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Origin and Geography  
of Cultivated Plants

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## Centers of origin of cultivated plants

Devoted to the memory of  
ALFONSE DE CANDOLLE  
Author of  
'Phytogéographie rationale' (1855)  
'Phytogéographie' (1880), and  
'L'origine des plantes cultivées' (1882)

### Introduction

WHEN STUDYING THE specific composition of cultivated plants it became necessary to establish a definitely natural system relating to the development of forms within the limits of Linnaean species and genera (Vavilov, 1920, 1922). By means of a thorough study, the variation of the inherited shapes and forms turned out to be subordinate to a well-composed system. As a result of collective work, we succeeded in constructing systems of varieties and races, and general schemes of the inherited variability, for entire families of the most important cultivated plants.

Table I, which illustrates the variation within the family Papilionaceae, can be used as an example of such a system. It illustrates the diversity of forms and differentiating characteristics according to which taxonomists concerned with cultivated plants can build up their own systems, not to mention the innumerable combinations into which the different alternative characteristics can be combined. In order not to make the table too unwieldy, not every characteristic has been included but only those most obvious and distinct, which are easy to recognize. (A more detailed scheme for the variability of grasses was furnished in my paper 'Toward an understanding of the soft wheats'; Vavilov, 1923.) The traits proposed for the description of the morphological and physiological characteristics, presently existing, i.e., the forms of different Linnaean species, are, correspondingly, indicated by the symbol '+' in the table.

Similar systems have been constructed for the grasses (Vavilov, 1924), Cucurbitaceae (Vavilov, 1924), Solanaceae (Bukasov, 1925), Cruciferae (Sinskaya, 1924), Linaceae and others. They are equally applicable to self-pollinating plants as to cross-pollinating ones. Studies of the system of variability revealed a striking resemblance between a number of morphological and physiological characteristics of closely related genera and species, which represent different

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Table I. General scheme of the variability within the species belonging to Papilionaceae

Variable hereditary characteristics	<i>Pisum sativum</i>	<i>Vicia sativa</i>	<i>Vicia faba</i>	<i>Ervum lens</i>	<i>Lathyrus sativus</i>	<i>Cicer arietinum</i>	<i>Phaseolus vulgaris</i>	<i>Soya hispida</i>	<i>Medicago sativa</i>	<i>Trifolium pratense</i>
<i>Flower characteristics</i>										
<i>Color</i>										
White	+	+	+	+	+	+	+	+	+	+
Pink	+	+	-	-	+	+	+	+	+	+
Red	+	-	+	-	+	+	-	+	+	+
Violet-blue	+	+	-	+	+	+	+	-	+	+
Yellow	-	+	+	-	+	+	-	-	+	+
Variegated (flag differs from wings)	+	+	+	-	+	+	+	+	-	-
Flag and wings spotted or striped	-	+	+	-	+	-	+	-	+	-
<i>Dimensions</i>										
Large	+	+	+	+	+	+	+	+	+	+
Small	+	+	+	+	+	+	+	+	+	+
<i>Pod characteristics</i>										
<i>Wall structure</i>										
With a papery layer	+	-	-	-	-	-	+	+	-	-
Without a papery layer	+	+	+	+	+	+	-	-	-	-
<i>Shape</i>										
Linear	+	+	+	-	-	-	+	+	-	-
Rhombic	-	-	-	+	+	+	-	-	-	+
Sickle-shaped	+	-	+	-	+	-	+	+	+	-
Swordlike	+	-	-	-	-	-	+	+	-	-
Moniliform	+	-	-	-	-	-	+	+	-	-
<i>Hairiness</i>										
Hairy	-	+	+	-	-	+	+	+	+	-
Glabrous	+	+	+	+	+	-	+	+	+	+
<i>Color of unripe pods</i>										
Yellowish	+	-	-	-	-	-	+	+	-	-
Greenish	+	+	+	+	+	+	+	+	+	+
Violet-brown (with anthocyanin)	+	+	-	-	-	-	+	+	+	+
<i>Color of ripe pods</i>										
Yellowish-green	+	+	+	+	+	+	+	+	+	+
Black (dark brown)	+	+	+	-	-	-	+	+	-	+
Spotted (or striped)	-	-	-	-	+	-	+	+	-	-
<i>Dimensions</i>										
Large	+	+	+	+	+	+	+	+	+	+
Small	+	+	+	+	+	+	+	+	+	+

Table I. (cont.)

Variable hereditary characteristics	<i>Pisum sativum</i>	<i>Vicia sativa</i>	<i>Vicia faba</i>	<i>Ervum lens</i>	<i>Lathyrus sativus</i>	<i>Cicer arietinum</i>	<i>Phaseolus vulgaris</i>	<i>Soya hispida</i>	<i>Medicago sativa</i>	<i>Trifolium pratense</i>
<b>Surface</b>										
(a) Smooth	+	+	+	+	+	+	+	+	-	+
Uneven	+	+	+	-	-	-	+	-	-	-
(b) Convex	+	+	+	+	+	+	+	+	+	-
Flat	+	+	+	+	+	-	+	+	-	+
<b>Seed characteristics</b>										
<b>Shape</b>										
Orbicular	+	+	+	+	+	+	+	+	+	+
Ovate (or egg-shaped)	+	+	+	-	-	-	+	+	+	+
Cylindrical	-	-	+	-	-	-	+	-	-	-
Flat (disk-shaped)	+	+	+	+	-	-	+	+	+	+
Angular	+	+	+	-	+	+	+	-	-	+
Kidney-shaped	-	-	+	-	-	-	+	-	+	+
<b>Surface</b>										
Smooth	+	+	+	+	+	+	+	+	+	+
Wrinkled	+	+	+	-	-	+	+	-	-	-
<b>Color</b>										
White	+	+	-	+	+	+	+	-	-	+
Yellow	+	+	+	+	+	+	+	+	+	+
Green	+	+	+	+	+	-	+	+	+	+
Grey	+	+	+	+	+	-	+	+	-	+
Pink	+	+	-	+	-	+	+	-	+	+
Red	+	+	+	+	-	+	+	+	-	+
Chestnut (brown)	+	+	+	+	+	+	+	+	+	+
Black	+	+	+	+	+	+	+	+	-	-
<b>Dimensions</b>										
Large	+	+	+	+	+	+	+	+	+	+
Small	+	+	+	+	+	+	+	+	+	+
<b>Pattern</b>										
Marbled	+	+	-	+	+	+	+	+	+	-
Dotted	+	+	+	+	+	+	+	+	-	-
Striped	+	+	+	+	+	+	+	+	-	+
<b>Color of cotyledons</b>										
Green (dull)	+	+	-	+	+	-	+	+	-	+
Yellow	+	+	+	+	+	+	+	+	+	+
Red (orange)	+	+	-	+	+	-	+	-	-	-
<b>Color of hilum</b>										
White	+	+	+	+	+	+	+	+	-	-
Brown	+	+	+	+	+	-	+	+	+	+
Black	+	-	+	+	-	-	+	+	-	+

Table I. (cont.)

Variable hereditary characteristics	<i>Pisum sativum</i>	<i>Vicia sativa</i>	<i>Vicia faba</i>	<i>Ervum lens</i>	<i>Lathyrus sativus</i>	<i>Cicer arietinum</i>	<i>Phaseolus vulgaris</i>	<i>Soya hispida</i>	<i>Medicago sativa</i>	<i>Trifolium pratense</i>
<b>Vegetative characteristics</b>										
<b>Leaf structure</b>										
With tendrils	+	+	-	+	+	-	-	-	-	+
Without tendrils	+	+	+	+	-	+	+	+	+	+
<b>Leaf shape</b>										
Linear	-	+	-	+	+	+	-	+	+	+
Cuneate (rhomboid)	+	-	-	-	-	-	+	+	+	+
Ovate	+	+	+	+	-	+	+	+	+	+
<b>Dimension of leaves</b>										
(a) Long	+	+	+	+	+	+	+	+	+	+
Short	+	+	+	+	+	+	+	+	+	+
(b) Wide	+	+	+	+	+	+	+	+	+	+
Narrow	+	+	+	+	+	+	+	+	+	+
<b>Leaf edges</b>										
Entire	+	+	+	+	+	-	+	+	+	+
Toothed	+	+	+	-	-	+	-	-	+	+
<b>Hairiness of leaves</b>										
Hairy	-	+	-	+	-	+	+	+	+	+
Glabrous	+	+	+	-	+	-	-	+	+	+
<b>Color of stipules</b>										
Green	+	+	+	+	+	+	+	+	+	+
With anthocyanin	+	+	+	-	+	+	+	+	-	+
<b>Leaf color</b>										
Yellowish	+	-	-	-	-	-	-	+	+	+
Green	+	+	+	+	+	+	+	+	+	+
<b>Waxy cover on plant</b>										
With wax	+	-	-	-	+	-	-	-	-	-
Without wax	+	+	+	+	-	+	+	+	+	+
<b>Stem structure</b>										
Straight	+	-	+	+	-	+	+	+	+	+
Coiling	+	+	-	-	+	-	+	+	-	-
<b>Growth shape</b>										
Upright	+	+	+	+	+	+	+	+	+	+
Creeping	+	+	-	+	-	+	+	+	+	+
<b>Height of plant</b>										
Tall	+	+	+	+	+	+	+	+	+	+
Intermediate	+	+	+	+	+	+	+	+	+	+
Low	+	+	+	+	+	-	+	+	-	+

Table 1. (cont.)

Variable hereditary characteristics	<i>Pisum sativum</i>	<i>Vicia sativa</i>	<i>Vicia faba</i>	<i>Ervum lens</i>	<i>Lathyrus sativus</i>	<i>Cicer arietinum</i>	<i>Phaseolus vulgaris</i>	<i>Soya hispida</i>	<i>Medicago sativa</i>	<i>Trifolium pratense</i>
Hairiness of stem										
Hairy	-	+	-	-	+	+	+	+	+	+
Glabrous	+	+	+	+	+	-	-	+	+	+
Shape of stem										
Cylindrical	-	-	-	-	-	+	-	+	+	+
Square	+	+	+	+	+	+	+	-	-	-
Fasciated	-	-	-	-	-	-	+	-	-	+
Color of shoots										
Green	+	+	+	+	+	+	+	+	+	+
With anthocyanin	+	+	-	+	+	+	+	+	+	+
Color of stem										
Green	+	+	+	+	+	+	+	+	+	+
Violet (with anthocyanin)	+	+	-	+	+	+	+	+	+	+
<i>Biological characteristics</i>										
Vegetative period										
Short (early-ripening)	+	+	+	+	+	+	+	+	+	+
Long (late-ripening)	+	+	+	+	+	+	+	+	+	+
Albinism	+	-	+	-	-	+	+	-	+	+

hereditary forms. The system of forms described resulted in Linnaean species and not in randomly composed races. The same applies not only to phenotypic but also to genotypic variation as long as it is subjected to study according to the method of hybridization.

The compilation of such systems for the purpose of building up strains based on a botanical classification revealed a large number of 'missing links', so far not known to taxonomists or not yet discovered but the existence of which could be predicted as a result of the laws of variability in the case of Linnaean species. During the search for the 'missing links' in the system, we succeeded in clearing up the geographical distribution of races and characteristics, the problem of the geographical centers for the development of forms and the process concerning the origin of the geographical centers of origin of cultivated plants. Consequently, questions arose: where to find the primary centers of variation, where to look for 'missing' forms, where to locate the maximum specific variability of a given Linnaean species and from where and how all the varieties of the forms of cultivated plants could be obtained.

The problem concerning the origin of cultivated plants has interested many scientists beginning with De Candolle (1855) and Darwin. Botanists, historians,

archeologists, physiologists and agronomists have been preoccupied with it as well. The origin of cultivated plants has given rise to an extensive literature among which, up till now, the classical synoptic work, 'L'origine des plantes cultivées' by De Candolle (1883; note, the first abbreviated edition appeared in 1882) is outstanding, although the comparatively scanty information available to De Candolle concerning the different groups of plants, has since been substantially augmented by new historical and archeological data and a number of botanical and genetical observations (Schweinfurth, 1872-73; Woenig, 1886; Buschan, 1895; Joret, 1897-1904; Solms-Laubach, 1899; Höck, 1900; Hoops, 1905; Bailey, 1906; Helweg, 1908; Reinhardt, 1911; Hehn, 1911; Gibault, 1912; Trabut, 1913; Schulz, 1913; Thellung, 1918; Laufer, 1919; Sturtevant, 1919; Zade, 1921; Schiemann, 1922; Schweinfurth, 1922; Carrier, 1923; Safford, 1925; and Cook, 1925). It should also be mentioned that among this extensive literature a wealth of data on the geographical centers of some plants can be found.

While concertedly approaching the problem concerning the origin of the cultivated plants for the purpose of utilizing the data on the geographical centers of origin in order to locate 'missing links', we soon became convinced of the imperfection of the majority of the data and of the discrepancies between the statements in the literature concerning the geographical centers of origin as well as of the definite inaccuracy of much data with respect to the important cultivated plants, not excluding those concerning the cereals.

Most recently, critical studies have compelled us to renounce the majority of the statements made and to make an attempt to solve the old problem about the native lands of cultivated plants from a fresh point of view and to combine with it the question about the origin by using, as far as possible, new and more accurate and objective methods for this purpose. When extending knowledge of the composition and differentiation of the species, the very problem of the origin of cultivated plants becomes much more complicated than it appeared at the time of De Candolle. At the same time it became absolutely clear that both the understanding of the dynamics of the evolution of cultivated plants and the genesis of the Linnaean species, as well as, to a great extent, the practical work of the plant breeders, depend on the correct solution of this problem. We have become convinced that a direct and exact establishment of the geographical centers of origin will open up extensive opportunities for a practical utilization thereof when the sources of a wealth of valuable strains are discovered.

The present paper is intended as a short review of our investigations concerning the origin of cultivated plants in the Old World and an account of the methods used for this research.

## CHAPTER I METHODS USED FOR DETERMINING CENTERS OF ORIGIN OF CULTIVATED PLANTS

To determine the native lands of cultivated plants, De Candolle (1883) relied, in principle, on the location of specific cultivated plants while distinguishing between the state of running wild (becoming naturalized) and the primitive

wild state, and separating the original discovery in the wild state from a later naturalization of a species in an area new to it. This was, in essence, the botanical method for determining the native land of the plants, such as understood by De Candolle. Archeological, historical and linguistic methods were used by him only as secondary methods, applied without any botanical basis.

In view of the present knowledge of the composition of the Linnaean species and their differentiation, such botanical methods evidently need to be revised, supplemented and changed.

### Criticism of the methods used for determining the native lands of cultivated plants

Neither De Candolle nor authors unfamiliar with botany distinguished strictly between the different Linnaean species *sensu strictu* and the different genetic groups of varieties into which the majority of cultivated plants have at present been broken up. The problem of the origin has conventionally been solved in relation to the plant in the wide sense, i.e. all the species and genetic groups composing it such as, e.g., all the cultivated kinds of barley, flax, oats and so on. Under such conditions, when the cultivated plants, e.g., wheat or oats, are represented by several Linnaean species, sharply differentiated and physiologically isolated from each other and unable to hybridize, it is evident that uniting them cannot but lead to definitely erroneous conclusions. Primarily, this circumstance makes many of the native lands established for some cultivated plants highly inaccurate. It was especially easy to make mistakes when utilizing historical, linguistic and archeological methods where an evaluation of the specific differences is absolutely impossible. However, De Candolle was the first to distinguish the origin of some species in the New World from that of the same species in the Old World while remarking, e.g., that individual species of cotton and grapes were typical of America, while others were typical of Asia. Sufficiently accurate distinction of geographic and genetic groups within the limits of the Old World was apparently not feasible 40 years ago. Later investigations did not solve this problem either.

The method used by De Candolle and other authors for determining the native lands, where habitats of a given cultivated plant in its wild state could be found, are far from always to be considered reliable; this is primarily so because many cultivated plants are not known except in a cultivated state and, secondly, because what is called 'wild ancestors' are only limited groups of forms with a not very large range of varieties, which are rarely genetically isolated and not able to explain all the rich variation that, as a rule, is shown by the cultivated plants themselves. More often, such plants appear to be wild genera or related forms but are not ancestors in the true sense.

The wild wheat, *Triticum dicoccoides* with 28 chromosomes, found by Aaronsohn in Syria, corresponds to some extent in its variation to the cultivated species of wheat with the same number of chromosomes. However, the existence of this wild emmer does not explain the occurrence of the large, genetically as well as physiologically isolated group of soft wheats with 42 chromosomes. In

essence, the relationship of *T. dicoccoides* to all the species with 28 chromosomes is not even entirely clear or even that to the cultivated emmer (*T. dicoccum*) with which Körnicke united it into one Linnaean species, because when crossed with cultivated emmer or hard wheat it results in first and later generations in a sharply expressed inclination toward sterility.

Wild barley (*Hordeum spontaneum*) is very close to one of the smaller groups of cultivated barley, i.e. the one with hulled, distichous and awned varieties, but can by no means be included among all the varietally differentiated species of cultivated, naked-grained and hulled barleys such as the awnless, furcate or two-rowed *deficientes* or the four-rowed or six-rowed barleys. The entire group of cultivated, naked-grained barley is isolated morphologically and physiologically from the wild distichous and hulled barley (*H. spontaneum*) by many characteristics. The presence of a naked-grained group in eastern Asia does not explain the existence in southwestern Asia of a large amount of wild, two-rowed and hulled barley. On the other hand, it is necessary to keep in mind the fact that wild barley has not been taken into cultivation to the same extent as wild wheat or oats since it does not lose the inherited brittleness of its spike and since it remains distinct from the cultivated forms. This makes its role as a direct ancestor more than doubtful.

An attempt by Schindler to cultivate mountain rye (*Secale montanum*), which botanists consider an ancestor of cultivated rye (*S. cereale*), did not succeed in making it into an annual from its perennial origin and did not turn its brittle spikes into those of the cultivated rye, however much the experimenter hoped it would. Just as unsuccessful were—and will be—the many attempts to turn *Avena fatua* into *A. sativa* or *Triticum dicoccoides* into *T. dicoccum*, and so on. Wild 'ancestors' or forms with adapted or induced self-propagation represent interesting groups of related forms corresponding to the cultivated plants and sometimes linking them (e.g. in the case of barley) to a member of cultivated forms within the limits of Linnaean species and tying them together with the wild species. However, the fact that they could be turned into cultivated forms, such as was believed by De Candolle and all the later authors, could not be proven. Therefore, the discovery of such questionable ancestors, which have been found during the last couple of years in the case of wheat, millet and hemp, does not yet solve the problem of the origin of cultivated plants at their centers of geographical variation.

Most of all—as shown by the examples—the investigation has demonstrated that the distribution areas of all these wild 'ancestral' forms are usually either fairly limited and confined to restricted and isolated areas, or, on the other hand, fairly wide, when attempts are made to use them for localizing the primary centers of cultivated plants. The full range of varieties of wild wheat, *Triticum dicoccoides*, has been preserved in Syria and Palestine, but only a few of its varieties have been found in Persia and Transcaucasia. The center of variation of the different species of cultivated wheat is far away from Syria and Palestine. On the other hand, wild barley, *Hordeum spontaneum*, is closely related to the cultivated kind, occupies a wide area stretching all the way from northern Africa to Asia Minor and is particularly common in the area of southwestern

Asia, the region of the specific center of development of strains of cultivated barley. As will be shown later, this center is confined to a fairly small geographic area. Where there is an infestation of wild barley in the foothill areas of Turkestan, in northern Afghanistan and in the mountains of Bokhara, we found a striking scarcity of varieties of cultivated barley. Wild melons (*Cucumis trigonus*), ancestral to the cultivated ones, are widely distributed from the Aral Sea to Fergana in areas where cultivated melons show an astonishing variation. The composition of cultivated melons in this area is rather a demonstration of remoteness from the source for their variation. The wild watermelon, *Citrullus colocynthis*, close to the cultivated *C. vulgaris*, embraces within its distribution area not only Africa – the geographical center of origin of watermelons – but reaches into Asia and is widely distributed in the desert areas stretching from Hindukush to Afghanistan, Persia and Belutchistan. However, we tried in vain to locate any native land for watermelons in Asia.

A number of wild species, corresponding to cultivated ones, have enormous distribution areas, extending all over Eurasia, such as, e.g., in the case of red clover (*Trifolium pratense*). Of course, such distribution areas do not furnish any real support for localizing the process of their introduction into cultivation.

Quite often the present distribution areas of the wild 'ancestors' do not coincide with the real centers where the strains developed, as will be seen, e.g., in the following discussion concerning cereals and other plants in the Old World.

#### Methods suggested for establishing centers of origin of cultivated plants

Detailed investigations during the last couple of years of the botanical composition of races and varieties of cultivated plants have allowed us to approach the problem concerning their origin from a fresh point of view, while enhancing and extending the methods used by De Candolle. After some decades of research done by the experimental agronomists at the Institute of Applied Botany and at other Russian experimental stations, the botanical and the qualitative structure of many plants within the European and Asiatic parts of the U.S.S.R. including Caucasia and Turkestan has to a great extent been cleared up. Expeditions have investigated agricultural areas of Persia, Bokhara, Korea, Mongolia, Afghanistan, Asia Minor and Mexico. English experimental stations in India, in particular the work done there by A. and G. Howard, Leach and Watts, have established the composition of many cultivated plants both in India itself and in Belutchistan, as well as in adjacent parts of Persia. The composition of plants in northern Africa has to a major extent been elucidated by American and French scientists. Published data from various countries in Europe, Africa and Asia permit – although far from completely – a more thorough approach to the questions regarding the centers where the strains of cultivated plants developed.

Studies of the cultivated vegetation of the Old World revealed one extraordinarily important fact, i.e. that in spite of the internationalization of cultivated crops and in spite of all the human migrations and colonizations as well as the

very antiquity of agriculture, it is still possible for students of taxonomy and geography to establish regions of definitely endemic varieties and races, to discover regions where the maximum primary variation of strains occurred and to establish a number of regularities concerning the distribution of inherited characteristics. Comparisons between data on the geography of varieties have revealed that the cultivated races, varieties and species are characterized by distinct geographical distribution areas and that, for a solution of the problem concerning centers of typification, the same methods can generally be used as those that botanists and zoologists apply for species of wild plants and animals.

As a basis for determining the centers of origin of this or that group or genus of animals and plants, taxonomists concerned with geography use the distribution of the species and the maximum concentration thereof within various areas. Naturally, just such a method for establishing the centers by means of regional concentration of varieties and by the use of extensive differentiation has already been applied to cultivated plants as well.

As a basis for determining the centers where the forms of different Linnaean species develop and in the light of the present representatives of the species as well as of polymorphic systems, we consider it necessary not only to establish the distribution area of an entire species, irrespective of the composition of its elements as developed up till now, but most of all to establish the distribution areas of all the parts composing it and the geographical concentration of all the inherited characteristics of the forms of this species. In other words, as a basis for the determination of the center, where the development of the forms of a given species took place, we must provide differentiating methods for establishing the racial composition of the species in question and the geographical distribution of the racial variation within countries and regions.

Just as a botanist or a zoologist establishes the exact specific composition of a genus and the distribution of its different species over the entire world when determining the geographic center of type-formation of a particular genus, so it is necessary, with respect to cultivated plants and their various Linnaean species, to apply differentiating methods for the racial and varietal composition, the racial variability of the species and the geographical distribution of all the Linnaean species, the so-called linneons.

Detailed botanical knowledge of the specific composition, of the complex of morphological and physiological characteristics and of the distribution within a region is necessary for the solution of those types of problems for every plant investigated.

Such a differentiating geographical method requires, of course, an enormous amount of botanical material from various countries, and studies of the different races by means of crops grown under identical conditions in order to ascertain inherited differences. In general, this always appears tedious and time-consuming but it furnishes distinct ideas about the actual centers where those strains were formed, which can then be used by plant breeders for practical work.

Acquaintance with the distribution area of the species *sensu lato* gives little information about the center where the forms developed. The distribution area of wild wheat, *Triticum dicoccoides*, reaches – as recently demonstrated – from

Palestine to western Persia and Transcaucasia as well as Asia Minor (according to P. M. Zhukovskiy) but the entire diversity of its races and varieties is, as far as is known, typical only of Syria and Palestine. Out of the immense diversity of the Syrian forms in Georgia and Persia only a few varieties are found. The area covered by cultivated rye is very large, the common types of it are widely cultivated from the Himalayas all the way to the Polar Circle; the area where all the racial variation of rye is concentrated is, as we will see below, considerably more limited.

