

University of Miami

The Genetic Origin of Spelt and Related Wheats

By ALFRED C. ANDREWS

KIHARA (1944) advanced the first sound theory regarding the genetic origin of spelt, *Triticum spelta* L. McFADDEN and SEARS in the same year (1944) reported the artificial synthesis of spelt and later (1946) independently advanced the same theory as KIHARA, but based it on detailed evidence rather than merely logical grounds. The last named article constitutes the point of departure for the present one, since all speculations regarding the origin of spelt which predate this theory are of historical interest only.

The conclusion of McFADDEN and SEARS regarding the genetic origin of spelt and related wheats was this: *Triticum aegilopoides* Bal. gave rise to *T. monococcum* L. *T. monococcum* × *Agropyron triticeum* Gaertn. produced *T. vulgare antiquorum* Heer. *T. dicoccoides* Kcke. gave rise to *T. dicoccum* Schrk. *T. dicoccum* (or *T. dicoccoides*) × *Aegilops squarrosa* L. produced *T. spelta*. *T. vulgare antiquorum* × *T. spelta* produced *T. compactum* Host and *T. vulgare* Vill. (now *T. aestivum* L. by the new taxonomic rules).

Their conclusions regarding the regions of origin and subsequent migrations were these: If *T. dicoccoides* was one of the parents of *T. spelta* and *Ae. squarrosa* the other, *T. spelta* can reasonably be assumed to have originated in southwestern Asia in a state of nature, since *T. dicoccoides* occurs only in that region, specifically in southern Armenia, northeastern Turkey, western Iran, Syria, and northern Palestine. But if *T. dicoccum* was one of the parents, it probably arose under cultivation, and the place of origin could have been either southwestern Asia or southeastern Europe, since *Ae. squarrosa* is endemic in both regions. Although southwestern Asia is usually considered the homeland of the hexaploid wheats, *T. spelta* could have originated in southeastern Europe either on the northern slope of the Caucasus or in the Crimea. From either of these areas migration would have been impeded on the south by the Caucasus mountains and the Black Sea and on the east by the Caspian Sea, arid climate, and cultural barriers. To the southwest, its migration into southern and central Europe would have been blocked by the Balkan and Carpathian mountains, as well as by cultural barriers and the presence of pre-existing free-threshing wheat. Its most natural course of spread was therefore to the northwest through the rich agricultural regions of the Ukraine, White Russia, Poland, and thence to Germany. There is linguistic evidence, they say, for the northern route in the existence of names for spelt in all the major Baltic and Atlantic languages from southern Russia to northern Spain (viz., Russian polba, Polish orkisz, German Dinkel, Saxon and English spelta, and Asturian Spanish escandia), while there is none for the southern route. The conjecture that spelt arose in southwestern Asia is difficult to prove on historical and archaeological grounds, since the

ancient peoples in much of the territory through which it would have to pass to reach western Europe have left no literature, and conditions in that part of Europe are unsuitable for the preservation of material as perishable as wheat.

SCHIEMANN (1947) reviewed the article by McFADDEN and SEARS and expressed full concurrence in the genetic findings.

BERTSCH (1949), obviously without having seen any of the above literature, published an article in which he argued that *T. compactum* is the oldest true wheat and that it arose from *T. monococcum* × *T. dicoccum* in southwestern Germany about 3,000 B.C. by crossing in cultivation. Having finally read SCHIEMANN's review, he attacked the theory of McFADDEN and SEARS in a longer article (1950), in which he argued that the artificial synthesized spelt of McFADDEN cannot survive in a natural state, pointed out that there has been no prehistoric find of spelt either in the assumed homeland or along the conjectured route, and rallied to the defense of his own theory, again arguing that spelt arose from *T. dicoccum* × *compactum* in southwestern Germany and that *T. vulgare* arose from the association of spelt and *compactum*, and maintaining that *T. vulgare antiquorum* is only a prehistoric form of *compactum*, hence his derivation is identical with that of McFADDEN and SEARS. He conceded that one troublesome factor in his derivation was the D genome, which occurs especially in the genus *Aegilops*, and disposes of this by assuming that an identical genome arose spontaneously in emmer and by assuming for *T. vulgare antiquorum* an unknown X genome which produced so radical a change that it must be equated with the B genome of emmer. He argued against the derivation of spelt from *T. dicoccum* × *Ae. squarrosa* and of *T. vulgare antiquorum* from *T. monococcum* × *Agr. triticeum* on the ground that *T. compactum* is the oldest form, and where it arose *Agr. triticeum* and all species of *Aegilops* are lacking, hence *T. vulgare antiquorum* arose as a mutation in central Europe.

