
Awn condition	115.03	Awn-glume ratio	1,237.85
Rachilla hairs	214.09	Awn-spike ratio	745.12
Awn-glume ratio	41.55	Awn condition and—	
Awn-spike ratio	137.59	Kernel color	75.23
Rachilla hairs and—		Awn-glume ratio	155.22
Head type	519.68	Awn-spike ratio	111.71
Kernel color	83.36	Kernel color and—	
Awn condition	91.80	Awn-glume ratio	150.77
Awn-glume ratio	379.27	Awn-spike ratio	344.23
Awn-spike ratio	251.16	Awn-glume ratio and awn-spike ratio	294.31

[1] Computed from comparisons of the actual proportions of collection strains constituted by the respective 2-character combinations with theoretical proportions of the strains they might have constituted had the pairing of the characters been at random within the limits of the proportions of the strains in which each character occurs.

COMBINATIONS THAT OCCUR IN GREATER OR LESSER PROPORTIONS OF STRAINS THAN WAS THEORETICALLY COMPUTED.—The proportions of the two-character combinations involving each character that occur in greater or lesser proportions of the strains than would have been expected had the characters been distributed at random are given in table 29. The proportions of the combinations whose actual

TABLE 29.—*Proportion of 2-character combinations in which each of 37 characters in 7 spike categories occur in a greater, equal, or lesser number of strains than theoretically computed or are missing among 6,200 strains in the World Collection of Barleys*

Spike category and character (code)[1]	2-character combinations in which number of strains was—			
	Greater than computed	Equal to computed	Lesser than computed	Missing
	Percent	*Percent*	*Percent*	*Percent*
Head type:				
6	62.5	3.1	34.4	0
2	25.0	6.3	59.4	9.4
D	25.0	6.3	40.6	28.1
I	37.5	6.3	18.8	37.5
U	21.9	15.6	34.4	28.1
Kernel color:				
W	41.9	3.2	54.8	0
LB	38.7	22.6	32.3	6.5
B	35.5	35.5	25.8	3.2
DB	41.9	6.5	45.2	6.5
Bk	51.7	6.5	29.0	12.9
P	38.7	6.5	22.6	32.3
Awn condition:				
R	59.4	3.1	37.5	0
Sm	21.9	6.3	50.0	21.9
SS	21.9	6.3	46.9	25.0
H	45.8	16.7	20.8	16.7
A	16.7	12.5	29.2	41.7
Caryopsis:				
C	45.7	17.1	37.1	0
N	37.1	11.4	42.9	8.6
Rachilla hairs:				
L	42.9	11.4	45.7	0
Sh	45.7	8.6	40.0	5.7
Awn-glume ratio:				
1.0	60.7	7.1	32.1	0
1.5	50.0	3.6	39.3	7.1
2.0	35.7	3.6	60.7	0
2.5	35.7	10.7	46.4	7.1
3.0	32.1	10.7	46.4	10.7
3.5	28.6	21.4	17.9	32.1
4.0	25.0	17.9	17.9	39.3
4.5	21.4	3.6	14.3	60.7
5.0	21.4	7.1	3.6	67.9
Awn-spike ratio:				
0.5	29.6	7.4	51.9	11.1
1.0	40.7	7.4	44.4	7.4
1.5	51.9	18.5	25.9	3.7
2.0	55.6	14.8	29.6	0
2.5	37.0	7.4	37.0	18.5
3.0	29.6	18.5	33.3	18.5
3.5	14.8	11.1	22.2	51.9
4.0	3.7	14.8	25.9	55.6

[1] For explanation of codes, see table 1.

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values equal the computed ones are also included. The characters whose numbers of strains per two-character combination deviate from the computed numbers for the greatest proportions of the combinations are generally the most predominant ones from the respective spike categories. Of the characters within each spike category that have the largest proportion of two-character combinations in which the numbers of strains are "greater" or "lesser" than the computed numbers, five in the "greater" column are the predominant characters within their respective spike categories and four in the "lesser" column are the second most predominant in their category.

Combinations Not Present

The two-character combinations that were not found in the collection are listed in table 30. High awn-glume and awn-spike ratios; deficiens, *H. irregulare,* and intermedium head types; purple kernels; and smooth, semismooth, hooded, and awnless types are involved in the greatest number of the missing combinations.

In nearly three-fourths of the missing combinations, at least one of the characters occurs in less than 3 percent of the strains.

TABLE 30.—*Possible 2-character combinations among 37 characters in 7 spike categories that are missing from the 6,200 strains in the World Collection of Barleys, and proportion of strains in which they might have occurred had distribution of characters been at random* [1]

Spike category and character (code) [2]	Missing	Proportion of strains in which they might have occurred had distribution been at random [3]
Head type:		*Percent*
6	None	----
2	4.5a-g	0.0251
	5.0a-g	.0126
	4.0a-s	.0502
D	A	.0080
	3.5a-g	.0220
	4.0a-g	.0100
	4.5a-g	.0020
	5.0a-g	.0010
	2.5a-s	.0520
	3.0a-s	.0340
	3.5a-s	.0080
	4.0a-s	.0040
I	Sm	.0720
	SS	.0324
	H	.0312
	A	.0048
	N	.1500
	3.5a-g	.0132
	4.0a-g	.0060
	4.5a-g	.0012
	5.0a-g	.0006
	0.5a-s	.0444
Head Type—Continued		*Percent*
I	3.5a-s	0.0048
	4.0a-s	.0024
U	P	.0175
	A	.0028
	4.0a-g	.0035
	4.5a-g	.0007
	5.0a-g	.0003
	2.5a-s	.0182
	3.0a-s	.0119
	3.5a-s	.0028
	4.0a-s	.0014
Kernel color:		
W	None	----
LB	4.5a-g	.0071
	3.5a-s	.0284
B	5.0a-g	.0083
DB	4.5a-g	.0131
	5.0a g	.0066
Bk	4.5a-g	.0057
	5.0a-g	.0028
	3.5a-s	.0228
	4.0a-s	.0114

See footnotes at end of table.

TABLE 30.—*Possible 2-character combinations among 37 characters in 7 spike categories that are missing from the 6,200 strains in the World Collection of Barleys, and proportion of strains in which they might have occurred had distribution of characters been at random* [1]—Con.

Spike category and character (code) [2]	Missing	Proportion of strains in which they might have occurred had distribution been at random [3]
Kernel color—Continued		*Percent*
P	Sm	0.1500
	SS	.0675
	A	.0100
	3.5a-g	.0275
	4.0a-g	.0125
	5.0a-g	.0012
	3.0a-s	.0425
	3.5a-s	.0100
	4.0a-s	.0050
	U	*.0175*
Awn condition:		
R	None	--------
Sm	3.5a-g	.0660
	4.5a-g	.0060
	5.0a-g	.0030
	3.5a-s	.0240
	4.0a-s	.0120
	I	*.0720*
	P	*.1500*
SS	3.5a-g	.0297
	4.0a-g	.0135
	4.5a-g	.0027
	5.0a-g	.0013
	3.5a-s	.0108
	4.0a-s	.0054
	I	*.0324*
	P	*.0675*
H	4.0a-g	.0130
	4.5a-g	.0026
	5.0a-g	.0013
	I	*.0312*
A	1.5a-g	.0360
	3.0a-g	.0240
	3.5a-g	.0044
	4.0a-g	.0020
	4.5a-g	.0004
	5.0a-g	.0002
	D	*.0080*
	I	*.0048*
	U	*.0028*
	P	*.0100*
Caryopsis:		
C	None	--------
N	5.0a-g	.0063
	3.5a-s	.1375
	I	*.1500*

Spike category and character (code) [2]	Missing	Proportion of strains in which they might have occurred had distribution been at random [3]
Rachilla hairs:		*Percent*
L	None	--------
Sh	4.5a-g	0.0391
	5.0a-g	.0196
Awn-glume ratio:		
1.0	None	--------
1.5	4.0a-s	.0180
	A	*.0360*
2.0	None	--------
2.5	3.5a-s	.0448
	4.0a-s	.0224
3.0	3.5a-s	.0240
	4.0a-s	.0120
	A	*.0240*
3.5	2.5a-s	.0286
	3.5a-s	.0044
	4.0a-s	.0022
	D	*.0220*
	I	*.0132*
	P	*.0275*
	Sm	*.0660*
	SS	*.0297*
	A	*.0044*
4.0	0.5a-s	.0185
	3.0a-s	.0085
	3.5a-s	.0020
	4.0a-s	.0010
	D	*.0100*
	I	*.0060*
	U	*.0035*
	P	*.0125*
	SS	*.0135*
	H	*.0130*
	A	*.0020*
4.5	1.0a-s	.0293
	1.5a-s	.0422
	2.5a-s	.0026
	3.5a-s	.0004
	4.0a-s	.0002
	2	*.0251*
	D	*.0020*
	I	*.0012*
	U	*.0007*
	LB	*.0071*
	DB	*.0131*
	Bk	*.0057*
	Sm	*.0060*

See footnotes at end of table.

TABLE 30.—*Possible 2-character combinations among 37 characters in 7 spike categories that are missing from the 6,200 strains in the World Collection of Barleys, and proportion of strains in which they might have occurred had distribution of characters been at random* [1]—Con.

