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WHEAT STUDIES

OF THE

FOOD RESEARCH INSTITUTE

VOL. IV, NO. 7 JUNE 1928

THE OBJECTIVES OF WHEAT BREEDING

THE objectives of wheat breeding are complex. They ordinarily involve the development of wheat varieties combining high yield with high protein content; but these are difficult to combine, and the breeder must often compromise. The farmer desires the high yields most common in soft winter wheats; but if protein content is too low or quality too poor, he may receive so low a price as to nullify the expected gain from high yield. Since wheat must be adapted to each locality in which it is grown, the breeder must add to his task the development of resistance to fungous and insect pests, to drought, to cold, to hot, dry winds, to a short growing period, and the like. Emphasis on quality in wheat breeding developed only with the advent and growth of world trade in wheat and with the introduction of roller milling in the 1870's. Changes in agricultural technique have also modified the objectives of wheat breeding. For example, lodging was unimportant when wheat was garnered with sickles; but the advent of the harvester and of the "combine" called for development of wheat that would not lodge and would not shatter its seed if allowed to stand in the field after maturity.

Only since 1900 has breeding become truly scientific. Before that date even the most adequate method, hybridization, was purely haphazard; for the laws under which the characters of the parents are transmitted to the offspring were unknown. Today the situation is complicated by the fact that many seed characters are not transmitted in the same way as the characters of the plant itself. During the last twenty years the principles of the science of genetics have been more and more applied to the complex practical problems of wheat breeding, and much progress has been made.

STANFORD UNIVERSITY, CALIFORNIA

June 1928

WHEAT STUDIES

OF THE

FOOD RESEARCH INSTITUTE

The central feature of the series is a periodic analysis of the world wheat situation, with special reference to the outlook for supplies, requirements, trade, and prices. Each volume includes a comprehensive review of the preceding crop year, and three surveys of current developments at intervals of about four months. These issues contain a careful selection of relevant statistical material, presented in detail in appendix tables for reference purposes, and in summary form in text tables and charts.

Each volume also includes six special studies bearing on the interpretation of the wheat situation and outlook or upon important problems of national policy. Subjects of issues already published are listed inside the back cover.

The series is designed to serve the needs of all serious students of the wheat market, in business, government, and academic circles, by summarizing and interpreting basic facts and presenting current developments in due perspective. The special studies are written not merely for students of the wheat market, but as well for various groups of readers who are especially concerned with the fields discussed.

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FOOD RESEARCH INSTITUTE

STANFORD UNIVERSITY, CALIFORNIA

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The Food Research Institute was established at Stanford University in 1921 jointly by the Carnegie Corporation of New York and the Trustees of Leland Stanford Junior University, for research in the production, distribution, and consumption of food.

THE OBJECTIVES OF WHEAT BREEDING

To increase yield per acre seems so self-evidently the dominant objective of wheat breeding that any detailed discussion of the subject might appear superfluous; yet, in reality, the factors determining the objectives of the wheat breeder are not merely complex, but they change with changing economic conditions and with changes in the economic factors determining farmers' profits. Large yields are desired not for themselves, but because they commonly result in larger profits than small yields. But the most prolific wheat is not necessarily the most profitable, for yield depends perhaps no more upon inherent multiplying power than upon the capacity of the plant to multiply in the special cultural conditions under which it is grown; and this involves the ability to resist disease, adverse climate, and other unfavorable conditions. The objective of the breeder, therefore, often resolves itself into indirect increase of yields through the development of disease-, drought-, and frost-resistant types of wheat.

Furthermore, the wheat that yields the most in spite of such adverse conditions as it may be called upon to resist is not necessarily the wheat that proves most profitable; for the buyer, commonly the miller, may decline to pay a good price for it because he cannot manufacture from it the type of flour desired by his customers. Thus the gain the farmer expects from increased yield may be nullified more or less by low price. It may pay better to grow some other kind of wheat of superior quality even though it yield somewhat less to the acre. The breeder and the farmer must, therefore, consider not yield alone but quality as well.

High quality in wheat for bread-making purposes is ordinarily associated with high protein content, though quality and protein content are not always parallel characteristics, because the physical properties of the protein are not equally good in all wheats. Superior proteins give to flour the capacity to absorb much water and to yield dough of exactly the proper toughness and resilience to hold the gas generated in the leavening process. If the proteins possess these qualities, the flour can be made into a well-risen, desirable loaf, provided there be enough of the good protein present. If there is not enough, the dough cannot be satisfactorily elastic and it will not absorb much water. If not much water is absorbed, the volume of the dough will be relatively small and the number of loaves per barrel the baker obtains will be few. If the protein is of inferior quality, then the dough is not satisfactorily elastic even though much protein be present; and the loaf will be poor in texture. As a matter of fact, there are varieties of wheat with high content of protein which nevertheless produce flour from which good bread cannot be baked because the proteins have not the proper elastic qualities to make good dough. Therefore, if the breeder is aiming at quality he must produce bread-wheat varieties with much protein of the proper physical character. Flour derived from such wheat is termed "strong"; flour of opposite characteristics, "weak."

It is evident, then, that the objectives of wheat breeding are complex rather than simple. The purpose of this issue of WHEAT STUDIES is to set forth some of the factors entering into the situation, and in particular to emphasize some of the economic aspects. The economic aspects now important are the outgrowth of a long evolution in agriculture, in milling and baking technology, in the science of genetics, and in standards of living. Hence, so far as appears desirable, the objectives of wheat breeding are considered historically; but only such consideration is given to the science of genetics as is indispensable to an understanding of wheat breeding by the layman.

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I. BREEDING FOR YIELD OR PROTEIN CONTENT

Local Character of the Wheat Market until Recent Times

Although quality as well as yield determines the farmers' profits, yield is nevertheless in many sections the most important determinant of profits. Farmers very generally want high-yielding wheats. In primitive conditions there were few factors operating to check the tendency to grow the highest-yielding sorts available, for there was little competition from imported wheat in the local market. Transportation was difficult and costly; except to a limited extent, and that only along sea or river routes, there was little trade in so bulky a commodity as wheat; and there were but few communities in which local and imported wheats competed with one another. It had been otherwise in the days of Imperial Rome, which depended largely upon Sicilian and Egyptian grain. In medieval Europe, and even up to recent centuries, the bulk of the grain consumed in most localities was grown locally or near by. Imported wheat rarely influenced the local market, partly because of transportation costs, partly because under the systems of agriculture then prevailing few localities produced surpluses for export. The miller was compelled to rely upon the local product; it was commonly all he could get. If it did not make very good flour and the flour did not bake out into a very good loaf, this was unfortunate but unavoidable, and was not laid to his door. Moreover, as there was no better foreign wheat to furnish a standard for comparison, there was little basis for contrast and complaint. Indeed, in the absence of standards for comparison, miller, baker, and consumer were uncritical. It probably rarely occurred to the miller to criticise the wheat at his disposal or to the consumer that the bread ought to be better. People did as their fathers had done and could not complain since they knew nothing else.

The principal basis for comparison was the variation in quality from year to year. If in one year the harvest was wet and the wheat and flour poor, it was still the only wheat obtainable. It was a misfortune for which no one was to blame; people had to eat the bread, such as it was, or go without. With but few localities where foreign wheat could be brought in in material amount, there could have been little check to the growing of the sorts of wheat giving the greatest yields, even though their quality might be poor as compared with other lower-yielding sorts of better quality equally well adapted for growth in the region. The principal check must have come from the farmers themselves who had their own wheat custom ground for their own use. Thus in India today the sorts of wheat preferred by the native cultivator for his own use are also those Indian wheats most esteemed by European millers. But quality is an elusive trait, while quantity—that is, yield—is plain to every man; and this in itself, even without conscious purpose of the farmer, would tend to favor the planting of the higher-yielding varieties. It is also not at all impossible that in earlier days the public taste was different; and this may be a factor in explaining what appears on present standards as a neglect of quality. Moreover, standards of living were unquestionably lower, and a far smaller fraction of the population was in a position to pay premiums for quality. Indeed, the public had to use the flour from unsound wheat even when it was regarded as unhealthful.

Though flour was made very largely from local wheat, millers in one and the same locality need not have paid the same price for all the local wheat; quite the contrary. Different parcels of the same variety inevitably vary in quality even when grown in the same general area, and were no doubt evaluated accordingly. Some parcels would be less sound than others, if local showers at harvest or bad storage caused damage. Aside from soundness, the chief concern of the miller in those days, and to a large extent today, was the plumpness and large size of the berries. This is well indicated by the weight per measured bushel, the so-called test weight; large, plump-berried wheat has a high weight;[1]

[1] The shape of the berries, determining the closeness with which they pack in the measuring vessel, is also a factor in determining test weight.

small, shrunken, shriveled wheat, a low weight. The millers' interest in the weight per bushel is due to the fact that large-berried, heavy wheat yields more flour per hundredweight than small-berried, light, shrunken wheat. But high crop yields and large size of berry (for the variety) go together. So in these early days, the judgment of the farmer and miller as to what was desirable in wheat did not conflict as much as in later days, when, besides yield, quality of flour for bread baking came more to be considered. There was little necessity to pay heed to flour quality; hence most of the high-yielding wheats developed in the early days of systematic wheat breeding yielded flour of far from superior bread-making quality.