SCHIEMANN (1951) repeated her view that the origin of hexaploid wheats as amphidiploids of a tetraploid wheat crossed with *Aegilops* gained new probability from McFADDEN and SEARS' synthesis of *T. spelta* as an amphidiploid from *T. dicoccoides* × *Aegilops squarrosa* with $n = 7 = D$ -genome. She pointed out that this presumed cross must have occurred in the common area of the two parents, which would imply the Caucasian center. From this area the hexaploid wheats, with the compact type as the initial representative, must have spread westward in the Neolithic period, while the lax forms of *T. aestivum* began to attain importance during the Roman empire. But in the same article she also called attention to the fact that hulled forms of hexaploid wheat of the lax type of *T. spelta* have never been found in Transcaucasia, but are endemic

in the upper and middle sections of the Rhine valley (Switzerland and southwestern Germany). Further, such forms do not appear in these countries before the Bronze age, which makes them later than the Neolithic wheats *T. monococcum*, *T. dicoccum*, and *T. compactum* (as well as a dense, six-rowed barley). These two facts led FLAKSBERGER and SCHIEMANN in 1939 to conclude that *T. spelta* originated in the Rhine valley at the beginning of the Bronze age from *T. dicoccum* (4 x-) \times *T. compactum* (6 x-).

HELBAEK (1952) pointed out that no Neolithic culture is known that was based on naked wheat (whether tetraploid or hexaploid), the traces occurring in Europe most frequently as insignificant admixtures with emmer and einkorn. Whenever it was possible to identify the actual variety with certainty, it was found to be *T. compactum*.

SCHIEMANN, this time in collaboration with STAUDT (1958), took cognizance of the second article of BERTSCH, fully exposing the inadequacy of his theory and again substantially supporting the theory of MCFADDEN and SEARS.

Meanwhile, SARKAR and STEBBINS (1956) had proposed *Ae. speltooides* as the source of the troublesome B genome; and RILEY, UNRAU, and CHAPMAN (1958) published supporting evidence.

SEARS in private correspondence has pointed out that BERTSCH was wrong in stating that the F_1 of emmer \times *Ae. squarrosa* is sterile and that the assumption, supported by SCHIEMANN and STAUDT, that *T. compactum* is the oldest hexaploid wheat implies that in the original synthesis of tetraploid wheat \times *Ae. squarrosa* the tetraploid involved was free-threshing and that *Ae. squarrosa* carried the *compactum* gene. MCFADDEN recognized this dilemma and tried to resolve it by suggesting that *T. vulgare antiquorum* was a tetraploid, a proposal which, according to SEARS, newer information renders untenable, for if it actually was a tetraploid, it could not have carried the *compactum* gene, C, since this is located on a chromosome of the D (*squarrosa*) genome, which *antiquorum* would have lacked. Therefore *T. spelta* \times *T. vulgare antiquorum* could not have given rise to *T. compactum*. SEARS points out that a greater difficulty lies in assuming the existence of the *compactum* gene in *Ae. squarrosa*, for not only is it lacking in all known strains of this now fairly widely collected species, but there is grave doubt that *Ae. squarrosa* could exist with the *compactum* gene. This gene practically sterilizes hexaploid wheat when it is present in four doses instead of the normal two, and in SEARS' opinion it is extremely unlikely that a diploid carrying it could exist, for it would almost certainly be completely sterile.