Spike category and character (code) [2]	Missing	Proportion of strains in which they might have occurred had distribution been at random [3]
Awn-glume ratio—Continued		*Percent*
4.5	*SS*	*0.0027*
	H	*.0026*
	A	*.0004*
	Sh	*.0391*
5.0	0.5a-s	.0019
	1.0a-s	.0147
	2.5a-s	.0013
	3.0a-s	.0009
	3.5a-s	.0002
	4.0a-s	.0001
	2	*.0126*
	D	*.0010*
	I	*.0006*
	U	*.0003*
	B	*.0083*
	DB	*.0066*
	Bk	*.0028*
	P	*.0012*
	Sm	*.0030*
	SS	*.0013*
	H	*.0013*
	A	*.0002*
	N	*.0063*
	Sh	*.0196*
Awn-spike ratio:		
0.5	*I*	*.0444*
	4.0a-g	*.0185*
	5.0a-g	*.0019*
1.0	*4.5a-g*	*.0293*
	5.0a-g	*.0147*
1.5	*4.5a-g*	*.0422*
2.0	None	
2.5	*D*	*.0520*
	U	*.0182*
	3.5a-g	*.0286*
	4.5a-g	*.0026*
	5.0a-g	*.0013*
Awn-spike ratio—Continued		*Percent*
3.0	*D*	*0.0340*
	U	*.0119*
	P	*.0425*
	4.0a-g	*.0085*
	5.0a-g	*.0009*
3.5	*D*	*.0080*
	I	*.0048*
	U	*.0028*
	LB	*.0284*
	Bk	*.0228*
	P	*.0100*
	Sm	*.0240*
	SS	*.0108*
	N	*.1375*
	2.5a-g	*.0448*
	3.0a-g	*.0240*
	3.5a-g	*.0044*
	4.5a-g	*.0004*
	5.0a-g	*.0002*
4.0	*2*	*.0502*
	D	*.0040*
	I	*.0024*
	U	*.0014*
	Bk	*.0114*
	P	*.0050*
	Sm	*.0120*
	SS	*.0054*
	1.5a-g	*.0180*
	2.5a-g	*.0224*
	3.0a-g	*.0120*
	3.5a-g	*.0022*
	4.0a-g	*.0010*
	4.5a-g	*.0002*
	5.0a-g	*.0001*

[1] Italics indicates reciprocal entry.

[2] For explanation of codes, see table 1.

[3] Example: 2-row occurs in 25.1 percent of the strains, and 0.1 percent of the strains have an awn-glume ratio of 4.5. Theoretical frequency for 2—4.5a-g= 0.251×0.001=0.0251 percent of the strains.

The theoretical proportions that each missing two-character combination might comprise of all entries, assuming a completely random distribution of the characters in the collection, are also given in table 30. The data indicate that 61 of the missing combinations would not be expected to occur in the 6,200 strains; i.e., less than 0.016 percent. Of the remaining 37 combinations, 23 would not be expected to occur in more than one entry. Only two combinations would theoretically occur in more than four entries.

Summary of Distribution of Combinations Among Entire Collection and Subdivisions

More different two-character combinations occur among the barleys from Africa and Asia than from any of the other subdivisions. An analysis of the occurrence of individual two-character combinations among the different subdivisions is afforded by table 31. The greatest diversity is found among the African-Asian strains and the least among those from the South Pacific and South and Central America. Although no other subdivision closely approximates the African-Asian diversity, the U.S. Breeding Lines subdivision ranks second. Most of the 172 combinations that have been obtained from all of the subdivisions include at least 1 character that is predominant in its respective spike category.

TABLE 31.—SUMMARY: *Distribution of 2-character combinations among 6,200 strains in the World Collection of Barleys and among strains from 5 source subdivisions*

2-character combinations	Strains	2-character combinations	Strains
	Number		*Number*
Possible among 37 characters in 7 spike categories	549	U.S. Domestic Selections	302
		South Pacific-South America	244
Present among all strains	451	Present only among strains from—	
Missing among all strains	98		
Present among strains from all source subdivisions	172	Africa-Asia	59
Present among strains from each source subdivision: [1]		U.S. Breeding Lines	9
Africa-Asia	445	U.S. Domestic Selections	1
U.S. Breeding Lines	364	Europe	1
Europe	317		

[1] From among the 451 combinations present among all strains.

Distinctive Two-Character Relationships Among Barleys From Some Specific World Areas

U.S. DOMESTIC SELECTIONS (RACHILLA HAIRS–HEAD TYPE).—Data in table 32 reveal that U.S. Domestic Selections with short or long rachilla hairs are 6-row or 2-row types to about the same extent as the strains in the foreign component of the collection. As previously noted, however, most of the domestic selections have short hair rachillas. On the other hand, long hair rachilla types are preponderant among the foreign strains. The domestic selections apparently do not constitute a random cross section of world barleys. They may have been drawn from a limited segment of the foreign barley population. The basic data for this study indicate that the following sources may be primary African-Asian centers of 6-row, short hair rachilla strains; i.e., comparatively large proportions of the strains from these areas have this combination of characters:

Ethiopia
Delta (Egypt)
North Africa
Turkey
Northeast Turkey
Transcaucasia
Manchuria

TABLE 32.—*Proportion of strains among the U.S. Domestic Selections subdivision and the foreign component of the World Collection of Barleys that have short- and long-haired rachillas, and proportion of these strains that have 6- and 2-row head types*

Segment of collection	Rachilla hairs		Head type	
		Percent		*Percent*
U.S. Domestic Selections	Short	71.8	6-row	95.2
			2-row	3.6
	Long	28.2	6-row	59.2
			2-row	35.7
Foreign component	Short	34.6	6-row	83.0
			2-row	10.5
	Long	65.4	6-row	61.8
			2-row	31.9

TURKEY (HEAD TYPE–AWN CONDITION).—It was noted in table 9 that the Black Sea area appears to be the main center of concentration for 2-row strains. Approximately 80 percent of the smooth awn strains in the foreign component of the collection are 2-row types. The data in table 21 indicate that 84.9 percent of all 2-row types have long hair rachillas. The results in table 33 indicate that the 2-row and long hair rachilla characters in barleys from Turkey occur in approximately the same proportions of strains having characters for barbed (rough) and barbless (smooth and semismooth) awns, respectively. A comparable picture is evident for the relationship between the 6-row and short hair rachilla characters as they occur with the awn types. Turkish 6-row types are almost exclusively characterized by rough awns and short rachilla hairs. Conversely, about one-third of the 2-row types from this area have smooth or semismooth awns and nearly all of them have long rachilla hairs.

TABLE 33.—*Proportion of strains from Turkey in the World Collection of Barleys that have 6- and 2-row head types and that have short- and long-haired rachillas, and proportion of these strains that have rough and smooth awns*

Items compared		Awns	
	Percent		*Percent*
Head type:			
6-row	37.9	Rough	98.7
		Smooth and semismooth	1.3
2-row	62.1	Rough	67.8
		Smooth and semismooth	32.2
Rachilla hairs:			
Short	35.7	Rough	93.8
		Smooth and semismooth	6.2
Long	64.3	Rough	71.5
		Smooth and semismooth	28.5

TURKEY (HEAD TYPE–RACHILLA HAIRS).—Rachilla hair proportions for the 6-row and 2-row strains from Turkey are compared with those of strains with these head types from the remainder of the collection in table 34. The preponderance of long hair rachillas among all 2-row types is evident. The combination of short hair rachillas and 6-row head types is not unique to the Turkish strains. It was noted in figure 3 that the strains from Ethiopia and Manchuria, most of which are 6-rowed, are characterized by a preponderance of short hair rachilla types. The picture for Turkey is unique because of the nearly opposite rachilla hair patterns for the 6-row and 2-row types.

TABLE 34.—*Proportion of strains from Turkey and of all strains (except from Turkey) in the World Collection of Barleys that have 6- and 2-row head types, and proportion of these strains that have short- and long-haired rachillas*

Segment of collection	Head type		Rachilla hairs	
		Percent		*Percent*
Turkey	6-row	37.9	Short	86.5
			Long	13.5
	2-row	62.1	Short	4.8
			Long	95.2
Entire collection (except Turkey)	6-row	75.9	Short	43.8
			Long	56.2
	2-row	19.6	Short	19.9
			Long	80.1

ETHIOPIA (*H. IRREGULARE*–OTHER HEAD TYPES).—*H. irregulare* occurs only among strains from Ethiopia. Only one strain of this type has been obtained elsewhere—that one was from Argentina, into which it was undoubtedly introduced. The data in table 35 afford a basis for comparing the occurrence of characters from spike categories II to V in *H. irregulare* strains with the occurrence of the same characters in Ethiopian strains that have the remainder of the head type characters. The character distribution patterns are surprisingly comparable. Thus, a head type character that has been very much isolated geographically occurs in strains that exhibit a diversity of type similar to that of strains from the same locale with the other head type characters, most of which are not limited to occurrence in that area.

TABLE 35.—*Proportion of H. irregulare and of other head types that occur with each character in 4 spike categories among Ethiopian strains in the World Collection of Barleys*

Spike category and character (code)[1]	Head type	
	H. irregulare	Other
	Percent	*Percent*
Kernel color:		
W	16.9	38.8
L	2.8	1.7
B	16.9	10.5
DB	19.7	8.8
Bk	18.3	26.4
P	25.4	13.8
Awn condition:		
R	100	100
Sm	0	0
SS	0	0
H	0	0
A	0	0
Rachilla hairs:		
L	23.9	28.7
Sh	76.1	71.3
Caryopsis:		
C	100	83.4
N	0	16.6

[1] For explanation of codes, see table 1.