It is natural that differentiation into varieties and races must precede the strict differentiation of a given cultivated plant into Linnaean species. Thus, by applying various methods such as cytology, hybridization, determination of resistance to parasites and the usual ones of taxonomy and morphology, the investigators have learned to delimit specific groups exactly, to isolate the actual Linnaean species from the artificial, vernacular-named species. The distribution areas of the genetically sharply isolated species of cultivated plants are often very different and not rarely typical of different continents.

The differentiating, taxonomical-geographical method suggested for the determination of centers of development of forms can be applied for various plants and consists of:

- (a) differentiating a given plant into Linnaean species and genetic units by means of various methods such as morphological-taxonomical ones, parasitological ones, etc.;
- (b) determining, if possible, the distribution areas of these species in the remote past when communications were more difficult than at present;
- (c) determining in detail the composition of the varieties and races (more exactly, the inherited variation of the characteristics) of each species and the general system of inherited variability; and
- (d) establishing the distribution of the inherited variation of the forms of the species in question and determining the geographical centers of accumulation of varieties. The region of maximum variation, usually including a number of endemic forms and characteristics as well, can usually also be considered as the center of type-formation.

Some examples follow below and illustrate the application of the differential method for determining the center where the forms developed.

For a more exact establishment of the centers of origin and the development of forms, a determination of that geographical center is necessary where there is a concentration of genetically closely related species. Just as with respect to wild plants, as a rule, the more closely the species are related, the more they are characterized by having adjacent or often overlapping distribution areas. It can also be understood that investigations of such species furnish valuable information for the determination of the centers of origin. Thus, as will be shown below, e.g., in the case of soft wheat (*Triticum vulgare*), the center of variation coincides with the geographical center of variation of shot wheat (*T. compactum*) and club wheat (*T. sphaerococcum*), i.e. species quite close to soft wheat, easily crossing with it and forming a single genetical unit together with it.

Finally, using necessary corrections and any supplementary information available when determining the areas of origin, establishment of the areas of

variation of closely related wild varieties or species of certain plants can be effected, while applying also the differential method of racial studies to them.

Usually this means components of such Linnaean species by which the cultivated plants are represented, but with additional characteristics that enable them to remain in the wild condition (e.g. elaiosomes at the base of the seed, brittle spike, grain splitting open when ripening, etc.). Botanists usually attached exceptional importance to the studies of such forms, viewing them as ancestors that still exist, and believing that once the wild form of the cultivated plant was found, the question of its origin could at the same time be answered.

While setting this not yet proven hypothesis aside for later discussion, there is no doubt that the wild forms, ancestral to the presently cultivated species, deserve the same research efforts as given the cultivated species.

On the basis of this kind of analytical botanical research, data from archeology, history and linguistics have acquired a great value. When related to a definite, botanical point of view, they can often, and in an important manner, supplement and enhance information about the past of cultivated plants.

The center of origin of a given group of cultivated plants is often characterized by many special parasites, widespread within that area and typical of that particular group of cultivated plants. That is, the centers of variation of the parasites, typical of a particular group of cultivated plants, coincides with that of the hosts. The greatest variation among the smuts of rye is found in southwestern Asia, the center of variation for this crop. Similarly, out of the 10 species of smut living on species of sorghum, the majority (*Tolysporium filiferum*, *T. volkensis*, *Sorosporium ehrenbergii* and *S. simii*) is found in Africa only, i.e. the native land of the sorghum (Reed and Melchers, 1925).

#### Primary and secondary characteristics of centers of diversity

As far as particular groups of plants are concerned, the centers of botanical diversity cannot always be considered as the primary foci of type-formation. There may be occasions when the present racial variation is the result of the similarity of different species and their hybridization with each other. In the case of cross-pollinating plants, where under natural conditions mainly dominant characteristics are present, perhaps an opportunity for isolation and exposure to external variation can arise far from the center of origin, or due to artificial breeding, e.g. inbreeding of recessive forms.

The maximum variation of some garden plants can often be found in horticultural nurseries. As a rule, this is apparently connected with the practice of hybridization. For example, in the case of the fruit fly, *Drosophila*, an exceptional variation is known to occur as a result of mutations within artificial surroundings. On the basis of recent cytological investigations of *D. melanogaster*, Jeffrey arrived at the conclusion that the exceptional inclination of this group toward mutations was linked to natural hybrids between this and other species of the same genus. His research revealed the same picture of abnormalities during mitosis and meiosis as found for *Oenothera lamarckiana* (cf. American Naturalist, 1925).

It is necessary to be prepared for the existence of such genera and to separate



critically the secondary development of forms from the primary one. However, actual investigations of a significant number of cultivated plants demonstrate quite definitely that the process of evolution occurred both in time and space. We have demonstrated by the examples above that the routes of geographical dispersal of forms, the foci of the genes and the basic centers of origin can still be established. Data from the geography of the specific variation of the cultivated plants do, on the whole, not oppose the basic condition for Willis' (1922) theory on the role of age and area for the evolution of plants.

Information on the center of variation of a species investigated and augmented by data on other ancestral species and wild forms and the simultaneous utilization of data from archeology, history and linguistics allow us to approach the establishment of a definite center of origin while keeping in mind the historical period most accessible to us. It may be possible to verify that many cultivated plants differentiated and formed different Linnaean species within the course of a certain period of time. It is possible also that other Linnaean species, that once originated from a single common geographic center, are separated today on different continents, although at present they are available for research only from the recent past. While interpreting the present distribution of a cultivated plant, it may be possible to start a reconstruction of its history in a more remote past. The interest in specific distribution and the foci of the genes in present time as well as during a historical period close to us can be of practical value.

Below we shall examine a number of actual examples of how to determine the centers of type-formation of the most important crops in the Old World by means of the differential-geographical method and show how we arrived at the facts established for a number of species.

## CHAPTER 2 GEOGRAPHICAL CENTERS FOR THE DEVELOPMENT OF FORMS OF CULTIVATED PLANTS IN THE OLD WORLD

### Geographical centers of type-formation of wheat

We shall start by establishing the geographical centers for the type-formation of the most important cultivated plants in the Old World, i.e. the wheats.

De Candolle believed that all the cultivated wheats had their origin in Asia. While distinguishing between hard, soft, English and emmer wheats, he did nevertheless not pay special attention to their differentiation into separate species. He was familiar with the experimental hybridization of wheats by Vilmorin but did not see any proof of an adequately expressed isolation of the individual species thereof. In his opinion, the absence of specific epithets for English and hard wheats in the Antique indicated that they were all *Triticum vulgare*. The hard wheats were, according to his judgment, established during the present era in Spain and Africa and underwent there a corresponding modification into *T. durum* and *T. turgidum*. De Candolle considered it necessary to single out only einkorn, *T. monococcum*, for which he pointed to Serbia,

Greece and Asia Minor where it is found in a wild state. Its definite physiological isolation, expressed by the difficulty of crossing einkorn with soft wheat, made it, in De Candolle's opinion, necessary to single it out.

In his comprehensive monograph, Percival (1921) was not concerned with the problem of the geographical centers of origin although the book contained much valuable information pointing toward a solution of the geographical problem. This question has also been pondered by other taxonomists and investigators (A. Schulz *et al.*) concerned with the problem of the origin of cereals.

Research during the last couple of decades has cleared up the differentiation of cultivated and wild wheats into individual Linnaean species.

By means of systematic investigations of the varieties of wheat, after many years of interspecific crosses and results obtained from cytology, parasitology and studies concerning the resistance of the species to diseases as well as serology, we have finally succeeded in distinguishing all the present kinds of wheat into the following genetic groups of species:

I	II	III
With $n = 21$	With $n = 14$	With $n = 7$
chromosomes	chromosomes	chromosomes
1 <i>T. vulgare</i> Vill.	5 <i>T. durum</i> Desf.	13 <i>T. monococcum</i> L.
2 <i>T. compactum</i> Host	6 <i>T. turgidum</i> L.	
3 <i>T. sphaerococcum</i> Perc.	7 <i>T. polonicum</i> V.	
4 <i>T. spelta</i> L.	8 <i>T. dicoccum</i> Schrank	
	9 <i>T. pyramidale</i> Perc.	
	10 <i>T. orientale</i> Perc.	
	11 <i>T. persicum</i> Vav.	
	12 <i>T. dicoccoides</i> Koern	

If there are doubts about the equivalence of the species or about the fact as to whether a given species is a subspecies or a species in the Linnaean sense, then they can be left within the limits of the group in which they are listed. On the whole, all three groups appear absolutely and without question physiologically and genetically isolated from each other and the division of wheats into three groups is not an arbitrary classification but an indisputable fact, proven simultaneously by various methods (Tschermak, 1914; Zade, 1914; Vavilov, 1914, 1919, 1925; Percival, 1921; Sax, 1921; Nikolayeva, 1923).

Group I (the *vulgare*) is characterized by  $n = 21$  chromosomes and all the species within its limits are easy to cross with each other and give rise to absolutely fertile offspring. On the whole, this group appears susceptible to infection by fungal diseases: smut, rust and mildew.

Group II (the *durum*) is characterized by  $n = 14$  chromosomes; all the species are easy to cross with each other and produce fertile offspring but differ considerably in their susceptibility to fungal diseases. They can only with difficulty be hybridized with species of groups I or III and display a more or less sharply distinct sterility in the first as well as later generations of the hybrids. *T. dicoccoides* shows some isolation resulting in a considerable degree of sterility when crossed with cultivated emmer, hard wheats or *T. persicum*. According to

the characteristics of the hybrids between *T. durum*, *T. dicoccum* and the other species of group II, they remind one of hybrids between distant species which, in spite of a considerable sterility, are able to produce a multitude of new types.

Group III (*monococcum*) has a karyotype with  $n=7$  chromosomes. It is distinguished by a strong resistance to infectious diseases and by sterile hybrids when crossed with species of the other two groups.

Let us now turn to the determination of the geographical centers of origin of these physiologically isolated groups.

### Centers of soft, shot and club wheats

During the course of the last nine years I and my colleagues (E.I. Barylina, G.M. Popova, A.A. Orlov and others) have worked out details of the distribution area from a botanical-geographical point of view in the case of the most complicated and intimidating of the species, i.e. *T. vulgare* (Vavilov, 1923). This species has lately been split by us into 67 botanical varieties, differing in the color of the spike, the grains and the awns, in the shape and size of the awns, in the pubescence of the glumes as well as the presence or absence of ligulae on the leaves. In addition, the varieties of soft wheat were studied from the point of view of racial composition. Not less than 166 characteristics were distinguished for the spike, the grains and the vegetative traits according to which different races could be separated and, thus, a botanical analysis was made – as far as possible in minute detail – of this polymorphic species.

Data from the special expeditions sent out from the Department of Applied Botany to Turkestan, Bokhara, Khorezm, Mongolia, Persia, Afghanistan and Asia Minor as well as literature data and the worldwide collections of the Dept. of Applied Botany were used as a basis for this research.

While not dwelling on details, in part already published (Vavilov, 1923), a slightly improved picture of the present geographical distribution of the varieties of soft wheats was obtained and is geographically represented by the resulting Fig. 1.

The taxonomic-geographical analysis demonstrated definitely that the varietal composition as well as the racial variation of soft wheats were concentrated in southwestern Asia. Studies of the geographical varieties and the racial characteristics demonstrated that the specific diversity increases in the direction toward Turkestan, India and Afghanistan. Proportionally, the farther away from central Europe and Siberia toward southwestern Asia, the more the number of botanical varieties and new, original races increases. All the diversity of the morphological and physiological characteristics of the soft wheats, existing at present, were found in the mountain areas of southwestern Asia. All the traits of the races, cultivated anywhere and typical of any variety of *T. vulgare*, are met with, although in different combinations, within this region where, together with the common European and Siberian forms, a large number of endemic varieties can be seen such as original, new non-ligulate forms with reduced leaves, or a number of new varieties with short awns or with colored edges to the hulls, never found except in this area.

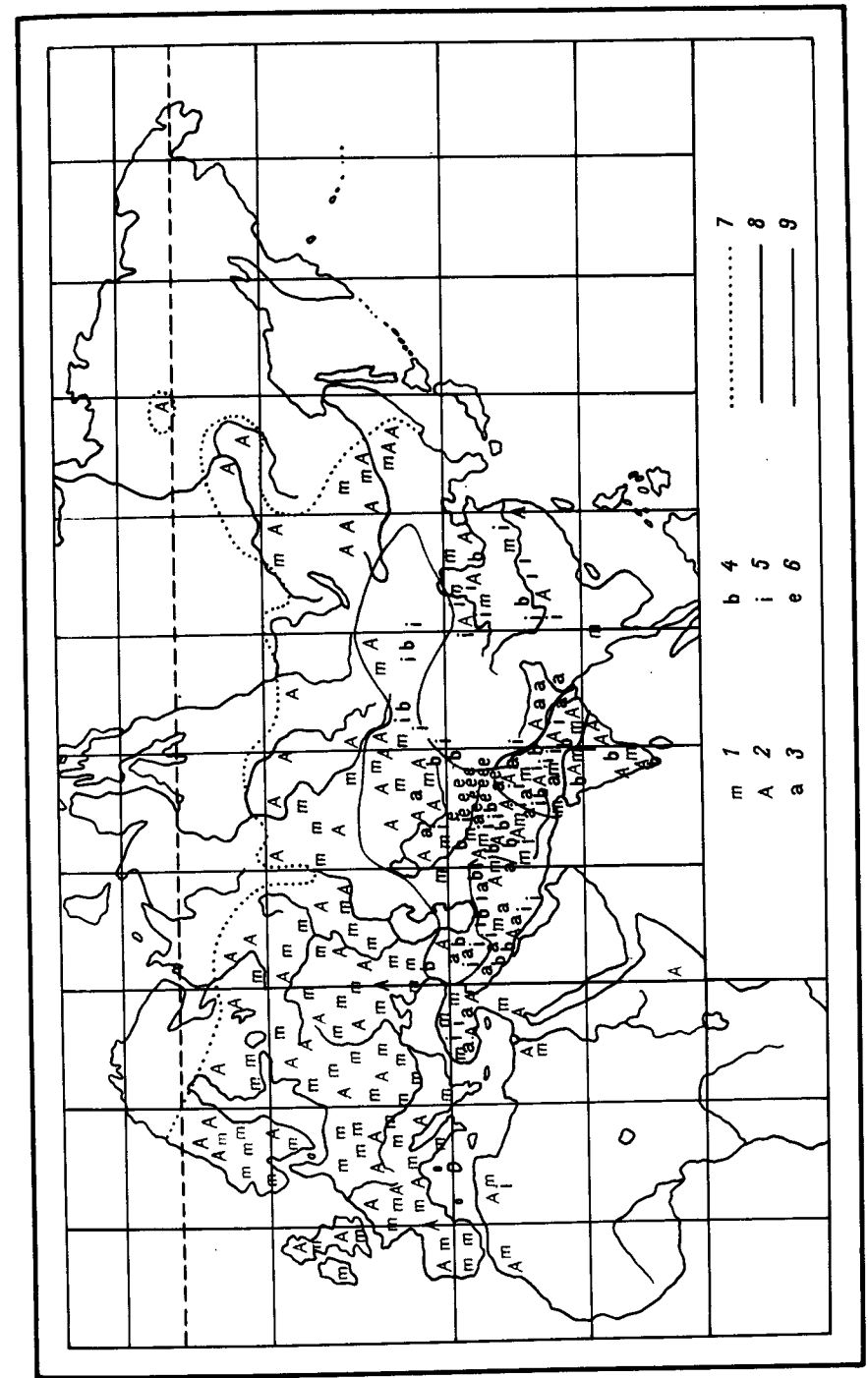


Fig. 1. Center of origin of the soft wheats. Geographical distribution of the varieties of soft wheat, including *Triticum sphaerococcum* Perciv. and *T. compactum* Host. 1. *Triticum muticum* Al.; 2. *T. vulgare aristatum* Al. (var. *europaeae*); 3. *T. vulgare aristatum* (vars. *asiaticae*, *endemicae*); 4. *T. breviaristatum* Vav.; 5. *T. inflatum* Flaksb.; 6. *T. elongatum* Vav.; 7. the northern limit of wheat growing; 8. the distribution area of *T. sphaerococcum* Perciv.; 9. ditto of *T. compactum* Host.

After studying the wheats of Afghanistan in 1924, it could be demonstrated that there was an especially rich variation of soft wheats in the area adjacent to the eastern part of Hindukush in the direction toward northwestern India. As far as we were able to find out, the non-ligulate forms of soft wheat are typical exclusively of Badakhshan, Chitral and the areas adjacent to them in Bokhara and, possibly also in Kashmir. They were not found in Turkestan, Khorezm, Persia, Mongolia or India, not to mention Europe or Siberia.

The number of types and the quality of the different racial characteristics decrease definitely from Afghanistan toward Mongolia (data from the expedition led by V.E. Pisarev) and central India (according to A. & G. Howard) as well as China (according to Percival).

All the European parts of the U.S.S.R., including northern Caucasus and Siberia, share only a small number of varieties of soft wheat. The number of varieties established for *T. vulgare* in Persia and Afghanistan amounts to 50, yet all of Europe has only 15–20. As could be expected because of the geographical and historical connections with Armenia, Georgia and Azerbaidzhan as well as southwestern Asia, the varietal composition of the wheats approaches that of Persia and southern Turkestan only in Transcaucasia.

As demonstrated by recent research by French authors (Boeuf, Miège, Duchêsne), soft wheat was not known in Africa until the colonization by Europeans. The introduction of different types into the oases of Sahara has not changed the picture of the world-wide geography of soft wheat. The New World adopted the cultivation of wheat from the Europeans and the botanical composition of cultivated wheats in the Americas is, in spite of the wide distribution of this crop in the U.S.A., Canada and Argentina, very poor in comparison with that in southwestern Asia (Clark *et al.*, 1922).

Thus, the method of differential studies of races and varieties very definitely allows us to approach the establishment of actual centers of variation and type-formation of the soft wheats. When making their way from Europe into southwestern Asia, the investigators, so to say, approach the center where the soft wheats arose and an advance from northwestern India toward Punjab and Upper Indus is accompanied by discoveries of more and more new types.

The study of the geographical distribution of the varieties of club wheat, *T. compactum*, which is closely related to soft wheat, fully corroborated our conclusions concerning the geographical center of soft wheat. The distribution area of club wheat is comparatively small. Club wheat is characterized by an important variation in the Khibinskiy oasis, and it is occasionally cultivated in the mountains of Bokhara, Transcaucasia and southern Turkestan, and occurs even in China. In Persia it is found just as a single variety in the Urmia area (A.A. Grossheim) but, in spite of special investigations, club wheat has not been found anywhere else in that country.

A detailed study by myself in Afghanistan in 1924 corroborated fully the theoretically predicted discovery of crops of club wheat in Hindukush. Crops of *T. compactum* were widely distributed there and – what is very important – many new, at that time unknown varieties of multi-awned and inflated club and shot wheats were also found there. The largest number of varieties of *T. compactum* occurred mainly in an area adjacent to northwestern India.

While bearing in mind that also a third species, closely related to the soft wheats, i.e. *T. sphaerococcum*, recently described by Percival, is found in its entire diversity only in northern India, it is evident that there is a complete overlapping of the areas covered by the varieties belonging to these three species. This confirms even better the veracity of applying the differential-geographical method for solving problems of origin.

Plant breeders must search for new types of soft wheat in the mountain areas of southwestern Asia. In the mountains of southwestern Afghanistan and the foothills of southwestern Himalayas, the process of type-formation of soft wheats and the species genetically related to them has been revealed. Northwestern India and the areas adjacent to it in Afghanistan, Chitral and Kashmir, display still the greatest diversity of the varietal and racial characteristics, many of which appear to be endemic. This area has a wealth of varieties and races. As demonstrated by *in situ* studies, all the enormous variety of spring and winter types of soft, club and shot wheats are represented here, together with the majority of the new races, which can be useful for practical breeding, if not directly then at least for the purpose of hybridization.

*T. spelta* is so far known only as a relict form, preserved as isolated crops grown in the mountains of Schwaben, Switzerland and, very rarely, in Urmia. It has been found by archeologists in a fossil condition in Egypt and in Asia Minor (Buschan, 1895). To establish exactly the center of its variation seems impossible at present. First of all, it may be assumed that this species, genetically related both to soft, shot and club wheats, should also have its center of variation and type-formation in the areas of southwestern Asia. However, in spite of painstaking efforts, this species has not been found in Khorezm, nor in Turkestan, Afghanistan, Persia or Asia Minor, or even in Mongolia. Additional research in this respect is desirable both in Asia Minor and northern India. Perhaps this species will turn out to be of hybrid origin?

### The center of hard wheats

Let us now turn to the study of the center of hard wheats. Summing up the results of research concerning the native land and the antiquity of the hard wheats, Buschan (1895) stated that this problem could not be solved for lack of data. Botanists at the Department of Applied Botany have studied this problem in detail under the guidance of my long-time assistant, A.A. Orlov (1923).

While carrying out similar work using differential-botanical analyses of hard wheats on the basis of a large number of specimens (ca. 1500) we were able to establish that the main source of the racial variation of hard wheats appeared to be northern Africa and, in general, the coast of the Mediterranean. There, a multitude of original and endemic types of this species, not known in Europe or Asia, are met with, and at the same time all the racial and varietal characteristics, typical of the entire species of *T. durum* including its European and Asiatic races, are concentrated here. All of Asia and also the area of Mesopotamia (according to Whimshurst) are very poor with respect to the variation of hard wheats. India, China, Turkestan, Bokhara and Siberia are characterized by a sharply

reduced variation in this species. Hard wheat is absent in the major part of southwestern Asia. In spite of painstaking efforts, we did not find a single spike of hard wheat among the innumerable fields of wheat we investigated in Afghanistan and Khorezm in 1924 and 1925. In spite of the striking variation in conditions for cultivation, varying from subtropical ones to the limits of agriculture in the mountains, Afghanistan with its primitive crops of wheat appeared to have been bypassed by this wheat when it dispersed. As we could see above, Afghanistan has, at the same time, a concentration of varieties of soft, club and shot wheats.

On the other hand, the basic focus of the types and the central area of all the polymorphism of *T. durum* seem to be found along the coasts of the Mediterranean, especially in Abyssinia, Algeria, Egypt and Greece. Such types as varieties of hard wheat with purplish-violet grains, pubescent leaves and sheaths or long-awned forms with elongated cilia on the auricles or at the base of the leaf blade, or with shoots distinguished by a brownish-violet color due to anthocyanin are known only from northern Africa.

A peculiar, non-ligulate hard wheat has, so far, been found only on the island of Cyprus (by Flaksberger, 1926). At the same time as endemic non-ligulate soft wheat was found by us in southwestern Asia in a secluded area of Badakhshan, endemic, non-ligulate hard wheats were discovered in the Mediterranean region, where we expected to find them.

According to investigations by A.A. Orlov, all the varieties of hard wheats can be determined according to 78 characteristics, including those of the grains, the awns and the spikes as well as vegetative ones (e.g. non-ligulate types) and reproductive ones.

All the races, characterized by the presence of a combination of the 78 characteristics, have been found only in the countries along the Mediterranean coast as well as in Abyssinia, whereas in Asia the diversity of the racial characteristics of hard wheats can be determined using only 51 traits.

Only the African region has a valid representation of the full range of polymorphism within *T. durum*. Only there the significance of the hereditary variability occurs to an extreme degree and the most extreme variants of the racial characteristics can be found there alone. Thus, e.g. there, groups of races can be met with which have awns more than 20 cm long and, at the same time, there are very short-awned races as well as 'semi-awned' types with awns less than 10 cm long. Exactly the same can be said about every characteristic typical of the races of hard wheat in Africa. The presence in northern Africa, and the islands close to it, of all the variations and all the forms of hard wheat, indicates, thus, that just this area is the main geographical center of the type-formation of the species of *T. durum*. It is necessary to study especially the countries along the Mediterranean coast and the banks of the Nile River all the way to Sudan in order to establish, in detail, the center of variation of the hard wheats.

The species close to *T. durum* are, unfortunately, still not as well studied in detail due to the lack of an adequate number of specimens, especially of *T. dicoccum*, *T. dicoccoides*, *T. turgidum* and *T. polonicum*, which are all typical of the same area. Large amounts and a great variety of the wild wheat, *T. dicoccoides*

with  $n = 14$  chromosomes, have been found in Syria and Palestine. Individual strains only of this species have reached as far as western Persia and Transcaucasia in the form of one or two varieties.