HELBAEK (1959) proposed that *T. compactum* arose in the Near East from emmer \times *Ae. squarrosa*. SEARS comments that the proposal is untenable, since it assumes the existence of a tetraploid wheat similar to *T. carthlicum* Nevski (formerly *T. persicum* Vav.) (for which there is no evidence) to serve as one parent and that the variety of *Ae. squarrosa* which served as the other parent carried the *compactum* gene, which is extremely unlikely.

With regard to the conclusion of FLAKSBERGER and SCHIEMANN that *T. spelta* arose in Germany from *T. compactum* \times *T. dicoccum*, SEARS says that simple

segregation from *compactum* \times *dicoccum* could not yield *spelta*; a mutation of C to c would also be necessary. He is dubious of reports of *spelta* types obtained from this cross, suspecting that some were *spelta-compactum* and others chromosome aberrants.

SEARS, on genetic grounds, is still convinced that *T. spelta* preceded *T. vulgare*. The free-threshing character of the latter is determined by a single gene, Q, located on one of the chromosomes of the A genome. Current einkorns all have the *spelta* allele of this gene, and, as in the case of the *compactum* gene, it is unlikely that a diploid wheat could exist with the *vulgare* gene.

SEARS' present conviction is that both the *vulgare* and the *compactum* genes arose as mutations from *T. spelta* by appearance of the Q gene after the polyploids were formed. The Q gene can have arisen at either the tetraploid or the hexaploid level, and probably only archaeological evidence can determine the actual level. But the *compactum* gene must have originated in a hexaploid wheat, and since *T. compactum* has both the Q gene and the *compactum* gene, it is two mutations away from the primitive type, q to Q on chromosome IX of the A genome and c to C on chromosome XX of the D genome (SEARS 1959). And since *T. vulgare* is a transitional type between *T. spelta* and *T. compactum*, it is logical to assume that *vulgare* (QQ) appeared first and *compactum* (QQCC) later. If the mutation of c to C preceded the mutation of q to Q, the resulting qqCC form would have been distinct from both *spelta* and *compactum*. But if C did precede Q, or especially if both appeared at about the same time, there would normally have been a crossing of *T. compactum* with the parental *spelta* form, which would have given rise to *T. vulgare*. On the other hand, if the prehistoric *compactum* was not genetically the same as modern *compactum*, perhaps differing from *spelta* by a single gene instead of two, hybrids with *spelta* would not have segregated the *vulgare* type. In that event, the modern *compactum* could have arisen later, after the appearance of *vulgare*, as a mutant from this form. In summary, SEARS' present view is that *T. vulgare antiquorum* is actually a form of *T. compactum* and that *T. spelta* originated by hybridization of *T. dicoccum* (or *T. dicoccoides*) \times *Ae. squarrosa* and that *T. compactum* arose by subsequent mutation. With specific reference to *T. vulgare antiquorum*, SEARS, in taking this to be actually *compactum*, is adopting the prevalent view. WATKINS (1930) expressed the view that all the earlier identifications of Neolithic samples of wheat as *vulgare* might be wrong. BERTSCH (1939) similarly refused to accept the samples as *vulgare*, commenting that the latter arose in the Bronze age. SCHIEMANN (1940) commented that scholars long before BERTSCH came to recognize that Neolithic finds of naked wheat were *compactum*. This *compactum* does differ from modern *compactum*. It has small, short, roundish kernels and thick awns.

I have proposed to SEARS that objections to the genetic theory that *T. spelta* arose from *T. dicoccoides* \times *Ae. squarrosa* in the natural area of the latter are answered if evidence exists that this hybrid became an element of a mixed crop of emmer and einkorn, but only a fractional one, and that this

medley was brought to southwestern Germany and northern Switzerland, where conditions particularly favorable to spelt caused it to emerge as a major crop. The present article aims to present the evidence supporting this hypothesis. In the course of correspondence with SEARS, the article by HELBAEK (1959) appeared, setting forth substantially the same proposal, but stressing different aspects of the problem.