COMMENTS

The two-character combination analysis has broadened our knowledge about the individual characters. For example, the 6-row character occurs not only in many strains from all over the world, but also in combination with all the characters from the other spike categories. Conversely, the *H. irregulare* head type, found only among strains from Ethiopia, is an example of a reverse situation in which some characters do not occur in combination with several of the characters in this study.

The occurrence of the predominant and individual characters in all possible two-character combinations; the presence of the different two-character combinations in from very small to major proportions of the strains; the failure of certain combinations to exist among the 6,200 strains—these findings point up the significance of the frequency of occurrence and geographic distribution patterns for the individual characters in determining the two-character combination picture. The most predominant individual characters are extensively distributed among strains from many African and Asian areas and some of the less preponderant characters are concentrated among strains from certain specific regions. The two-character combinations that occur in large proportions of the strains involve at least one predominant character. The less preponderant two-character combinations involve characters that occur in limited proportions of the strains.

The least preponderant of all the characters, a 5.0 awn-glume ratio, does not occur in 20 of 28 possible combinations. More than 85 percent of the missing two-character combinations would not be expected to occur in more than one strain.

To a considerable degree, the extent to which a character exists in different two-character combinations may be a function of the number of strains in which it occurs. The number of different strains bearing certain individual characters may be a function of the extent to which these characters are concentrated in barleys from specific world regions. The concentration of certain characters among strains from specific regions may be a function of such things as the evolutionary age of the characters, the impact of the characters on the adaptive qualities of the plants in which they occur, the role of the character in determining the productivity of the plant, or the suitability of the characters for meeting the needs of man.

A different picture is evident when only the breeding lines are considered. Here the needs and desires of man have been important in determining the composition of the genotypes. In certain instances, characters that occur in only very limited proportions of the world's barley strains or that are concentrated among strains from given world areas have been incorporated into large proportions of the lines developed through hybridization.

Although numbers are of considerable significance in determining the two-character combination proportions, "frequency" determinations may not afford a true insight into the relationships between the characters. For example, it is not enough to determine only the proportion of the strains that are 2-row, white kernel types. To be complete, the analysis must reveal how the characters are associated with one another; e.g., to determine what proportion of the 2-row strains are white and, conversely, what proportion of the white kernel types are 2-rowed. From the "frequency" approach we learned that a little less than one-fifth of the collection strains have the 2-row, white kernel combination. The "association" approach revealed that more than three-fourths of all 2-row types have white kernels, whereas only a little more than one-third of the white kernel strains are 2-rowed. Different evolutionary backgrounds for these characters are suggested by the data that show that the 2-row character is somewhat restricted in its areas of geographic distribution, whereas the white kernel character is not.

The forces governing the concentration of certain characters in some rather specific world areas undoubtedly have had much to do with the two-character combination picture as it is evidenced by the collection strains. For example, the concentration of purple kernel and short hair rachilla types among the Ethiopian-derived strains is undoubtedly responsible for the large proportion of the *H. irregulare* strains that have these characters. The markedly greater proportion of smooth awn types from the Black Sea area that are 2-rowed, as opposed to 6-rowed, reflects the concentration of both the 2-row and smooth awn characters in this part of Asia. This suggests an initial evolutionary tie between the 2-row and smooth awn characters. Of these, the 2-row character occurs more frequently in the collection strains and its geographic distribution is more widespread. One might speculate, therefore, that the smooth awn character arose at some time subsequent to the evolution of the 2-row character.

Many of the results of this study indicate a remarkable intermingling of the genetic factors governing the expression of the spike characters. Geographic barriers have been surmounted for some of the combinations to have come into being. The deficiens-hooded combination is a case in point. These two characters seem definitely to be concentrated among strains from the Ethiopian and Central Asian regions, respectively. The collection records indicate that all but one strain with this combination were developed through hybridization in North America.

The African-Asian strains, with all of the individual characters, afforded the greatest number of two-character combinations. A considerable number of the combinations were found only among strains from this subdivision. Most of these must have evolved through natural processes, with man exerting some selection pressure and acting as an agent for migration. The U.S. Breeding Lines constitute the next most important source of two-character combination diversity. Many of these combinations were undoubtedly obtained in strains from other subdivisions, but a number of them were effected through controlled hybridization involving introduced strains. The third most important source of diversity was Europe. Here, too, new combinations involving foreign derived germ plasm may have been created through hybridization. Thus, we have a picture of substantial evolutionary change occurring in a natural way in African and Asian barleys over the centuries and of additional accelerated change through controlled hybridization among strains acquired from diverse sources.

The different rates and directions of evolutionary activity in barleys from different world areas are indicated by several exceptions among the subdivisions to the two-character combination pattern for the entire collection. For example, the combinations in strains from Europe reflect the preponderance of the 2-row character in that subdivision. The comparatively large proportion of short hair rachilla types among strains from the Americas and the isolated occurrence of *H. irregulare* strains among Ethiopian strains are the foundations for some two-character patterns that are unique.

The role of man in fostering evolutionary change is most evident in the U.S. Domestic Selections and Breeding Lines. The very presence of the crop in North America is evidence of man's significant role as an agent for the migration of plant germ plasm. Thirty-four of the characters in this study are represented among the U.S. Domestic Selections. These characters occur in 302 of the 549 possible two-character combinations. From these and other introduced strains, 364 two-character combinations have been incorporated into the U.S. Breeding Lines.

Possibly the best indication of the impact of modern plant breeders on the world barley population is the story of the 6-row, smooth awn combination among the collection strains. The U.S. Breeding Lines are made up of a much higher proportion of strains with this combination than are those from any other subdivision. Approximately 95 percent of the U.S. Breeding Lines with smooth awns have a 6-row head type.

Although the smooth awn character is concentrated among 2-row strains from the Black Sea area, it also occurs in a limited number of 6-row strains. One of these, the variety Lion from southern Russia, was used in the United States as the first parental line to incorporate the smooth awn character into adapted varieties. The Lion gene for smooth awn has been the basis for the development of nearly all of the smooth awn types in the United States.

FIVE-CHARACTER COMBINATIONS

RESULTS

Combinations Present

Combinations involving individual characters from spike categories I to V are referred to as five-character combinations. In all, 600 such combinations are possible. Only 169, or 28.2 percent, are present, although the collection includes more than 10 times the minimum number of strains needed to represent each combination.

Proportions of Possible Combinations in Which Individual Characters Occur

The proportions of the possible five-character combinations in which the individual characters occur are given in table 36. Major differences exist between the proportions for the characters within the respective spike categories. Only the 6-row and rough awn characters are present in more than half of the combinations in which they might theoretically occur.

TABLE 36.—*Proportion of possible 5-character combinations in which each of 37 characters in 7 spike categories occur among 6,200 strains in the World Collection of Barleys*

Spike category and character (code) [1]	Percent	Spike category and character (code) [1]	Percent
Head type:		Awn condition:	
6	55.8	R	68.3
2	41.7	Sm	30.0
D	19.2	SS	18.3
U	15.0	H	16.7
I	9.2	A	7.5
Kernel color:		Caryopsis:	
W	44.0	C	39.7
B	30.0	N	16.7
DB	25.0	Rachilla hairs:	
LB	35.0	L	31.7
Bk	21.0	Sh	24.7
P	14.0		

[1] For explanation of codes, see table 1.

Proportions of Existing Combinations in Which Individual Characters Occur

The numbers and proportions of the combinations in which each of the characters occur are given in table 37.[12] This table also includes a record of the proportions of the strains with each character that

TABLE 37.—*Proportion of all 5-character combinations among 6,200 strains in the World Collection of Barleys in which individual characters occur; proportion of these combinations that constitute 8 percent or more of the strains in which each character occurs; and proportion of strains having each character that occurs in these predominant combinations*

Spike category and character (code)[1]	Number	All combinations	Combinations that constitute 8 percent or more of the strains	
			Combinations	Strains
		Percent	*Percent*	*Percent*
All 5-character combinations	169	100.0		
Head type:				
6	67	39.6	4.5	42.5
2	50	29.6	4.0	64.9
D	23	13.6	17.4	57.9
I	18	10.7	11.1	46.5
U	11	6.5	45.5	73.6
Kernel color:				
W	44	26.0	9.1	78.0
Bk	35	20.7	8.6	56.0
B	30	17.8	10.0	80.5
DB	25	14.8	8.0	79.4
LB	21	12.4	14.3	75.6
P	14	8.3	21.4	62.3
Awn condition:				
R	82	48.5	3.6	43.3
H	36	21.3	8.3	55.9
Sm	22	13.0	13.6	61.8
SS	20	11.8	15.0	56.8
A	9	5.3	44.4	78.2
Caryopsis:				
C	119	70.4	2.5	43.6
N	50	29.6	4.0	51.4
Rachilla hairs:				
L	95	56.2	5.3	67.7
Sh	74	43.8	4.1	61.5

[1] For explanation of codes, see table 1.

[12] Five-character combinations involving each character that occur in 8 percent or more of the strains having that character are included in table XI of the appendix referred to on p. 13.

occur in five-character combinations involving 8 percent [13] or more of the strains with that character. For most of the characters a few combinations represent large proportions of the strains. Nearly half of the 6-row strains occur in only 4.5 percent of the combinations that involve this character. The proportions for most of the characters run higher than this. More than 80 percent of the strains with blue kernels occur in only 10 percent of the combinations in which this character occurs.