Cultivated emmer increases in diversity toward N. Africa. In Abyssinia, black-spiked, white-spiked and red-spiked types and forms with fringed, dark-pigmented hulls, not known anywhere else, have been found there. Emmers, easy to thresh, also exist in that area (according to Harlan). An enormous amount of spike-types of emmer have also been discovered in the tombs of the Egyptian pharaohs.

All the varieties of the so-called poulard wheat, *T. turgidum*, are typical of the Mediterranean coasts.

The Polish wheat, *T. polonicum*, is characteristic of Egypt and the countries contiguous with it and all the strains of *T. pyramidale* are typical of northern Africa. *T. orientale* is also a Mediterranean species.

In general, this group of species which are difficult to delimit, easily hybridize with each other, are characterized by their resistance to infectious diseases, have the same number of chromosomes ( $2n = 28$ ), and have distribution areas along the coast of the Mediterranean (see Fig. 2).

Some years back, I distinguished a new species of hard wheat under the name of *T. persicum*. It has recently been discovered in a great number of varieties in Georgia, Armenia, Daghestan and Persia (Vavilov, 1919; Atabekova, 1925; Dekapredelevich, 1925). P.M. Zhukovskiy (1923) described white-spiked, black-spiked and red-spiked varieties as well as a multitude of races, distinguished by vegetative and other generative and biological characteristics. This species represents a morphological as well as a transitional group of forms between hard and soft wheats. Due to its external aspect, it was previously unhesitatingly referred to the soft wheats by the taxonomists but, according to the hereditary, physiological characteristics and the number of chromosomes, this species is undoubtedly closer to the hard wheats. *T. persicum* hybridizes easily with hard wheats and produces completely fertile offspring. The geographical distribution area and the center of variation of Persian wheat (i.e. Armenia, Georgia and Asia Minor) occupy an area intermediate between the Afro-Mediterranean area of the hard wheats and southwestern Asia, the center of the soft wheats (Vavilov and Yakushkina, 1925). In addition, *T. persicum* has been found between Khorosan and Seistan in Persia. This species of wheat, occupying a position genetically intermediate between groups I and II of the wheat species, possibly originated from hybridization of this species and some other species belonging to either of these two groups, such as could be expected from the geographical concentration of its variation along the borders between the areas of groups I and II.

### The center of einkorn

Finally, group III of the wheats, einkorn (*T. monococcum*), known mostly in its wild form, is found in large numbers in a wild state in Asia Minor, Syria, Kurdistan, Transcaucasia, Crimea, Greece, Mesopotamia and Palestine (Flaks-

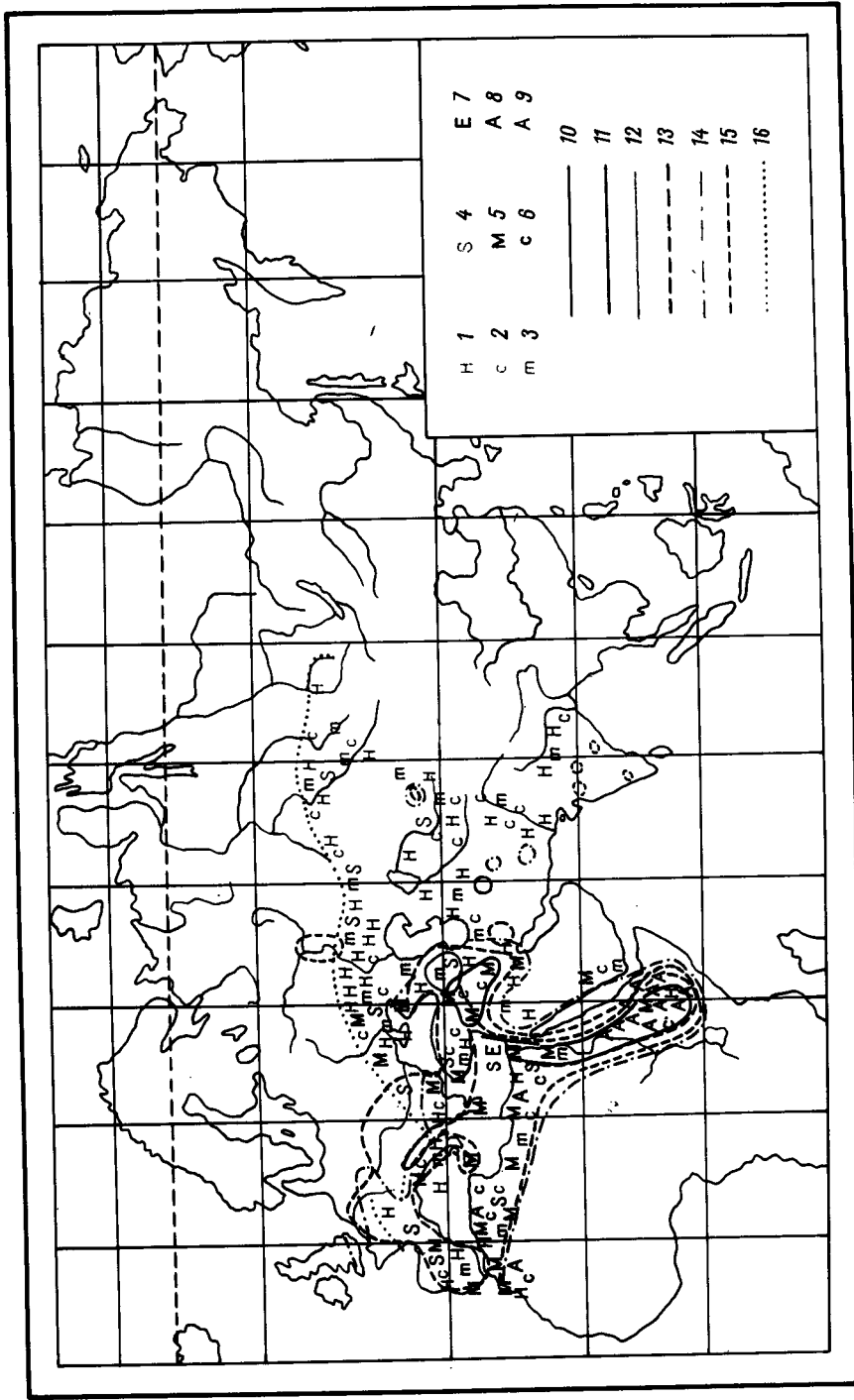


Fig. 2. Center of origin of the hard wheats. Geographical distribution of *Triticum durum* Desf. and the groups of species with  $n = 14$  chromosomes. 1-3: *Communes*: *hordeiforme* Host (1), *coarvalescens* Bayle (2), *melanopus* Al. (3); 4. *subcommunes*: e.g. *leucom Al.*, *leucomelan Al.*, *affine* Koern.; 5. *mediterranea*: e.g. *affricanum* Koern., *egyptiacum* Koern., *italicum Al.*, *apulicum* Koern.; 6. *circumflexae*; 7. *eligulatae* var. *aglossicon* Flaksb.; 8. *africanae*: *duro-compactum* incl. *T. pyramidale* Perciv.; 9. *abyssinicae caryopsidibus violaceis*; 10. *T. dicoccoides* Koern.; 11. *T. pyramidale* Perciv.; 12. *T. periscium* Vav.; 13. *T. polonicum* L.; 14. *T. turgidum* L.; 15. *T. dicoccum* Schrank; 16. northern limit of the distribution of the hard wheats.

berger, 1925). In addition, it occurs in Spain, in the mountain areas of France, in southern Germany (Württemberg, Tübingen, Baden and Brandenburg), in Switzerland and northern Caucasus (in the Terskaya district), Morocco and Algeria (Miège, 1924). During prehistoric time, einkorn was distributed in the mountain areas of Asia Minor, the Balkans and the Alps as well as the Carpathians. Einkorn was known to Aristoteles as forage for pigs. Galen, Theophrastes and Dioscorides also mentioned it (Buschan, 1895).

In spite of special searches for it, einkorn has not been found either in a wild or in a cultivated form in southwestern or eastern Asia. The distribution area and the center of einkorn are without doubt placed outside the center of type-formation of the soft wheats and isolated from the area of the greatest variation of the hard wheats as well. Most likely, the region of Asia Minor and the areas adjacent to it appear to be the center of einkorn variation. At first, the greatest variation of einkorn was found in Crimea, where it had been subjected to a special investigation (by P. Larianov and E.I. Barylina). Subsequent research concerning the distribution area of einkorn has, however, shifted the center of variation to Asia Minor, where this species appears to be a common weed in the crops of the cereal grasses (P.M. Zhukovskiy).

Thus, the differential, taxonomic-geographical method clearly outlines three independent groups of wheat and furnishes a comparatively accurate picture of the concentration of the centers of type-formation of the different groups thereof. The distribution of the centers of variation of wheat species bears witness to the isolation of two groups of Linnaean species over a span of many thousands of years. There can be no doubt that the ancient inhabitants of northern Africa and southwestern Asia based and developed their agriculture on different kinds of wheat. The present absence of hard wheat in Afghanistan, and in many areas of India, China and Khorezma is indicative of this. The ancient agricultural civilizations of Mesopotamia and along the Indus were developed on the basis of both soft and hard wheats, while those of Egypt, Crete and around the Mediterranean were, as they are now, based on the group of hard wheats.

The ecological type of hard wheat is different from that of the soft ones. The strains of hard wheat are (as a unit) plants that require moisture, particularly during the early stage. In a mature state they tolerate drought well, in this respect not yielding to, but definitely surpassing the soft wheats. This difference is apparently linked to the native area of hard wheats. The maximum precipitation along the coasts of the Mediterranean occurs usually during the autumn and spring, the times of seeding and development of the early stages, whereas in Europe and Asia, the precipitation falls mainly during the winter months (Scharfetter). The vegetative rhythm of the species does, as demonstrated by Scharfetter, usually correspond to the climatic rhythm of the region where the plants originated.

The facts stated above indicated to the plant breeder where he should search for material suitable for plant breeding both for hard and for soft wheats. At the same time, these facts reveal that to unite hard and soft wheats on the basis of their origin, which is still done, while not taking into consideration the

geographical peculiarities of the species, leads simply to confusion in respect to the history and origin of wheats.

### The distribution area of emmer

The taxonomic-geographical investigation of emmer (*T. dicoccum*), the bread wheat of the ancient agricultural peoples, turned up a very interesting group of phenomena for the elucidation of the antiquity of wheat cultivation.

As is already known from archeological discoveries, emmer was cultivated in the past in considerable quantities in Egypt (Schulz, 1913). Grains of it have also been found from the Stone Age in Germany (at Worms) and from the Iron Age in Italy (at Aquilaia) and in Switzerland (at Auvernier) according to Buschan (1895).

The racial composition of emmer and the history of its cultivation have, during the past couple of years, been thoroughly studied at the Department of Applied Botany (Stoletova, 1925). The investigations have revealed that out of the ancient crops of emmer in the Old World only isolated sites remain. They are almost exclusively associated with backward or isolated populations. As indicated by statisticians in the U.S.S.R. and in other countries, this plant is becoming extinct and is being replaced by other crops.

Thus, in Russia, the area under emmer was reduced by almost 50% between 1888 and 1916 in spite of the fact that the areas of other field crops were increased by almost the same figure during the same period. A similar decrease took place in Serbia. Only the following isolated areas remain where emmer is grown in the Old World: in respect to the area covered, the Pri-Kama region takes first place, i.e. the areas along the rivers Volga and Kama, including the Tatar and the Bashkir republics, the autonomous territory of the Chuvashi (the upper Kazán, Simbirsk and the Ufa Governates) and a portion of the Votskaya Autonomous Territory as well as the Province of Perm. In 1916 up to 170000 hectares of emmer were grown there. Important areas of emmer are found along Lower Volga (more than 20000 ha) and in the Cis-Uralian region (more than 15000 ha). Sites with emmer occur also in northern Caucasus and Transcaucasia but especially in Armenia, Georgia, and Azerbaidzhan (in Caucasus up to 5000 ha). Insignificant localities under emmer remain in Crimea (see Stoletova, 1925, for more details). In western Europe, emmer occurs mainly in the mountains of Switzerland, Germany (Baden, Schwaben, Württemberg), Spain, France and Italy, and in the Balkans in the mountain areas of Serbia, Bulgaria, Chernogora and Croatia. In the Pyrenées it is still grown by the Basques. In addition to Asia Minor, emmer is found in small areas of Persia, according to our experience almost exclusively among Armenian settlers of the area. In India, emmer is occasionally grown in Bombay, Madras and Mysore as well as in the central provinces (A. & G. Howard, 1909). In Africa, it is grown mainly in the mountain areas of Abyssinia (Kostlan, 1913).

The absolutely certain remainders of the ancient cultivation of emmer are linked, in the Old World, to the ethnographical picture. In the U.S.S.R., emmer is cultivated by the Tatars, the Bashkirs, the Chuvashi and the Votyaki, in the

Caucasus by the Yaphetids [Indo-European peoples]: Armenians, Gortsians, Georgians, Pshabi, Tushini, Rachintsi, Khevsuri and Ossetini; in Germany it is grown by backward Schwabians and in Spain by the Basques. In Abyssinia, emmer is grown by tribal Masai and Amharans and along the Tigris and Euphrates by the Kurds, i.e. by people associated with remote antiquity in respect to their customs and civilizations. V.S. Sbojev (1856), the explorer of the Chuvashi, called them 'repositories of Antiquity'.

Studies of specimens, collected by us from all the areas where emmer is cultivated, revealed that in Europe and Asia only two botanical varieties are almost exclusively grown, i.e. *T. dicoccum* var. *farrum* and var. *rufum*. In addition, a black-spiked winter-emmer, *T. dicoccum* var. *atratum*, is occasionally grown in France. In other words, at first glance the varietal composition grown in Europe and Asia is very poor and monotonous. Only Abyssinia constitutes in this respect an exception, as demonstrated by recent research done by Harlan (1923). This revealed a major variation in the forms of emmer in that country.

Detailed, multifaceted research at the Institute of Applied Botany on the forms of emmer from various areas has shown that, although emmer is grown in different countries and belongs either to a variety of *farrum* or *rufum*, the racial composition of these is sharply differentiated. After detailed studies by means of crops grown it could be shown after some years that the different races within the limits of these varieties differed in some dozens of well-expressed morphological and physiological, hereditary characteristics. We shall present the characteristics of the major traits of the geographical races belonging to var. *farrum*.

Table 2 demonstrates, with a description of the geographical races, what profound differences can be found behind the 'exterior' of a single variety. At the same time as both the botanical varieties and the conventional taxonomic units differ in one or two characteristics (e.g. white, red, or black spikes), the races within the limits of a single variety can differ by dozens of traits. Simultaneously, the table as set up, illustrates facts concerning the sharp divergence of the races depending on 10 or more morphological and physiological traits. The presence of such a divergence of characteristics can only mean that the species of *T. dicoccum* was once represented by a major, polymorphic species as in the case of the other species of wheats and that, apparently, it was widely distributed in the Old World. The present existence of differentiating racial characteristics linked to different areas is evidence for the past diversity of emmer. The various geographical races remaining and the isolated areas, where major crops of the polymorphic species are grown, indicate the profound antiquity of emmer and of all the crops of wheat. Some races, remaining in isolated areas of emmer cultivation and differing in many characteristics, create an opportunity for a reconstruction of the entire system of alternating characteristics, making up the species of *T. dicoccum*.

Although it may be possible to establish the original center of variation of some other species of wheat, such as *T. vulgare*, *T. compactum* or *T. durum*, in the case of emmer the initial composition of the variation can be restored only by summing up the complex of all the characteristics of the different races found in the Old World.

Table 2. Races characteristic of the variation within *Triticum dicoccum* var. *farrum*

Characteristics	Races found in				
	Abyssinia and India	Persia	Transcaucasia	The Pri-Kama region	Germany Spain
Color of shoots	Violetish, with anthocyanin	Violetish, with anthocyanin	Violetish or green	Violetish	Green Green
Growth shape	Upright	Upright	Upright	Upright	Spreading
Color of stem	Violetish	Violetish	Violetish	Violetish	Green
Height of stem	Low	Medium	Tall	Tall	Tall
Culm diameter	Medium	Slender	Slender or medium	Slender	Slender
Culm filled or not filled with pith	Filled	Filled	Not filled	Not filled	Not filled
Hairiness of nodes of leaves	Glabrous	Very hairy	Very hairy	Hairy or glabrous	Glabrous
	Smooth but with small prickles along veins	Very hairy, almost woolly	Very hairy	Very hairy	Very hairy
of secondary axis	Hairy along the segments	Hairy along the segments	Glabrous or hairy segments	Hairy at the base of the spike	Hairy along the segments on a significant portion of the axis and at the base of the spike
of sheaths	Glabrous	Hairy	Hairy	Hairy or glabrous	Glabrous
Consistency of leaves	Rigid, leathery	Soft, velvety	Soft, velvety	Soft, velvety	Soft, velvety
Color of leaves	Yellowish-green	Bluish	Bluish	Bluish	Bluish
Color and hairiness of nodes	Colored, hairy	Colored, hairy	Colored, hairy	Colored, hairy	Not colored, glabrous
Type of awns	Coarse	Coarse	Average	Tender	Tender or coarse
Diameter (in $\mu\text{m}$ ) of stomata	Large, 65.1	Average, 53.1	—	Average, 56.2	Small, 49.2
Life type	Spring-type	Spring-type	Spring-type	Spring-type	Spring-type
Vegetative period	Very short	Medium long	Medium or long	Medium	Long
Size and shape of teeth on glumes	Short, pointed	Short, pointed	Short or long, hooked	Short, blunt or conspicuous	Elongated (forms exist with hooked or with straight teeth)
Resistance to					
<i>Enisyphe graminis</i>	Strong	Weak	Strong	Medium	Strong
<i>Puccinia glumarum</i>	—	Weak	Strong	Weak	Strong
<i>P. triticea</i>	Strong	Weak	Strong	Weak	Strong
<i>P. graminis</i>	Strong	Weak	Strong	Weak	Strong

The crops of emmer associated with ethnic differentiation appear to be interesting examples of the geographical distribution of species about to become extinct and represent instructive examples of the expediency of the differential phyto-geographical method for studying cultivated plants.

Thus, the solution of the problem of the geographical origin of cultivated wheat can be drawn up. We shall select the two basic, independent centers of type-formation with respect to the two major groups of Linnaean species of wheat with  $n = 14$  and  $21$  chromosomes, respectively, and belonging to two continents. The theory of a polyphyletic origin of wheat according to Solms-Laubach (1899) borders on the acknowledgement of a miracle and seems less than believable. It was confirmed only by a method that Solms-Laubach himself had outlined but of which he could not take full advantage due to the lack of data at that time, i.e. a comparison of the botanical composition between the species in northern Africa and those in Asia. Instead of confirming the assumption of Solms-Laubach about the unity of the wheat species of Abyssinia and those in eastern Asia, where he was inclined to place the native land of wheat, a comparison of the species, varieties and races of the wheats on the two continents confirms the opposite fact, i.e. that there is a sharp difference between the Asiatic and the African groups of wheat.

De Candolle cursorily launched a hypothesis that the soft wheats, in his opinion originally from Mesopotamia, changed into hard wheats. This reasoning is at present impossible to substantiate; all objective and irreproachable data force us to speak of independent type-formation within either center. We may later succeed in linking together both centers, to understand the origin in general of all the species of wheat and to tie together the genesis of all the species of wheat into one genus, *Eutriticum*, but this is a matter for future investigations. It is a problem of general importance, which affects all the questions concerning the origin of Linnaean species. There is no doubt that this problem can also be solved by painstaking studies of the entire composition of the varieties and races of all the wheats in the Old World by means of detailed geographical investigations, especially of the mountain areas in Africa and Asia and by means of experimental syntheses of the species after hybridization.

In any case, plant breeders may be satisfied with a temporary solution to the problem regarding the centers of type-formation of wheats since the detailed geographical data allow us to build practical plant breeding work from them.

In order to understand the origin of the Linnaean species of wheat it is necessary to include not only the species of wheat but also those of the genus *Aegilops* [the goat grasses] within the scope of the investigations. Some species of this genus hybridize easily with wheats, although this results mainly in sterile offspring.

The distribution areas of many species, belonging to *Aegilops*, overlap those of the wheats. As demonstrated by research made by G.M. Popova, species of *Aegilops*, although polymorphic, remind one in this respect of the species of wheat. Most of all, their differentiation into groups is similar to the division of the wheat species. Species such as *Ae. cylindrica*, *Ae. squarrosa* and *Ae. crassa* correspond in their response to fungal parasites and to 'hollow straw' disease to

that of the soft wheats; in their resistance to these diseases as well as in the character of the pith, *Ae. triunciales* and *Ae. ovata* remind one of the hard wheats (Popova, 1923). Apparently, the former easily hybridize with the soft wheats as well. By selecting similar species of the genus *Aegilops* and resorting to complicated hybridization between them and wheat, an investigator can perhaps come close to a solution of the problem concerning the speciation of these closely related genera. Under the conditions in Turkestan, extensive hybridization between wheat and *Aegilops* is a common phenomenon. However, these hybrids are usually sterile and cannot give rise to fertile forms. The role of species belonging to *Aegilops* in the origin of the cultivated species of wheat is at present highly problematic and requires very complicated research.

### The geographical centers of type-formation of barley

De Candolle looked for the native land of barley in the area where the distichous, hulled barley, *Hordeum spontaneum*, grows in its wild state.

At present we are able to add considerably to the information available to De Candolle about the geographical area of wild barley; it extends across northern Africa all the way from Morocco to Abyssinia and on into Asia Minor, Turkestan, Bokhara, Persia and northern Afghanistan as well as Transcaucasia (Vavilov, 1918).

Our studies of wild barley, *H. distichum* var. *spontaneum*, in southwestern Asia (Persia, Bokhara, Turkestan and Afghanistan) have revealed a number of new varieties and races. In addition to the usual yellow-spiked form, we know now of a black-spiked variety of this wild barley, i.e. *H. distichum* var. *transcaspicum*. In northern Afghanistan, there is a new variety with brown glumes, a genetically dominant characteristic. In the Transcaucasian area (Turkmenistan) around Anau, our expedition (under D.D. Bukinich) found a race of distichous barley with a comparatively rigid rachis. In addition to the ordinary races of winter barley, we also found a spring barley.

Nevertheless, studies comparing wild and cultivated barleys in the Old World have demonstrated that, in general, the former is represented by a very limited group of forms, composed of a series of distichous, hulled barleys, but in no way corresponding to the rich diversity and polymorphism found among cultivated barleys. The large number of cultivated varieties and races described during the last couple of years is characterized by a multitude of varietal and racial traits, both recessive and dominant when crossed, but not typical of the wild barleys so far described. For instance, such characteristics as compact spikes, multistichous spikes, underdeveloped lateral spikelets (*deficientes*), the formation of three-lobed appendages instead of awns (*trifurcatum*), short awns, no awns, smooth awns, naked grains, wide leaves (as in the case of many races of var. *coeleste*) and broad glumes have been noted.

Plant breeders have looked in vain for forms of wild barley suitable for practical purposes within the major portion of its distribution area where it occurs as a weed on loess soils in northern Afghanistan, Transcaucasia and Bokhara. While ecologically clearly related to the cultivated races of distichous,



hulled barley, wild barley (*H. spontaneum*) displays only a fraction of the hereditary variation typical of *H. sativum* (*s. lat.*) in which plant breeders are interested.

A group of barley, sharply isolated from the wild one in southwestern Asia, is represented by the naked-grained barleys of southeastern Asia and the elevated mountain areas of Central Asia. These have wide leaves and thin-walled stems of an anatomically peculiar structure and coarse, rough awns (Vavilov, 1921). They are also characterized by a comparatively satisfactory resistance to mildew (*Erysiphe graminis*). The wild barley, i.e. *H. spontaneum*, is usually not common in the mountain areas of Afghanistan, Bokhara and Turkestan above 1800–2000 m.s.m. Naked-grained barley, on the other hand, is typical at the limits of cultivation. As a rule, it is grown in southwestern Asia above 2500 m. In the alpine areas of Tibet, Ladakh and Hindukush, it occurs up to 4000 m elevation.