By way of preface, it must be pointed out that the linguistic evidence presented by MCFADDEN and SEARS for a northern route for spelt from southwestern Europe to western Europe actually demonstrates nothing of the sort. The following is the actual linguistic picture.

To begin with, no Classical Greek name positively denotes spelt. Furthermore, there is no reliable evidence that spelt was raised in classical Greece or Asia Minor, nor is there any sound ground for assuming, in the face of the lack of specific semasiological evidence, that it was raised there, for this region lies somewhat south of the optimum range of spelt, which today is cultivated only in scattered sections of Europe. But conditions in Italy, more especially in the north, were relatively more favorable for raising spelt, and it is therefore possible that it was cultivated there in the classical period. The Latin nomenclature is the chief key to solution of the problem.

The most important, perhaps the only, wheat raised by the early Romans was usually called far. This was a hulled wheat and probably specifically emmer, *T. dicoccum*. The manner in which the term far is used in the late republican and early imperial periods and the descriptive epithets applied to the wheat it denoted are sometimes perplexing, but there is no clear evidence that the wheat was spelt. But survivals of the term in Italian mostly denote spelt, and this suggests a shift of application from emmer to spelt at some indeterminable time between the early imperial and the modern period. The source of far (earlier *farr) (SOMMER, 1914) may be (1) *bhar-es- 'bristling awn, bearded grain' (HOOPS, 1905; SCHRADER, 1917—18); (2) *bher-(e)s- 'break, crush', developing the meaning 'eat', then becoming *bher-'split,' the source of various terms for edibles; or (3) *bher-es- 'be pointed, bristle' (TUCKER, 1931). Cognate with far are Gothic barizeins 'made from barley', Old Norse barr 'grain, barley', Old English bere 'barley', Old Church Slavonic buru 'millet', and Russian borosno 'rye-meal' and boru 'millet'. HROZNY (1914) calls attention to Arabic burr or barr, the basic meaning of which he takes to be 'naked (grain) separated (in the threshing), freed (from the hulls)', thus a term more especially for hulled wheat as opposed to naked wheat, since hulled wheat requires special processing in the milling to free the grain from the hulls. He notes the similarity of the Semitic term to the European group and suggests that the Semitic term may be the source, commenting that in any event some connection apparently exists. The diversity of denotations of the Indo-European cognates indicates that in primitive Indo-European, prior to the dispersal through Europe, that word attained no greater specificity than as a term for bearded cereals. As for the connection with the Arabic word, it is more likely that the origin of both the Semitic and the

Indo-European words is to be sought in Syria or Asia Minor. The early Romans used far as a term for emmer. The prehistoric European emmer constitutes a distinct type, var. *europaeum* Vavilov, which was probably developed in the Syrian center and reached Europe very early. According to SCHIEMANN (1932), the route by which it reached western Europe was Syria — Asia Minor — the northern Balkans — Bosnia — the Dinarian Alps — Upper Austria — Bohemia — southwestern Germany and northern Switzerland. The word which is the source of far may not have become limited to the meaning 'emmer' until it reached Italy, or again it may have acquired this specific meaning somewhere along the route taken by emmer. The prime factor is that both the word and the cereal almost certainly came up the Danube valley.

Scandula is reported by PLINY (N. H. 18.62) to be a Latin term for a kind of far raised by the Gauls, which they called brace. The Latin term, originally denoting a shingle or splint, was probably applied to types of wheat with glumes which covered the kernels like shingles, hence hulled wheat in general (SCHULZ, 1918). In the Po valley it became and remained a specific term for spelt, with some extension to *Hordeum distichum* L. (PENZIG, 1924) and some spread to the Iberian peninsula (e. g., Asturian Spanish escandia) (MEYER-LUEBKE, 1935; SCHULZ, 1911, 1918). The basic meaning of brace in Celtic was 'malt, grain soaked in water to germinate so that it can be used for making beer'. Since far usually denoted emmer, some scholars have taken brace to be a type of emmer (e. g., JASNY, 1944); but what apparently occurred was an extension of the term from barley to spelt (WARTBURG, 1928—46). The Celts accordingly acquired spelt from the Germanic area, as is clear from the cultivation of spelt in northeastern France in the early medieval period (GRADMANN, 1909), but without a name, and extended the term brace to it, since they also used spelt for making beer, as is still the practice today.