PROPORTIONS OF COMBINATIONS VS. PROPORTIONS OF STRAINS.—Data in table 38 corroborate the previous observation that the proportions of the combinations in which the individual characters occur are not necessarily of the same magnitude as the proportions of the strains in which they occur. The 6-row head type is present in 71.0 percent of the strains. It is found in only 39.6 percent of the combinations. On the other hand, the intermedium head type occurs in only 0.7 percent of the strains, but it occurs in 10.7 percent of the combinations. The least preponderant characters occur in larger proportions of all the combinations relative to the total number of strains involved than do the predominant characters. The average proportions of the strains that occur in each five-character combination generally become larger as the proportions of the strains in which the individual characters occur become smaller.

Example:

On the average, each of the five-character combinations involving white kernel color occurs in 77 strains. The white kernel character occurs in 3,413 strains.

There are about 11 strains, on the average, that have each of the combinations involving purple kernel color. It occurs in 154 strains.

The figure 77 comprises a lesser proportion of 3,413 than 11 does of 154. The white kernel character occurs in more than 22 times as many strains as the purple character. However, white occurs in only slightly more than three times as many five-character combinations as does purple. If the proportions of all five-character combinations in which these characters occur were of the same order as the number of strains in which they occur, the ratio for the number of five-character combinations would be 93 to 4 instead of 44 to 14.

The relatively high proportions of the combinations in which the intermedium and hooded characters occur are traceable to modern breeding procedures for barley improvement. (See table 7.)

In all instances, the proportions of combinations in which the predominant characters from each spike category occur are less than the proportions of strains in which they occur. The opposite situation prevails for all other characters. The ratios for the spread between the proportions of strains vs. combinations generally become greater as the numbers of strains in which the characters occur become smaller.

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[13] Base value arbitrarily established after inspection of the data.

TABLE 38.—*Proportion of all strains in the World Collection of Barleys that bear each character and proportion of all 5-character combinations in which these charac ers occur*

Spike category and character (code)[1]	All strains	Strains having each character that occur in each 5-character combination (average)	5-character combinations
	Percent	*Percent*	*Percent*
Head type:			
6	71.0	1.5	39.6
2	25.1	2.0	29.6
D	2.0	4.3	13.6
I	1.2	9.1	6.5
U	.7	5.6	10.7
Kernel color:			
W	55.1	2.3	26.0
B	16.5	3.3	17.8
DB	12.1	4.0	14.8
LB	7.1	4.8	12.4
Bk	5.7	2.9	20.7
P	2.5	7.1	8.3
Awn condition:			
R	88.3	1.2	48.5
Sm	6.0	4.5	13.0
SS	2.7	5.0	11.8
H	2.6	2.8	21.3
A	.4	11.1	5.3
Caryopsis:			
C	87.5	.8	70.4
N	12.5	2.0	29.6
Rachilla hairs:			
L	60.9	1.1	56.2
Sh	39.1	1.4	43.8

[1] For explanation of codes, see table 1.

Principal Combinations

Only 16 five-character combinations occur individually in more than 1 percent[14] of the strains. These will be referred to as the *principal* five-character combinations. They are listed in table 39. The number of strains in which each of these combinations occurs is given alongside a computed number of strains in which it might have occurred had the distribution of characters been at random. Percentages of the deviation of the actual numbers from the theoretical numbers are also listed. The computed figures were obtained by multiplying together the actual proportions of entries in which the individual characters occur, as explained in the two-character combination section.

The 16 principal five-character combinations represent more than three-fourths of the 6,200 strains. Two-thirds of the principal combinations occur in more strains than might have been expected if

[14] Base value arbitrarily established after inspection of the data.

the characters had been distributed at random within the scope of the collection. Four of the five principal combinations that have fewer entries than expected differ from a comparable combination among that group by only the rachilla hair characteristic. The principal combinations involving the 6-row character with fewer strains than the calculated number have long rachilla hairs. The principal combination involving the 2-row type with fewer than the calculated number of strains has short rachilla hairs. The great preponderance of long hair rachilla types among 2-row strains was noted previously. More than half of the strains with the 6-W-R-C-Sh combination were obtained from Ethiopia, Turkey, and Manchuria—centers of concentration for 6-row, short hair rachilla strains. Thirteen of the principal combinations involve the 6-row character; only two involve 2-row. The same ratio occurs for rough vs. smooth awns and covered vs. naked caryopsis.

TABLE 39.—*Actual and computed number of strains for each of 16 5-character combinations that occur in 1 percent or more of 6,200 strains in the World Collection of Barleys*

5-character combination [1]	Strains		Deviation from computed
	Actual	Computed	
	Number	*Number*	*Percent*
2-W-R-C-L	885	397	+122.9
6-W-R-C-Sh	831	725	+14.6
6-W-R-C-L	651	1,129	-42.3
6-B-R-C-Sh	402	219	+83.6
6-DB-R-C-L	387	251	+54.2
6-B-R-C-L	326	342	-4.7
6-W-R-N-L	302	162	+86.4
6-DB-R-C-Sh	260	161	+61.5
6-LB-R-C-Sh	177	94	+88.3
2-W-R-C-Sh	126	255	-102.4
6-LB-R-C-L	115	147	-21.8
6-W-Sm-C-L	99	78	+26.9
6-B-R-N-L	97	49	+98.0
6-Bk-R-C-L	80	118	-32.2
6-W-Sm-C-Sh	69	50	+38.0
2-W-Sm-C-L	62	27	-129.6

[1] For explanation of character codes, see table 1.

Combinations Not Present

Nearly three-fourths of the possible five-character combinations do not occur among the collection strains.

Data in table 40 indicate that 45 percent of the five-character combinations existing in the collection include three or more predominant characters; 87 percent include two or more. The data in table 37 indicate that some of the less preponderant characters occur in comparatively few combinations. These data indicate that the very secondary awnless character might not occur in more than nine combinations with any other character, whereas the predominant covered caryopsis and long hair rachilla characters might occur together in as many as 95 combinations.

TABLE 40.—*Number of 5-character combinations and proportion of all combinations involving from 5 to 0 predominant individual characters among 6,200 strains in the World Collection of Barleys*

Predominant characters (number)	5-character combinations	
	Number	Proportion of total combinations (percent)
5	1	0.6
4	14	8.3
3	61	36.1
2	71	42.0
1	19	11.2
0	3	1.8

COMMENTS

To have a potential for the occurrence of all possible five-character combinations in the collection, it probably would be necessary for the characters within each spike category to occur in approximately like proportions of the strains, perhaps with not more than about 25 percent deviation from equal values.

Example:

Proportions of strains having each character.	*Spike Categories*						
		I	II	III	IV	V	
	Equal	0.20 ×	0.166 ×	0.20 ×	0.50 ×	0.50 =	0.00166 (10+ strains out of 6,200)
	25 percent deviation (minus) from equal.	0.15 ×	0.12 ×	0.15 ×	0.38 ×	0.38 =	0.00039 (2+ strains out of 6,200)

It would further be necessary for the characters from the different categories generally to occur with one another in a random way. These conditions do not prevail!

The disparities in the frequency of occurrence and geographic distribution of the individual characters are reflected in the five-character combinations. Nearly three-fourths of the possible combinations are not present.

It may be hypothesized that the predominant and widespread characters from each spike category have occurred in strains that have undergone relatively more evolutionary change than have those bearing their less preponderant counterparts. The occurrence of the

predominant characters in the greatest numbers of five-character combinations (with the lowest proportion of strains, on the average, per combination) seems to support this idea. The widespread geographic distribution of the predominant individual characters and their thorough intermingling with the other characters in two-character combinations would seem to explain the fact that fewer strains have the 6–W–R–C–L combination than might have been expected; i.e., although there are many strains with the 6–W combination, neither of these characters is restricted to association with the other one, etc.

In contrast to the deficiency of 6–W–R–C–L strains, there are more than twice as many 2–W–R–C–L strains as might have been expected had the characters been distributed at random. About 57 percent of the 2-row strains have the W–R–C–L combination. Nearly 65 percent are characterized by the W–R–C combination. The DB, LB, and N characters exhibit a similar tendency to occur with certain characters. It was noted previously that the 2-row head type and naked caryopsis characters are concentrated in barleys from definite areas in Asia. Less pronounced, but significant centers of concentration are evident for the DB and LB kernel color characters. These findings suggest that the strains bearing the 2, DB, LB, and N characters may be the product of appreciably less change than those in which the more predominant characters occur.

The general limitation of the 2-row types to the W–R–C–L combination suggests a possible explanation for the relatively high proportions of the five-character combinations in which the less preponderant characters occur (table 27). The following data from tables 5 and 21 illustrate a hypothesis in this regard:

6-row (71.0 percent):	*Percent*	2-row (25.1 percent):	*Percent*
White	(47. 8)	White	(78. 9)
Colored	(52. 2)	Colored	(21. 1)
	100. 0		100. 0

Assuming a random distribution of the collection strains in a field planting, we find that about one-half (0.710×0.710=0.504) of randomly distributed natural crosses might involve 6-row × 6-row. Somewhat more than one-third of them might involve 6-row × 2-row. Only slightly more than one-twentieth might be 2-row × 2-row, most of which would involve white × white. It is evident that a greater change in the proportion of white vs. colored kernels would occur among 2-row than among 6-row types as a result of outcrossing. It might be reasoned, therefore, that by virtue of strains bearing the 6-row character having undergone greater evolutionary change than their 2-row counterparts, any change involving the 2-row strains is more apt to result in a new combination of characters than is a change among the 6-row strains.