Perhaps future studies of the genetics will help solve the problem concerning the wild ancestors of the cultivated barleys. At present it is obvious that the existence in nature of a large amount of distichous, hulled barley, *H. spontaneum*, in southwestern Asia does not solve the problem concerning the origin of cultivated barleys or where the source of the wealth of strains of cultivated barleys can be found.

Investigations at the Department of Applied Botany during the last couple of years by means of special expeditions to Mongolia, Afghanistan, Persia, Turkestan, Bokhara and Asia Minor, and studies of north-African material sent to us from the Department of Agriculture in the U.S.A. (through Dr. Harlan) as well as a comparison of materials from various countries obtained from experimental stations in India, Burma, China, Algeria, Tunisia, Egypt and other countries, have helped us approach the problem of the geographical centers of varietal diversity of cultivated barleys. Our access to this material of strains revealed, thanks to detailed taxonomic-geographical studies that there are *two* basic centers of variation as far as cultivated barleys are concerned.

One center of type-formation appears to be related to northeastern Africa, especially the mountain areas of Abyssinia, where there is a particular wealth of forms of hulled barley. A whole series of peculiar varietal and racial characteristics are found exclusively among the barleys cultivated in Abyssinia. Varieties with broad glumes, distichous barley with entirely under-developed lateral spikelets, forms of barley with pubescent paleas (the pubescence is visible even in the field) or with brightly anthocyanin colored stems are known only from Abyssinia.

The following botanical varieties appear to be endemic in Abyssinia and northeastern Africa:

- 1 var. *gracilius* Koern.,
- 2 var. *schimperianum* Koern.,
- 3 var. *latiglumatum* Koern.,
- 4 var. *atriscipatum* Koern.,
- 5 var. *eurylepis* Koern.,
- 6 var. *platylepis* Koern.,
- 7 var. *contractum* Koern.,

- 8 var. *heterolepis* Koern.,
- 9 var. *glabro-heterolepis* Vav. (with a compact spike of type *erectum* and with smooth awns),
- 10 var. *steudelii* Koern., (rarely met with also in Arabia)
- 11 var. *atterbergianum* R. Reg. (syn. *subglabrum* Beaven.)
- 12 var. *africanum* Vav. (belonging to the group of *deficientes* f. *erectum* with yellowish spikes)
- 13 var. *copticum* Vav. (distinct from the preceding varieties by having black spikelets)
- 14 var. *abyssinium* Sér.,
- 15 var. *macrolepis* R. Reg.,
- 16 var. *leiomacrolepis* R. Reg.,
- 17 var. *melanocrithum* Koern., and
- 18 var. *deficiens* Steud. (frequent also in Arabia and India).

Algeria, Tunisia, Morocco, Tripolitania, Arabia and Mesopotamia yield to Abyssinia as far as the diversity of the barleys is concerned and come closer to the composition of the varieties in the European countries. Persia, Turkestan, Bokhara, Khorezm and India are characterized by a small number of common varieties. As far as our investigations of the composition of the strains are concerned, and in spite of the abundance of wild barleys and the diversity of conditions for cultivation, only four to five varieties of barley are grown in Afghanistan, while in Abyssinia all the European varieties such as vars. *pallidum*, *nigrum*, *pyramidatum*, *nutans*, *erectum*, etc., are met with. As far as can be judged from the material available to us, Abyssinia appears to be the single most important one of the major centers where the forms of barley developed.

As shown by the comparative-geographical study of the strains in the Old World, southeastern Asia, China, Japan and the area adjacent to Tibet (and, perhaps, also Nepal) appear to represent a second center of varietal and racial diversity with respect to the barleys. There, varieties with naked grains, short awns, no awns or varieties where the awns are replaced by three-lobed appendages (different kinds of *trifurcatum*) occur. The racial composition of this group of varieties is always variable and includes both extremely late-maturing and extremely early-maturing races. Judging from all the material not yet published and the collections available to us, eastern Asia appears, in general, to have a concentration of naked-grained, furcate, no-awned or short-awned forms. On the other hand, Abyssinia appears to be the main center of the awned, hulled forms.

The following varieties turned out to be endemic in and known only from southeastern Asia:

- 1 var. *brachyatherum* Koern.,
- 2 var. *tonsum* Koern.,
- 3 var. *nigritonsum* Koern.,
- 4 var. *japonicum* Vav. (hexastichous, hulled; the palea of the central spikelet carries a short awn, the lateral spikelets are almost completely without awns, the spike is dense and yellowish)
- 5 var. *revelatum* Koern.,
- 6 var. *nudipyramidatum* Koern.,

- 7 var. *asiaticum* Vav. (hexastichous, with an open spike and naked grains; the paleas carry short awns; it is cultivated in Japan and India),  
 8 var. *brevisetum* R. Reg., and  
 9 var. *trifurcatum* Schlecht.

The ecological type of the Asiatic group of naked-grained barleys differs from that of the previous group. In Asia the races of barley are grown mainly on irrigated soils. In the elevated mountain areas of the southwestern area naked-grained barley is, as a rule, also grown on irrigated soils but, at the same elevation, hulled barley often succeeds on non-irrigated soils.

The New World adopted the cultivation of barley from Europe and is of no importance for the solution of the problem concerning the origin of this crop. The varietal composition of barley in Canada, the U.S.A. and Argentina reminds us, in general, of that in Europe.

Thus, the application of the differential, taxonomic-geographical method proved the presence of two basic centers where forms of cultivated barley developed (Fig. 3).

The existence of two independent centers could also be confirmed by data from experimental hybridization between the Asiatic and the African forms. Between 1915 and 1918 we made a large number of crosses between different varieties of naked-grained and hulled barleys. Studies of the F<sub>2</sub>, F<sub>3</sub> and F<sub>4</sub> generations revealed a definite presence in such combinations of a noticeably expressed interrupted spike. Although all the races and varieties of the wild and cultivated barleys are easy to cross and not as clearly isolated from each other as hard and soft wheats, some differentiation between the east Asiatic and the east African groups is indicated by a display of partial sterility in the form of an under-development of the reproductive organs of many plants or in the form of a so-called interrupted spike. In the case of the hybrids between the races within a single group, the interrupted spike is more or less completely absent or only weakly developed.

The striking fact of an isolation between the east Asiatic and the African group was revealed to us in 1925 while we were investigating the second generation hybrids between *H. vulgare* var. *pallidum* f. *coerulescens* (no. 3316 from Abyssinia) and *H. vulgare* var. *coeleste* (no. 3426, a low-growing type from Japan). The first generation in 1924 was normal, hulled, tall-growing and reminded us of the Abyssinian type. The first generation was also similar to the wild barley, *H. spontaneum*, because of the brittleness of the rachis. In the second generation, out of 301 seeds that germinated, 12 plants turned out to be completely sterile; half of the remaining seedlings were generally weakly developed in spite of absolutely normal growing conditions in the greenhouse, while the other half developed normally with thick spikes, which were, however, nevertheless completely sterile. These plants stood with open glumes for a long time (several days) during anthesis, reminding one of the common type of behavior of sterile hybrids. On 46 plants, grains developed in some spikes only; a part of the spikelets of these plants were completely sterile; 197 plants displayed more or less of interrupted spikes, while 46 had normally fertile spikelets (K.V. Ivanova calculated the figures).

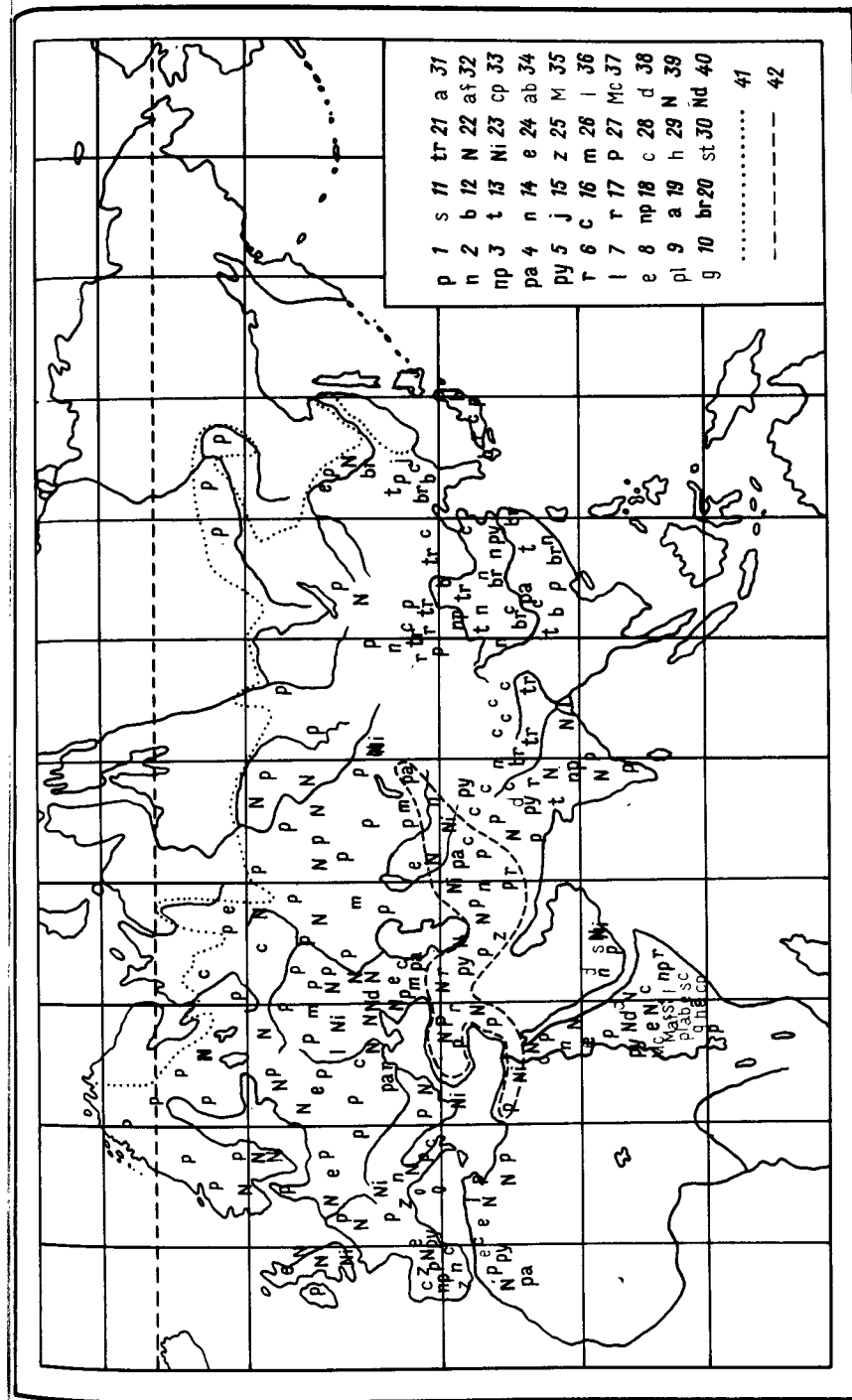


Fig. 3. Geographical distribution of the varieties of cultivated barley and *Hordeum spontaneum* C. Koch. 1. *Hordeum pallidum* Sér.; 2. *nigrum* Willd.; 3. *nigropallidum* R. Reg.; 4. *parallellum* Koern.; 5. *pyramidatum* Koern.; 6. *ricotense* R. Reg.; 7. *leirithychnum* Koern.; 8. *eurylepis* Koern.; 9. *platylepis* Koern.; 10. *gracilis* Koern.; 11. *schimperianum* Koern.; 12. *brachyatherum* Koern.; 13. *tonsum* Koern.; 14. *nigritonsum* Koern.; 15. *japonicum* Koern.; 16. *coeleste* L.; 17. *revelatum* Koern.; 18. *nudipyramidatum* Koern.; 19. *asiaticum* Vav.; 20. *brevisetum* R. Reg.; 21. *trifurcatum* Schlecht.; 22. *nutans* Schuebl.; 23. *nigricans* Sér.; 24. *erectum* Schuebl.; 25. *zeorithum* L.; 26. *medium* Koern.; 27. *persicum* Koern.; 28. *contractum* Koern.; 29. *heterolepis* Koern.; 30. *stuedelii* Koern.; 31. *atterbergianum* R. Reg.; 32. *africanum* Vav.; 33. *copticum* Vav.; 34. *abyssinicum* Sér.; 35. *macrolepis* R. Reg.; 36. *leiomacrolepis* R. Reg.; 37. *melanocrothum* Koern.; 38. *deficiens* Steud.; 39. *nudum* L.; 40. *nudificiens* Koern.; 41. northern limit of cultivated barley; 42. distribution area of *H. spontaneum* C. Koch.

The facts stated above concerning the appearance of completely sterile plants following hybridization between representatives of barley from Abyssinia and Japan clearly show that the two basic geographical groups of barley are quite well isolated from each other. In spite of the common opinion that *H. sativum* is a single species, different characteristics of it are, as shown above, entirely isolated due to the appearance of disharmony during the development of the reproductive organs after hybridization. It could be that in a remote past, the different groups of cultivated barley originated from a single center, although we can only guess about that. The present isolation of the groups is so obvious to the plant breeder that he is able to draw corresponding practical conclusions from it.

From the simple hypothesis of De Candolle, we have now arrived at some very complicated ideas. The problem concerning the origin and the evolution of cultivated barley has, over the past 40 years, turned out to be much more involved and intricate. The distribution area of *H. spontaneum* is shown in Fig. 3. Just as could be expected, it does not coincide with the two centers, where cultivated barleys developed, but corresponds more closely to that of the African group of the cultivated, hulled barleys.

#### The geographical centers of type-formation of cultivated oats

An even more complicated picture was revealed with respect to the origin of oats. In his agronomical monograph on oats, published in 1918, Zade writes: 'Es gibt wohl keine zweite Getreideart oder sonstige Graminee, deren Verwandtschafts und Abstammungsverhältnisse wir so klar zu durchschauen vermögen wie die des Hafers'. [There is hardly any other kind of cereal or similar grass, the relationship and evolutionary condition of which we can understand as easily as that of oats.] Later arguments have revealed the falseness of this opinion.

De Candolle ascribed a European origin to the oats while mainly basing his opinion on conclusions drawn from historical and philological facts. The cultivation of oats is, apparently, not very old. Neither the early Egyptians nor the early Europeans grew oats. Old data in the literature indicate that, as a European crop, oats were a speciality of the northern countries – ancient Germany, Scotland and Norway (Buschan, 1895). European oats are represented by a large group of quite different races, clearly differing in the color of the glumes, the shape of the grains and leaves, vegetative characteristics and resistance to parasites. A number of forms of cultivated oats are without question at present typical only of northern and central Europe.

In addition to the European group of *Avena sativa*, studies over the last decade (Trabut, 1913) have revealed the presence of a large Mediterranean group of oats, comparatively sharply isolated from *A. sativa*, i.e. *A. sterilis* and *A. byzantina*. Northern Africa turned out to be the center of a large group of cultivated oats, in general characterized by resistance to the European types of smut, *Ustilago avenae*, and rust, *Puccinia coronifera*, and physiologically isolated from the European oats by a considerable degree of sterility after hybridizing with the latter. Apparently a number of wild oats, belonging to the subgenus *EuAvena*, can also be included in the group and are met with in northern Africa.

In northwestern Europe it is also necessary to distinguish another independent group of oat species, in addition to *A. sativa*, i.e. *A. strigosa* and *A. brevis*, half weedy but in part also cultivated and characterized by a low number of chromosomes,  $2n = 14$  instead of  $2n = 42$  (or close to that), typical of the former group, i.e. *A. sativa* and *A. byzantina* (Nikolayeva, 1920). The major part of the forms of *A. strigosa* and *A. brevis* are, according to our experiments, and as confirmed in America by Reed (1920), characterized by resistance to smut, *Ustilago avenae*, and rust, *Puccinia coronifera* as well as mildew (Vavilov, 1919). The physiological isolation of this group is the reason why it is impossible to hybridize *A. strigosa* and *A. brevis* with forms of *A. sativa* and *A. byzantina* (Zhegalov, 1920).

Marquand (1921, 1922) described a considerable number of varieties of *A. strigosa* from Wales. He distinguished var. *alba f. fusca* (ssp. *pilosa*), var. *albida f. cambrica* (ssp. *glabrescens*), and vars. *flava*, *intermedia* and *nigra* (ssp. *orcadensis*); some of them are apparently at present endemic in Great Britain. We have established a number of new forms for the European parts of the U.S.S.R., France and Germany. During our experiments with infection of *A. strigosa* with smut, rust and mildew, it could be demonstrated that there were two clearly different strains within that species: one very susceptible to all the parasites enumerated and another very resistant to them. *A. strigosa* appears to be distributed as a weed in cereal crops in Byelorussia and Estonia. It is found as an important crop on sandy soils in England and France. *A. strigosa* and *A. brevis* are not known as a cultivated species nor as weeds in the southern areas of European U.S.S.R., nor in the Asiatic parts of it (Turkestan, Bokhara, Khorezm, Persia or Afghanistan). The geographical distribution area of *A. strigosa* and *A. brevis*, both when in a cultivated state or as weeds among cereal crops, seems to be related to western Europe only. The center of their variation is restricted to the northwestern and western parts of Europe.

There is no doubt that the question about the origin of *A. brevis* and *A. strigosa* must be singled out just as the problem concerning the origin of einkorn (*T. monococcum*) was in the case of wheats. The presence among oats of two physiological groups, either resistant or susceptible to smut and other diseases, indicates that the genesis of this group is not straightforward.

The widely held opinion that the ordinary cultivated oats, united under the epithet of *A. sativa*, should be a definitely north European crop only is not very convincing to us. Studies in Mongolia and northern China have revealed a large number of varieties and races of *A. sativa*, typical of those countries. There, all kinds of colors are found on the glumes from white to black as well as peculiar ash-colored races (var. *grisea*) and some with a heavy coating of wax on the hulls. Oats are grown in many parts of China and Tibet but have so far not been investigated botanically there.

Transcaucasia (Georgia and Armenia) and parts of Persia are characterized by the presence of a very large number of weedy races of hulled oats belonging to *A. sativa* among emmer and barley crops. There, a multitude of peculiar, endemic forms of *A. sativa* appear, in addition to *A. fatua* and *A. ludoviciana*, which are widely distributed all over southwestern Asia (Turkestan, Bokhara, Persia and Afghanistan). We have also found peculiar races of *A. sativa* in the

fields of the Pri-Kama area in crops that no doubt originated from more southerly areas.

Most of all, the large- and naked-grained oats, genetically related to the oats cultivated in Europe and characterized by one of the chromosome numbers ( $2n = 42$ ), easily hybridizing with each other and reacting similarly to parasitic fungi, are undoubtedly typical, especially of China. The center of its variation must be there. Europe learned about naked-grained oats from China. The very name of one of the widespread varieties, *A. nuda* var. *chinensis*, demonstrates the Chinese origin of the large-grained, naked-grained oats. It is also known from data in the literature that naked-grained oats were brought from China during the fifth century A.D. (Breitschneider, 1881). An expedition from the Department of Applied Botany (under V.E. Pisarev) in 1922 discovered new varieties of naked-grained oats (e.g. *A. nuda* var. *mongolica*) in some settlements in Mongolia. These have dark spots on the exterior paleas. Naked-grained oats are still widespread in eastern Asian crops. The presence in eastern and southeastern Asia of both hulled and naked-grained oats from which, later, endemics were no doubt developed, speaks in favor of the presence there of a basic center of variation and of the possibility for a transfer of the cultivation of oats in part also from Asia.

The small-grained forms of naked-grained oats, found as weeds and very rare in the crops of northern Europe, must necessarily be sharply distinguished from the Chinese naked-grained oats. As shown by our experiments, these forms are very easy to hybridize with *A. brevis* and *A. strigosa*, but are different in their resistance to the parasitic fungi (Vavilov, 1918).

These forms do not hybridize with the common oats or the large- and naked-grained forms. Morphologically they are close to *A. brevis* and *A. strigosa* with respect to the vegetative characteristics as could be assumed on the basis of the data available. Cytologically (according to A.G. Nikolayeva), they also turned out to belong to the group of *A. brevis* and *A. strigosa* ( $2n = 14$ ). All the authors, starting with Koernicke, erroneously united them (because of the naked grains and the many florets) with the large- and naked-grained ones into one basic species, *A. nuda*. We consider it more correct to distinguish the naked- and small-grained oats as a basic species, *A. nudibrevis*. This species forms a special group together with *A. strigosa* and *A. brevis*, the genesis of which developed independently of that of the *A. sativa*. In both groups we can find parallel, homologous series of forms as is common during the evolution of plants. *A. nuda*, the large- and naked-grained oats, corresponds to a similar series of *A. sativa*, while the small- and naked-grained oats, *A. nudibrevis*, correspond to the group of *A. brevis* and *A. strigosa*.

The genesis of cultivated oats is no doubt linked to that of weedy as well as wild species, i.e. *A. fatua*, *A. ludoviciana*, *A. sterilis* and *A. barbata*. The common wild oats, *A. fatua* and *A. ludoviciana*, are associated with the crops of *A. sativa* just like *Hordeum spontaneum* is associated with crops of *H. sativum*. The similarity of their karyograms (chromosome numbers), the reaction to parasitic fungi, the general morphological similarity and the possibility of obtaining fertile hybrids between them all indicates this. All the species of wild oats are

extremely polymorphic and they can, in their turn, be distinguished into physiological groups as well. *A. fatua*, *A. ludoviciana* and *A. sterilis* are characterized by 42 chromosomes (or close to that) while a number of races of *A. barbata*, studied by A.G. Nikolayeva and Kihara, occupy a position intermediate between *A. nuda* on the one hand and *A. strigosa* and *A. fatua* on the other ( $2n = 32$  according to Nikolayeva, 28 according to Kihara); according to Nikolayeva (1922) *A. clauda* and *A. pilosa* from the Yelizavetopol Governate have 14 chromosomes.

As shown by our experiments, *A. sterilis* and *A. barbata* can, in the same way as *A. strigosa*, be distinguished into two physiological groups. One group is at the same time strongly susceptible to smut, *Ustilago avenae*, rust, *Puccinia coronifera*, and mildew, *Erysiphe graminis*, while the second group is immune to all these parasites. Strongly affected forms of *A. barbata* are typical of Persia. Among them, races are found where the effect of the smut is localized on the anthers only, but in the majority of these forms it affects all the organs of the flower. *A. clauda*, *A. pilosa* and *A. wiestii* proved to be susceptible to smut and rust only. In our experiments with infections we have tested races of *A. wiestii* and *A. pilosa* from the Yelizavetopolsk District and *A. clauda* from the same district as well as from Transcaucasia.

The distribution area of *A. fatua* covers an enormous area from the northern districts of the European parts of the U.S.S.R. all the way to Hindukush. It infests cereal crops in the mountain areas of Afghanistan, Transcaucasia, Ukraine and the Vyatskaya Autonomous Territory. A somewhat less wide but still very large area is typical of the races of *A. ludoviciana*; it is especially widespread in southwestern Asia, Transcaucasia and the southern areas of the European U.S.S.R. The areas of *A. fatua* and *A. ludoviciana* overlap in general with the main areas of the racial and varietal diversity of *A. sativa*. There is no doubt that together with the large-grained *A. nuda* these four species form one single group. It is very hard to tell where the geographical center of their type-formation is found. In any case, it would be erroneous to state that the cultivated oats are definitely linked to Europe only. The existence in China of endemic groups of *A. sativa* and *A. nuda*, the wide distribution of *A. fatua* and *A. ludoviciana* in a wild as well as in a weedy state in Turkestan, Bokhara and Afghanistan, Persia, Armenia and Transcaucasia and the presence there of many peculiar groups of weedy and wild oats all point to the participation of Asia in the development of the forms of *A. fatua*, *A. ludoviciana*, *A. sativa* and *A. nuda*.

In Abyssinia, the cultivated and weedy oats are represented by a peculiar group (*A. abyssinica*, *A. schimperi*, *A. hildebrandtii* and *A. braunii*), so far not very well studied. Specimens furnished us by Harlan proved according to the investigations made by E.K. Emme, to have  $2n = 28$  chromosomes.

The African group of cultivated, wild and weedy oats, the investigation of which was initiated by Trabut (1913), needs to be subjected to a special study but at present there is nothing fundamental in favor of uniting them with the European or Asiatic species.