Latin spelta must originally have been a term for hulled grain, then a little more specifically a term for hulled wheat, somewhere in the Germanic area (PICTET, 1877; HOOPS, 1905; SCHRADER, 1906—07). In that area spelt presumably became the most important of the three hulled wheats, and the term accordingly acquired the specific meaning of spelt (SCHULZ, 1911). Such exports of wheat as were made from the Germanic area to Italy presumably consisted largely of spelt. Although, on the basis of PLINY, spelt was being raised in the Po valley in his time by Gauls, there is no clear evidence that it was being shipped to other sections of Italy. But even if it was being shipped, the quantity must have been insufficient to meet the demand. It is therefore not surprising to find evidence that wheat was being shipped in undetermined quantities from the Germanic area, especially Pannonia, to central and southern Italy (SCHULZ, 1911; BERTSCH, 1949). And since it is specifically with Pannonia that Hieronymus (In Ezech. 8.14) associates the term spelta, it can be assumed that this wheat was mostly spelt. Hence the name was brought with spelt imports to central and southern Italy, precisely the area where

current Italian dialectic variants of the word tend to have the specific meaning of spelt (PENZIG, 1924). This explains the use of the two names *scandula* and *spelta* in the Edict of DIOCLETIAN (1.8) in 301 A.D. The former became current in the Po valley and the latter in central and southern Italy. Spelt had gained in production in the Po valley and as an import in the rest of the peninsula, and meanwhile emmer had waned in production, giving ground to naked wheat, and perhaps was being raised in Italy only for local use. Hence the drafters of the Edict omitted far, i. e., emmer, from the Edict, but since they recognized the importance of spelt in Italy (although not in the East), they not only listed it, but gave the names by which it was known respectively in northern Italy and in central and southern Italy. Moreover, the listing of *spelta munda* in the Edict (1.7) without a synonym implies that this was imported German spelt, shipped with the hulls removed as a routine measure to reduce the cost of transportation.

The term *scandula*, as already pointed out, remained largely confined to the Po valley, with some extension to the Iberian peninsula. *Spelta* became the prevalent term, spreading to the Celtic area, where it displaced brace and became Modern French *épeautre*. It was also borrowed in Germanic, since Pannonia was no longer a part of the Germanic area and meanwhile had sharply declined in spelt production (cf. BECKER-DILLINGEN, 1927), appearing in Old High German as *spelta*, which developed into Germanic *Spelz*, Anglo-Saxon, English, and Danish *spelt*, and Swedish *spält*. This word also spread to the east, appearing in Polish as *szpelta*, in Czech as *sspalta*, and in Russian as *polba*.

The Celts presumably acquired spelt from the contiguous area of southwestern Germany and northern Switzerland, and since they extended their term brace to it, they acquired it without a name. Today in most of Germany spelt is called *Spelz*, but also *Schwabenkorn* with allusion to the concentration of spelt production in Swabia in southwestern Germany. But in Swabia *Spelz* is not in popular use, but rather such terms as *Dinkel*, *Einkorn*, *Fesen*, and *Korn*, mostly non-specific in character. This strengthens the Celtic evidence that at the time of acquisition of spelt neither *spelta* nor any other specific name for spelt was in use in southwestern Germany.

Let us return now to the theory of MCFADDEN and SEARS. BERTSCH, having published in 1949 a theory regarding the origin of *T. compactum* which he considered eminently plausible, and then discovering in 1950 that MCFADDEN and SEARS had three years previously promulgated a theory with which his clashed, amassed factual evidence to support his own theory. Ironically, much of the factual data he accumulated, when correctly interpreted, actually supports the genetic conclusions of MCFADDEN and SEARS regarding the origin of spelt by shedding light on the transmission route and the cultural dissemination center.