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SEVEN-CHARACTER COMBINATIONS

RESULTS

Combinations Present

Combinations involving individual characters from spike categories I to VII are referred to as seven-character combinations. In all, 43,200 such combinations are possible. It is significant to note that only 14.4 percent of these might occur among 6,200 barleys. Actually, only about one-seventh of this maximum number of combinations for the collection are present—2.1 percent (885) of the possible number.

Proportions of Possible Combinations in Which Individual Characters Occur

The proportions of the possible seven-character combinations in which the individual characters occur are cited in table 41. None of the individual characters occur in as many as one-tenth of the combinations in which they might possibly be manifested. Fourteen of the 37 characters exist in less than one-hundredth of the combinations in which they might possibly occur.

TABLE 41.—*Proportion of possible 7-character combinations in which each of 37 characters in 7 spike categories occur among 6,200 strains in the World Collection of Barleys*

Spike category and character (code) [1]	Percent	Spike category and character (code) [1]	Percent
Head type:		Rachilla hairs:	
6	6.7	L	2.3
2	1.9	Sh	1.8
D	.7	Awn-glume ratio:	
I	.6	1.0	7.2
U	.4	2.0	3.2
Kernel color:		1.5	2.5
W	4.0	2.5	2.3
B	2.4	3.0	1.7
Bk	1.7	3.5	.7
DB	1.6	4.0	.5
LB	1.6	4.5	.08
P	.9	5.0	.06
Awn condition:		Awn-spike ratio:	
R	7.6	1.5	4.8
Sm	1.1	1.0	3.7
H	.7	2.0	3.6
SS	.6	0.5	1.1
A	.1	2.5	1.0
Caryopsis:		3.0	.6
C	3.1	3.5	.2
N	1.0	4.0	.1

[1] For explanation of codes, see table 1.

Proportions of Existing Combinations in Which Individual Characters Occur

The numbers and proportions of the combinations in which each of the characters occur are shown in table 42.[15] This table also includes a record of proportions of the strains with each character that occur in the seven-character combinations involving 2 percent[16] or more of the strains having that character. The predominant individual characters occur in large proportions of the combinations, but only a small proportion of the strains bearing these characters are marked by any given combination. There are some distinct differences among the seven-character combination patterns for the individual characters. For example, less than one-tenth of the 6-row strains occur in combinations that individually comprise 2 percent or more of the strains with that character, whereas nearly two-thirds of the 2-row strains occur in such combinations. All the awnless and high awn-glume and awn-spike ratio strains occur in combinations that involve 2 percent or more of the strains having these characters.

Proportions of combinations vs. proportions of strains.—Data in table 43 indicate that the previously noted relationship between proportions of strains and proportions of combinations in which individual characters occur holds true for the awn-glume and awn-spike ratio characters. The average proportions of the strains having each character that occur in each combination are appreciably lower in the seven-character combination analysis than in the two- and five-character combinations. The magnitudes of the proportions of the existing seven-character combinations in which the individual characters occur most closely approximate those for the proportions of the strains in which the individual characters occur. In addition to the 6, W, R, C, and L characters, previously mentioned as occurring in a lesser proportion of the five-character combinations than of the total number of strains, the 2-row and 1.0 awn-spike ratio characters occur in lesser proportions of the seven-character combinations than of the total number of strains.

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[15] The seven-character combinations involving each character that occur in 2 percent or more of the strains having that character are given in table XII of the appendix referred to on p. 13.

[16] Base value arbitrarily established after inspection of the data.

TABLE 42.—*Proportion of all 7-character combinations among 6,200 strains in the World Collection of Barleys in which individual characters occur; proportion of these combinations that constitute 2 percent or more of the strains in which each character occurs; and proportion of strains having each character that occurs in these predominant combinations*

Spike category and character (code) [1]	Number	All combinations	Combinations that constitute 2 percent or more of the strains	
			Combinations	Strains
		Percent	*Percent*	*Percent*
All 7-character combinations	885			
Head type:				
6	585	66.1	0.5	7.7
2	163	18.4	4.3	65.4
D	58	6.6	22.4	58.9
I	48	5.4	31.3	54.6
U	31	3.5	3.2	23.3
Kernel color:				
W	289	32.6	2.4	38.0
LB	116	13.1	8.6	38.8
B	174	19.7	5.7	40.5
DB	119	13.4	10.9	58.5
Bk	121	13.7	8.3	39.5
P	66	7.5	18.2	45.2
Awn condition:				
R	664	75.0	.6	19.0
Sm	98	11.1	12.2	49.1
SS	55	6.2	16.4	59.4
H	59	6.7	13.5	54.1
A	9	1.0	100.0	100.0
Caryopsis:				
C	676	76.4	.6	19.4
N	209	23.6	3.8	34.5
Rachilla hairs:				
L	501	56.6	.6	23.6
Sh	384	43.4	3.6	40.4
Awn-glume ratio:				
1.0	344	39.2	2.0	34.2
1.5	122	13.9	11.5	51.3
2.0	153	17.3	8.5	54.8
2.5	111	12.5	9.9	59.6
3.0	83	9.5	9.6	51.4
3.5	35	4.0	42.8	70.9
4.0	22	2.5	100.0	100.0
4.5	4	.5	100.0	100.0
5.0	3	.3	100.0	100.0
Awn-spike ratio:				
0.5	58	6.6	17.2	64.7
1.0	200	22.6	5.5	56.9
1.5	262	29.6	3.8	38.8
2.0	192	21.7	4.2	31.9
2.5	56	6.3	17.8	60.1
3.0	32	3.6	21.9	71.2
3.5	10	1.1	100.0	100.0
4.0	6	.7	100.0	100.0

[1] For explanation of codes, see table 1.

TABLE 43.—*Proportion of all strains in the World Collection of Barleys that bear each character and proportion of all 7-character combinations in which these characters occur*

Spike category and character (code) [1]	All strains	Strains having each character that occur in each 7-character combination (average)	7-character combinations
Head type:	*Percent*	*Percent*	*Percent*
6	71.0	0.2	66.1
2	25.1	.6	18.4
D	2.0	1.7	6.6
I	1.2	2.1	5.4
U	.7	3.3	3.5
Kernel color:			
W	55.1	.3	32.6
B	16.5	.6	19.7
DB	12.1	.8	13.4
LB	7.1	.9	13.1
Bk	5.7	.8	13.7
P	2.5	1.5	7.5
Awn condition:			
R	88.3	.2	75.0
Sm	6.0	1.0	11.1
SS	2.7	1.8	6.2
H	2.6	1.7	6.7
A	.4	11.3	1.0
Caryopsis:			
C	87.5	.1	76.4
N	12.5	.5	23.6
Rachilla hairs:			
L	60.9	.2	56.6
Sh	39.1	.3	43.4
Awn-glume ratio:			
1.0	55.2	.3	38.9
2.0	16.8	.7	17.3
2.5	11.2	.9	12.5
1.5	9.0	.8	13.8
3.0	6.0	1.2	9.4
3.5	1.1	2.9	4.0
4.0	.5	4.5	2.5
4.5	.1	25.0	.4
5.0	.05	33.3	.3
Awn-spike ratio:			
1.5	42.2	.4	29.6
1.0	29.3	.5	22.6
2.0	17.0	.5	21.7
0.5	3.7	1.7	6.6
2.5	2.6	1.8	6.3
3.0	1.7	3.1	3.6
3.5	.4	10.0	1.1
4.0	.2	16.7	.7

[1] For explanation of codes, see table 1.

Principal Combinations

Thirteen of the seven-character combinations occur individually in 1 percent [17] or more of the strains. These will be referred to as the *principal* seven-character combinations. They are listed in table 44. Only seven of the principal five-character combinations listed in table 39 occur in this group. The principal five-character combination, 2–W–R–C–L, is subdivided by two combinations of awn-glume and awn-spike characters; 6–W–R–C–L by two; and 6–W–R–C–Sh by five. The 6–B–R–C–L combination and the last seven of the five-character combinations listed in table 39 do not occur among the principal seven-character combinations. Eleven of the principal seven-character combinations occur in a greater proportion of the strains than might have been expected had the characters been distributed at random within the scope of the collection. The principal combination that occurs in the greatest proportion of the strains, 2–W–R–C–L–1.0a–g–1.0a–s, occurs in more than 10 times as many strains as might have been expected. The two combinations that occur in fewer strains than expected are comprised of the predominant characters from each spike category, considering both the 1.0 and 1.5 awn-spike ratios as predominant characters. More than half of the 2-row barleys in the collection are characterized by the combination W–R–C–L–1.0a–g with a 1.0 or 1.5 awn-spike ratio. No comparable situation exists for any other character. Not as many as half of the strains with any other character occur among all principal combinations involving that character.

TABLE 44.—*Actual and computed number of strains for each of 13 7-character combinations that occur in 1 percent or more of 6,200 strains in the World Collection of Barleys*

7-character combination [1]	Strains: Actual	Strains: Computed	Deviation from computed
	Number	*Number*	*Percent*
2–W–R–C–L–1.0–1.0	[2] 475	44	+979.5
2–W–R–C–L–1.0–1.5	[2] 334	92	+263.0
6–W–R–C–Sh–2.0–1.5	123	51	+141.2
6–W–R–C–Sh–2.5–1.5	112	34	+229.4
6–W–R–C–Sh–2.5–1.0	104	24	+333.3
6–W–R–C–L–1.0–1.5	79	261	−69.7
6–W–R–N–L–1.0–1.0	72	26	+176.9
6–B–R–C–Sh–1.0–1.5	71	51	+39.2
6–W–R–C–L–1.0–1.0	69	183	−62.3
6–DB–R–C–L–1.0–1.5	69	58	+19.0
6–W–R–C–Sh–2.0–2.0	63	21	+200.0
6–DB–R–C–Sh–1.0–1.5	62	37	+67.6
6–W–R–C–Sh–2.0–1.0	62	36	+72.2

[1] For explanation of character codes, see table 1.
[2] 52 percent of all 2-rows occur in these combinations.