It seems impossible to reduce the origin of the cultivated oats to a single geographical center. The cultivated oats have no doubt a polyphyletic origin.



considered the problem of the native area of millet still open: 'Millet is usually referred to East-India', he writes, 'but there is no proof favoring this assumption'.

Let us now turn to a taxonomic-geographic analysis of the various kinds of millet. At present, the botanists have described more than 60 botanical varieties of *P. miliaceum* (Arnold, 1925). The density of the inflorescences, the color of the paleas and glumes and the roughness of the paleas were used as basis for the division into varieties.

Studies of the racial composition of millet at the Department of Applied Botany together with I.V. Popov revealed even more taxonomic characteristics such as the dimensions of the grains, the pubescence of the leaves, the length of the vegetation period, the height of the plants, and so on.

A study of the complex of millet in various regions of the European and Asiatic parts of the U.S.S.R., Bokhara, Khorezm, Persia, Afghanistan, Mongolia and China demonstrated clearly that the variety of forms increased toward the east in Asia. The maximum diversity was established in eastern and central Asia, where the entire racial and varietal complex of the Linnaean species of *P. miliaceum* is found. So far China has hardly been studied at all but, nevertheless, Mongolia and northeastern China – the areas of the most advanced Chinese civilization – display an exceptional diversity of morphological and biological characteristics.

In the districts of the European parts of the U.S.S.R., an increasing diversity of millet crops can be observed toward the east and southeast. At the same time as in the Voronezh district 22 varieties were found after detailed investigations (by I.V. Yakushina), there were 40 in the Saratov District (Arnold, 1925). In the areas of Bokhara, Chinese Turkestan and the countries adjacent to them, endemic forms not known in Europe are found. There, large quantities of membranaceous and naked-grained millets are grown. In Mongolia, extremely late-maturing kinds of loosely spreading millet, such as never seen in Europe, are found and races with glabrous leaves and large grains have also turned up.

In some parts of Mongolia, races of millet with a characteristic type of rachis, on which the glumes sit, are found. It disarticulates when maturing. This type of formation reminds of the elaiosomes of wild oats. A.K. Holbach established a whole scale of brittleness based on the Asiatic strains. Some cultivated Asiatic races are characterized by the florets dropping off when the grains mature, littering the soil, behaving like wild plants and multiplying as self-sown crops. Some millets actually become weedy.

Apparently, millet dispersed from Asia to Europe together with nomadic people. Among the crops grown by these nomads in Asia, millet appears to be the favorite cereal. It can be sown very late or at different times, and does not tie the nomads down to one place. To seed a 'desyatina' [2.7 acres] only a very small quantity of seeds is required. Millet is extremely easy to transport, universal with respect to its utilization, usually drought resistant and succeeds even on soils where other plants (except for watermelons) do not thrive. Therefore, it is still indispensable to the nomadic economy in the semi-desert areas of Asia and the southeastern European parts of the U.S.S.R.

The mountain regions of Mongolia have an especially large variation of forms with respect to the color of the seeds, the shape of the panicle and the length of the vegetation period.

Studies of the complex of millet strains and their geographical distribution are still in progress, but already now it is possible to definitely outline the general traits of the centers where the forms of this crop developed. The center is not located in Egypt, nor in Arabia, as suggested by De Candolle, but in eastern and central Asia. According to critical studies by Buschan (1985), crops of millet were not found in Egypt in prehistoric times. Persia and Turkey (Asia Minor) cultivated only small quantities of millet in the form of a comparatively poor variety of strains. The variation in Afghanistan was, according to our experiences, also rather small. There, as in Turkey and Persia, it is mainly forms with light-colored grains that predominate. Everything indicates that the diversity increases toward Mongolia, China and eastern Asia. East-Siberian black-colored, brown and dark gray millets come, as shown by the research done by V.E. Pisarev, from the mountain areas of Mongolia. In eastern Europe, the southeastern parts of the European U.S.S.R. and Romania, millet was found also during pre-historic times, as demonstrated by the discoveries by archeologists (Cocuouteni) in Romania of millet from the Stone Age. There is also definite evidence of its cultivation there during the fourth century B.C. (Buschan, 1895). Already, in his *Historia Naturalis*, Plinius stated that millet was an important crop among the Slavic tribes (the Sarmatians). Columella (in his *De re rustica*, vol. II) mentioned the preparation of bread baked with millet flour and consumed while still hot.

Italian (or foxtail) millet, *P. italicum* [now = *Setaria italica*], has a very unfortunate epithet since this millet has little in common with Italy. It is grown in large quantities in the mountain areas of southwestern Asia, in Afghanistan, Bokhara and Uzbekistan. Italian millet (also known by several local common Russian names such as 'chumiza', 'gomi' and 'mogare') is often grown in Asia mixed with panicked millet (*P. miliaceum*). In many areas of Bokhara, Turkestan, Afghanistan and Kazakhstan (formerly the Turgay district), the crops of millet grown by the nomads and the settlers consist of both species, *P. miliaceum* and *P. italicum*.

Biologically, both these species are extraordinarily close and it is difficult to separate the species by the seeds. Although these species are sharply delimited genetically as well as physiologically (e.g. in their response to parasitic fungi), the centers where both seem to have formed apparently overlap.

Eastern Asia, including China and Japan, where millet is grown as a cereal crop, appears to be the main center of the Italian millet, *P. italicum*. In Europe, it is grown mainly as a forage crop. Apparently this millet is of alien origin in Transcaucasia, imported there from eastern Asia.

The dispersal of the strains of millet (both *P. miliaceum* and *P. italicum*) into Europe is, as we have succeeded in clearing up, definitely quite regular. Toward the north, the forms cultivated are mainly those branching into loose panicles and having small seeds; toward the south the large-grained and late-maturing forms are increasingly common; in between there are intermediate forms with

dense inflorescences, which are drooping or nearly so. Their dispersal is apparently linked to the length of the vegetation period, which correlates with the shape of the inflorescence and the dimensions of the seeds.

The so-called 'mohar' (*P. italicum moharicum*) – a kind of Italian millet with a short, non-branching inflorescence – dispersed toward the north; on the other hand, the branched form with a compound inflorescence is essentially a plant of the south and has a very long vegetation period. The typical forms of millet are grown in Transcaucasia and China. In intermediate areas (e.g. Bokhara) there is a full range of transitional forms from branched Italian millet (*P. italicum maximum*) to non-branching millet with small inflorescences. In the elevated mountain areas the non-branching type of millet predominates, while at lower elevations with a longer vegetative period the branching type is most common.

The ranges of *Setaria glauca* and *S. viridis* [sometimes also called foxtail millet] are very close to that of *P. italicum*, and cover very large areas. These common weeds are widespread in Europe and Asia and, as far as their habitats are concerned, it is necessary to draw conclusions about their centers of type-formation from that of the group close to them, i.e. *P. italicum*.

### The geographical centers of type formation of cultivated flax

In his thorough review of the origin of flax and its cultivation in the past, Oswald Heer (1872) suggested that the ordinary cultivated flax originated from the wild species, *Linum angustifolium*, while assuming that winter flax, *L. hyemale-romanum* and *L. ambiguum*, should be the ancestral forms of *L. angustifolium* and *L. usitatissimum*. He considered the native land of the cultivated flax to be located within the Mediterranean area, where *L. angustifolium* still occurs in its wild state. Thus, on the basis of this opinion, Heer referred the discoveries in the pile-dwellings in Switzerland of remnants of stems and seeds to *L. angustifolium* cultivated during the Stone Age.

The questions concerning how the different races of flax originated or how they became cultivated for the sake of the fibers and seeds were not touched upon by Heer (1872) but the establishment of a connection between cultivated flax and the wild forms appeared to him quite important; that would be where the solution of all the problems concerning the origin of the cultivated flax was supposedly hidden.

However, more recent data according to Gentner (1921) compel us to consider Heer's determination of the flax from the pile-dwellings as *L. angustifolium* to be erroneous and instead to assign it to the ordinary winter flax, *L. hyemale romanum*.

De Candolle's opinions changed drastically from 1855 to 1882. In his *Géographie botanique raisonnée* (De Candolle, 1855) he assumed on the basis of 1. the existence of many names for flax among various people, 2. the antiquity of the flax crops in Egypt, and 3. the cultivation of flax in India only for linseed but in other countries both for its fibers and its oil that the cultivation of flax was polyphyletic in origin and originated initially from two or three species, which had become united into one single species, *L. usitatissimum*. In 1885, De Candolle

began to doubt that the species of flax cultivated in Egypt could be the same as the Russian and the Siberian types of flax. In his *L'Origin des plantes Cultivées* (De Candolle, 1883), he changed his original opinion and leaned toward that of Heer, assuming that the people of the pile-dwellings had cultivated *L. angustifolium*. He looked for the ancestors of the commonly cultivated flax among the wild flax of Asia while basing himself mainly on doubtful discoveries of it in the westerly areas of that continent. In *L'origine des plantes cultivées*, De Candolle acknowledged that *L. usitatissimum* must have arrived in Europe from Asia while assuming that the Egyptian and the Mesopotamian as well as all the presently cultivated kinds of flax came initially from wild flax, originating in localities between the Persian Gulf and the Caspian and Black Seas.

During the last 10 years we have, together with E.V. Ellad', conducted detailed phyto-geographical research on the kinds of flax grown in the U.S.S.R. and other countries. During special expeditions and through the courtesy of correspondents, we have collected more than 1400 samples of flax from all areas where flax is cultivated for fibers or seeds, thus gaining a comparatively complete understanding of what represents cultivated flax as such in relation to the variation of the different kinds thereof. Taxonomic-geographical studies of the kinds of flax grown in various parts of the U.S.S.R. at the experimental stations of the Department of Applied Botany revealed that the first solution of the problem according to De Candolle in 1885 was closer to the truth than the opinion to which he arrived at in 1882. Studies of the botanical complex of the cultivated types of flax and their geographical distribution in Eurasia have to some extent revealed the presence of two basic centers of variation with respect to flax and two major geographical groups of cultivated flax.

According to all the data available, ancient areas for cultivation of flax appear to be found in Asia, i.e. in India, Bokhara, Afghanistan, Khorezm and Turkestan, and along the Mediterranean coasts in Egypt, Algeria, Tunisia, Spain, Italy and Asia Minor. In remote prehistoric time, flax was cultivated also in Central Europe (Heer, 1872; De Candolle, 1883; Buschan, 1895). Among the areas at present covered by cultivated linseed flax, India takes so far first place in the Old World, only recently having a competitor with respect to the cultivation of linseed in Argentina, where its cultivation has developed during the last couple of decades. Just as in Bokhara, Afghanistan, Turkestan and Khorezm, India grows flax exclusively for linseed oil both at present as well as in earlier times (Howard and Khan, 1924). According to the information now available, flax is grown in Asia Minor both for fibers and oil. Ancient Egypt, too, grew flax for both purposes.

Studies of the many specimens of flax collected in southwestern Asia revealed a concentration there of an enormous variety of hereditary forms. In river valleys and lowland habitats, characteristic, low-growing, late-maturing, densely leafy, branched and typically bushy types (gr. *brevimulticaulis*) are concentrated and occasionally also forms with a spreading growth (gr. *prostrata*). Among the typically bushy forms (gr. *brevimulticaulis*) there are races with brownish, amber or pale-yellow colored seeds and endemic races with narrow, crimped petals (var. *angustipetalae*). Entire areas, such as the Khivinskiy



oasis, are characterized mainly by the cultivation of yellow- (or white-) seeded forms. In the mountain areas of Fergana, Bokhara and Afghanistan, races are grown that occupy a position, with respect to the branching and the length of the vegetation period, intermediate (gr. *intermediae*) between the typical North-Russian tall-growing early-maturing types and the South-Turkestan bushy types with a long vegetation period. At the altitudinal limit of cultivation in Pamir and Badakhshan one occasionally meets with typical, early-maturing, tall-growing flax (gr. *elongatae*), cultivated for the seeds. In India alone Howard and Khan (1924) have determined 26 botanical varieties and 123 races of linseed flax.

Comparisons between the Indian types described in detail by Howard and Khan, and the races known to us from Turkestan, Afghanistan, Bokhara and Persia revealed a number of characteristics among the former that make us consider them endemic in India. Side by side with races from other countries, we increased experimentally the crops of 20 samples obtained from different areas in India. Excluding the vars. *bicolor*, *vulgatum* and *commune*, described from India but found by us in other countries as well, 23 varieties remain, which were described by Howard and Khan but are not found anywhere else among our enormous material. These varieties are: *luteum*, *lutescens*, *indicum*, *cyaneum*, *purpureum*, *albidum*, *album*, *albocaeruleum*, *officinale*, *bangalense*, *agreste*, *meridionale*, *gangeticum*, *laxum*, *praecox*, *pratense*, *minor*, *herbaceum*, *pulchrum*, *caesium*, *campestre*, *tinctorium* and *sativum*. The general peculiarities, typical of the Indian forms but not found in the races of Turkestan, Bokhara, northern Afghanistan, Persia and Transcaucasia are firm and hard capsules, difficult to thresh (of type *rigidum*) and white flowers not opening fully during anthesis. While in some of the races from Turkestan and Bokhara and those of the African and European types of flax, the petals fall off after anthesis, in the case of the many Indian forms they remain adhered after flowering. Under the conditions in the territory of Kuban' (where the flax was tested) the strong development of anthocyanin in the shoots and the capsules when ripening appears to be a characteristic trait of the Indian forms. Such intensely colored races have been found by us only in Asia Minor. In India there are also typical and peculiar races with light-colored seeds and narrow-petaled flowers, and also typical races with large seeds (up to 6 mm long), which at the same time have white flowers. Forms with very small seeds (from the western parts of India), measuring 3.5–3.75 mm in length, are also found.

During the studies of flax in Asia and Europe, the general impression was that in the direction toward India the composition of the types became more variable. The complex of characteristics distinguishing the races and varieties in Europe and in Asia was especially variable in India, where the maximum variability of the types is concentrated. However, at the same time, the flax of Bokhara and Afghanistan and the countries adjacent to them display a number of endemic characteristics and combinations, not typical of the Indian flax and, perhaps not of those of Europe either. In the areas on both sides of Hindukush and in the mountain areas of Bokhara a number of peculiar types are hidden away; low-growing, branching and bushy races with open flowers and peculiar white-seeded races are found in Khorezm and Persia, although they are distinct

from the white-seeded Indian types. The capsules of the Turkestan, Afghani and Bokharan types are easier to thresh than those of the Indian races. In southern Afghanistan, adjacent to India, we found the typical Indian forms growing together with the Afghani races.

In the composition of the ordinary European races, large- and white-seeded races with large flowers, narrow petals and a typical bushy growth and races with capsules difficult to thresh are absent. With respect to the seeds, the flowers and the type of open flowers as well as the leaves, the European races are linked by a gradual transition to the types of flax in southwestern Asia (Afghanistan and Bokhara). In the mountain areas of Bokhara and in Badakhshan, different sites can be found with crops of types similar to fiber flax and impossible to distinguish from the present European types of flax.

In general, in all of Asia (except for along the Mediterranean coast, i.e. Palestine and Syria) and in Europe, including the Caucasus and the European parts of the U.S.S.R., mainly small-seeded (or medium-seeded), small-flowered and small-capsuled races of flax are typical, with tall-growing and bushy as well as intermediate growth-forms. Although an increase in the size of seeds can be observed toward the south of Europe (fiber flax seems to have smaller seeds than the bushy linseed flax), all the larger-seeded European and Asiatic races of the bushy type cede with respect to the size of seed to the typical Mediterranean forms (Kappert, 1921). The center of variation of the large group of small-seeded flax is confined to southwestern Asia.

In the future, investigations of the northern areas of India, Kashmir, Asia Minor and China will allow us to establish more exactly the centers of concentration of the maximum variability of that group of flax.

The Mediterranean coast can be sharply distinguished from Central Europe and southwestern Asia with respect to the complex of flax cultivated there. Mainly large-seeded, large-flowered and large-capsuled forms of linseed flax are typical of the countries extending along the Mediterranean coasts. Egypt, Algeria, Tunisia, Morocco, Tripolitania, Palestine and Syria grow races with large flowers (25–30 mm wide), large seeds (5–6.1 mm long), and large leaves. The European and the Asiatic races have flowers 15–18 mm wide (fiber flax) and up to 18–24 mm (linseed flax). The common Russian fiber flax has seeds 4–5 mm long, but only 3.5–3.75 mm long in the case of the small-seeded types. This group is clearly distinct from the common Asiatic and European races. Large flowers, large capsules and large seeds appear, as a rule, to be genetically linked characteristics, determined by a few genes (Tammes, 1911).

Judging from the eight samples we obtained from Abyssinia, peculiar small-capsuled, low-growing, small-leaved and small-flowered forms are grown there. The dimensions of the seeds are either medium or very small (3.75 mm) in size. Endemic forms were found in Abyssinia, linking a yellow color of the seeds to a blue color of the corolla at the same time as there are also ordinary forms with yellow-colored seeds linked to white flowers.

The large-seeded races of the Mediterranean coasts are, in turn, represented by different varietal types. According to our investigations of 26 samples (from Morocco, Algeria, Tunisia, Egypt and Palestine), there are two types: Morocco, Algeria, Tunisia and parts of Egypt grow large-seeded forms with very large



flowers (up to 30 mm or more in diameter), large capsules and large leaves. In Egypt, large-seeded linseed flax with small flowers (16.3–21.7 mm wide), very small and rarely vernate leaves, single stems, similar in type to fiber-flax are also found. The capsules of the latter type are extremely hard, difficult to thresh and have an intense anthocyanin coloring when ripe. The shoots are also of an anthocyanin color. This second type approaches the Indian forms with respect to the small flowers, the threshing difficulties and the anthocyanin coloration of the capsules and the shoots.

When comparing data concerning the dimensions of the seeds of cultivated flax, found during archeological digs at Dra-Abu-Negga, Asserif and Scheich as well as Abd-el-Qurna in Egypt, with those of the African large-seeded forms of linseed, it could be seen that the large-seeded forms were grown in Egypt in the remote past as well. Thus, in his review of the archeological sites of flax, Buschan (1895) furnishes the following measures of the ancient Egyptian seeds: 4.5, 5.0 and 5.5 mm. The present large-flowered linseed flax is characterized by similar dimensions, ranging from 6 to 6.1 mm in length, while Asiatic forms of flax from northern India, Turkestan, Afghanistan and Bokhara, as well as the European forms associated with them, are characterized by seed length from 3 to 4.5 mm. Various races of *L. angustifolium*, in which Heer and De Candolle were inclined to see the 'ancestors' of cultivated flax and which seem to have been grown in prehistoric times, have seeds measuring from 2.5 to 2.9 mm in length.

Taxonomic studies of cultivated flax force us, therefore, to distinguish, as far as possible, between two basic groups: the large-seeded and large-flowered one, genetically associated with the Mediterranean coastal area, and the small-seeded and small-flowered one, belonging to southwestern Asia. It is possible that more thorough studies of flax in Abyssinia will reveal still another group or form.

'Cracking flax' (*L. crepitans*), a kind of flax with capsules that crack when they ripen, is presently grown on small plots in Ukraine (e.g. in the Chernigov district), in the Primor'e area, and in the Alps, the Black Forest and Württemberg in Germany, as well as in Switzerland, mainly in mountain areas. It is also found as an admixture to ordinary flax with closed capsules. As far as the type is concerned, this flax approaches the Asiatic-European groups. The seeds are medium-sized (4.5 mm), brownish with a weakly developed 'beak'; the capsule is not hard, the flowers are small and blue, the height of the plant and the branching remind one of the intermediate types (gr. *intermediae*) and the capsules are few in number. According to the length of the vegetative period, it can be distinguished into early- and late-maturing forms. The capsules crack wide open when ripe, throwing out the seeds. It is interesting to note that this flax, in essence characterized by 'wild' traits, should still remain in cultivation in spite of the fact that a large amount of its seeds is lost at the time of harvesting or even before that.

Winter flax, *L. hyemale romanum*, is grown on small plots in Spain, northern Italy and the Alps, and in Carinthia and Krain in the mountain areas of Austria (Kramer, 1923). In growth type, this flax approaches the Asiatic kinds with a

spreading growth (gr. *prostrata*), being very leafy and characterized by a prostrate habit.

Of all the many species belonging to the genus *Linum*, the wild flax, *L. angustifolium* with its small seeds and narrow leaves comes closest to *L. usitatissimum*. Only this species produces fertile hybrids with ordinary flax. The geographical area of *L. angustifolium* reaches from the Canary Islands to western Persia and Asia Minor, including all the Mediterranean coastal area (Fig. 5). This species is also represented by a large number of forms (cf. Ascherson and Graebner, 1914), easily hybridizing with the cultivated flax and, no doubt, genetically close to the common type of flax (Tammes, 1923). It could perhaps be correct to unite *L. angustifolium* with *L. usitatissimum* into a single Linnaean species *L. usitatissimum* s. lat., as suggested by Heer (1872). However, there is no objective reason for considering this narrow group of plants as the ancestors of all the European and African kinds of flax, just as there is little reason for considering the distichous barley as the ancestor of all the cultivated types of barley. In our opinion, *L. angustifolium* represents a group of types, closing the cycle of varieties within the species of *L. usitatissimum*. It is no doubt very close to it and genetically related, but just barely so. It is also possible to fit *L. crepitans*, with its capsules that crack open, into the morphological series between typical *L. angustifolium* and typical *L. usitatissimum*. Just like wild barley or wheat, *L. crepitans* can easily persist in the wild state or in the form of a weed. The different types of *L. crepitans* and *L. angustifolium* occupy the same positions within the system of *L. usitatissimum* s. lat. as races of *Hordeum spontaneum* within the system of *Hordeum sativum* s. lat.

It seems likely that the two geographical groups of flax that exist at present were once united and had a common center of origin and that, physiologically, these groups of flax were not sharply delimited. However, in a very remote time, these groups apparently became isolated, of which the discoveries of exclusively large-seeded forms in the Egyptian diggings bear witness. The ancient agricultures of Mesopotamia, India and the countries adjacent to them grew crops of special kinds of flax, different from the Egyptian ones, from which, in turn, an independent kind of crop arose.