The reasoning goes thus. The genetic theory of the origin of spelt proposed by MCFADDEN and SEARS is sound. This means that spelt originated in southwestern Asia, if *T. dicoccoides* was one of the parents,

and in southwestern Asia or southeastern Europe if *T. dicoccum* was one of the parents. KUCKUCK (1957) found *T. spelta* being grown in Iran, within the natural range of *T. dicoccoides*, with no indication of introduction from Europe. This fact, in conjunction with the failure of Russian botanists (cf. VAVILOV, 1926), despite systematic search, to find any spelt in Khorasan, Tukestan, Afghanistan, Asia Minor, or Mongolia, suggests that spelt culture in Iran may be a phenomenon of the same sort as that postulated for southwestern Germany and northern Switzerland, viz., the emergence of spelt to the status of an independent crop under favorable conditions. It also tends to point to southwestern Asia rather than southeastern Europe as the area of origination. In any event, conditions in the general area are not conducive to the preservation of perishable material. It is therefore not surprising that early prehistoric remains have not been found either in the presumed area of origination or along any conjectured migration route.

BERTSCH states that the oldest remains of naked wheat belong to *T. compactum* and come from the spiral-ceramic settlement of Öhringen, the band-ceramic settlement of Böckingen, and two Rössener settlements of Heilbronn about 2.2 km. apart. All four settlements are in southwest Württemberg in southwestern Germany. The remains date ca. 3,000 B.C. (full Neolithic period) and are limited in quantity. Larger amounts of emmer and einkorn were also found at these four stations, but no spelt. By the late Neolithic period *compactum* became the dominant cereal in the palafitte area. The earliest identified remains of spelt come from the late Neolithic settlement of Riedschachen in the Federsee and consist of three ears of spelt, with much more numerous specimens of emmer, einkorn, club wheat, and barley. In the late Bronze age (ca. 1,000 B.C.) spelt was the chief cereal of the Swabian area, as well as Federsee and Zurichsee in northern Switzerland. Swabia was apparently also the center of diversity of spelt, and BERTSCH comments that geneticists take such an area to be the area of origination of a species of grain. BERTSCH also says that the band-ceramic people, who migrated from east to central Europe in the full Neolithic age, did not have spelt, and it was still lacking for the palafitte people on the large lakes of the Alpine foreland. He also notes that emmer and einkorn were raised as a mixed crop in the prehistoric period, *compactum* later being a component.

These facts require reevaluation. Let us assume that spelt originated in southwestern Asia or southeastern Europe, as the theory of MCFADDEN and SEARS postulates. If it arose from *T. dicoccoides* × *Ae. squarrosa*, it intruded into cultivated crops of emmer and einkorn. If it arose from *T. dicoccum* × *Ae. squarrosa*, it became a part of the same mixed crop. If the specific ecological conditions prevailing were such that spelt, after arising, was barely able to survive against the competition of emmer and einkorn, it would constitute so small a fraction of this crop that its presence would probably not be detected even if prehistoric remains of this mixed crop were found. This condition would prevail both in the area of origination and up the entire length of the Danube valley, the route of transmission of

emmer and einkorn. But in Swabia different conditions prevailed. This is the area of maximum spelt production today, to such a degree that spelt is often referred to as Schwabenkorn, because conditions there are highly favorable to raising spelt and less favorable to raising other types of wheat. Contrary to BERTSCH, not all geneticists maintain that the center of diversity of a cultivated cereal is presumably the center of origination. EDGAR ANDERSON, of the Missouri Botanical Garden, maintains that disturbance of the ecology of an area by man in the course of the cultivation of plants upsets the balance and renders possible the survival of variants which normally would perish. This creates the impression of a center of origination, of the type postulated by VAVILOV, whereas actually the area is only one in which variants have a better chance to survive. In the case of spelt, which was already a constituent of a mixed crop, the activity of man played a role only in bringing this crop from a relatively warm climate to a relatively cool one, more favorable to spelt and less favorable to emmer and einkorn. Then toward the end of the Bronze age the climate in that area became cooler and moister, producing conditions still more favorable to spelt. The change in the character of the mixed crop would not have been opposed by farmers, since spelt was more resistant to disease, less subject to raids by birds, equally productive, and superior in the quality of its meal (cf. BERTSCH, 1949). So spelt was present in a mixed crop of emmer and einkorn and came in time to constitute a substantial fraction of that crop, at the same time producing variations which survived. This was a situation favorable to the origination of *T. compactum* and *T. vulgare* by mutation, and the former is attested for the late Neolithic period.