In time agriculture became more and more nearly rational and more and more efficient. Better crop rotations began to be used; deep plowing displaced mere scratching of the surface; heavy manuring was introduced, especially with artificial fertilizers. These practices tend to increase the vigor and duration of growth and also the yield, but the protein content tends to go down. The grains become starchier and more floury (with certain exceptions which need not be considered here), while quality frequently tends to become poorer. At the same time such very favorable cultural conditions insure the survival of all the different strains in a crop. It is only in recent years that the seed sown consists at all frequently of a single pure strain. When the crop consists of several strains or varieties of which one is much more prolific than the rest, its seeds must be present in greater proportion in the harvested crop than those of the less prolific strains, even though in the seed as originally sown the proportions may have been similar. If for succeeding crops seed is sown without selection, it follows that ultimately the crop must consist chiefly of the most prolific strain. It is obvious that, where cultural conditions are so good as not to handicap prolific strains, in the long run yields must go up even when there is no purposeful selection. Since the highest-yielding strains tend to be of poorer quality, quality must go down. There is reason to believe that this actually occurred with improvement in agricultural technique in Western Europe. Indeed, the phenomenon is one of the factors accounting for the so-called deterioration of wheat when seed of high-quality wheat but not of a pure strain from one region is used in another region. Climate and other growing conditions account for a part of the change, but the gradual domination of the more prolific poorer-quality strains accounts for a part of it if, under the changed environment, the prolific strain finds conditions as favorable as the less prolific ones.

Effects of World Trade in Wheat

It is obvious then that in early times there were many factors favoring the culture and the development of high-yielding wheat. When deliberate, purposeful wheat breeding began, the principal objective was naturally the development of high-yielding sorts. Wheat breeders began seriously to breed for quality as well as yield only long after a general world trade in wheat had been established. They were no doubt stimulated thereto by the premiums paid for certain types of high-quality wheat which formed an important fraction of that trade.

The world trade in wheat was the direct result of the growing industrialization of civilization. Science and invention industrialized the world, increasing the number of mouths to be fed, and at the same time furnishing through cheap transportation a world market for the surplus of goods produced by industrialized countries. The sale of this surplus furnished the means for the purchase of the extra food needed, and cheap transportation made such purchase feasible. At the same time a surplus of wheat for exchange against manufactured goods became available through the opening of new lands in America and elsewhere. Much of this was grassland which, through science and invention, could be brought for the first time under the plow. Besides the steamboat and the railroad, the inventions involved were well-digging and agricultural machinery; for much of the grassland of the world is semi-arid, and its per-acre yields are usually comparatively low. If, then, the farmer is to exist, and also produce the surplus which he requires to exchange against necessities not producible upon grasslands, he must cultivate an acreage larger than is possible without the use of agricultural ma-

chinery and the aid of considerable power, whether supplied by animals or machines. With the inauguration of the world trade in foodstuffs, the economic isolation of the Western European wheat farmer was gone. Except in so far as he was sheltered behind tariff walls he had to face the competition of the world. In England the tariff walls, the corn laws, were radically reduced in 1846 (effective in 1849), and all duties were abolished twenty years later; for a generation after 1865, trade was less hampered by tariffs in Europe than at any time before or since.

The earliest competition came probably from Hungary and the Balkan countries. The river systems of Central Europe furnished cheap transportation. The United States was also an early exporter. Soon southern Russia became a factor and was followed by India, Australia, Argentina, and finally Canada, as sea freight rates went down, and railroad mileage increased, and as Australia, Argentina, and Canada came to be more populated.

Much land has a climate wherein only varieties with a short growing period can be grown. Such wheat tends to be hard, flinty, vitreous,[1] and high in protein content —a type of wheat new to millers when it first came to Western Europe. They did not know how to handle it. Their machines, millstones, were not well adapted to producing flour from it. In consequence it was not fully appreciated, and lower prices were paid for it than for the better classes of local wheats. This state of affairs did not at first affect the United States seriously. Wheat was not yet produced on the semi-arid Great Plains, which were not yet settled sufficiently to produce a surplus. The wheat exported came from nearer the Atlantic seaboard. In the first third of the nineteenth century Virginia was a great wheat state and in the middle half of the century Rochester, New York, was the greatest milling center. Hence, in those days the bulk of the wheat exported from the United States was soft winter wheat.[2]

The objectives of the wheat breeders were still to produce finer types of high-yielding wheat that would mill out the maximum of flour. Relatively little attention had to be paid to breeding high-protein wheats since they did not command better prices. The development of better spring wheats came later in drier and colder portions of the country when these came to be settled. As wheat acreage expanded in these regions, the effort of wheat breeders was in the direction of increasing the winter hardiness of winter wheats, and where this failed to insure a crop, to resort to spring wheats. The desire for winter wheats where possible is due not solely to the fact that they incline to be heavy yielders but also to the fact that the growing of winter wheat brings with it a better distribution of farm labor through the year. On the other hand, the spring-wheat grower has the advantage that in the spring the probable price of the crop can be somewhat more accurately fore-

[1] The vitreous appearance of some wheats is apparently merely a physical property. In such wheats the starch granules are closely imbedded in the matrix surrounding them, whereas in the non-vitreous types the granules are less closely imbedded so that fissures or air spaces separate them to a greater or lesser degree from the surrounding matrix. From the surface of these tiny internal cavities light is reflected, giving the grain an opaque or whiter appearance. Vitreous wheat may be made opaque by merely soaking in water and then drying. This treatment, as may be demonstrated with the microscope, causes internal air spaces to develop. Since opaque wheat contains more air spaces than vitreous wheat, it is less dense, i.e., has a lesser specific gravity. This is of commercial importance, since the average density of the berries is one of the factors determining the weight of a measured bushel, i.e., the test weight.

[2] The term "winter wheat" is applied to the varieties of wheat which are customarily planted in the fall and harvested the following summer. If planted in the spring, most of them grow during the ensuing summer but do not head and produce seed until the summer of the following year. They commonly exhibit a creeping habit of growth, covering an appreciable surface of ground by the process known as stooling or tillering. By tillering is meant the habit which wheat shares with many other grasses of dropping some of its branches to the ground and so growing roots at the nodes on the branches. Because of this habit of growth, they produce more stalks and ears per plant than spring wheats. These have a shorter growing period than the winter wheats, being customarily sown in the spring and harvested in the late summer; they tiller less; and they produce fewer ears per plant. In some climates, California for example, spring wheats are sown in the fall and harvested in the early summer. Therefore, to speak of the two sorts as winter and spring wheat is not strictly accurate. It would be better, at least in scientific work, to speak of them as wheat with winter and wheat with spring habits of growth, respectively. Common winter wheat and common spring wheat are varieties of the same species, *T. vulgare* Vill. Indeed, between the two habits of growth as well as in length of growing period all intermediate gradations may be found. Club wheat, *T. compactum* Host., may be of either winter or spring habit. Durum wheat, *T. durum* Desf., is usually of spring habit.

seen than six months earlier and consequently the area under wheat can be increased if conditions appear to justify it.

Introduction of Hard Wheats

In breeding spring wheats the effort was at first not in the direction of producing hard, high-quality varieties, but rather to produce drought- and rust-resisting forms of early maturity, in order to avoid frost damage in the fall. That varieties with these characteristics were usually hard, high-protein sorts was rather a misfortune at first, for these wheats were not highly prized by millers. Farmers everywhere would have preferred high-yielding soft winter wheats. These were displaced by lower-yielding hard spring wheats only where climatic conditions made the growing of soft winter wheats too hazardous or impossible.

This state of affairs continued until the introduction of the roller process of milling. It is perhaps not an accident that the process was invented in Hungary, which produces fairly hard wheat. The process began to be widely employed in the United States in the late 1870's. Thereafter hard wheats came to be appreciated because, if properly milled, they produced whiter flour of superior quality from which better bread might be baked. Hard wheats, instead of being discounted by millers, began to carry premiums over many sorts of winter wheats. The introduction of the process of roller milling proved an important factor in changing the wheat map of the world.