[17] Base value arbitrarily selected after inspection of the data.

Combinations Not Present

More than 97 percent of the possible seven-character combinations are not represented among the collection strains.

Data in table 45 indicate that 21.9 percent of the seven-character combinations in the collection include five or more of the predominant characters; 50.8 percent include four or more; and 81.0 percent include three or more. The data in table 42 indicate that some of the rare high awn-glume and awn-spike ratio characters might not occur in more than three to six combinations among the collection strains, whereas some of the predominant characters might occur together in several hundred combinations.

The findings presented in table 46 indicate the extent to which the different awn-glume and awn-spike two-character combinations are affiliated with the predominant characters. The average number of awn-glume–awn-spike ratio combinations per five-character combination becomes less as fewer and fewer predominant characters occur in the five-character combinations. Not only are there fewer five-character combinations in those instances where the number of predominant characters is low, but there are fewer awn-glume–awn-spike ratio combinations per five-character combination.

TABLE 45.—*Number of 7-character combinations and proportion of all combinations involving from 7 to 0 predominant individual characters among 6,200 strains in the World Collection of Barleys*

Predominant characters (number)	7-character combinations	
	Number	Proportion of total combinations (percent)
7	5	0. 1
6	83	2. 8
5	267	19. 0
4	336	37. 9
3	168	30. 2
2	25	9. 4
1	1	. 6

TABLE 46.—*Number of 7-character combinations involving from 5 to 0 predominant individual characters among 6,200 strains in the World Collection of Barleys, and the average number of awn-glume–awn-spike ratio combinations per 5-character combination*

Predominant characters (number)	7-character combinations	
	Number	Average number of awn-glume–awn-spike ratio combinations per 5-character combination
5	43	43.0
4	242	17.3
3	365	6.0
2	204	2.9
1	28	1.5
0	3	1.0

COMMENTS

The great increase in the number of possible seven-character combinations over that for the five-character combinations is a result of the numerous classes used in recording the awn-glume and awn-spike ratios. This is indicative of the impact of quantitative characters on diversity within a plant population.

Many of the attributes that determine plant productivity and quality of product are quantitative in nature. The implication of the data on the proportions of the possible seven-character combinations present in the collection strains would seem to be that only a small fraction—seemingly an infinitesimal one when the great numbers of plant characters are taken into account—of the potential barley genotypes have been acquired.

The comparatively large numbers of different awn-glume–awn-spike ratio combinations associated with five-character combinations involving four or more predominant individual characters versus those involving fewer predominant characters is further evidence that strains bearing the predominant characters have undergone more evolutionary change than their less preponderant counterparts.

In addition to the tendency for 2-row strains to be limited to the W–R–C–L–1.0a–g–1.0a–s/1.5a–s makeup, the 6-row, short hair rachilla combination stands out amount the principal seven-character combinations. Slightly more 6-row strains in the collection have long hair rachillas than have short. The comparatively large numbers of strains from Ethiopia, Turkey, and Manchuria—centers of concentration for the 6-row, short hair rachilla combination—undoubtedly account for the large proportions of strains with this combination of characters.

TWO-, FIVE-, AND SEVEN-CHARACTER COMBINATIONS

RESULTS

Summary of Proportions of Possible Combinations

The proportions of the possible two-, five-, and seven-character combinations among the collection strains are summarized in table 47. The collection affords a fairly complete representation of the two-character combinations that are possible among the 37 characters in seven spike categories. The representation of the genotypic potential is markedly less among the five-character combinations and only a very small proportion of the possible seven-character combinations are present among the collection strains.

TABLE 47.—SUMMARY: *Possible number of 2-, 5-, and 7-character combinations of 37 characters in 7 spike categories, and actual number present, among 6,200 strains in the World Collection of Barleys*

Type of combination	Possible	Present	
	Number	*Number*	*Percent*
2-character	549	451	82.1
5-character	600	169	28.2
7-character	43,200	885	2.1

Minimum Numbers of Strains Required To Represent All Individual Characters and All Possible Two-, Five-, and Seven-Character Combinations

The minimum numbers of strains required to embody all the individual characters in this study and all possible two-, five-, and seven-character combinations are given in table 48. The individual characters and all possible two-character combinations might be included in a very few strains. Many more strains would be required to represent all possible five-character combinations. The collection includes nearly 10 times the minimum number of strains required for embodying all possible five-character combinations, yet only slightly more than one-fourth of the possible combinations are present. A very large number of strains would be required to represent all the seven-character combinations; the 6,200 collection strains represent approximately one-seventh of this number, and they include only about one-fiftieth of the possible seven-character combinations.

TABLE 48.—*Minimum number of strains of barley required to embody each of 37 characters, and all possible 2-, 5-, and 7-character combinations, in each of 7 and in all spike categories*

Spike category	Strains			
	Individual characters	2-character combinations	5-character combinations	7-character combinations
Head type:	*Number*	*Number*	*Number*	*Number*
All characters	5	45	600	43, 200
Any given character	1	9	120	8, 640
Kernel color:				
All characters	6	54	600	43, 200
Any given character	1	9	100	7, 200
Awn condition:				
All characters	5	45	600	43, 200
Any given character	1	9	120	8, 640
Caryopsis:				
All characters	2	18	600	43, 200
Any given character	1	9	300	21, 600
Rachilla hairs:				
All characters	2	18	600	43, 200
Any given character	1	9	300	21, 600
Awn-glume ratio:				
All characters	9	72	------------	43, 200
Any given character	1	9	------------	4, 800
Awn-spike ratio:				
All characters	8	72	------------	43, 200
Any given character	1	9	------------	4, 800
Each character and all possible combinations	9	72	600	43, 200

Summary of Proportions of Possible Combinations in Which Individual Characters Occur

The proportions of the possible two-, five-, and seven-character combinations in which the individual characters occur among the collection strains are listed in table 49. Comparisons within proportions given for the individual characters bear out the relationships noted in table 47. On the basis of each of the characters, the differences between the proportions for the two-, five-, and seven-character combinations are somewhat greater for the less preponderant characters within each spike category than for the predominant ones.

TABLE 49.—SUMMARY: *Proportion of the possible 2-, 5-, and 7-character combinations of individual characters within 7 spike categories in which each of 37 characters occur in the World Collection of Barleys*

Spike category and character (code) [1]	Combination		
	2-character	5-character	7-character
	Percent	*Percent*	*Percent*
Head type:			
6	100.0	55.8	6.7
2	91.9	41.7	1.9
D	71.9	19.2	.7
I	62.5	9.2	.6
U	71.9	15.0	.4
Kernel color:			
W	100.0	44.0	4.0
B	96.8	30.0	2.4
DB	93.6	25.0	1.6
LB	93.6	35.0	1.6
Bk	87.1	21.0	1.7
P	67.8	14.0	.9
Awn condition:			
R	100.0	68.3	7.6
Sm	78.1	30.0	1.1
SS	75.0	18.3	.6
H	87.5	16.7	.7
A	68.8	7.5	.1
Caryopsis:			
C	100.0	39.7	3.1
N	94.3	16.7	1.0
Rachilla hairs:			
L	100.0	31.7	2.3
Sh	94.3	24.7	1.8
Awn-glume ratio:			
1.0	100.0	----------	7.2
2.0	100.0	----------	3.2
2.5	92.9	----------	2.3
1.5	92.9	----------	2.5
3.0	80.3	----------	1.7
3.5	67.9	----------	.7
4.0	60.7	----------	.5
4.5	39.3	----------	.08
5.0	28.6	----------	.06
Awn-spike ratio:			
1.5	96.6	----------	4.8
1.0	93.1	----------	3.7
2.0	100.0	----------	3.6
0.5	89.7	----------	1.1
2.5	82.8	----------	1.0
3.0	82.8	----------	.6
3.5	51.7	----------	.2
4.0	48.3	----------	.1

[1] For explanation of codes, see table 1.