When the above evidence is meshed with the linguistic evidence, a clear, consistent picture emerges. *T. spelta* arose by crossing somewhere in the general area of southeastern Europe and southwestern Asia and became a fractional component of a mixed crop of emmer and einkorn. This mixed crop moved up the Danube valley, eventually reaching southwestern Germany and northern Switzerland, where particularly favorable conditions caused spelt in time to become the dominant cereal in the mixed crop. Spelt was present in this crop, but not in identifiable quantities, as early as 3,000 B.C., and the accelerating impact of cooling climate did not occur until the late Bronze age, about 1,000 B.C. The shift in composition of the crop was therefore gradual, and the farmers felt no need of a special term for the spelt component of the crop. The Alamanni migrated to this region and conquered it about 500 B.C. They adopted spelt as a crop and became habituated to it. When later they moved to Pannonia, they took along the cultivation of spelt, although people living in Pannonia were raising emmer and einkorn. A distinguishing term for spelt thus became necessary, and the Alamanni restricted a general Germanic term to the specific meaning of spelt. This term was the source of Latin *spelta*. As spelt acquired greater importance as an independent crop, the need for this name continued, since spelt was now in active competition with naked wheat. Hence Latin *spelta* not only moved to France and displaced the native Celtic

term but also to Germany (except Swabia) and from there west to England, north to the Scandinavian countries, and east to Poland, Czechoslovakia, and Russia.

Summary

The genetic theory of McFADDEN and SEARS regarding the origin of spelt and related wheats is defended. This theory postulates that *T. spelta* arose from *T. dicoccum* (or *T. dicoccoides*) \times *Ae. squarrosa* in the natural area of the latter. This hybrid became a component of a mixed crop of emmer and einkorn, but only a fractional one, and this medley was brought to southwestern Germany and northern Switzerland, where conditions particularly favorable to spelt caused it to emerge as a major crop.

Zusammenfassung

Die genetische Theorie von McFADDEN und SEARS über den Ursprung des Spelzes und verwandter Weizen wird unterstützt. Nach dieser Theorie ist *T. spelta* aus der Kreuzung *T. dicoccum* (oder *T. dicoccoides*) \times *Ae. squarrosa* im natürlichen Areal von *Ae. squarrosa* entstanden. Diese Hybride wurde ein, allerdings nur in Spuren vorhandener Bestandteil einer aus Emmer und Einkorn bestehenden Mischkultur, und dieses Gemisch gelangte nach Südwestdeutschland und der nördlichen Schweiz, wo für den Spelz besonders günstige Bedingungen zu seiner Entwicklung als selbständige Kulturpflanze führten.

Literature

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Aus dem Institut für Pflanzenzüchtung Kleinwanzleben der Deutschen Akademie der Landwirtschaftswissenschaften zu Berlin

Die Hypokotylfarbe als Markierungsfaktor von Genomstufen der Zuckerrübe

Von HANS EBERHARD FISCHER und KLAUS FÜRSTE

1. Problemstellung

Mit zunehmender Ausweitung des Anbaues anisoploider *Beta*-Rüben ist ein kontinuierlich ansteigender Arbeitszeitaufwand zur zytologischen Kontrolle von Zuchtmaterial und Saatgut notwendig. Diese Kontrolle erfolgt in der Hauptsache durch Chromosomenzählungen (HUTIN 1962, NEEB 1962, RADERSMA 1962). Andere Methoden, wie die Trabantenchromozentren- und die Plastiden-Methode (REITBERGER 1956, GRAF 1958, 1959, BUTTERFASS 1958, 1961) sind mit Nachteilen sowie Schwierigkeiten verbunden und konnten sich nicht allgemein durchsetzen (vgl. FISCHER, SCHNEIDER und ENDERLEIN 1963).