As harder wheats came to be sought, wheat breeders began to pay increasing attention not merely to the production of high-yielding varieties but also to the production of hard, flinty, vitreous, high-quality sorts both of winter and of spring habit of growth. In the United States and Canada the first steps were in the direction of the introduction of high-quality wheats from other regions with similar climates. Useful sorts were introduced from southern Russia, from the Mediterranean littoral, from India, and elsewhere. These were the foundation stocks with which breeders operated. In the beginning the efforts were to produce types with very hard, dark, vitreous berries. Little attention was paid to protein content because the chemical analysis of wheat for the determination of protein content was difficult. It was not till 1883 that the Danish chemist, Kjeldahl, made public a relatively simple method for the quantitative estimation of nitrogen; from nitrogen content protein content may be calculated.

This method made it possible for the plant breeder to substitute an exact quantitative measure for the rough subjective estimates based on hardness, color, and translucency. However, few breeders took advantage of the chemical method, perhaps because the protein in a small sample or in a single kernel could not be estimated by the method in its original form. To use the method the breeder had to have at his disposal an appreciable amount of seed. In selecting a plant for propagation he very naturally hesitated to sacrifice most of the seed in order to learn more accurately than was possible by inspection how much protein was in the seed. Thus Saunders in developing Preston and Marquis wheats used the chewing test. The kernel is chewed slowly till most of the starch is removed, leaving most of the protein, which is known as gluten, behind between the teeth. From its feel in the mouth an experienced person may gain a fair idea of the amount of protein in the wheat and of its physical properties.

Within the last few years the Kjeldahl method of estimating nitrogen has been much improved by the development of the so-called micro-method, which requires only a minute amount of material. With its help the amount of nitrogen in a single seed and indeed even in only a part of a seed can be determined accurately. Thus it should be entirely feasible to dissect an individual seed into its principal organs—the seed coat or bran, the main part of the berry; the endosperm, which yields the flour; and the embryo—and to estimate nitrogen separately in each. This should be helpful in estimating the probable protein content of the flour, for this is always less than that of the berry because, in milling, the bran and embryo, which contain more protein than the endosperm, are eliminated. It should also give some help in judging probable flour yields, for these depend not merely upon test weight, but also upon

thickness of bran coat and size of embryo.[1] Though the micro-method should be an invaluable help to breeders, it does not as yet seem to have been used by them.

Changes in the Milling and Baking Industry in Recent Times

One of the most potent factors in forcing upon the breeder the development of high-protein rather than of merely high-yielding wheats has been the change which for more than a generation has been taking place in the milling and baking industries. Milling was a small local business before the days of cheap freight rates. Just as in most of Europe the wheat of the farmers of one locality did not much compete with the wheat of farmers in another locality, so the flour produced by the millers of a given locality did not much compete with that produced in another locality. It was a local gristing business, custom milling. Moreover, the millers in a given locality all had the same wheat, the same raw material to work upon. The difference in the flour of two locally competing millers was due primarily to differences in their respective skill. As the international trade in wheat and flour developed and as millers began to have a choice of raw materials, they were enabled to control the quality of flour by selection of the sorts of wheat purchased for milling. The art of blending wheats for milling developed. Thus competition between wheats was established and the judgment of the individual miller in the purchase of his raw material and in blending different sorts of wheat became as potent a factor in his success as skill in the mere mechanical operations of milling.

Naturally, these developments were first most pronounced in Europe, since to Europe began to flow all kinds of wheat from the corners of the globe, and in particular high-quality wheats from North America. Naturally, the mills situated at the seaboard were first affected; the practice of using imported wheat spread only gradually into the interior of Europe. Indeed, in many countries milling tended to be concentrated at seaports; even today in the several countries of Europe it is still so concentrated. At present great milling centers are located either close to, if not actually in, a region where high-quality wheat is produced, or at some point toward which transportation routes from many wheat-producing sections converge. In the United States such milling centers as Minneapolis–St. Paul and Kansas City exist because they are close to regions producing excellent wheat. Budapest in Hungary owes its pre-eminence in milling to the same cause.

The concentration of milling in these favored localities made possible larger and more efficient units, a movement that was favored by the introduction of the roller process which required more investment in machinery. However, the most important factor causing the establishment of large mills and the gradual disappearance in many countries of the small local mill was increasing concentration of population in large cities. The net result was that wheat was milled where the miller could buy it most advantageously and ship flour to the consuming centers, having due consideration for the costs of transportation inward and outward and the markets for mill by-product, millfeed. In Europe these centers are commonly at seaports except in a few countries which import only a minor fraction of their wheat and flour requirements. In the United States and Canada, which export both wheat and flour, milling centers, as above stated, are developed near wheat-producing regions or at points of convergence of transportation routes.

In buying wheat, the large mill, the existence of which is the consequence of the world wheat trade, finds it of the utmost importance to pay especial attention to quality. At first, and indeed until recently, wheat was bought on the judgment of the buyer. Many of the wheat buyers acquired an uncanny skill in foretelling from appearance and physical properties, such as weight per bushel, color, soundness, hardness, vitreousness, et cetera, the quality of flour that could be produced from a given parcel of wheat. On this basis the grain trade of the United States gradually evolved a series of grades which were a general, though far from precise, expression of wheat qualities. These grades were crystallized into the

[1] Clark, Martin, and Ball have found that the size of the embryo is a very constant varietal character. *Classification of American Wheat Varieties* (U.S. Department of Agriculture Bulletin 1074), November 8, 1922.

United States official grain standards in 1916, but the range between any two of these grades is still wide enough to leave ample play for the judgment of the individual wheat buyer. The grades are not based primarily on chemical analysis. They did, however, in their day help higher quality in wheat to receive recognition.[1]

Just as the gradual concentration of milling in larger factories resulted in greater emphasis upon quality in wheat, so the more recent concentration of baking in larger plants is exerting an analogous effect. In America bread baking is leaving the home kitchen more and more and passing into the bakery. While in the United States this transition is far from complete, in many countries of Europe home baking practically disappeared years ago. Nevertheless, in these countries, as well as in the United States, bakeries until a few decades ago were small units using but little machinery and furnishing a relatively small output per plant. This has been changing. Large bakeries in most countries are growing more numerous; in recent years they are using more and more machinery. While under any conditions that one can foresee for the more immediate future there is no prospect that a bakery will be able to supply as wide a territory as a mill, because bread is so much more perishable than flour, nevertheless bread baking is being more and more concentrated in fair-sized plants.[2] In consequence greater care is being devoted to the purchase of flour. Indeed, the larger bakeries find it advantageous to employ chemists to buy flour, as well as other supplies, on chemical analysis and on specification. There were few bakeries a generation ago large enough to warrant employment of chemists; indeed this is still true of a very large proportion of them. The baking chemist introduced the purchase of flour on specifications in which protein content plays an important rôle. This does not mean that the larger bakeries are more dependent on high-quality flour than heretofore; quite the contrary. The housewife must have a high-grade, foolproof flour; but the efficient baker can get results with less good kinds. Indeed, bakers tend to use less patent flour than formerly, but they tend to buy it upon chemical specifications that include protein content, though a high protein content is not invariably demanded.

One reason for the baker's eagerness to purchase high-protein flour is high bread yield, which is vital to him since it is an important factor in determining his profits. Flour with much protein of high quality absorbs much water in being doughed and yields more loaves to the barrel of flour. This is therefore the type of flour most desired by the baker. It is one of the reasons why he specifies a minimum protein content of flour and why he is often willing to pay a premium for it.

So keen is the skilful baker to incorporate as much water as he can into the loaf without reducing its acceptability to the consumer that he resorts to a number of devices to achieve that end. Only one of these, the mechanical high-speed mixer, is of interest here. This is a machine for kneading the dough mechanically. Introduced as a labor-saving device to imitate hand-kneading, it was soon found that the machine incorporated water more thoroughly than the journeyman baker, and so increased bread yields. When the machines are run at relatively high speeds, the absorption of water into the dough can be increased sufficiently to pay. Hence, hand-kneading is gradually disappearing. The change is vastly facilitated by the general availability of small electric motors. Everyone knows that mechanically working an elastic material ultimately injures its elastic properties. Obviously, the new mechanical method of kneading is a severer strain upon the elastic properties of dough than hand-kneading. Under the new method flour proteins in the dough must be able to stand more "punishment" than before. Varieties of wheat satisfactory for hand-kneading may prove less so when kneaded by machine. Blackhull wheat, a new Kansas variety of high-protein winter wheat, is said to behave in this way. It is reported as making satisfactory bread if kneaded in the ordinary way, but bread not quite so good if worked in a high-speed mixer. It seems likely that the mechanization of bakeries

[1] Cf. "Protein Content: A Neglected Factor in Wheat Grades," WHEAT STUDIES, February 1926, II, 164–76.

[2] C. L. Alsberg, *Combination in the American Bread-Baking Industry, with Some Observations on the Mergers of 1924–25* (Miscellaneous Publications of the Food Research Institute, No. 3), February 1926.

has introduced new problems for the wheat breeder to solve.