In Table 3, we shall make a short review of the geography of the diversity of the kinds of flax in the Old World, compiled according to the most variable characteristics by myself and E.V. Ellad'. From the tables one can see that the most variable characteristics, and consequently also most of the forms, are concentrated within the Indian area. From India we have data from Howard (40 samples) and our own observations of 20 samples, obtained from there. These studies of a small number of samples have already revealed a more or less definite concentration of the largest diversity of types in this country. An important variability characterizes also the areas of Afghanistan and Bokhara, adjacent to India. In spite of detailed investigations of a very large number of specimens (over 1000) in comparison with the small number of samples studied from India, and in spite of the widespread cultivation of fiber flax in the north, in Europe and Siberia, the diversity there is not large. The number of forms definitely decreases from southwestern Asia in the direction toward the Euroasiatic northlands. In

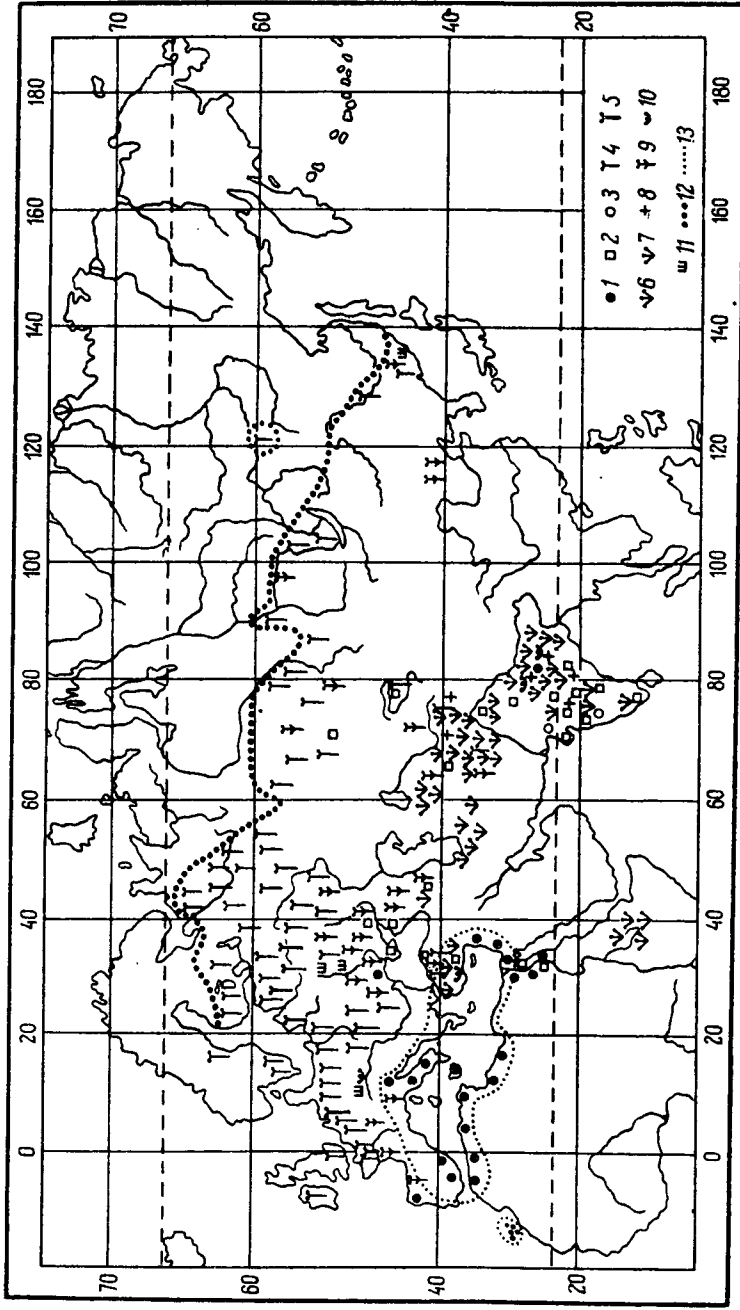


Fig. 5. Geographical distribution of the varieties of *Linum usitatissimum* L. and *L. angustifolium* Huds. 1-3: The *macrosperrmae* group: 1. var. *grandiflorae*; 2. var. *parviflorae*; 3. var. *leucanthae*; 4-10: the *mesosperrmae* group: 4. var. *elongatae* (4. var. *coeruleae*, 5. var. *albiflorae*); 6-8: *brevimulticaules* (6. var. *brunnea*, 7. var. *leucosperrmae*, 8. var. *angustipetalae*); 9. *intermediae*; 10. *prostratae*; 11. the *microsperrmae* group: var. *crepitans*; 12. northern limit of flax cultivation; 13. the distribution area of *L. angustifolium* Huds.

Table 3(a)-(d). Geography of the type-formation of flax in the Old World  
(a)

Area	Group of forms		Characteristics						
	<i>elongatae</i>	<i>intermediae</i>	Shoots			Flowers			
India	-	+	+	+	+	+	+	+	+
Afghanistan	+	+	+	-	+	+	-	+	+
Turkestan and Khiva	+	+	+	-	+	+	-	+	-
Bokhara	+	+	+	-	+	+	-	+	+
Persia	-	-	+	+	+	-	-	+	-
N. and Central parts of RSFSR	+	+	-	-	+	+	+	+	+
Ukraine and southern RSFSR	+	+	-	-	+	+	-	+	-
Transcaucasia	-	+	+	-	+	+	-	+	-
Siberia	+	+	-	-	+	-	-	+	-
N. Africa	-	+	-	-	+	+	+	+	+
Abyssinia	-	-	+	-	+	+	-	+	-
Palestine	-	+	-	-	+	-	-	+	-
Asia Minor	-	-	+	+	+	-	-	+	-
Italy	-	+	-	-	+	-	-	+	-

(b)

Area	Characteristics of the flowers									
	White	Open	Convolute	Large	Medium	Small	Broad-petaled	Narrow-petaled	Blue anthers	Yellow anthers
India	+	+	+	+	+	+	+	+	+	+
Afghanistan	+	+	+	-	+	+	+	-	+	+
Turkestan and Khiva	+	+	-	-	+	+	+	-	+	+
Bokhara	+	+	-	+	+	+	+	+	+	+
Persia	+	+	-	-	-	+	+	-	+	+
N. and Central parts of RSFSR	+	+	-	-	-	+	+	+	+	+
Ukraine and southern RSFSR	-	+	-	+	+	+	+	-	+	-
Transcaucasia	-	+	-	-	+	+	+	-	+	-
Siberia	+	+	-	-	+	+	+	-	+	-
N. Africa	-	+	-	+	+	+	+	-	+	+
Abyssinia	-	+	-	-	-	+	+	-	+	-
Palestine	-	+	-	+	-	-	+	-	+	-
Asia Minor	-	+	-	-	+	+	+	-	+	-
Italy	-	+	-	+	+	+	+	-	+	-

(c)

Area	Characteristics of the capsules									
	Closed	Cracking open	Large	Medium	Small	Septa glabrous	Septa pubescent	Hard to thresh	Medium hard to thresh	Easy to thresh
India	+	-	+	+	+	+	+	+	+	-
Afghanistan	+	-	-	-	+	+	+	+	+	-
Turkestan and Khiva	+	-	-	+	+	+	+	-	+	-
Bokhara	+	-	-	-	+	+	+	-	+	-
Persia	+	-	-	-	+	+	+	-	-	-
N. and Central parts of RSFSR	+	-	-	-	+	+	+	-	-	+
Ukraine and southern RSFSR	+	+	-	+	+	+	+	-	+	+

(c) (cont.)

Area	Characteristics of the capsules									
	Closed	Cracking open	Large	Medium	Small	Septa glabrous	Septa pubescent	Hard to thresh	Medium hard to thresh	Easy to thresh
Transcaucasia	+	-	-	+	+	+	+	-	-	+
Siberia	+	+	-	-	+	+	+	-	-	+
N. Africa	+	-	+	+	-	+	+	+	-	-
Abyssinia	+	-	-	-	+	+	-	-	+	-
Palestine	+	-	+	-	-	-	+	+	-	-
Asia Minor	+	-	+	+	+	-	+	-	+	-
Italy	+	-	-	+	+	+	+	+	+	-

(d)

Area	Characteristics of the seeds						Number of samples
	Brown	Umber-colored	Yellow	Large	Medium	Small	
India	+	+	+	+	+	+	33
Afghanistan	+	-	+	-	+	-	25
Turkestan and Khiva	+	+	+	+	+	-	24
Bokhara	+	-	+	-	+	-	23
Persia	+	-	+	-	+	+	19
N. and Central parts of RSFSR	+	-	-	-	+	-	21
Ukraine and southern RSFSR	+	-	-	+	+	-	22
Transcaucasia	+	-	-	+	+	-	19
Siberia	+	-	-	-	+	-	18
N. Africa	+	-	-	+	-	-	21
Abyssinia	+	-	+	-	+	+	16
Palestine	+	-	-	+	-	-	13
Asia Minor	+	-	-	+	+	-	19
Italy	+	-	+	+	-	-	19

India we could record 33 variable characteristics (34, if Afghanistan is included), whereas we know of only 21 variable characteristics within the R.S.F.S.R. and 18 within Siberia.

The countries around the Mediterranean are adequately studied and, while putting together a special morphological and genetical group, it was necessary to treat it differently from the preceding groups, originating from southwestern Asia.

There are definite regularities with respect to the distribution of flax over the Old World, which are important for an understanding of all the different groups of flax and for the interpretation of the plant breeding work with flax.

While studying flax of different origin by means of crops grown under uniform conditions we were able to reveal that northern types, mainly fiber flax, are as a rule characterized by a short vegetative period. Investigations of about 1500 samples from different regions indicated that there is an inverse correlation with respect to flax between the vegetative period and the height of the plants: the shorter the vegetative period, the taller the flax. The closer it comes to the ordinary type of fiber flax, the less the plants are branched and the lower is the production of seeds. With an increasing vegetative period, the branching increases, just like the number of stalks and that of capsules but, correspondingly, the height of the stalks is reduced.

The distribution of hereditary forms of flax in the direction from south toward north is definitely linked to the length of the vegetative period. Toward the north there are mainly early types with a short vegetative period and tall stalks, not branching but used for the long fibers; toward the south the branching, low-growing races, producing many capsules, are used for their seeds.

The fiber flax of the northern parts of European U.S.S.R. belongs to early types. Linseed flax – low-growing, many-stalked types producing many capsules and having a prolonged vegetative period – turns out properly to be typical of southwestern Asia. The southern races of flax grown in the Ukraine, northern Caucasus and the southeastern portion of the European U.S.S.R. belong to types with a long vegetative period but are still closer to fiber flax than the present types of linseed flax (*f. brevimulticaules*).

In Tables 4–6, the characteristics of the types of flax in different areas of origin are listed. A comparison between the inherited differences between these forms was carried out under uniform conditions by means of crops grown at the North-Caucasian Branch of the Institute of Applied Botany, belonging to the Institute of Applied Agronomy (the Kammenaya Step' in the Voronezh District), and at the Central Plant Breeding and Genetical Station (i.e. Detskoye Selo in the Leningrad District).

A pronounced abbreviation of the vegetative period can be clearly seen from these tables to be an inherited characteristic of flax when it disperses from Afghanistan toward northern Europe. From the center of its variation and the actual focus of its origin in southwestern Asia, flax differentiated according to its vegetative period when dispersing northward. Those races that have a long vegetative period remained in the south while the early-maturing forms were dispersed northward because of natural selection.

Table 4. Height of the plants and the vegetative period of strains of flax of different geographical provenance.  
The North-Caucasian Branch of the Otrada Kubanskaya Station, 1925

Provenance of the strains	Latitude (°N)	No. of samples	Mean height of the plants (in cm)	No. of days from sprouting to maturity (vegetative period)
Northern and northeastern regions (districts of Arkhangelsk, N. Dvina, Perm, Vyatsk and Vologod)	65–56	36	75	87
Northwestern region (districts of Leningrad, Novgorod and Pskov)	61–55	95	83	88
Districts of Tversk, Rybin and Yaroslav	59–56	25	74	86
Districts of Moscow and Vladimir	57–54	20	71	88
Altai	55–46	1	66	87
Byelorussia	56–51	35	66	88
Districts of Kaluzh, Tul', and Ryazan	55–52	6	63	88
Districts of Orlov, Tambov and Penzensk	55–51	19	63	89
Districts of Samara and Saratov	51–48	27	61	95
Districts of Kursk and Voronezh	54–49	10	61	93
Districts of Chernigov, Poltava and Kharkov	52–49	26	61	93
Districts of Volyn and Podolsk	52–47	18	63	94
Districts of Kiev and Yeakerinoslav	51–48	26	62	96
Crimea	46–44	8	56	95
Northern Caucasus	46–40	61	58	95
Turkestan (at different elevations)		28	58	97
Khorezm	43–40	19	44	99
Afghanistan (at different elevations)	43–40	4	42	102
	38–30	57	48	100

Table 5. Height of the plants and the vegetative period of strains of flax of different geographical provenance.  
The Central Plant Breeding Station at Detskoye Selo, 1922

Provenance of the strains	Latitude (°N)	No. of samples	Mean height of the plants (in cm)	No. of days from sprouting to maturity (vegetative period)
Northern and northeastern regions (districts of Arkhangelsk, Perm, Vyatsk and Vologod)	65-56	23	86	85
Northwestern region (districts of Leningrad, Novgorod, Pskov and Vitebsk)	61-55	24	91	86
District of Tversk	59-56	11	77	85
Byelorussia	56-51	5	83	87
Districts of Penzensk and Simbirsk	56-53	3	68	105
The south-east	51-48	16	68	104
Turkestan (different strains collected at different elevations)	43-55	8	64	100
Khiva	43-40	1	55	Did not ripen
Pamir and Bokhara (different strains, collected at different elevations)	43-40	69	47	98
Afghanistan	38-30	3	58	Did not ripen

Table 6. Height of the plants and the vegetative period of strains of flax of different geographical provenance.  
The Central Plant Breeding Station at Detskoye Selo. Means of 1921, 1922 and 1925

Provenance of the strains	Latitude (°N)	No. of samples	Mean height of the plants (in cm)	No. of days from sprouting to maturity (vegetative period)
Northern and northeastern regions (districts of Arkhangelsk, N. Dvina and Vologoda)	65-56	50	83	89
Northwestern region (districts of Leningrad, Pskov and Novgorod)	61-55	61	87	93
District of Yaroslav	59-56	6	83	92
Byelorussia	56-51	22	80	97
Districts of Kaluzh and Ryazan	55-52	2	62	105
Districts of Orlov, Tambov, Penzensk and Simbirsk	55-51	15	71	110
Districts of Kursk and Voronezh	54-49	2	73	103
Districts of Poltava and Voronezh	52-49	2	70	111
Districts of Volyn and Podol'	52-47	6	75	110
Districts of Samara and Saratov	51-48	34	68	112
Districts of Kiev and Yekaterinoslav	51-48	5	70	114
Northern Caucasus	46-40	2	67	118
Turkestan (at different elevations)	43-55	25	61	112
Pamir and Bokhara (at different elevations)	43-40	151	51	106

The distinction of flax into fiber flax and linseed flax is the result of natural selection in the direction from south toward north. The concentration in the north of crops of flax grown for their fibers and in the south of bushy and intermediate forms of flax, grown for the seeds, can be simply explained by the action of natural selection, reflected toward the north in the short vegetative period required by early-maturing flax and, consequently, also in long-stalked flax especially suited for obtaining a satisfactory yield of long fibers. In the south, there was of course a concentration of those races that were able to utilize a longer vegetative period, and consequently, grow more stalks of a lower stature but bear a large number of capsules and, thus, produce more seeds when ripe.

When dispersing northward from southwestern Asia, the crops of flax grown in their native land mainly for linseed oil, became naturally converted into crops of long-staple flax in the north. As demonstrated during the investigation at our biochemical laboratory (by Ivanov, 1926), the percentage of oil in the seeds of some pure-bred strains of flax did not change when transferred from the south to the north or vice versa. The alteration affected the quality of the oil, however (the iodine index has a tendency to increase in the northerly direction). Geographical experiments with crops of 12 different pure-bred lines at 58 sites in the U.S.S.R. demonstrated that in the south there was, in general, a reduction in the height of the flax plants but an increase in the number of stalks and in the number of capsules. The reverse phenomenon was observed when southern types of flax were transferred to the north. Fiber flax grew more stalks of lower stature when moved from the north toward the south. Linseed flax grew taller in northern Europe. The individual variability went in the same direction as the selection of inherited characteristics from south toward north. It is necessary to distinguish the individual variability of the pure-bred lines, which depend on geographical effects, from the inherited differences, typical of the geographical races.

As our research demonstrated, common flax in the high mountains has a tendency to increase the height of the stalks but to decrease the branching. Typical fiber flax from the Pskov district underwent a sharp reduction in height and an increase in the number of branches when moved from the north to the south but in the mountain areas of Transcaucasia, e.g. in Bakurian at 1760 m.s.m., and at an elevation of 2000 m south of Tashkent, it can hardly be distinguished from the typical fiber-flax of Pskov.

Flax is very successfully grown for its fibers at an elevation of 7000–9000 feet in Kenya, right on the equator. Tests at the Belfast College of Technology have shown that this flax surpasses the Russian long-staple-flax in quality (Wigglesworth, 1923).

During our investigations among the high mountains of Bokhara (Roshan and Shugnan) we found in some secluded localities at an elevation of about 2700–3000 m.s.m., settled by Tadzhiks – the ancient inhabitants of Turkestan – some isolated plots of fiber flax, grown for the seeds. During tests, this flax turned out to be almost identical with the present Russian fiber flax of the northern type. In the majority of cases in southwestern Asia and at high elevations, the ordinary low-growing flax is cultivated for its seeds. However,

the existence of isolated plots of fiber flax, preserved in southwestern Asia, supports the accuracy of our conclusions concerning the origin of the cultivation of flax in these areas. As can be expected a priori, all the initial types both of the future northern crops of early-maturing fiber flax and the southern, branched and late-maturing types, are concentrated here thanks to the exceptional diversity of habitat conditions. The mountain areas of southwestern Asia favored both the formation and the preservation of the different morphological and physiological types of flax. It is possible that, during detailed studies in southwestern Asia, crops of flax in remote areas of the high mountains will turn out to produce such types of flax that, possibly, became utilized for cultivation of fiber flax in northern Europe. In Asia Minor, flax is still grown for its fibers in mountain areas (data from the expedition led by P. M. Zhukovskiy).

In southern and central areas of India, in North Africa and Palestine, we have discovered low-growing, comparatively rapidly maturing linseed flax that is ephemeral. Such races are often distinguished by hard capsules with seeds that are difficult to thresh out. The intensely hot climate has forced a selection of races with a very short vegetative period, able to utilize the moisture of the winter and spring months and to avoid the summer heat. Early ripening during climatic conditions characterized by drought often results in good quality, just as in the north in the case of a short vegetative period. These races represent a special ecological type with a particular kind of root system (Howard and Khan, 1924) and it is necessary to distinguish them from the relict crops of flax in southwestern Asia and Europe.

Thus, under the conditions in northern Caucasus (at Otrada Kubanskaya Experimental Station), crops grown in 1925, belonging to a number of different lines of flax (Table 4) from Morocco, Algeria and Tunisia (17 samples), reached a mean height of 48 cm and had a mean vegetative period of 98 days. Flax from Abyssinia (8 samples) reached a mean height of 29 cm during a mean vegetative period of 86 days and Egyptian flax (5 samples) grew 41 cm tall after an average of 90 days, while flax from India (15 samples) grew an average of 32 cm tall after a mean of 92 days. At the same time, a series of races, common in Turkestan, Afghanistan and Khivinsk, had a vegetative period of 100 days.

Detailed, systematic and zonal investigations of flax from the mountain areas of India, Asia Minor and northern Africa will no doubt turn up much interesting data, which can be utilized for the cultivation of flax on the European lowlands.

In many cases, it is definitely clear from the facts mentioned above that the center for this type formation of *Linum usitatissimum* can still be traced to southwestern Asia and northern Africa, where plant breeders should go for material of strains for practical purposes. In the case of seed crops, no doubt interest should focus on the large-seeded types of the Mediterranean coastal areas, distinguished by a high percentage of oil, as indicated by the research done by Howard and ourselves.

In the Russian northlands and in Siberia, as well as the northern parts of European U.S.S.R., the cultivation of flax has selected out races with a shorter vegetative period due to both natural selection and the efforts made by Man

through the centuries. As far as the presence of a direct correlation between short vegetative period and long stalks is concerned, the Russian North appears long since to have been the possessor of valuable races of fiber flax that force us to pay special attention to a study of the North-Russian flax in areas of more ancient cultivation at the limits where flax can mature and where discoveries of especially practical and interesting types of flax can be expected.

We have examined in detail the cultivation of flax, wheat, barley, oats and millet, in order to demonstrate that, at present, the problem of the local origin of crops and the homeland of any given plant can be solved by means of differential, phyto-geographical methods. Using flax as an example, a number of geographical regularities could be revealed for the dispersal of races and to a great extent for determining the work of plant breeders. It may be possible to find many more examples of complex and more complicated origins of cultivated plants. Investigations at the Institute of Applied Botany have led us to draw the conclusion that the majority of legumes have *two* centers of origin. Cultivated peas, lentils and horse beans come initially from two centers, one of which seems to be concentrated in southwestern Asia, the other, apparently, in northern Africa, or in general, within the Mediterranean area. The same can be said for the castor bean, *Ricinus communis* (Popova, 1926). By means of methods that use detailed analyses of the racial composition, it was possible to establish the centers of type-formation of many cruciferous plants.

The problem of the origin of cultivated plants has turned out to be more complicated than was believed at the time of De Candolle, Heer and many other authors. The discovery of plants in a wild state, which are close to those cultivated and which clearly belong to a single Linnaean species, still tells too little about the local origin of the cultivated plants to form a basis for plant breeding work with them, and to indicate where to look for the initial types of these plants. Wild oats are very close to cultivated oats, but this does not mean that the latter originated directly from the wild oats. The distribution areas of wild and weedy oats do not determine the centers of type formation of the cultivated oats. The wild oats (*Avena fatua* and *A. ludoviciana*) are met with in enormous quantities in southwestern Asia in such wild and weedy conditions, as were never known by the cultivated oats.

The differential taxonomic-geographic approach to the problems concerning origins offers a possibility for utilizing the solutions thereof for practical plant breeding, by means of which it was previously impossible to arrive at an even approximate solution.

Although by means of artificial selection, a plant breeder located far from the native land of the plants can, by crossbreeding of types, produce a race with new characteristics, not revealed by immediate study in their native land, it does not, in essence, change the general concept about the geographical distribution of the variety and its connection with the center of origin. By inbreeding, it is possible to single out a number of recessive types (e.g. in the case of maize, non-ligulate types or a large number of abnormalities). But all of these recessive types are, nevertheless, in their basic genetics, associated with the initial centers of origin and on the basis of these primary varieties one can look for the geographical center of a given crop.

## CHAPTER 3 WEEDY PLANTS AS ANCESTORS OF CULTIVATED PLANTS

### The origin of cultivated rye

During the study of the geography of to the varietal diversity of rye we ran into an interesting group of facts which, subsequently, turned out to be of general importance.

The rye cultivated in Europe, the European parts of U.S.S.R. and Siberia is botanically very uniform and is, in essence, represented by a single botanical variety, *Secale cereale* var. *vulgare*, with straw-colored and short-awned spikes and an admixture of var. *monstrosum*, a branched type. Enormous areas of northern Europe and Asia, many millions of acres, are sown with these ordinary varieties of rye. Although within the limits of these varieties it is also possible to distinguish forms according to the color of the grains or the more or less pronounced density of the spikes, these characteristics are not localized and do not have particular distribution areas, typical of the varieties of rye where such characteristics are not found.

Figure 6 outlines the northern limits of the cultivation of rye in Europe and Asia and a line south of which crops of wheat predominate over those of rye, but north of which crops of rye are more common than those of wheat.

Investigations by V.F. Antropopov and myself on specimens of rye from various countries demonstrate that all the variation and all the wealth of types of rye are concentrated in those areas where rye is either of secondary or no importance at all as a cultivated plant. The main botanical variation of rye is found in Afghanistan, Persia, Transcaucasia (Georgia and Armenia), Asia Minor and Turkestan. There, rye is known mainly as a weed, infesting wheat and barley crops, in particular the crops of winter wheat. It is also met with among winter barley. The crops of barley are particularly strongly infested by rye in northern Persia and the Transcaucasian areas, where races of winter barley are grown in large quantities.