Summary of Proportions of Existing Combinations in Which Individual Characters Occur

The proportions of the existing two-, five-, and seven-character combinations in which the individual characters occur are summarized in table 50. As was noted previously, if the individual characters in

TABLE 50.—SUMMARY: *Proportion of the existing 2-, 5-, and 7-character combinations in which each of 37 characters in 7 spike categories occur among the 6,200 strains in the World Collection of Barleys*

Spike category and character (code) [1]	Combination		
	2-character	5-character	7-character
	Percent	*Percent*	*Percent*
Head type:			
6	25.2	39.6	66.1
2	22.8	29.6	18.4
D	18.1	13.6	6.6
I	15.7	6.5	5.4
U	18.1	10.7	3.5
Kernel color:			
W	18.3	26.0	32.6
B	17.8	17.8	19.7
DB	17.2	14.8	13.8
LB	17.2	12.4	13.1
Bk	16.6	20.7	13.7
P	13.0	8.3	7.5
Awn condition:			
R	24.4	48.5	75.0
Sm	19.1	13.0	11.1
SS	18.3	11.8	6.2
H	21.4	21.3	6.7
A	16.8	5.3	1.0
Caryopsis:			
C	52.2	70.4	76.4
N	47.8	29.6	23.6
Rachilla hairs:			
L	51.5	56.2	56.6
Sh	48.5	43.8	43.4
Awn-glume ratio:			
1.0	14.9	----------	39.2
2.0	14.9	----------	17.4
2.5	13.8	----------	12.7
1.5	13.8	----------	13.9
3.0	13.3	----------	9.5
3.5	10.1	----------	4.0
4.0	9.0	----------	2.5
4.5	5.9	----------	.5
5.0	4.3	----------	.3
Awn-spike ratio:			
1.5	15.0	----------	32.1
1.0	14.4	----------	24.5
2.0	15.5	----------	23.5
0.5	13.9	----------	7.1
2.5	12.8	----------	6.9
3.0	12.8	----------	3.9
3.5	8.0	----------	1.2
4.0	7.5	----------	.7

[1] For explanation of codes, see table 1.

each spike category occurred in equal proportions of the strains and if the characters were associated with one another in a random way, they might occur in equal proportions of the combinations; for example, head type characters, each 20.0 percent; kernel color characters, each 16.7 percent; caryopsis characters, each 50.0 percent; etc. The proportions for the two-character combinations most nearly approximate this condition; those for the seven-character combinations digress the most from this theoretical situation.

The predominant individual characters from the respective spike categories occur in the greatest portion of the two-, five-, and seven-character combinations involving characters in their respective spike categories. They occur in relatively greater portions of the combinations as the number of characters in the combinations becomes larger; e.g., 6-row occurs in 25.2 percent of the two-, 39.6 percent of the five-, and 66.1 percent of the seven-character combinations. For most of the other characters the reverse of this pattern is in evidence. As additional numbers of characters are included in the combinations, the general tendency is for the proportions within each spike category to more closely approximate the values for the proportions of the strains with the individual characters. (See table 5.)

The greatest ranges between the proportions of the characters that occur in the largest and the least number of combinations within the respective spike categories occur in the seven-character combination values.

Relative Diversity of Spike Types Among Strains From Some Major Sources

An attempt was made to evaluate the relative diversity of spike types found among strains from eight major African and Asian sources. The results of this analysis are presented in table 51. The diversity among the Ethiopian strains as compared with the uniformity of those from Manchuria has been observed in field planting of the collection. The Manchurian and Japanese strains were ranked low for all measures of diversity used. The strains from other sources, for example, Turkey, indicate considerable diversity when certain measures are applied and very little when others are considered. Ethiopian barleys demonstrated fewer different individual characters than did those from four of the sources, but they evidenced the greatest diversity from the standpoint of most of the measures applied to the character combinations.

TABLE 51.—*Strains from 8 African-Asian sources in the World Collection of Barleys ranked according to relative diversity of type (based on data for 37 characters in 7 spike categories, and 2-, 5-, and 7-character combinations thereof)*

Source	Individual characters		Combination: 2-character: Average entries per combination		Combination: 2-character: Proportion of possible combinations		Combination: 5-character: Average entries per combination		Combination: 5-character: Proportion of possible combinations		Combination: 7-character: Average entries per combination		Combination: 7-character: Proportion of possible combinations		All ranks, mean
	Number	*Rank*	*Number*	*Rank*	*Percent*	*Rank*	*Number*	*Rank*	*Percent*	*Rank*	*Number*	*Rank*	*Percent*	*Rank*	
Ethiopia	28	5	1. 4	5	46. 2	1	7. 8	2	7. 8	1	1. 9	1	0. 45	1	2. 3
Russia	29	4	. 9	2	39. 5	4	6. 0	1	6. 2	3	2. 0	4	. 26	4	3. 1
China	30	1	. 9	2	38. 7	6	9. 4	3	3. 5	5	1. 9	1	. 24	5	3. 3
India	30	1	2. 0	6	42. 7	3	15. 3	5	5. 3	4	3. 9	6	. 29	3	4. 0
Turkey	30	1	3. 2	8	44. 4	2	18. 3	7	7. 3	2	5. 8	7	. 32	2	4. 2
Korea	24	7	. 8	1	29. 7	7	14. 9	4	1. 5	7	1. 9	1	. 16	7	4. 9
Japan	28	5	1. 2	4	39. 1	5	15. 8	6	2. 8	6	2. 8	5	. 23	6	5. 3
Manchuria	24	7	2. 7	7	28. 1	8	48. 2	8	1. 5	7	8. 1	8	. 12	8	7. 6

COMMENTS

The very low proportions of the possible five- and seven-character combinations that are present among the 6,200 collections strains are of special significance when the germ plasm potentials of the collection and of the world barley population are considered. These findings, together with the previously noted concentration of certain characters in specific world regions, seem to suggest that much of the potential diversity among world barleys may never have been realized because of the relative geographic isolation of strains bearing many of the plant characters.

The occurrence of the predominant individual characters in large proportions of the different character combinations appears to be a reflection of their widespread geographic distribution and may indicate that they are comparatively aged evolutionwise. This is particularly evident when comparisons are made between the results for the seven- and five-character combinations. The results presented in figure 3 suggest a possible explanation for the occurrence of the 6-row character, for example, in a greater proportion of the seven- than of the five-character combinations. There are very few strains with head types other than 6-row in the collection from the areas from which strains with the lowest or highest awn-spike ratio types have been obtained; e.g., the greatest portion of the strains with awn-spike ratios of 2.5 or higher were obtained from North Africa, an area that has yielded barleys that are almost exclusively 6-rowed.

The comparative diversity of types obtained from different sources is of significance in attempting to evaluate the extent of evolutionary change in different areas. This diversity is a rather elusive thing to measure. Within the scope of this study, Ethiopian barleys express fewer individual characters than do those from, say, Turkey. On the basis of this single criterion, which certainly is an important facet of evolutionary change, Turkish barleys might be thought to have undergone more change than those from Ethiopia. When the character combinations among the collection strains are taken into account, however, Ethiopian barleys seem to be more diverse than those from the other sources considered.

Diversity resulting from the evolution of new characters, particularly those that are governed by single genetic factors, is attributed to the phenomenon of mutation. Diversity that is reflected through new combinations of characters may be due to mutation or to recombinations following cross-fertilization. Even in a self-fertilized crop such as barley, individual characters may achieve widespread distribution within the world population more readily through cross-fertilization than through mutation.

It may be that mutational change has occurred at a more rapid rate or for a longer time among Ethiopian barleys than among those from other areas, but this is open to doubt since strains from some other sources include a greater number of individual characters. The results of this study suggest that much of the diversity among the Ethiopian strains has been derived through cross-fertilization. The environment at the high elevations may in some manner result in structural or developmental peculiarities in barley flowers so that airborne or insect borne pollen may reach receptive stigmas.

DISCUSSION

The frequency of occurrence and geographical distribution of the various characters would seem to have evolutionary significance. That is, frequent occurrence along with widespread distribution would imply agedness or adaptiveness of certain characters, or perhaps their desirability to man. Moreover, the occurrence of these predominant characters in all possible two-character combinations and in relatively large parts of the five- and seven-character combinations would indicate that they have been involved in a long succession of evolutionary events.

The concentration of some of the less preponderant characters in specific world areas—the center of concentration for one character being geographically removed from that for another—implies that evolutionary changes have occurred across the far reaches of the barley growing areas. The "centers of concentration" concept holds great significance for plant exploration and improvement work. Certain world areas may be the most fruitful source of certain characters. This assumes a special importance when characters such as disease and insect resistance are considered.

Many important plant traits, such as yielding ability and hardiness, are quantitative in nature and are governed by the interaction of several or many genes—combinations of characters. To the extent that individual characters are isolated from one another by whatever means, the world's plant germ plasm fails to realize its full genotypic potential. When the picture for the world's barley population, as it is reflected by this study, is enlarged to include all of the plant characters, only a tiny fraction of the genotypic potential may have been realized.

Selections have been drawn from the whole of the world's barley germ plasm for use in plant improvement work. The transition from the broad base of germ plasm to the tiny component constituted by modern advanced breeding lines and improved varieties might be visualized spatially as a pyramidlike configuration with irregular angulation. This angulation, as it rises from the base of the pyramid, depicts varying phases of advancement, leveling off, and retrogression, but overall a discernible trend toward improvement. The blocks that we might imagine near the pinnacle of the ever-unfinished pyramid embody the modern breeding lines and improved varieties. They represent a very small component of the germ plasm base; a component in which the constituent parts may have the greatest number of traits in common.

Each new requirement placed on the world's germ plasm for meeting the needs of man and animals has served to shunt aside as unsuitable another segment of the whole. The following data from the collection illustrate this principle, each additional character being considered as a new requirement to be met in developing or acquiring a superior barley strain:

Composition of Strains	*Number*
6	4, 402
6-W	2, 102
6-W-R	1, 828
6-W-R-C	1, 482
6-W-R-C-L	651
6-W-R-C-L-1.0a-g	290
6-W-R-C-L-1.0a-g-1.5a-s	79

To the need for compatible parental germ plasm embodying survivability and reproducibility have been added the requirements for general adaptation to environment. More specific demands now exist for such things as greater productivity of grain or foliage or for a superior quality of product. For given world areas, only *very small* proportions of the world's barley genotypes embody the characteristics required for growing the crop efficiently in those areas. The significance of this cannot be overemphasized, for man has enjoyed only limited success in artificially inducing or synthesizing plant characters that have not been found previously among Nature's living herbarium. To an even lesser extent have ways been found to match natural forces for stabilizing new characters in genetic backgrounds affording vigorous well-adapted plants.