Flours with the maximum of good-quality protein are desired by the baker for several other reasons besides the high bread yields he is able to obtain with them. One of these is that it is less difficult to produce acceptable bread from good high-protein flour than from good low-protein flour. Strong flours require long fermentation periods because the rate of maturation of the dough is slow. Hence, the baker has considerable latitude; a little longer or a little shorter fermentation time does not spoil the bread. If there is a breakdown of machinery while the dough is fermenting, he has some leeway to make repairs. Weak flours, on the contrary, mature very rapidly and should be fermented only a relatively short time. The dough must be molded into loaves and placed in the oven at exactly the right stage. The baker, if any delay occurs, has little leeway and runs greater risk of uneven quality of his product.

There is still another reason why in America the baker is so eager for high-protein flour; it produces the type of loaf preferred by the American public. This is a large, very white, puffed-up loaf, baked in pans rather than on the oven's hearth. High-protein flours lend themselves better to the production of this type of bread than flours poor in protein. The taste for this type of bread is largely connected with the fact that in America bread is being used more and more as a vehicle for spreads. A puffed-up loaf naturally serves this purpose better than a more compact loaf of the same weight. Moreover, size rather than weight is an important factor in the sale of bread in America. The consumer feels that the larger loaf contains more bread even though its weight be less than that of a less puffed-up, competing loaf. Even where there are legal standards for weight of loaves, this is a factor which bakers do not ignore. It favors the production of the puffed-up loaf and the use of high-protein flours. In Europe the type of loaf preferred is different, and the bakers' demand for the very high-protein flour is apparently less insistent. Millers there rarely produce flours from the hardest wheats alone. Nearly always the bread flours preferred seem to consist of blends of hard with softer wheat. It is stated that with such blends the European baker secures more nearly the desired bread of the European consumer than is possible with flour from a single kind of wheat. Australian wheat, for example, is said to give the loaf a particularly fine bloom. Other sorts of wheat are used in the blends for flavor which in Europe seems more important than in America, perhaps because in Europe bread is for the most part made from flour, salt, and yeast alone, whereas in America, in addition to these, other ingredients, sugar, shortening, and milk, are generally used. Naturally, in bread containing a number of ingredients the flavor of any single one is less important. There are, nevertheless, indications that the European baker is becoming aware of the desirability of buying flour on chemical and other specifications, and it is to be anticipated that the trade there is not unlikely to follow the practices in buying becoming current in the United States.

It is a characteristic of the American consumer's demand that he desires a white loaf without tinge of gray or of yellow. Some good sorts of wheat yield flour of a creamy tint and this makes them less desirable. The objection to such kinds of wheat is less nowadays than it used to be because of the general practice in America of bleaching flour. In Europe, where bleaching is not so widely practiced, inherent flour color is more important, even though it would seem that the European consumer is less exacting in his demands for a very white loaf than the American. Consequently European millers in blending wheat must pay especial attention to color.[1] No doubt the greater skill now being exercised both in Europe and in America by the great bread-baking companies has been an important factor in changing the objectives of wheat breeding or at any rate in making them more precise.

[1] The color of flour is not due to the color of the wheat from which it is milled. In red wheat the pigment resides in the seed coats, which are removed in making flour. White wheat is devoid of this pigment. The flour from both sorts is white. Flours with a creamy color owe this trait to the presence of a yellow carotinoid pigment in the endosperm. It is present in all or nearly all wheats, but in varying amounts. The whitening of flour in ageing is due to the gradual fading of this pigment. When flour has a grayish tint or contains specks this is due to the imperfect removal of the bran. The bran left in flour from red wheat is of course more conspicuous than that from white wheat. The gray color of inferior clear and low-grade flour is due to the presence of appreciable amounts of finely divided bran.

Premiums for High Protein Content in Wheat

The effect upon the miller has been profound, for he is now often required to furnish flour with the specified minimum of protein. He in turn has been compelled to modify his methods of buying and evaluating, adding to his basis of judging wheat its protein content. He, too, is compelled to employ chemists for the purpose. In milling flour he is required to blend wheats in such proportion that the resulting flour has, as exactly as may be, the specified protein content. If it has less, the flour is likely to be rejected; if it has more, the miller's costs will be more than they need to be and his profits less, since as a rule high-protein wheats are more expensive than low. The effects upon prices paid for wheat have been profound. Very large premiums are paid for high-protein wheats in seasons when these are scarce; premiums of sixty cents a bushel and more above the base for the grade are not unknown. Such wheat is blended with less expensive, lower-protein wheat to produce a flour meeting the bakery chemist's specification.[1]

Naturally, this growing practice on the part of the baker has its effect upon the wheat farmer. It creates more favorable economic conditions for the farmer so situated that he can grow only short-growing-period wheats—since these are commonly high-protein wheats. The premium paid for these wheats serves to some extent to counterbalance the low yields. To be sure, ever since these hard wheats began to be appreciated, more was usually paid for them than for most soft wheats.[2] The grading of the grain exchanges and the federal grain standards were adjusted to give them recognition in a general way; but present methods of evaluating flour have served to increase appreciation for them and to cause the adoption of what amounts to a sliding scale of prices based on protein content for a given grade, other things being equal. The result has been to stimulate the farmer more than ever to produce high-protein wheat and this in turn is now stimulating the wheat breeder to attempt to produce improved and higher yielding high-protein varieties for the regions naturally endowed with a climate capable of producing high-protein wheat.

Even in regions where only soft winter wheats thrive, it is realized that there is no necessity to plant sorts with the very lowest protein content. For such localities it is possible to find or produce varieties which contain a fair measure of protein, even if the high figures of the best hard wheats cannot be attained. With such wheats it will be necessary to blend only relatively small quantities of wheat of distinctly high protein content in order to produce good flour.

Thus over much of the globe today an important objective of the wheat breeder is to give the farmer wheats with higher protein content than at present. The object is to do so without unduly sacrificing yields; to produce a wheat that will fetch a better price, yet not to sacrifice so much in yield as to absorb the increment in price. This, for example, is a principal objective in England at the present time and has already resulted in the production of the Yeoman variety, which is fairly high in protein and yields about as much as other varieties generally grown in England.

In some sections of the United States lower yields of high-protein wheat give a better net profit than larger yields of softer wheat, but for the most part this does not seem general; and naturally, in many sections farmers do not grow the lower-yielding sorts. Moreover, the protein premium paid in the terminal market upon the individual parcel of grain is not everywhere and at all times fully reflected back to the farmer who grew it, partly because the official grades take no direct cognizance of protein content, partly because there is no

[1] With full appreciation of the commercial value of protein, there are indications that the protein premiums are being overdone. Not unnaturally, the pendulum of chemical analysis has swung too far. We doubt whether the very high premiums paid for protein during the past season could be justified by many of the mills paying them. One-tenth of one per cent of protein lies within the error of the total process of sampling and analysis, yet it has figured in many commercial transactions during recent months.

[2] In the United States, however, in seasons of short crop or poor quality of soft red winter wheat, high-grade wheat of this kind commands a premium. In Europe, imported hard wheats usually sell at higher prices than domestic soft wheats, even where tariffs are inoperative. But for special reasons Australian wheat ordinarily commands as high prices as any but the superior grades of hard wheat, like No. 1 Northern Manitoba.

good, simple system of estimating protein content at country shipping points.[1]

While injustice may be done to the individual grower, the general effect upon wheat growing is less than might be supposed, because the official grades divide wheat into classes corresponding roughly to the amount and quality of protein they usually possess. Moreover, in the markets the place of origin of the different parcels is important. Buyers know the general quality of the different sorts of wheat and they also know in a general way the most probable protein content of the wheat from a given territory. This knowledge results in the adjustment of the general price level of a particular sort of wheat from a particular region in accordance with the esteem in which the variety is held, the general character of the wheat originating in the territory in question, and the demand and supply relations of the moment for that type and quality of wheat. Thus the general price level of the wheat of a given region may be high even though some farmers whose wheat is above the average of the region fail to receive the protein premium to which they are really entitled. Hence the discouragement to growing the highest-protein wheat possible is not as serious in all sections as one might suppose, though it is a real factor.

Moreover, variations in protein content of individual parcels of the same variety of wheat from the same region are accidental and rarely due to the deliberate act of the grower. They are, within the variety, the result of differences of climate, soil, season, and the like, and commonly not within the control of the farmer—at least in the United States. Furthermore, being largely due to the weather, the individual farmer who one year has wheat above the average quality, is just as likely as not to have wheat below the average the next season. Nevertheless, there can be no question that if it were possible to reflect back the premium to each individual grower this would not merely be ordinary justice but would also be economically most helpful to those sections which can grow only high-quality, low-yielding types of wheat.

While protein is at the moment perhaps the objective most in the public eye, the reader should not get the impression that it is the only objective. Yield will probably always remain the most important. The breeder of today is endeavoring to develop wheats combining high yields with high quality; to the breeder of the middle nineteenth century yield was the important objective and quality as understood today quite secondary. Quality meant for the most part large, plump, free-milling traits. Today there are other factors also that are important.