Among these weedy types of rye an exceptional variety can be established that is not represented within the European agriculture. In Afghanistan alone, where rye is known mainly as a weed, 18 botanical varieties have been found. In southwestern Asia (in a wide sense), red-spiked types and varieties with long awns and pubescent hulls are known. In Armenia, Georgia and eastern Persia as well as in Asia Minor, floral variations are typical: red-spiked, brown-spiked and, occasionally, even black-spiked forms occur. White-spiked forms are typical mainly of Afghanistan, Bokhara, Khorezm and Turkestan. In Badakhshan and the mountain areas of Bokhara adjacent to it (Shugnan and Roshan), we have found a peculiar variety without ligulas or auricles, var. *eligulatum*. In Asia Minor, on the other hand, races with a very large kind of auricles (var. *auriculatum* Vav.) are established. Races with rough spikes and rough awns, with or without a waxy coating or with shoots almost without any anthocyanin (var. *viride* Vav.) are also found. In Shugnan (in Pamir), we succeeded in 1916 in finding forms of cultivated, brittle spring rye. When threshed, the spikelets disarticulate from the upper portion of the spike (Vavilov, 1917). A large

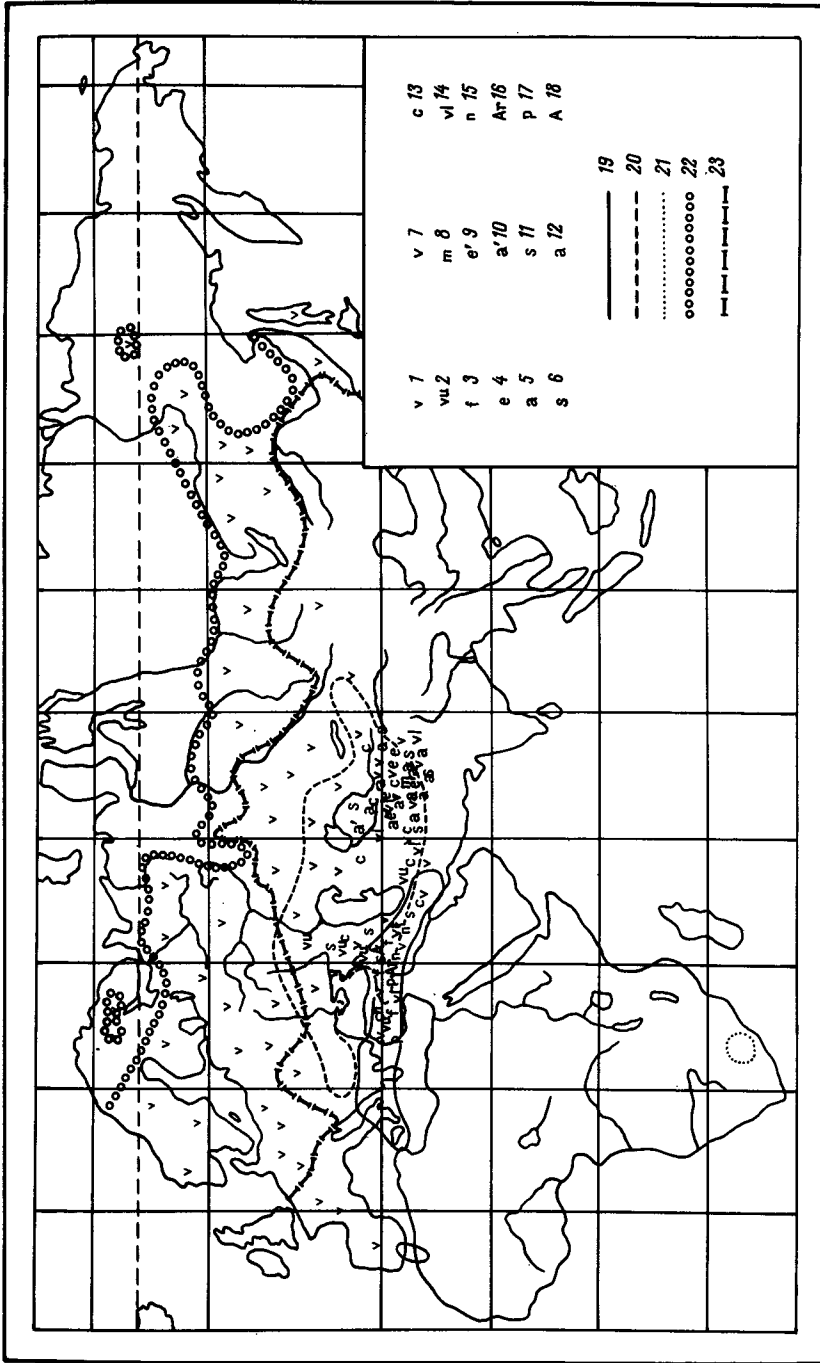


Fig. 6. Centers of origin of cultivated rye. Geographical distribution of the botanical varieties of *Secale cereale* L. and the distribution areas of other species of rye. 1. *vulgare* Koern.; 2. *vulpinum* Koern.; 3. *fusum* Koern.; 4. *eligatum* Vav.; 5. *afghanicum* Vav.; 6. *scabrisculum* Vav.; 7. *viride* Vav.; 8. *multicum* Vav.; 9. *eprunosum* Vav.; 10. *articulatum* Vav.; 11. *subarticulatum* Vav.; 12. *asiaticum* Vav.; 13. *clausopaleatum* Vav.; 14. *velutinum* Vav.; 15. *nigrescens* Vav.; 16. *armeniaticum* Zhuk.; 17. *persicum* Vav.; 18. *auriculatum* Vav.; 19. distribution area of *S. montanum* Guss.; 20. area of *S. montanum* M.B.; 21. area of *S. africanum* Stapf; 22. northern limit of rye cultivation in the Old World; 23. line south of which crops of wheat predominate over those of rye and north of which rye predominates over wheat.

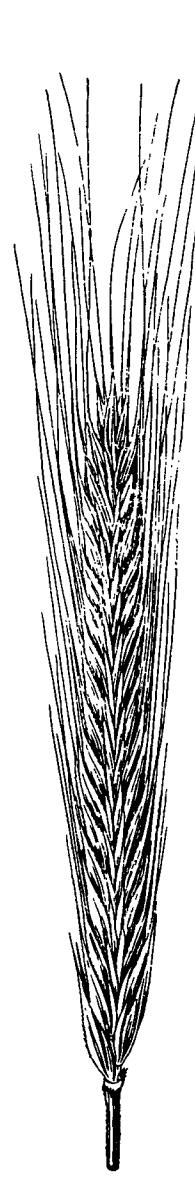


Fig. 7.

Fig. 7. Spike of *Secale cereale* var. *afghanicum* Vav. Drawing based on a green, not yet ripe and still not disarticulated spike.



Fig. 8.

Fig. 8. Spikelets of *Secale cereale* var. *afghanicum* Vav. Drawing by M. Lobanova.



diversity of forms (14 varieties according to our own estimate) has been found in Georgia and Armenia by P.M. Zhukovskiy (1923 a, b), N.A. Maysurian (1925) and E. A. Stoletova. Among the rye infesting the fields, especially in Afghanistan, Persia and Turkestan, races predominate that have enclosed, non-shedding grains and adpressed awns, while in Transcaucasia (Armenia) and Asia Minor such races of weedy rye are found, in considerable quantities, that have spreading awns and florets that do not enclose the grains, which are easily dislodged and remind one of the type found in cultivated rye.

In other words, in southwestern Asia, including Transcaucasia, the investigator encounters, in fact, a striking diversity of rye, reminding one of the varietal complex of soft wheat and, in addition, rye is also found in different forms there, mainly as weedy plants among crops of soft and club wheat as well as winter barley.

A general picture is furnished of the distribution of the botanical varieties of rye, studied by us, from various parts of Eurasia (Fig. 6).

During the basic classification of the variation, according to which the diagram of the geographical distribution is drawn up, we touched upon such characteristics as the presence or absence of ligulae and auricles on the leaves, the brittleness of the rachillae, the color of the spikes, the pubescence of the hulls, the enclosure of the grains, the type of awns and the presence or absence of a waxy coating on the plants. These characteristics are definitely geographically differentiated and make it possible to establish exactly the centers of the inherited variability. For the sake of convenience we excluded characteristics concerning the colors of the grains, listed by N.A. Maysurian (1925) in his classification of the varieties of rye, since they are geographically indeterminate and present within all the areas.

A somewhat abbreviated review of the information available to the Institute of Applied Botany illustrates, nevertheless, that the variation is concentrated in the direction toward southwestern Asia.

#### BRITTLE *SECALE CEREALE*

In 1924, when sent out to Afghanistan specially to study rye and wheat, i.e. crops that, according to our geographical hypothesis, should display a maximum variability there, we encountered rye that, with respect to morphological and biological characteristics, reminded us of wild oats. In Afghanistan, rye occurs not only as a common weed among soft and club wheat, but most of all it is found (in addition to the common non-disarticulating, Turkestanian type of rye) in the form of extremely brittle types, definitely disarticulating when threshed. With respect to the character of the rachillae, this rye reminds us of wild barley, *Hordeum spontaneum*. Its spikes disarticulate when threshed and behave like the florets of wild oats. Together with wild oats, this weedy, brittle type of rye often covers the ground in enormous quantities after the wheat has been harvested. Biologically, it is in no way distinguishable from wild oats. In northern Afghanistan, this rye is not even distinguished by name from wild oats. The inhabitants of the Herat Province call both brittle rye and wild oats 'tak-

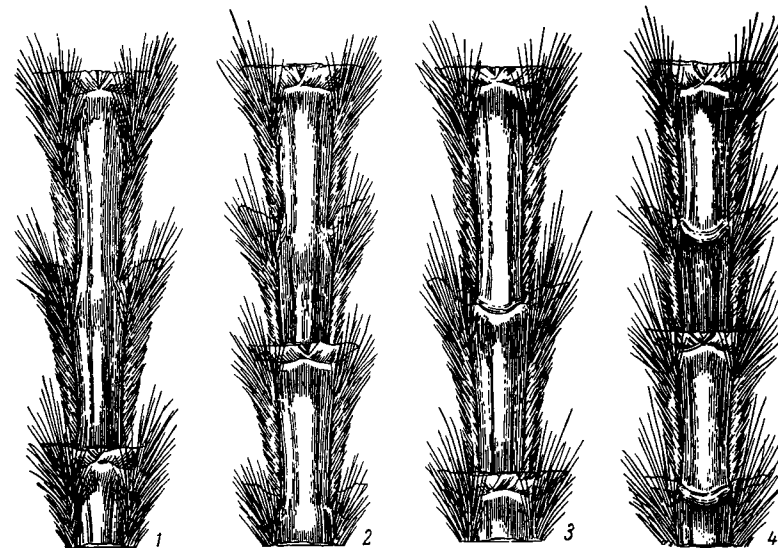


Fig. 9. Types of articulated spikes of cultivated and weedy rye (the rachis of the spikes is illustrated). 1. Ordinary European rye; the rachillae are fused with and delimited by the rachis of the spike; 2. type of north-Caucasian non-disarticulating weedy rye; 3. type of weedy rye from Turkestan; 4. type of disarticulating weedy rye, *Secale cereale* Var. *afghanicum* Vav.

tak'. An enormous quantity of brittle rye is, in particular, found in Hindukush, around Kabul, among *Triticum compactum* [shot wheat] which is frequently cultivated in southeastern Afghanistan. There, after the wheat is harvested, the ground is often literally covered by spikelets of brittle rye, constituting a serious scourge for the cultivation of wheat. In order to clean the fields, the farmers sometimes sweep the spikelets of this rye from their fields with brooms. I have named this variety of weedy, brittle rye *Secale cereale* var. *afghanicum*, although in other respects its characteristics (i.e. the dimensions of the grains, the morphology of the spike, etc.) do not differ from those of ordinary rye.

A Latin diagnosis of this new variety of rye follows below:

*Secale cereale* L. var. *nova afghanicum*, spica lineari elongata, rachis fragilis, spiculae 2-3-floris, aristae 2 vel 3 cm longae; caryosides clausae. Valde affine varietatii *vulgares Secalis cerealis*. Hab. frequens in segetis *Tritico vulgari* hiberno et *T. compacto* hiberno. Ar. geogr. Afghania, imprimis im parte meridionale prope Herat. (Figs. 7,8)

Thus, there is now a complete morphological series for brittleness and type of rachilla, ranging from the typical, brittle Afghanistani kind all the way to the forms that are definitely not brittle, and are cultivated in the north. The brittle races are characterized by segments jointed to the rachis at right angles; the segments of the rachillae are in the case of this variety easily dislodged (Fig. 9). In the case of the races cultivated in the north, and as the result of an unconscious



participle of the verb 'dashtan' ('to be', 'to be found in'); 'der' with a short 'e', as pronounced in other areas, is the present participle of the verb 'derun' (torment) and gives us the literal meaning, 'the plant tormenting barley or wheat'. The Persian epithet is widespread all over southwestern Asia from Turkey to India. The philological analysis of the epithet and its wide distribution all over the East bear witness to the fact that the local inhabitants of southwestern Asia, Persia, Afghanistan and Tadzhikistan from time immemorial have known rye as an annoying, weedy plant, hard to get rid of since it often completely infests the crops of wheat and winter barley or even displaces them, at present sometimes with disastrous results.

When I traveled around Bokhara, Persia, Turkestan, Khorezm and Afghanistan, I had a chance to listen to the complaints of the local inhabitants concerning the difficulties they met with in their fight against rye. Aitchison (1881, 1888) also heard such remarks in Afghanistan. Rye occurs as a weed of ill-repute also in Transcaucasia and Asia Minor (according to P.M. Zhukovskiy) and in Syria as well as in Palestine (according to Aaronsohn, 1910). The grains of wheat are difficult to distinguish from those of rye even for the best contemporary specialists in the sorting of grains, and therefore the complaints heard by the travelers concerning rye in Afghanistan, Persia, Turkestan and Asia Minor can be understood. In northern Caucasus – the granary of winter wheat – such an infestation of wheat by rye is a total disaster, causing a reduction in the value of the crop. An intense campaign is made by the land management for mowing the plots of land at the time when the rye flowers. At that time the contaminated fields have, literally, two tiers: the upper one is represented by the spikes of the rye, the lower one by those of the wheat. It is possible to mow down the rye carefully and not damage the wheat. An intense campaign is being made for this action in the war against rye infesting the wheat crop. In 1925, the land owners were free from taxes if they took such preventive measures.

#### THE APPEARANCE OF RYE AS AN INDEPENDENT CROP

However, rye does not occur as only a weedy plant in southwestern Asia. In the high mountains of Bokhara, Afghanistan and Asia Minor, it is possible to observe how, when ascending the mountains, rye gradually turns from a weedy plant into an independent crop. In the high mountain areas of Afghanistan, around Kabul and along the Khazariyskaya Road, in the mountains of Bokhara, in Shugnan and Roshan and in Badakhshan, rye has become a cultivated plant. The same can also be seen in southern Fergan. Also, its name changes there. The Tadzhiks of Badakhshan call this rye 'kal'p' or (in Roshan) 'lomak'. At the same time the inhabitants of the valleys still use the epithets 'chou-der' or 'gandum-der', i.e. 'the weed of wheat and barley'.

It is possible to draw a picture of the gradual displacement of wheat by rye and of the replacement in the high mountain areas of winter wheat by rye. According to our own observations, this substitution occurs especially intensely in Afghanistan on slopes facing north, but also on those facing south in

Hindukush at an elevation of 2000 m.s.m. and more. Pure crops of winter rye are associated with elevations of 2000–2500 m.s.m. G.A. Balabayev (1926) established for Zeravshan and other areas that a gradual displacement of winter wheat occurred from 2000 m and upward. Above 2500 m, the areas of spring cereals begin and types of winter rye, both the cultivated and the weedy ones, disappear.

G.A. Balabayev calculated the percentage of wheat infested by rye at various elevations and at different localities; accordingly, a clear picture was obtained for all the areas studied concerning the replacement of wheat by rye in relation to the progress toward more elevated sites. Thus, for instance, the picture shown in the first table developed with respect to the district of Dzhizak.

Settlement	Elevation (m.s.m.)	Percentage of rye in wheat crops
Yam-Dzhizak	345–457	3.1
Zaamin-Rabat	457–1000	8.9
Sanzar	350–1535	11.9
Turulyash	1535–2330	39.0

Among the settlements in the mountains of Zeravshan the increase toward the more elevated zones showed the proportions shown in the second table.

Zone	Elevation (m.s.m.)	Percentage of rye in wheat crops
Lower	1130–1448	13.3
Median	1535–1860	25.0
Upper	1886–2439	41.7

G.A. Balabayev and I observed that the process of replacement of wheat by rye in the upper zone (in Central Asia at elevations of 2000 m.s.m. or more) was faster than in the lower zone (from 300–1200 m.s.m.). In relation to the ascent into the mountains, the extent to which rye is distributed is noticeably increased.

As is well known, rye is biologically hardier, tougher and more frost resistant and it is therefore natural that, when the crops are transferred into more severe conditions, rye starts to replace the less hardy plants of winter wheat and, particularly, winter barley. Schindler (1923) wrote: 'The modest demands of this cereal is evident already from the geographical distribution of rye crops. It could actually be said that among the cereals it is the most modest one . . . The minimum temperature tolerated by rye when growing is 1–2 °C lower than that tolerated by all the other cereals. At a soil temperature of 4–5 °C rye can start to sprout in 4 days, while wheat under the same conditions requires 4–6 days . . . Neither is rye sensitive to superfluous moisture . . . Dry, sandy loam is considered as the true soil for rye, providing a steady yield. Even such sandy soils, where only lupines thrive, can be utilized for growing rye in combination with the lupines.'

Concerning its biology, rye has specific characteristics, conditioning it as a

wild plant and correlating its growth with the more severe conditions on barren soils under severe winter conditions. In comparison to barley or wheat, its root system possesses a greater capacity for assimilation; it tolerates a higher acidity and is able to utilize less soluble compounds. Physiological investigations by Stoklase and others have cleared up the lesser demands of rye on the substrate in comparison with those of wheat or barley.

Factors not favoring the growth of wheat can be favorable for the cultivation of rye. The replacement of wheat by rye under severe conditions depends, naturally, on this factor, just as happens in the mountains of Central Asia and Transcaucasia. Such a process evidently also occurred during the progress of the cultivation of wheat toward the north. Gradually during the transfer of the crops from their basic focus, i.e. from southwestern Asia and Transcaucasia toward the north, northeast and northwest, the rye infesting them replaced them and became, itself, a pure crop. With much thanks to the wishes of Man, the former weed became a cultivated plant. On poor soils and under severe conditions in the north, rye was, according to a statement by A.D. Thaeer 'a better gift from God' and, thus, the people began, without knowing it, to sow rye together with the wheat so that, at present, the farmers of the northern and central districts voluntarily sow only rye and not wheat.

If the above facts are taken into consideration, the history of the origin of cultivated rye becomes straightforward and very simple. The ancient crops of winter wheat and winter barley, when transferred from the south toward the north, east and west (the reduction in the varietal diversity of wheat proceeds in that direction and, consequently, the dispersal of the crops must also have gone in the same direction) brought with it the rye in the form of a weed. When cultivated under more severe conditions with colder winters and on poor, podsollic soils, rye began to overpower the weaker wheat and barley types. Barley was the first one to be 'knocked out'. Barley crops could only grow under the conditions such as in Transcaucasia, the Transcaspian region and the southern valleys of Turkestan. Gradually, during further progress toward the north, wheat, too, began to diminish, and, finally, in Siberia and the European parts of the U.S.S.R. and Germany, rye became a pure crop.

In central Persia as well, rye was tougher and hardier than wheat when grown under uniform conditions and rye, which had been constantly and intentionally weeded out by the farmers elsewhere, turned there into a pure crop. Due to the lesser hardiness of the wheat, rye was allowed to replace winter wheat toward the north, with much thanks to the efforts of Man.

It is interesting that, at the border of the 'struggle' between winter rye and winter wheat, the farmer has long since, and even now, purposely sown a mixture of rye and wheat. Not counting on success with winter wheat every year, the farmer willingly sows a mixture of grains of rye and wheat in the hope that, should the wheat fail during an unfavorable winter, at least the rye will survive and produce half a harvest. The peasants in Normandy and the Russian farmers in the Kuban and Terek River areas and the Stavropolis Governate sow both intentionally and involuntarily a great amount of so-called 'surshy' [mixed crop, D.L.], i.e. a mixture of rye and wheat. In France, they often grow 'le méteil', the flour of which is more valued than that of rye alone. According to

information from Pallas, mixed crops of wheat and rye are common also in the Crimea.

It is still possible to trace in detail the entire process of the emergence of rye as a crop. In order to understand the origin of cultivated rye, it is necessary to associate it with the cultivation of wheat. Cultivation of rye originated from the cultivation of wheat and, in part, that of barley; therefore, it is natural that the areas overlap where the greatest diversity of soft wheat and of rye occur.

Thus, rye in the form of a field weed and the varieties thereof appear to be the ancestors of cultivated rye. The plant breeder, interested in the selection of varieties of rye, must turn his attention to the weedy rye that infests the fields of Transcaucasia, Asia Minor, Turkestan, Persia, Bokhara and Afghanistan.

Still, very little has been achieved in this direction. Plant breeders have worked mainly with the uniform west-European rye populations. Although these are suitable for the humid conditions of western Europe and the western districts of the European parts of the U.S.S.R., there should definitely be a greater interest in obtaining seed material from the areas of weedy rye for our southern and southeastern regions.

Our research has demonstrated that it is actually possible to find exceptional varieties, e.g. among the weedy rye of Persia, not only from the point of view of morphology but also that of physiology. In Persia, forms can be found that are especially tolerant to drought and which have, apparently, been selected for this for centuries in these drought-stricken areas (Vavilov, 1922). The southeastern races of rye, more tolerant to drought, are known to us from a complex of weedy rye in southwestern Asia. With respect to its productivity, the dimensions of the grains, its spikes and its sturdiness, weedy rye does not yield to the ordinary, cultivated rye.

Apparently, winter rye became cultivated in Europe and in Asia along two basic pathways: one from Transcaucasia and the other from the area of Turkestan, Afghanistan and areas adjacent to them. The difference between the two geographical groups of weedy rye indicates this fact.

During the dispersal of cultivated rye from the south toward the north, some regularity, similar to that concerning the geography of flax crops, could apparently be observed as demonstrated by the investigations made at the Institute of Applied Botany by V.I. Antropopov and V.F. Antropopova. Toward the north (in the Vyatsk, Vologod and Olonetz districts) races occur that are characterized by tall culms and open spikes, which are easy to thresh. Races with shorter culms and denser spikes that shed their spikelets are more frequent toward the south (Kuban, Crimea and Ukraine). A spreading form of growth is typical of many southern races of cultivated rye, such as the so-called 'bushy' type in contrast to the so-called 'tall-one' of the north.

#### SPRING RYE

The origin of cultivated spring rye was somewhat different. Studies of cultivated vegetation in Afghanistan allowed us a closer approach to the understanding of that process.

In the mountain areas of Badakhshan (northern Afghanistan) crops of winter

wheat and weedy winter rye give way to those of spring cereals, i.e. barley and spring wheat, at an elevation of 2700–3000 m. Spring rye is a common field weed among spring wheat and, more rarely, barley. When studying a considerable-sized area of Badakhshan, from Faizabad to Ishkashim (in Pamir), we were able to demonstrate that the replacement of spring wheat by spring rye was particularly intense in areas with sandy soil. It was evident that such soil conditions worked as a factor of natural selection in favor of the spring rye. It is well known that rye does better than barley and wheat on light, sandy and only slightly loamy soils. Thus, for instance, cultivated spring rye is often grown on sandy soils in the southeastern parts of the U.S.S.R.

The spring rye of eastern Siberia, the Transbaikalian area and the Far East (locally called 'yaritsa') had, evidently, also developed into pure crops from weeds among spring wheat and barley. The expedition to Mongolia, led by V.E. Pisarev, found that spring wheat and barley in northern Mongolia are heavily infested. According to information from the expedition sent out from the Department of Applied Botany, the Siberian and Far East field crops had been adopted from Mongolia. As shown by experiments made by agriculturists in Transbaikal and eastern Siberia, spring rye is hardier here than spring wheat. The winter cereals do not succeed without a snow cover during the winter months.

The development of spring rye into an independent crop can be followed in the high mountains of Bokhara, in Roshan and Shugnan. There, along the river Gunt and farther north, we were able to prove the presence of pure crops of a peculiar, tall-growing, large-grained type of rye with exceptionally large anthers, almost twice the size of those belonging to ordinary European spring and winter rye. Among this kind of rye, we discovered endemic, non-ligulate forms as well as races with semi-brittle spikes. We also found strange, low-growing rye, grown as pure crops on the border to Fergana (in the mountains of Bokhara) at the Pakshif pass. There, as well as in other areas, it is possible to find a complete transition from pure crops of spring wheat to pure crops of spring rye in every kind of proportion. It is interesting that in these high mountain areas of Badakhshan there are large thickets of wild, brittle rye, *Secale fragile*, growing on sandy soils at elevations of 2600 m.s.m.

All the stages in the evolution of cultivated rye can, in general, be followed in minute detail and the information can also be utilized for practical purposes within plant breeding.

The local origin of rye crops was without doubt polyphyletic. As can still be seen, the process of adopting rye into cultivation occurred simultaneously and independently in several localities. The diversity of the rye populations in different isolated areas bears witness to this. The 'yaritsa' [spring rye] with light-colored (mainly yellow) grains and short spikes, found in Siberia, is very different from the rye with large anthers, thick spikes and large grains found in Pamir or from the low-growing spring rye in the Karateginskiy Range. The spring rye of the Astrakhan district is distinguished by long awns and a strongly developed waxy coating on the spikelets, etc.

The distribution area of the wild, montane rye, *Secale montanum* – a species

still considered by botanists to be an ancestor of cultivated rye – does not help solve the problem of the local origin of cultivated rye, *S. cereale*, with an accuracy that is satisfactory to plant breeders. According to Flaksberger (1913), the distribution area of *S. montanum* embraces Morocco, southern Spain, Sicily, Dalmatia, Serbia, Greece, Asia Minor, Persia, Turkestan, Central Asia, the Turkish portion of Armenia, northern Caucasus and Transcaucasia (Abkhazia and Armenia).