Es wäre eine wesentliche Erleichterung, wenn man zur Genomstufenanalyse makroskopisch sichtbare Merkmale verwenden könnte. Bisher zeigte sich jedoch, daß die Variabilität morphologischer Merkmale, wie z. B. die des Längen-Breiten-Indexes der Blätter, recht groß ist und keine Trennung der einzelnen Pflanzen nach ihrer Genomstufe erlaubt.

Eine weitere Möglichkeit, die Genomstufe zu identifizieren, besteht in der Verwendung von Markierungsgenen, besonders solchen, die auf Grund intermediären Erbganges des betreffenden Merkmals auch heterozygote Pflanzen erkennen lassen. Wenn man den einen Faktor eines entsprechenden Faktorenpaares auf eine tetraploide Population überträgt, den anderen auf eine diploide, so werden bei Kreuzung beider Populationen Nachkommen erzielt, deren Genomstufenzusammensetzung unmittelbar festzustellen ist. Um die Pflanzen innerhalb einer Population frühzeitig nach ihren Genomstufen trennen zu können, muß es sich um Merkmale handeln, die bereits am Keimling auftreten. Hierfür ist die Hypokotylfarbe geeignet.

2. Durchführung und Auswertung der Beobachtungen und Untersuchungen

Nach DUDOK VAN HEEL (1931) sowie FILUTOWICZ und SZOTA (1961) bestimmt bei der Zuckerrübe ein

Faktorenpaar die Hypokotylfarbe, das von den letztgenannten Autoren mit R-r symbolisiert wird. R ist für die Bildung von roten Farbstoffen aus der Gruppe der Betanine verantwortlich. Läßt man tetraploide Populationen mit grünem Hypokotyl und diploide mit homozygot rosa Hypokotyl untereinander abblühen, so finden sich neben tetraploiden „grünen“ und diploiden „rosa“ Pflanzen, die durch Befruchtungen innerhalb der entsprechenden Population entstanden sind, triploide Pflanzen, deren Hypokotyl weniger stark bzw. etwas anders gefärbt ist als das der diploiden. Die heterozygoten Pflanzen besitzen demnach offenbar weniger Betanine im Hypokotyl als die diploiden homozygoten „rosa“ Pflanzen. Sie weisen eine Hypokotylfarbe auf, die Hellbraun oder Beige näher steht als Hellrosa. Tetraploide „grüne“ Pflanzen werden mit rrrr, diploide homozygote „rosa“ Pflanzen mit RR und triploide Bastarde mit Rrr symbolisiert. Da im Rahmen der vorliegenden Arbeit keine genetischen Analysen beabsichtigt waren, muß die Frage offen bleiben, ob es sich bei den betreffenden Faktoren um das Allel R oder um ein anderes Allel handelt. (Nach FILUTOWICZ und SZOTA liegt multiple Allelie vor.)

Die Unterscheidung der bei reziproker Kreuzung (RRRR × rr) entstehenden RRr-Pflanzen von RRRR-Individuen bereitet Schwierigkeiten, da RRr-Typen den in bezug auf den Farbfaktor homozygoten Pflanzentypen farbmäßig recht ähnlich sind. Man kann daher eine Kreuzung von rr- mit RRRR-Rüben für den genannten Zweck nicht empfehlen, zumal es relativ schwierig ist, RRRR-Populationen zu finden und unter Kontrolle zu halten. Brauchbare Ergebnisse konnten nur erzielt werden, wenn rrrr- mit RR-Pflanzen gekreuzt wurden, so daß wir uns auf die Wiedergabe dieser Ergebnisse beschränken.

Die Untersuchungen erstreckten sich über die Jahre 1960, 1961 und 1962. Es wurden di- und tetraploide Pflanzen verwendet, von denen auf Grund von Beobachtungen an den Vorgenerationen anzunehmen