II. BREEDING FOR PLANT CHARACTERISTICS

Problems Raised by the Mechanization of Agriculture

The mechanization of agriculture has also modified the objectives of the wheat breeder. When wheat was grown in small tracts and labor was relatively abundant, harvesting was done by hand with a sickle. The harvest was adjusted exactly to the most favorable stage of maturity and almost every stalk was garnered individually. The stalks were carefully bound into sheaves, so that losses during harvesting were reduced to a minimum. As the area in wheat relative to available labor became greater and as labor-saving machinery began to be introduced, the harvesting operation became larger scale and less careful. First came the scythe, and then the cradle. These were followed by the reaper and binder and still later by the combined harvester-thresher, which cuts and threshes in one operation. Each successive one of these inventions handles the wheat less carefully and more roughly than its predecessor. The losses from shattering are therefore greater with each successive improvement in harvesting machinery. With the increasing mechanization of agriculture, therefore, it became necessary for the breeder to add to his objectives the development of non-shattering qualities in wheat.

It was, of course, always the object of

[1] See, however, the promising method recently proposed by Shollenberger and Kyle for hard spring wheat. "Correlation of Kernel Texture, Test Weight per Bushel, and Protein Content of Hard Red Spring Wheat," *Journal of Agricultural Research*, December 15, 1927, XXXV, 1137–51.

wheat breeders to produce varieties with straw that would not easily be beaten down in the field by rain or wind and would not lodge when conditions were favorable for rank growth. However, while wheat was garnered with a sickle, the tendency to lodge was not as serious a defect in wheat as it later became with the introduction of harvesting machinery. As such machinery became larger, heavier, more completely automatic, ability to stand upright quite as much as non-shattering qualities became of great importance, and more and more attention had to be devoted to this wheat character.

The introduction of harvesting machinery emphasized the importance of stiffness of straw and non-shattering qualities also because it made difficulties for the individual farmer in harvesting his fields at exactly the ideal moment of maturity, before much shattering or lodging had time to occur. While wheat was cut by hand or by horse-driven machines, shocked by hand, and then threshed from the shock at some convenient time, each farmer could own the necessary machines (except threshers) and harvest at or near the ideal time so long as his field was small. Where the combined harvester has come into use, the capital investment has become so large few farmers can afford to own a harvester if it is to be used only in their own fields. Most farmers find it advantageous to have harvesting done for them. However, a given farming community warrants the maintenance of only a limited number of machines; individual farmers must wait their turn so that it is often necessary to leave the wheat standing in the fields for days after the grain is fully ripe. Hence stiff straw and non-shattering characteristics are important properties where a dry harvesting season makes it feasible to leave the wheat in the fields for several days uncut. These properties are especially important where there are high winds to buffet the grain about. Conditions of this sort prevail in many sections of the Pacific Coast states and are responsible in part for the continued growth there of club wheats which do not lodge or shatter in marked degree, though they are rather poor for bread-making purposes. In Canada, on the other hand, the large machines enable the farmer to allow the field to dry before cutting, in conditions that would necessitate cutting the field wet with a small self-binder.

The standing capacity of the straw is, moreover, in some European countries a limiting factor on output because farmers do not dare to fertilize beyond a certain degree for fear that the resulting rank growth will cause enough lodging to nullify the increased formation of seed. Danger of lodging may be obviated either by breeding varieties so stiff they will stand in gales or with straw so pliable they will by bending relieve the strain on the roots. Ability to withstand lodging is not merely a matter of straw characteristic but also of how effectively the plant is buttressed with roots, the so-called adventitious roots. It is plain, then, that lodging may be lessened in a number of ways: either by stiffening the straw or making it more pliable, by increasing the number and strength of the adventitious roots, by shortening the straw and so lessening the leverage of the wind. These ends can be attained by breeding special varieties or by modifying cultural conditions. A rank-growing variety, for example, may produce the right length of straw where rainfall is scanty but will lodge where there is heavier precipitation.

What matters to the farmer is quantity and character of grain, rather than the nature of the plant that produces the grain. The plant is the means to an end; its characters are important only in so far as they are conditions for seed production and especially for high yields, so long as high yields mean high profits. High yields may be attained either by increasing the hereditary capacity of the plant to produce seed, or by adapting the plant to overcome local conditions of climate, soil, planting, cultivation, or harvesting that prevent the inherent capacity of the variety to produce seed from becoming manifest. If a hardier variety developed by the breeder is grown and the farmer does not suffer loss by winter-killing, early frost, or too low temperatures at unfavorable times, obviously his yield is greater than it would otherwise have been. He finds it advantageous to grow the hardier wheat since production is less hazardous, even though the hardy variety possesses less inherent capacity to produce high yields than some other variety.

Hardiness in Wheat

Hardiness in winter wheat is a somewhat different character from hardiness in spring wheat. In the former it is principally ability to resist severe winter weather and in particular repeated and alternate freezing and thawing. In spring wheat it means, rather, ability to make satisfactory growth even if the weather is not hot, and above all to resist early frosts. Hardiness of winter wheat, therefore, can be developed only by increasing the inherent resistance of the plant; whereas the danger to spring wheat from early autumn frosts may be met in this way or by developing early-maturing sorts. It seems that varieties showing greater resistance to cold have firmer tissues, a higher dry-matter content, and a more concentrated sap, i.e., a sap with more material dissolved in it. They hold on to the water they contain more tenaciously than less cold-resistant varieties. The discovery of these traits of hardy plants is of practical importance since it should enable the breeder to test the hardiness of individual plants without being compelled to wait until he is fortunate enough to have severe weather come at just the right time. In many sections winters of the peculiar type of severity that tests the hardiness of winter wheat come at quite irregular and unpredictable intervals. This is of course also true of premature autumn frosts.

Analogous to frost resistance is the ability to germinate at low temperatures. It is obvious that this too is an important objective of the breeder, for a variety that is able to germinate at low temperatures may be planted later in the fall or earlier in the spring, as the case may be. Under some circumstances this may be of great advantage not merely as it affects distribution of farm labor, but also because it may be helpful in giving the young wheat plant a good start. Moreover, if the seed bed is too dry at the time of sowing winter wheat but rain falls later when the weather is cold, it is obvious that ability to germinate in spite of low temperature is of the utmost importance. The first few weeks of the life of the wheat plant are critical. Recent experiments seem to indicate that the extent to which the seedling exhausts the endosperm determines the size of the first leaf.[1] But the size of the first leaf determines the size of the second leaf, and the first and second leaves together, the size of the third, and so on, till in the end the size of the first leaf determines the size of the plant itself, at least for spring wheat. It is obvious, then, why the period from germination to the full development of the first leaf is so critical for the plant. Indeed, too little attention seems to have been paid by wheat breeders to the requirements of the wheat plant in the first few days during and after germination. Adaptation to the temperature and moisture conditions then prevailing is vital. Early tillering is also important so that the plant may cover the ground as early as possible and thus fight weeds more successfully.

If earliness with hardiness and high-yielding capacity can be combined in one strain for cultivation on lands located far north or at high altitudes, the wheat acreage of the world may be substantially increased. Earliness, however, is usually conceded to be attained at the sacrifice of yield; a larger world acreage can be put into wheat, but per-acre yields are not increased except in far northern or high-altitude lands. Drought resistance is analogous to earliness. The development by the breeder of more drought-resistant forms makes possible an increase in wheat acreage; but it tends to increase yields only in semi-arid regions. Analogous to drought resistance is ability to germinate with a minimum of moisture. In view of what has already been said concerning the first developmental stage of the wheat plant as a critical period, the importance of this objective of wheat breeding is obvious in regions where the seed bed may be too dry for ordinary varieties. This is especially true in many sections of India. The introduction of early-maturing and drought-resisting forms has been an important factor in permitting the spread of wheat culture in the western portion of the Great Plains and intermountain country of the United States and much of Canada. Indeed, the Canadians have taken the lead in developing early-maturing varieties, such as Ruby, Garnet, and Prelude.

Earliness is useful and affects yields favorably, not merely in regions where early frost or drought are to be feared, but also in humid regions where yields are reduced

[1] Observation of H. L. van de Sande Bakhuyzen at the Food Research Institute, as yet unpublished.

by stem and leaf rust, smut, bunt, mildew, or insect attack. Earliness in maturity in a disease-susceptible strain may counteract the defect by allowing the wheat to be harvested before a serious infection occurs. Yields may thus be increased even though the early variety in question may not be unusually prolific under ideal conditions. Reduction in yield from disease may be counteracted in another way, by the development of varieties that are by nature resistant to the particular form of disease that does the damage. More attention than formerly has been paid in recent years to the development of disease-resistant forms, especially in America and in the newer wheat-growing countries. The reason is perhaps to be found in the fact that in America disease is a more important factor than in Europe. This is because wheat is planted in vast, continuous areas, which favors the spread of disease, whereas in Western Europe the areas are smaller, discontinuous, and cut up into separate sections by ridges and mountain ranges, which offer more or less impediment to the spread of parasitic infection. The development of resistant strains has been facilitated by study of the parasites. Gradually the life history of the parasitic fungi is becoming known through the investigations of phytopathologists, and this knowledge enables the wheat breeder to do his work more intelligently.