It is of interest to speculate about the origin of the basic adapted types that served as the foundation blocks for the U.S. small grain industry, many of whose characteristics may still be observed in current varieties. They came into being before the advent of controlled hybridization as a tool in plant improvement work. Their evolution may have required a great period of time. It may have involved the phenomona of mutation, cross-fertilization, and natural selection, perhaps with the latter two forces being the more important. To a considerable extent, they must have been developed within the scope of the germ plasm that was endemic to their immediate areas.

It may be that new basic adapted types will need to be evolved before substantial gains in productivity can be added to those already achieved through hybridization. The basis for this thought might be best explained by discussing one aspect of the hard red winter wheat industry in the United States. This industry in the Great Plains "breadbasket" became possible with the introduction of winter-hardy Turkey wheat from southern Russia. The hardiness of this type of wheat is not known to be equaled by any other. For this reason, it serves as a basic type among winter varieties grown in areas of rigorous winter climate in this country. Although numerous advances have been made by selecting superior strains from within the original heterogeneous type and by incorporating disease and insect resistance and other attributes into hybrid progenies, the Turkey germ plasm of necessity pervades all U.S. hard red winter wheat varieties. It follows then that, in general, this germ plasm may set the productivity ceiling for hard red winter wheats developed by conventional breeding.

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Although Turkey wheat best illustrates the point of the above discussion, the condition described is not peculiar to hard red winter wheats. The comments about a basic type pervading commercial varieties have considerable application to other small grains. Crosses between standard varieties and advanced breeding lines unquestionably represent an exceedingly narrow germ plasm base compared with that of the world grain population.

The potential for developing new hard red winter wheat varieties with the marked increases in productivity that will be needed in the future to feed an expanded population may be limited unless new high-yielding *basic* hardy genotypes are secured to supplant or complement the Turkey germ plasm. The results of the barley study indicate that it may be possible to do this. The data suggest that only a segment of the genotypic composition of world wheats may have been present in the geographic locales in which the Turkey type arose.

Germ plasm from all over the world is available for inclusion in today's breeding nurseries; strains bearing genes that may have been isolated from one another may be brought side by side. The phenomena mentioned as possibly being involved in the evolution of basic adapted types are component parts of present-day breeding efforts. In general, methods exist or are within the realm of possibility for bringing to bear all these evoluntionary forces in a sequence of plant improvement events much expedited and intensified over that found in Nature.

The results of this study indicate that a great potential for new combinations exists among strains in the World Collection of Barleys. The approximation of the diversity of type noted among the U.S. Breeding Lines to the centuries-in-developing African and Asian diversity indicates that the rate of evolutionary change through recombination has been increased manyfold since the advent of purposeful hybridization.

Evolutionary change has occurred at different rates in different world areas. This was noted by comparing the relative diversity of type among strains from such sources as Manchuria and Ethiopia. The basic data for this study show that nearly 84 percent of the Manchurian barleys have the combinations 6–W–R–C–Sh or 6–W–R–C–L. Only slightly more than 20 percent of the Ethiopian strains have the above combinations. Most of them occur in combinations that involve less than 8 percent of the strains.

Evolutionary change may be measured in different ways. It was noted that more individual characters occur among the Turkish than among the Ethiopian strains, yet the Ethiopian barleys reflect the most diversity of type.

This study serves to emphasize the evolutionary significance of genetic recombination following cross-fertilization. It is necessary to postulate hundreds of successful mutations, many of them in types in which one or more mutations already have become fixed, in order to rationalize the evolution of the many seven-character combinations through this medium alone. On the other hand, a modest number of mutations, particularly in the case of the several characters that are known to be controlled by single factors, followed by cross-fertilization would readily account for all of the combinations.

As a matter of conjecture, it might be hypothesized that the original cultivated barley plant was comprised of the predominant individual characters from the seven spike categories. One would not speculate that these characters entered into all the combinations with the other characters through the mutational process. Cross-fertilization seems to be deserving of greater recognition as a force in evolutionary change. Seemingly, little variation might exist without mutation, but assuredly little variation would be in evidence without the cross-fertilization mechanism for the recombination of the characters.

SUMMARY

Data classifying 6,200 strains from the World Collection of Barleys for 37 morphologic characters in 7 spike categories were analyzed in an attempt to (1) gain a new understanding of the nature and scope of the collection, (2) evaluate some world barley population characteristics as they are reflected by the collection, and (3) acquire additional insight into the evolutionary background for this crop.

Individual characters occur in as few as 3 (0.05 percent) and in as many as 5,475 (88.3 percent) of the strains.

Predominant characters in the spike categories are:

I	6 rows of kernels.
II	White kernels.
III	Rough awns.
IV	Covered kernels.
V	Long rachilla hairs.
VI	Glume-awn-equal-to-length-of-glume.
VII	Lemma-awns-extend-beyond-tip-of-spike-to-a-distance-equal-to-1½-times-the-length-of-the-spike.

They are widely distributed geographically. The less preponderant characters are limited to more localized areas.

No consistent relationship is evident between the preponderance of the characters and genetic dominance or recessiveness, although most of the less preponderant characters are considered to be controlled by dominant factors.

Distinct differences exist between barleys from different world areas. World "regions" representing some different barley types are postulated on the basis of "character distribution patterns" (proportions of the strains having each of the characters): e.g., North Africa, Ethiopia, Black Sea Area, Caucasus area, Near East. . . .

African-Asian regions yielding greater proportions of strains with specific characters than other regions are designated "centers of concentration" for these characters. Centers are postulated for most of the less preponderant characters; e.g., *H. irregulare* (Ethiopia)—smooth awns (Black Sea area)—hooded (central Asia) . . . .

Within Africa and Asia, characters are not derived from any one or two centers of evolutionary activity, but are obtained from different locales over the whole of the barley-growing area.

The greatest number of the characters found among the Old World barleys are also present among strains from the United States, into which the crop was introduced. Certain characters concentrated in limited world locales and occurring in only a few introductions have been incorporated into many U.S. Breeding Lines.

About 82 percent of the possible two-character combinations (the joint occurrence of individual characters from two spike categories) are present in the collection.

Predominant characters occur in all possible two-character combinations. The principal combination in each two-way conjunction of spike categories is comprised of the predominant characters from those categories.

The distribution of the characters in two-character combinations is not at random within the scope of the collection. Some characters, particularly the less preponderant ones, are associated with, but not genetically linked with, certain characters to the general exclusion of other characters with which they might be associated. Certain combinations are peculiar to strains from specific areas.

The greatest number of two-character combinations is found among strains from Africa and Asia, the next largest among U.S. Breeding Lines.

Most of the two-character combinations that are not present in the collection involve the least preponderant characters. The frequency of occurrence of these characters is generally so limited that most of the missing combinations might not theoretically occur within this collection.

About 28 percent of the possible five-character combinations (the joint occurrence of individual characters from categories I to V) are present.

The predominant characters occur in the greatest proportions of the five-character combinations, although only the 6-row head type and rough awn characters occur in as many as one-half of the combinations in which they might be manifested. About 45 percent of the combinations include three or more predominant characters; 87 percent include two or more. However, the combination involving all of the predominant characters occurs in only slightly more than one-half as many strains as might be theorized if the characters were associated with one another in a random way within the scope of the collection. On the other hand, other combinations involving less preponderant characters occur in more than twice as many strains as would be theorized.

For most of the characters a few five-character combinations represent large proportions of the strains. However, only 16 of the 169 existing combinations occur individually in more than 1 percent of the strains. Two-thirds of these occur in more strains than might have been expected had the characters been distributed at random.

Only about 2 percent of the possible seven-character combinations (the joint occurrence of individual characters from the seven spike categories, two of which involve quantitative characters) are present.

The predominant characters occur in the largest proportions of the seven-character combinations, but only small proportions of the strains bearing these characters are marked by any given combinations. None of the individual characters occur in as many as one-tenth of the combinations in which they might possibly be manifested. Only 13 of the 885 existing combinations occur individually in 1 percent or more of the strains.

Nearly 60 percent of the seven-character combinations include four or more of the predominant characters; about 22 percent include five or more.

The combination that involves all of the predominant characters occurs in less than one-third as many strains as might be theorized if the characters were associated with one another in a random way within the scope of the collection. On the other hand, the same combination, except that 2-row is substituted for 6-row, occurs in more than three times as many strains as might be theorized. Another combination involving 2-row occurs in more than 10 times as many strains as might be theorized.

A minimum of 9 strains would be required to embody all of the individual characters in this study; 72 for all the possible two-character combinations; 600 for the five-character combinations; and 43,200 for the seven-character combinations.

The rough awn character occurs in 100 percent of the two-, 68.3 percent of the five-, and 7.6 percent of the seven-character combinations in which it might possibly occur. No other character exceeds these proportions.

The predominant characters occur in greater proportions of the five- than of the two-character combinations and in greater proportions of the seven- than of the five-character combinations. The reverse of this is true for most of the less preponderant characters.

Strains from Ethiopia manifest more diversity of type than do those from some other major Old World sources, although those from some of the sources include more different individual characters than do those from Ethiopia.

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