Finally, as in part pointed out above, breeding for certain physical characteristics such as stiff straw, tight chaff, shape of kernel, dense head, has a tendency to increase yield by purely mechanical means in connection with harvesting by machinery.

III. BREEDING OF SOFT AND DURUM WHEATS

Uses of Low-Protein Wheat

Hitherto, it has been tacitly assumed in the present discussion that the sole objective of the wheat breeder is the improvement of bread wheat; and this is indeed usually true. However, bread is by no means the only form in which wheat is consumed. Very large quantities of flour are used, for example, in cake, cracker, and biscuit making. For these types of products it is not so essential that high-protein wheats be used. The better kinds of moderately soft wheats are entirely satisfactory. The wheat breeder developing wheats for cake and cracker flour need not follow the same objective as the breeder of bread wheats. He may work toward high-yielding, large, plump-berried varieties, provided he does not at the same time permit the quality of the protein to deteriorate too much. While statistical data are not available, it is probable that in countries like the United States with a high standard of living and a large and increasing per capita sugar consumption, the use of flour in cakes, crackers, biscuits, pies, and "sweet goods" generally represents an increasing proportion of the per capita flour consumption. Flour in these forms and also as bread is becoming more and more a vehicle for sugar, fruits, and fats, and less and less a food *per se*. This trend is likely to increase the demand for good soft wheats and to moderate more and more as time goes on the demand of the commercial baker for flours with high protein content. Certainly it means a sharper differentiation of the two types of flour, strong and weak.

Another form in which flour is consumed is in alimentary pastes. These are of two sorts: macaroni and spaghetti types, and noodle types. The wheat requirements of the two are quite different. The best macaroni and spaghetti are not made from flour at all but from semolina. Semolina is granular endosperm free from bran and germ. In the roller-milling process the wheat is not reduced to the fineness of flour in a single operation. Reduction is performed in a series of steps by passing the wheat between successive pairs of rolls, of which the earlier pairs are so adjusted as to produce as little flour and as much coarse granular material as possible. Only after this coarse granular material has been freed from bran and germ by sifting and by air currents is it reduced to the fineness of flour. Before this final grinding, it is known as purified middlings or semolina. It is this material from which the best macaroni is produced. It is obvious that the hardest wheats must produce the most and the largest granules, because their endosperms are hard and

tough; whereas soft wheats with friable endosperms must produce the least. Therefore, the very hardest wheats are preferred for macaroni manufacture. As the durum wheats are the hardest, these are the macaroni wheats *par excellence,* and indeed are so called.[1] They are a drought-resistant, short-growing-period variety, grown principally in dryer sections where, because of their drought and rust resistance, they outyield the common wheats of spring habit of growth. Obviously, in view of the principal uses to which durum wheat is put, the objectives of breeders of durum wheat are not at all points the same as those of breeders of common wheat.

For alimentary pastes of the noodle type, flour too poor in protein content and protein quality to be satisfactory for bread or even cracker and cake may be used. If a breeder desires to develop wheat for this special use he may concentrate his efforts on all those characters that make for high yields. As a matter of fact, wheats are not grown specifically for noodles as durum wheat is grown for macaroni. There is enough soft, low-protein wheat in the world. Moreover, in the production of the higher grades of flour, the so-called patent flours, poorer flour is a by-product which may be used in these softer kinds of alimentary pastes. Indeed, the mills of the Pacific Coast of North America dispose of these flours, so-called clear flours, by exportation to the Orient whenever conditions permit. In the Orient little leavened bread is baked, but there is a considerable consumption of noodles and related products, for which clear flours and flours from club wheats so largely grown in the Pacific Northwest are entirely suitable. The sale of the clear flours in the Orient is much facilitated by heavy bleaching in the mills. It is the demand for yeast-leavened loaf bread that has brought about the insistent demand for high-protein wheat, and the breeder of wheat to be used in pastry or noodles need not make high protein content one of his major objectives.

Finally, wheat is grown for forage and feed as well as for food. In some regions wheat is cut—usually when the seed is in the dough stage—and cured for hay. For this purpose varieties with luxuriant growth are desirable. In other regions winter wheat, if weather conditions are favorable, may be pastured during the winter or early spring, and then permitted to produce a crop. The tillering power and the ability to grow at lower temperatures are important characters if wheat is to be pastured. In some countries the straw has other uses than as feed or manure. For example, straw was largely used in England as a packing material, especially for pottery and other fragile manufactures. Farmers situated close to the seat of such industries obtained a material return from straw and were led to plant varieties with fine, stiff, long straw. As these are often very high-yielding but low-quality varieties, this use of straw unquestionably exerted a material influence on wheat breeding in England. In more recent times straw has been replaced for this purpose by other substances. In some regions, England and California for example, an important use of wheat is as poultry feed. The poultry feeder buys wheat on its appearance, not on chemical analysis. He prefers large, plump, white wheat, and it is reported that in England the grower of such wheat (which there is often rather poor for bread-making purposes) not uncommonly receives more for it from poultry feeders than from millers. Naturally, this has not been without its effect on the choice of wheats there grown. The bran and germ fraction of wheat from which the flour has been removed by the miller is also used for feed. There seems to be a widespread preference for white bran. Why feeders should prefer white bran to red is not clear. Possibly it is because white bran seems to them to contain more flour. In modern milling the by-product, millfeed, is an important item of income. Competition is so keen that the return on the bran must enter into the miller's calculation both in the sale of flour and in the purchase of wheat. Now the color of the bran does not determine the quality of wheat, though it is true that among the high-protein, hard, flinty, vitreous sorts red varieties prevail. There are also high-quality white wheats. In breeding, therefore, the color of the bran coat is a factor to be considered.

[1] But it must not be assumed that good durum and good hard spring wheats (for example, Marquis) of the same protein content behave identically in the making of bread and paste—quite the contrary. Flour from Marquis wheat makes the best bread, and semolina from amber durum wheat makes the best paste.

IV. HISTORY OF WHEAT BREEDING

The breeder in his efforts to achieve the many diverse objectives of wheat breeding, and to give to the farmers of each district the particular variety of wheat that is most profitable under the special conditions prevailing in that district, has to use as foundation stock the varieties of wheat now in existence. These are the raw materials out of which he must create the special wheats for special purposes. To understand the character of his work and the obstacles he has to surmount, it is helpful to inquire how present-day varieties came into existence and how present-day methods of breeding were developed.

Origin of the Wheat Plant

Botanically, the wheat plant belongs to the genus *Triticum*. Botanists are far from agreement concerning the number of distinct species that belong to this genus or of their relationships to one another. Botanists differ also concerning the origin of the different sorts of wheat. Some believe that at least certain of the different kinds were developed each from a single wild species; others, that they arose from accidental hybrids and perhaps also from mutations.[1]

The idea that domesticated wheats may have originated from hybrids of different wild species finds support in the fact that wheat is normally self-fertilized, that is, the seed is the product of the female and male element (pollen) of the same flower. Cross fertilization does occur occasionally without human interference; but the fact that it is the exception rather than the rule favors the maintenance of new varieties arising from hybrids that have appeared either accidentally or as the deliberate act of man. If such a hybrid possesses characteristics that enable it to survive, it will continue to be inbred indefinitely, since it will be self-fertilized. Hence, in the long run, a wheat hybrid will develop into strains or lines that have lost their hybrid character in that they breed true. Each of these strains or lines may represent a new variety since each may contain different combinations of the characters of its ancestors. Thus may be formed what is essentially a new type of plant.[2] If the types are suited to the environment they will survive; if any one new type is better suited than its ancestors it may in time displace them. In the course of the ages many of the varieties of wheat have perhaps developed in this way. There was accidental hybridization. A new type arose. This was better suited to its environment than the types from which it was derived, and for this reason replaced them. Or else it appealed to man as superior, so that it was deliberately selected and propagated.

Deliberate, purposeful plant breeding by hybridization was practiced in ancient times: in China with various flowers; with roses in the Roman Empire; and in the seventeenth century by Dutch flower fanciers. However, no one knew anything concerning the laws of heredity and no one could prophesy the characteristics of hybrids or of their offspring. The method was essentially one of trial and error. Indeed, nothing was known about the sexuality of plants before it was established by Camerer in 1694.[3] Not until 1760 was the first successful scientific hybridization experiment performed by Kölreuter in crossing two species of tobacco.[4] Though the phenomenon was much studied thereafter, its application to the improvement of crop plants remained for more than a century largely a matter of trial and error, for little was known about the laws determining the manner of inheritance by the hybrid of the characters of its parents. Moreover, the difficulties were multiplied because the progeny of hybrids vary in ways that were then quite mysterious; the hybrid usually fails to breed true.

[1] The spontaneous origin of new characters is known as mutation. Individuals with new characters are known as mutants. Little is known concerning how mutation, which is comparatively rare with most plants, comes about. In some cases, certainly, mutants have turned out to be individuals with a hybrid in their more or less remote ancestry.

[2] This is not the place for a full discussion of the laws and mechanism of inheritance. For such a discussion the reader is referred to E. B. Babcock and R. E. Clausen, *Genetics in Relation to Agriculture* (New York, 1927).

[3] *Epistola de sexu plantarum*, quoted by Babcock and Clausen, *op. cit.*, p. 335.

[4] Vorläufige Nachricht von einigen, das Geschlecht der Pflanzen betreffenden Versuchen und Beobachtungen, nebst Fortsetzungen 1, 2, und 3 (1761–1766)," edited by W. Pfeffer, as No. 41, in *Ostwalds Klassiker der Exakten Wissinschaften* (Leipzig, 1893).

Its progeny may be of many types, each representing a different combination of the characters present in the wheats used in the original cross.

Efforts, no doubt, were made by primitive peoples to improve wheat; but the technique used was not that of hybridization, but mass selection. It consists simply in picking out choice plants from the main crop and sowing the seed from them for the next crop. When systematic plant breeding began in Europe in the latter part of the eighteenth century, and soon thereafter in America, this was the general method used. Applied to wheat, which is self-fertilized, no lasting success could be achieved and no new varieties developed unless it happened that accidental hybrids or mutants were selected for propagation. In order to maintain improvement it is necessary to keep on selecting the best plants. Indeed, strains developed by this method have rarely been able to maintain themselves permanently unless based originally on the selection of hybrids or mutants, accidental or artificial. An improvement of the method, though no change in principle, was introduced when single individual plants were selected for propagation. When these happened to be hybrids or mutants, new varieties, which sometimes proved to be of great value, were originated.

Artificial Hybridization

The breeding of wheat by artificial hybridization was begun during the middle of the nineteenth century. It represented an immense advance, since by this method it is possible deliberately to produce new varieties. In the beginning the procedure was relatively simple: two kinds of wheat were crossed, the seed of the hybrid plant was sown, and selection was made from its progeny. Breeders later resorted to multiple crosses: the first hybrid was crossed with another form, and sometimes the hybridization continued for a number of generations.

However, while the introduction of the method of selecting plants with desirable characters from the descendants of artificial hybrids introduced a new era in wheat improvement, nevertheless the work remained rather haphazard so long as the laws of inheritance of characters were not applied to the problems of wheat improvement. Wheat breeders endeavored to help themselves out of their difficulties by seeking correlations between characters. By correlation is meant that two characters which, so far as appearances go, are not physiologically related to each other, seem always to be transmitted together. The idea underlying these studies was that if one could ascertain what traits are inherited together, one should be able to select more intelligently the parents for a cross. For example, if redness of the bran coat were always associated with high protein content, this knowledge would be enormously helpful in the process of selecting the most promising parents for a cross, and subsequently in making selection from among their hybrid progeny.

An immense amount of work was done to establish such correlations as guides in breeding and selecting, but on the whole with but few results of practical value. Such correlations as were uncovered served merely as makeshifts employed by the breeders of the second half of the nineteenth century for lack of real knowledge of the laws of heredity. Yet two of the fundamental laws had been discovered by Gregor Mendel as early as 1865. Unfortunately, his publication was overlooked and remained generally unknown till unearthed by deVries, Correns, and Tschermak about 1900, when Mendel's laws were rediscovered and verified[1] by them and also by Johannsen. Only since that time has a real science of genetics arisen which is capable of explaining many of the phenomena of heredity, and of serving as a guide to the breeder. Only since the turn of the century has truly scientific breeding been possible. Breeders before then crossed varieties on their personal judgment and experience, guided only by what had been established in the way of correlation of characters. The result was largely a question of trial and error; yet in this period some of our most valuable varieties were produced. Noteworthy examples are to be found in Farrer's Australian wheats, Federation and Comeback, and Saunders' Canadian wheats, Marquis and Preston.

[1] For an exposition of the character of these laws the reader is referred to the book of Babcock and Clausen above cited.

Scientific Breeding by Experiment Stations

With the introduction of artificial hybridization, the practice of breeding wheat gradually passed more and more out of the hands of farmers, practical men, amateurs, and seedsmen into the hands of scientists. This is due in part to the fact that as scientific methods began to be applied, scientists naturally had the advantage over amateurs. The main reason, however, is that as systematic methods came into use it was found necessary for the best results to test out many hundreds of progeny of hybrids each year and to grow the plants chosen for propagation over a series of years. All this involves great expense and a long continuance of the work. Few private persons are able to support such work for long. Scientists are commonly connected with permanent institutions, such as agricultural colleges, agricultural experiment stations, universities, or botanic gardens, supported out of public funds or private endowments. These commonly possess the resources and the facilities to undertake large-scale, long-continuing investigations such as nowadays are required in wheat breeding. And so it is not astonishing that at the present time the practice of systematic wheat improvement has passed very largely out of private hands and is now being conducted by agricultural colleges and experiment stations. This does not mean that no new varieties are ever at the present time introduced by others; such introductions are, however, the exception. It happens now and then that a farmer is struck by some individual plant in a field of wheat, saves its seed, and propagates it. If it is a hybrid or a mutant, this may result in the introduction of a new strain or variety. The recent introduction of Blackhull wheat in Kansas is an instance of this kind.

While it is perhaps to be regretted that with the reduction in numbers of the private wheat breeder there has been a loss of individual initiative in crop-plant breeding, there are many compensations. So long as it was possible for private individuals to work successfully in originating new varieties, it happened not infrequently that varieties inferior to those already being grown, or at least not superior, were foisted upon farmers by seedsmen and others as improvements. If the variety caught the farmers' fancy, very considerable profits accrued to the introducer. Occasionally an old and well-known variety was merely given a new name and the seed sold to farmers at high prices. This sometimes happened purely from ignorance. Indeed, so long as there was a great commercial element in wheat breeding, involving the chance for large profits, possibilities of fraud upon the farmer and of injury to the reputation of the wheat from a given locality were serious.

Injury of reputation is a most significant matter. The place of origin of wheat is an important consideration in the minds of purchasers in determining price. It is therefore important that the wheat of a given geographic section be as uniform as possible and consist preferably of but a single variety. The more perfectly a wheat-growing region can standardize its wheat, the more uniform and invariable it is, the greater the sense of security of the buyer. Anything that lessens this uniformity lessens the sense of security of the buyer and induces a correspondingly unfavorable reaction in regard to the price he is willing to pay.[1] The introduction of a new variety, unless it is manifestly superior to those already grown, has this effect. Indeed, there are wheat-growing regions where relatively low average prices are received because many varieties are grown and no one is standard. No doubt one of the factors responsible for the good prices paid for the wheat of western Canada is its uniformity, for it consists predominantly of a few varieties only, indeed largely one. Experiment stations have no commercial interests at stake and painstakingly study new varieties for years and consider the economic effects of their introduction before offering them for general use. Moreover, they carefully test old or new varieties recommended by others, and oppose or encourage their introduction as their respective merits seem to the scientists of the experiment stations to warrant. On the whole, it would seem that the all-important rôle now played by the experiment station brings in its train benefits which rather more than counterbalance the general disappearance of private initiative.

[1] For assurance in purchases, millers map the wheat-growing regions.

V. COMPLEXITY OF THE PROBLEM OF WHEAT BREEDING

Great as has been the progress toward truly scientific breeding, that goal is far from having been reached. There are many obstacles still to be surmounted. One of these is the difficulty of knowing what the characters of the plant as it stands in the field, for example, length of straw, have to do with the characters of its seed. In the last analysis the farmer is interested in the seed rather than in the plant that produces it. The plant is merely a means to an end, a machine to produce seed. Its characteristics interest him only in so far as they determine the quantity and characteristics of the seed harvested.[1] Unfortunately, it is difficult to prophesy from the characteristics of a wheat plant what sort of seed it will produce. How immensely complex are the correlations between the characteristics of the plant itself and of its seed is in part dependent upon the fact that the seed is not exactly a single individual, like the young of animals. It is in fact a sort of pair of twins, because in seed-bearing plants fertilization is in a way double.

In seed-bearing plants both the male and the female reproducing cells, when mature, have two nuclei which in fertilization pair off, giving rise to two new nuclei, one of which produces the embryo, while the other produces the endosperm. The embryo or germ is the new individual; from it the daughter plant develops. It is but a small portion (less than 4 per cent by weight) of the seed, and is situated at one pole of the berry opposite to the crease or furrow that is found along one side of the seed. The endosperm is a relatively large store of reserve food which is utilized in germination by the embryo as it grows into the seedling. It enables the seedling to grow until a root system adequate for drawing nourishment from the soil has been formed. On germination the embryo becomes a parasite upon the endosperm; in its early life the embryo consumes the endosperm in order that it may grow.

[1] This naturally ceases to be true where straw has sufficient value to be a joint product of importance, or where wheat is cut for hay.

[2] The comparison of a seed with a hypothetical pair of dissimilar twins is not, scientifically speaking, strictly warranted; but as a metaphor it is accurate enough to be useful in the present connection.

One may therefore think of a seed as a sort of pair of Siamese twins, but a pair of twins in which the two individuals are not merely dissimilar[2] but in which one, the embryo, becomes a parasite upon the other, the endosperm. It must follow that the correlation of plant characters with the inheritance of endosperm characters is complex; the endosperm, though formed by the same parents, may have a somewhat different inheritance from its embryo twin, just as two children need not necessarily possess exactly identical combinations of the characters of their parents. The miller is not interested in the embryo; he endeavors to remove it as completely as possible from flour and he would pay a premium for wheat without any embryo at all. His interest lies in the other twin, the endosperm. Yet it is through the embryo that the inheritance of endosperm characters is passed down from generation to generation.

It is easy to understand that the wheat breeders of the last half of the nineteenth century encountered difficulties when they endeavored to establish correlations between endosperm and plant characters, i.e., when they endeavored to foretell from the character of the wheat plant what would be the characters of its seed and to predict the characteristics of the seed of its progeny. It is obvious that the establishment of such rules would facilitate breeding immensely. An enormous amount of experimentation was done with comparatively meager results owing to the complexity of conditions. Certain correlations were, however, established in a general way, though subject to numerous exceptions. Some of these are of interest in the present connection.

Established Correlations

It was established that in general, though subject to exceptions, a longer growing period is usually accompanied by greater yield, larger size of individual berry, and, unfortunately, by lower protein content also. As a rule, wheats that produce flour with characteristics desired by bakers of bread, have a high protein content, though to this there are exceptions. Hence, it may be said that generally the highest yields are usually incompatible with the highest

protein content.[1] Large size of the wheat berry, as has been stated, is apt to go with low protein content. Usually, too, glassy or vitreous appearance and translucency of the endosperm indicate high protein content, though not invariably. In short, with some exceptions, a long growing period and high yields go together, and are usually incompatible as a rule with high protein content. To put it still another way, most of the long-growing-period wheats, to which the most widely grown of all wheats, the so-called winter wheats, belong, are usually heavy yielders of the softer kinds of wheat, whereas most of the short-growing-period wheats, the so-called spring wheats, are usually light yielders of the harder, higher-protein sorts of wheats. Under favorable circumstances hard winter wheats have been developed and perfected. For a given variety, cultural conditions which favor a long growing period, such as deep plowing, heavy fertilization, thin seeding, plenty of moisture, result usually in lowering protein content. Climate alone has an immense influence not only on the yield but also on the chemical composition of the seed of a given variety of wheat.

Especially important seems to be the length of the period between flowering and maturity. It seems that as the fertilized flower begins to develop into the seed the protein is deposited in it first; the starch accumulates more gradually later, and over a longer period. Hence, for a given variety, the longer the interval between flowering and maturity the more time is there for starch to be deposited and accumulate in the seed. The proportion of protein to starch in the mature seed must be reduced thereby, though the absolute quantity may not be changed. Therefore, anything that lengthens the period between flowering and seed maturity tends to reduce the percentage of protein in the ripe seed. This usually means a reduction in bread-making quality since, other things being equal, quality for this purpose depends upon the percentage of protein. At the same time it is obvious that, if the protein content does not much change, whereas the percentage decreases due to increasing deposition of starch as the period after flowering is prolonged, the size of the seed must increase and with it the crop yield. And this is in accord with the correlations above mentioned.

Environmental Factors

And so it also becomes obvious that anything that lengthens the period between flowering and ripening should lower protein content and increase yield. A long growing period may be an inherent characteristic of a given variety, but this period may more or less be lengthened or shortened by climate, weather, or method of cultivation. Thus statisticians have established the probability that cool, cloudy, or even rainy weather at the time of flowering favors high yields. The physiological reason for this correlation[2] is that at the time of blossoming there is an enormous increase in the water requirements of the plant because transpiration, i.e., loss of water from the surface of the plant, is greatly increased. The sudden demand for moisture that accompanies blossoming is difficult for the roots of the plant to meet. The result is more or less rapid dessication of the annual plant leading to its final death. The more dessication, the greater the corresponding injury and the shorter the subsequent life of the plant, the smaller the seeds, the smaller the yield, and the higher the protein content. Hence, it follows that anything that reduces transpiration, i.e., the loss of water from the plant's surface, would tend to reduce the extent of the dessication at the time of blossoming, as well as the extent of the injury resulting therefrom and would lengthen the subsequent life of the plant. This in turn would tend to increase yield while reducing the percentage of protein. It is obvious that high humidity of the atmosphere would tend to reduce evaporation. And this explains why rainy and cloudy weather at the time of flowering tend to increase yields. Other things being equal, wind would increase evaporation and tend to have the opposite effect.

[1] It follows that it is obviously unfair, as is done so frequently, to assert that agriculture in one country is more efficient than in another because wheat yields are greater. The character of the varieties it is possible to grow in the two countries with very different climates is probably at least as important a cause of differences in yields as agricultural technique.

[2] This has been established by the experiments at the Food Research Institute. See H. L. van de Sande Bakhuyzen, "Studies on Wheat Grown under Constant Conditions," *Plant Physiology*, January 1928, III, 1–30.

It is obvious, then, that yield and protein content are not solely determined by heredity but that the effects of inheritance are modified by environment from season to season and from place to place. Therefore, it is difficult to know in any one year to exactly what extent the yield and protein content of that year are due to inheritance and to what extent they are due to environment. For this reason a new variety must be tested for many years so as to eliminate the effect of yearly fluctuations in environment before one can estimate the part played by inheritance in determining yield and protein content. In wheat-breeding work it would therefore seem worth while, in addition to growing field plots, to grow a few plants of each variety under test in rooms in which all environmental conditions are kept constant. This does not hitherto seem to have been attempted, but the writer is convinced that the time that could be saved and the information that can be obtained in only this way, not merely concerning protein content but also concerning growth rates at different stages, would many times pay the added cost.

Inheritance of Qualitative Characters

Yield and protein content are characters that are sometimes termed quantitative to distinguish them from other types that are qualitative. A qualitative character is one that is either present or absent; presence or absence of awns and presence or absence of pigment in the seed coat are such characters. A quantitative character is one that is always present but to varying degree. The mode of inheritance of qualitative characters is understood; they obey Mendel's laws. Unfortunately, however, they have little or no economic importance. Grain-yielding capacity, on the other hand, perhaps the most important character to control, like almost all quantitative characters either does not obey Mendel's laws or else does so under conditions so complex that it has as yet been impossible to unravel them under field conditions. Similar conditions prevail for other characters desirable to control, such as length of growing period, resistance to drought, to frost, to lodging (stiffness of straw), to shelling out, and to disease. The conditions under which these characters are inherited seem very complex and are not yet clearly understood. Nevertheless, progress is being made; and even with what is already known, more rapid advance is being achieved in wheat improvement than would have been possible in the days before the recognition of the significance of Mendel's fundamental discoveries.

It must by this time be obvious to the reader that all purposes cannot be met in a single variety of wheat any more than with domestic animals. A horse cannot at one and the same time be an ideal draft animal and also a good racer. The purpose of the wheat breeder is not to produce a single, in all respects ideal, variety, but a series of varieties, each of which is as nearly ideally adapted as possible to the economic conditions of the particular wheat-growing section for which it is designed. Yield will usually be the foremost objective of the wheat breeder; but he must also consider quality. He will oftenest produce varieties that represent a compromise between the highest yielding power and the highest quality. The need for continuing wheat improvement seems unlikely to disappear for many years to come. In the past the objectives of wheat breeders have had to be modified to meet changing conditions of agriculture and of civilization. The wheat that is most profitable for extensive one-crop farming may prove the reverse when the type of farming becomes more diversified and more intensive. The type of flour that is satisfactory to the consumer in one generation may no longer prove so in a later generation, when taste changes and when methods of converting the raw wheat into the food that comes to the table are altered. There will be work for the wheat breeder for years to come, and it is therefore gratifying that so much progress is being made through purely scientific investigations in learning the nature of the fundamental laws of heredity, knowledge of which must inevitably facilitate enormously the approach to perfection in wheat cultivated for any given purpose.

This issue is the work of Carl L. Alsberg, with the assistance of E. P. Griffing

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