It appears to us that placing the beginning of the cultivation of rye in Turkestan (S.I. Korzhinskiy, Koernicke, A. Schulz), Serbia (Kerner) or the Balkans (Engelbrecht) is unfounded; it seems much more likely that in this case Persia, Asia Minor, Afghanistan, Bokhara and Transcaucasia, should also be included.

Growing rye crops appears rather to be the result of natural selection when allowing the weed, winter rye, to replace winter wheat or winter barley or letting the field-weed spring rye displace spring wheat on light soils toward the north and high up in the mountains or in the harsh climatic conditions of eastern Siberia. It is quite natural that such a selection among the populations of rye should occur when they appear in the company of wheat crops and barley as a specialized weed acting similarly to corn cockle [*Agrostemma githago*], Italian rye-grass [*Lolium perenne*] or bachelor buttons [*Centaurea cyanus*]. When those hereditary types that were most fit for cultivation were singled out, the people had only to multiply them.

This fact is in complete agreement with the origin of cultivated rye from weedy crops of wheat and barley according to the data available from linguistic, archeological and historical information, disclosing that the cultivation of rye developed much later than that of wheat and barley. This could be expected since the cultivation of one led to the cultivation of the other in crops of the two main cereals. All the information available to us concerning the cultivation of rye indicates that the beginning thereof took place at the start of the Christian era and no later than during the first centuries of that era.

Thus, the problem concerning the origin of cultivated spring rye can be solved to an extent such as needed by plant breeders and biologists for determining the concentration of the sources where the type-formation of a given crop occurred. It is evident that such a solution is only a first approximation toward the elucidation of the problem concerning the origin of the Linnaean species of *Secale cereale*. That problem affects a more general and more difficult area, i.e. that concerning the origin of Linnaean species in general.

In its genesis, the Linnaean species *Secale cereale* is apparently linked both to the perennial rye, *S. montanum* (in a paper by Engelbrecht, 1917, there are hints at a link between the cultivated and the weedy forms of rye, however, like other authors, Engelbrecht was led astray by the identification by A. Regel of the weedy rye of Turkestan as *S. montanum*) and the annual, brittle rye, *S. fragile*, of sandy soils. The latter is found in large amounts in the former territories of Ural, Turgay, Semireche, Syr-Darya and Transcaspia, in northern and north-eastern Afghanistan (Badakhshan) as well as, toward the south, in the Saratov and the Astrakhan districts. Recently, A.A. Grossheim (1924) discovered an annual

type, new with respect to its spike, that reminds one of that of *S. montanum*; he named it *S. vavilovii* Grossh. and considered it a link between *S. cereale* and *S. montanum*. As studies by E.K. Emme in the cytology laboratory of the Institute of Applied Botany demonstrate, all these species are characterized by the same chromosome numbers (normally  $n = 7$ , exceptionally  $n = 8$ ). *S. montanum* is able to cross with *S. cereale* (according to E. Tschermak). Thus we have a comparatively narrow group of types, which are genetically close to each other. In order to widen the approach to the genesis of these species, a detailed differential-geographical study of the wild species of rye is necessary, similar to that carried out in the case of cultivated rye. Asia Minor is apparently of exceptional interest for solving the problem concerning the genesis of the *Secale* species since, according to investigations made by P.M. Zhukovskiy, all the species of wild rye are found there in great amounts as well as a great variety of weedy *S. cereale*. According to observations by Zhukovskiy, *S. montanum* – a species ecologically different from *S. cereale* – occurs in the fields of wheat there and has become a weed in the vicinity of Yuzdar, displaying a number of races that show how much this species approaches *S. cereale*.

The problem concerning the origin of the species of *Secale* is, apparently, quite complicated, as demonstrated by a discovery in South Africa – in the Cape colony – of large amounts of a species close to both *S. montanum* and *S. cereale*, i.e. *S. africanum*.

According to investigations carried out by E.K. Emme, this species also has  $n = 7$  chromosomes which are impossible to distinguish from those of the species discussed above. The discovery of *S. africanum* in South Africa indicates – as an example of the geographical dispersal of species of *Secale* to the most isolated areas – a considerable age for the *Secale* species, the origin of which must go back to long before our present era.

Thus, the weedy rye of southwestern Asia appears to be the direct ancestor of cultivated rye. The wild species of *Secale* are no doubt close to *S. cereale* proper. Coherent forms (including brittle as well as non-brittle races) uniting these were possibly in the remote past distinguished into groups of populations, developing into the complex of specialized weeds infesting ancient wheat and barley crops. The discovery of brittle rye, *S. cereale* var. *afghanicum*, in Afghanistan and of a whole series of transitions with respect to brittleness in *S. cereale*, the establishment by A.A. Grossheim of a new, wild, annual rye, *S. vavilovi*, with a spike of the same type as the perennial *S. montanum*, and finally, the discovery by P.M. Zhukovskiy in Asia Minor of an exceptional concentration of species, including a large variety of weedy as well as cultivated kinds of rye, make it possible to reconstruct, morphologically as well as physiologically, a well-composed evolutionary series of rye. A detailed study of the multiformity of the wild species of rye in areas where their variation is concentrated promises to lead the investigator on to the problem concerning the development of the Linnaean species of *S. cereale*. However, at present, we do not believe that there is any reason for the suggestion that the ancestors of cultivated rye should be *S. montanum* and *S. fragile*, such as has been considered acceptable up until now. In this case, the differential-geographical method has allowed us to come closer to

a solution of the problem concerning the ancestors right up to the establishment of the sources for the diversity of the types. So far, these sources have not been utilized by plant breeders because of the distraction on the part of *S. montanum*, which – although a closely related species – does not have any direct relationship to the genesis of cultivated rye.

#### OATS AS WEEDS AND THE PROBLEM CONCERNING THE ORIGIN OF CULTIVATED OATS

Studies of other plants have revealed that the manner in which cultivated plants become grown from weeds is fairly common.

In 1916, during our travels around Persia, we happened to come across a number of villages in the vicinity of Khamadan [W. Iran] where large amounts of emmer (*Triticum dicoccum*) were grown. In general, the cultivation of emmer was not known in Persia, except for in the Armenian settlements established there about 300 B.C. by Abbas the Great. In that area, it was still possible to see a few isolated fields of this crop, which was imported from Turkish Armenia. Studies of these emmer fields revealed a heavy infestation by oats, *Avena sativa*. This is that much more remarkable since oats were not known in cultivation in Persia, nor in Afghanistan, Bokhara, India or Turkmenistan and since, in Persia, oats appeared to be an unavoidable attribute only of emmer crops. In some fields, it was even possible to observe that the oats were displacing the emmer.

During detailed studies of the crops of these Persian oats and a comparison between them and the kinds known in European crops, it turned out that what we had seen of oats among emmer was represented by independent races, which until then were not known to be cultivated. They were distinguished by peculiar, unilateral, atypical panicles, so far not described by botanists in the case of cultivated oats. Both the paleas and the glumes of this kind of oats are much longer than those of ordinary oats. A full range of glume color from whitish to dark brown could be observed. I singled out the forms discovered as special botanical varieties under the names of *A. sativa* var. *iranica* Vav. (white-grained), var. *persica* Vav. (yellow-grained) and var. *asiatica* Vav. (brown-grained; see Figs. 10 and 11).

The fact that we had found peculiar races of oats in the form of weeds among crops of an almost extinct kind, attracted our attention and made us also investigate the weeds among emmer in other countries.

The studies of emmer (*Triticum dicoccum*) in the Pri-Kama region, in the upper Kazan, Ufa and Simbirsk Governates revealed similar facts. There, too, cultivated emmer was heavily infested by oats, and there, as in Persia, we found a multitude of new, peculiar races and a species, *Avena diffusa*, previously not known in crops. Thus, for instance, it was strange to find *A. sativa* with leaves covered by a dense pubescence, f. *pilosiuscula*, a trait definitely rare among ordinary oats.

In addition to the common forms, characterized by florets not firmly articulated to the panicle and falling apart (as grain) when threshed, there were also peculiar races with firmly articulated spikelets that did not fall apart when



Fig. 10.

Fig. 10. Weedy oat from a field of emmer in Persia.

Fig. 11.

Fig. 11. Spikelet of weedy oat from a field of emmer in Persia.



Fig. 12. Different races of weedy oats (*Avena sativa* L.) From a field of emmer along the Volga. 1-3: Typical races with firmly articulated flowers and short pedicels, found among emmer; 4-6: ordinary races or weedy oats with brittle, disarticulating florets (separating into different florets when threshed); the races illustrated differ from each other with respect to the extent of pubescence at the base of the florets.

threshed (Fig. 12). The rachis, on which the two florets sit in the case of such forms, is short and sessile; because of this the articulation of the florets becomes rather firm so that, if you try to separate the florets from the panicle, they do not disarticulate from the rachis as usual in the case of cultivated oats, but only a portion of the hull is torn off. When passing through the threshing machine, such kinds of oats always leave pairs of spikelets, i.e. the florets (grains) remain united (*firme coalitae*). Among the races of oats in the Volga area we discovered, in general, races with panicles morphologically somewhat reminding one, in their compact structure, of the spikes of *Triticum spelta* or *T. dicoccum*. The separation of such spikelets and florets is more difficult than in the case of ordinary, hulled oats. Such forms of oats are found exclusively among crops of emmer. Among these peculiar forms of oats in emmer we also found a number of varieties, distinguished by the color of the glumes and by the awns: white-grained ones with awns (i.e. var. *kasanensis* Vav.) and without awns (var. *volgensis* Vav.) and yellow-grained ones with awns (var. *bashkirorum* Vav.) and without awns, (var. *segetalis* Vav.). The names given refer to those of the localities and the areas where emmer is grown (around lower Volga and in the Kazan Governate).

Detailed investigations of oats among emmer, made by A.I. Mordvinkina, led to the distinction of a multitude of transitional forms ranging from the races typical among emmer to common forms impossible to separate from the usual kind of cultivated oats with respect to the articulation of the spikelets. Among all the varieties growing among emmer, there are special races with short bristles



at the base of both the grains (florets), and among var. *kasanensis* Vav. some peculiar forms with long bristles at the base of both florets. So far these forms are definitely not known among cultivated oats.

A number of races were discovered among emmer grown in Dagestan. These have unusually broad glumes. In the Volga area, a new race of *Avena strigosa*, with short awn-like appendages also occurs as a weed.

Studies of emmer brought to northern Caucasus (Dagestan, Ossetia) from Transcaucasia (Armenia, Georgia and Azerbaidzhan), Asia Minor, Bulgaria, Crimea and those grown by the Basques in the Pyrenées, as well as some from Abyssinia, invariably revealed the presence among them of oats as a constant attribute; in these cases, the emmer crops actually turned out to be the 'preserver' of a diversity of oats, and of a peculiar concentration of kinds of oats not known in cultivation. At the same time, ordinary types, such as those well known in cultivation, were also found there. We began to study these weedy oats in detail just as we had done in the case of emmer itself. It turned out that the centers in the world where emmer still remains in cultivation were actually at the same time also the centers of variation in the case of oats. In Transcaucasia, where there are no cultivated oats, there is a large variation of *Avena diffusa*, characterized by a series of glume colors and by firmly articulated florets, although not as clearly expressed as in the case of the group around the Volga. In Transcaucasia, there are also constant forms of var. *transiens* with dark-brown bristles covering the glumes. This type was so far known only as rare hybrid forms, intermediate between oats and the wild oats of the Balkan peninsula. Among winter emmer, obtained with great difficulty from the Basques in the Pyrenées, we found peculiar, late-ripening races of *Avena sativa*. In Abyssinia, the emmer is, just like other cereals, accompanied by peculiar forms of oats, *A. abyssinica* and so on. Emmer from Bulgaria was infested by an enormous amount of oats, represented by different varieties.

Table 8 provides a brief review of the diversity of the varieties and the races ('jordanons') of oats found by us so far among emmer crops. By now, we have studied about 100 samples of emmer and we do not doubt that, in the future, still more new races of oats will be found when investigating emmer from Transcaucasia, Bulgaria and other countries.

Oats appear to be common weeds also among einkorn [*Triticum monococcum*], the cultivation of which is preserved by the Tatars on small plots in the Crimea, in Asia Minor, Bulgaria and in the northern Caucasus. We were able to confirm the presence of weedy oats in samples of einkorn from Bulgaria, Transcaucasia, N. Caucasus and Crimea studied in our laboratory. In the northerly areas (e.g. the Vyatskaya Governate), oats often appear to infect crops of barley (the local epithet of such a crop is 'soritsa', [i.e. the 'weedy one'; D.L.] just as observed in Transcaucasia.

In the Povolzhe area, the amount of oats in emmer takes on such dimensions that, statistically, these crops can be distinguished from those of emmer by the epithet 'supolby' ['emmer companion'; D.L.].

In this case, we are talking only of oats belonging to the cultivated type and sharply distinguished from wild oats, *A. fatua* and *A. ludoviciana*, which

frequently, together with ordinary oats, infest emmer, einkorn and barley crops (in Transcaucasia and Bulgaria).

### THE DISPLACEMENT OF EMMER BY OATS

Farmers sowing emmer around the Volga and in Crimea and Transcaucasia complain constantly about oats infesting their emmer. The oats lower the quality of the groats and the flour, spoiling them somewhat, and therefore oats are considered an undesirable admixture. Emmer heavily infested by oats is ordinarily not used for groats or flour but only as forage for cattle. According to all information available to us, oats are considered a hardier plant than emmer in the north. Observations by local agronomists in the Pri-Kama region unambiguously indicate that the emmer there is being displaced by oats. In a paper from the first half of the last century (Belikov, 1840) we can read as follows: 'Who among us does not know that oats overpower emmer so that from an almost imperceptible number of grains of oats, falling by chance among grains of emmer, after a few harvests, the field, even the entire desyantina [1.2 acres; D.L.] appears to have been sown with oats alone, among which a few specimens of emmer are by chance mixed in'. This means that in a given case we can observe a development similar to the penetration of rye into wheat and barley crops. According to some folklore, collected by E.A. Stoletova from the Kazan territory, there is, for instance, a statement used by the local inhabitants: 'Ask any old man, ask any young man and all will tell you that emmer degenerates into oats' (Stoletova, 1925). Frequently there are instructions to the peasants that they should stop sowing emmer because the wild oats will stifle it.

The ancient authors knew oats only as weeds among crops of other cereals (Theophrastes). Hehn explains the German epithet 'Hafer' as 'Bocksgras', i.e. a weedy grass [actually, 'Devil's grass'; D.L.].

### THE ORIGIN OF CULTIVATED OATS

In view of the above-mentioned facts, the problem concerning the origin of cultivated oats has suddenly become clearer and many intricate data concerning the geography of the varietal diversity of oats and examined by us with respect to the center of origin, can now be understood and make full sense when cultivation of oats is associated with the cultivation of emmer, which is about to die out. The link between the cultivation of oats and the oldest cereals in the world, emmer and einkorn, becomes at the same time definitely obvious. Just as rye was brought along with soft wheat, when the latter dispersed toward the north, the ancient crops of emmer during their dispersal over the Old world took along a collection of weedy oats. When the crops were transferred to the north or into much more severe conditions, the weedy oats began to displace the main crop. Thanks to these conditions, more favorable for oats, they turned into crops in their own right. In that manner, the cultivation of oats originated within a number of areas. It is most likely that this led to the origin of the crops of oats in the Pri-Kama region. In the Vyatskaya Governate, many kinds of



Table 8. *Varieties of the kinds of oats that infest emmer (Triticum dicoccum)*

	Area					
	Around Volga	Transcaucasia	Persia	Crimea	Altai	Spain
<i>Botanical variety</i>						
<i>Avena diffusa</i>						
var. <i>mutica</i>	+	+	-	+	+	-
<i>aristata</i>	+	+	-	+	+	-
<i>aurea</i>	+	+	-	+	-	-
<i>krausei</i>	+	+	-	+	+	-
<i>grisea</i>	+	+	-	+	-	+
<i>cinerea</i>	+	+	-	+	-	-
<i>brunnea</i>	+	+	-	+	-	-
<i>montana</i>	-	+	-	-	-	-
<i>transiens</i>	-	+	-	-	-	-
<i>setosa</i>	-	+	-	-	-	-
<i>iranica</i>	-	+	+	-	-	-
<i>persica</i>	-	+	+	-	-	-
<i>asiatica</i>	-	+	+	-	-	-
<i>volgensis</i>	+	-	-	-	-	-
<i>kasanensis</i>	+	-	-	-	-	-
<i>segetalis</i>	+	-	-	-	-	-
<i>bashkivorum</i>	+	-	-	-	-	-
<i>A. orientalis</i>						
var. <i>tatarica</i>	+	-	-	-	-	-
<i>obtusata</i>	+	+	-	-	-	-
<i>A. strigosa</i>	+	-	-	-	-	-
<i>Racial characteristics</i>						
<i>Shoots</i>						
Pubescent	+	-	-	-	-	-
Glabrous	+	+	+	+	+	+
<i>Growth form</i>						
Caespitose	+	+	+	+	+	-
Semicaespitose	-	+	-	-	-	+
<i>Leaf blade</i>						
Pubescent	+	-	-	-	-	-
Glabrous	+	+	+	+	+	+
<i>Culms</i>						
Tall	+	+	-	+	+	+
Short	-	+	+	-	-	+
<i>Nodes</i>						
Glabrous	+	+	+	+	+	+
Pubescent	+	+	+	+	+	-
<i>No. of culms</i>						
Many	-	+	+	-	-	-
Few	+	+	-	+	+	+

Table 8. (cont.)

	Area					
	Around Volga	Transcaucasia	Persia	Crimea	Altai	Spain
<i>Panicle</i>						
Spreading	+	+	+	+	+	+
Unilateral	-	-	+	-	-	-
Single-crested	+	+	-	-	-	-
<i>Articulation</i>						
Firm	+	+	-	-	-	-
Not Firm	+	+	+	+	+	+
<i>Pubescence at base of grain</i>						
Only on lowest floret	+	+	+	+	+	+
On both florets	+	-	-	-	-	-
<i>Rachilla</i>						
Long	+	+	-	+	-	-
Short	+	+	+	+	+	+
<i>Dimensions of hulls</i>						
(a) Very long	-	+	+	-	-	-
Long	+	+	+	+	-	+
Short	+	+	-	+	-	+
(b) Wide	+	+	-	-	+	-
Narrow	+	+	-	+	+	+
<i>Awns</i>						
(a) Long	+	+	+	+	+	+
Short	+	+	-	+	+	-
(b) Coarse	+	+	+	+	+	+
Fine	+	+	-	+	+	-
<i>Shape of grain</i>						
Elongate	-	+	+	-	-	-
Ovate	+	+	-	+	+	-
Type of cultivated						
'Probshteykiy type'	+	+	-	-	+	-
Type intermediate						
between needle-like						
and the cultivated						
'Probshteykiy' types	+	+	-	+	+	+
<i>Vegetative period</i>						
Long	-	+	-	-	-	+
Intermediate	+	+	+	+	+	-
Short	+	+	-	-	+	-

locally cultivated oats cannot be distinguished from the kinds of oats found in emmer. The type called 'chernoviy' ['the black one'; D.L.] recently produced by the Vyatskaya Experimental Station, and based on local oats, is characterized by firmly articulated spikelets, which do not separate into florets (grains) when threshed, which, as we have seen, is often typical of a number of the weedy oats among emmer in the Pri-Kama region.

In Abyssinia, Kostlan (1913) observed the displacement of barley crops by oats in the mountain areas; in the case of late barley crops (ripening in July) and during cold and harsh weather, half the barley crop when harvested consisted of oats. Such grain, sown in the following years, eventually gave rise to a pure crop of oats.

Just like rye, oats are, according to all historical and archeological data, a younger plant than wheat, barley or emmer, the information about which dates back to thousands of years before our present time. As in the case of rye, the first information about crops of oats does not go further back than to the first centuries of the Christian era (Schulz, 1913). The comparative youth of the cultivation of oats can be understood, since these plants were brought along by other ancient crops when dispersing from the south toward the north.

The reason for the dying out of emmer cultivation remains to be understood. At the same time as it was transferred into areas where it could be cultivated, the crops of naked-grained wheat, grown rather than the hulled emmer, which is less suitable for grinding, were to a considerable extent responsible for the reduction of the acreage under emmer, which also, because of natural selection, had been replaced by oats. Just as in the case of rye, oats were taken into cultivation by Man voluntarily or even against his will.

The absence of a single center of origin of oats can also be understood from this. Oats, like rye, were taken into cultivation simultaneously and independently in various places. This happened not only in the case of different Linnaean species but also within the limits of the single Linnaean species, *Avena sativa*, itself.

As we have seen, the centers of emmer in Transcaucasia, the Pri-Kama region, Spain, Abyssinia and Germany are, to a great extent, represented by different morphological and physiological types, accompanied by corresponding groups of weedy oats. In the past, the weedy oats associated with early-ripening emmer grown around the Volga, turned out to be early-maturing. It was natural that different lines of such oats among emmer should initially give rise to different groups of cultivated oats, as shown by the strains still preserved in plots of cultivated emmer. When considering the very large amount of material of oats among emmer, preserved by primitive people in Eurasia and Africa, there is no doubt that it is still possible to interpret the details of how oats became cultivated and to trace the different lines or groups of oats, which were associated with the different groups of emmer. However, this process cannot be completely retraced since the original cultivation of emmer still occupies the stage to a considerable extent and much of the history about how oats became cultivated cannot be fully traced either. In this respect, the most interesting fact is the petering out toward the north of emmer cultivation, which by now is

almost extinct. This is even more obvious in the case of the other ancient, cultivated plant, einkorn, now practically extinct as a crop. Displaced in the north by oat crops, emmer and einkorn themselves died out. Spikes of emmer (*Triticum dicoccum*) are only rarely recorded, demonstrating the link between the oats grown at present and the basic crops of emmer that are now dying out.

It is impossible to understand fully the geographical diversity of oats cultivated in the Old World without associating them with isolated plots of emmer and, perhaps, also with such plots of barley. For instance, in Abyssinia, the plots of emmer still act as 'carriers' of an exceptional variety of oats. New types, suitable for introduction, should be sought by plant breeders in such basic centers of variation. There, chances exist for finding new races, which could be valuable for this or that reason. Experiments, testing strains at our Steppe Station, have shown that some races of oats from emmer crops in the Kazan area, surpass the west-European races with respect to productivity under the conditions present on the Russian steppes.

The cultivation of emmer, the origin of which extends, as we have seen, along the coastal area of the Mediterranean, where an exceptional diversity of forms is concentrated in the mountain areas and where there are areas of multiformity adjacent to it has, thus, taken a close part in the creation of the crops of European oats. During the advance to the north, the cultivation of oats developed in the form of different strains from the weeds in the ancient crops. Without any knowledge of emmer crops, it is impossible to understand the genesis of cultivated oats, just as it is impossible to understand the origin of cultivated rye without associating it with the more ancient cultivation of wheat and winter barley.

Hence, it is not such an incredible fact that the roots of cultivation of oats in the north must – just as in the case of the other northern crop, rye – be searched for in the mountains of the more southerly areas. In the case of *Avena sativa*, this may be a question of the countries extending along the northern part of the Mediterranean coast from the Balkan peninsula to the Pyrenées.

We still have not enough reason to convince ourselves that all the cultivated oats developed in this manner. As we have seen in the chapter on the centers of type-formation, cultivated and wild oats have a polyphyletic origin. The cultivation of oats could also belong to the same type as that of *A. byzantina*, which originated along the Mediterranean coast, perhaps in Africa, where it still constitutes an important crop. Apparently, *A. brevis* and *A. strigosa* came from weeds among barley and other cereal crops in northwestern and northern Europe. They are still, to a considerable extent, weedy plants in Byelorussia and adjacent areas. Their hardiness on light and sandy soils, on which they are still grown in England and France, served no doubt as a favorable factor, operating to the benefit of the selection of these oats into cultivation.

Further studies are necessary, but we do not doubt that the establishment of a connection between the cultivation of oats and its development from that of other crops will be of decisive importance for a detailed elucidation of the genesis of cultivated oats.

When retracing the history concerning the origin of cultivated oats, we must

necessarily take into consideration the considerable complications that caused the disappearance of the basic crops, that brought oats with them. As far as the fragments of emmer cultivation are concerned, i.e. that which once occupied a broad belt from the Pyrenées to the Caucasus (as demonstrated by the isolated plots preserved of the now almost extinct races of emmer, *T. dicoccum*), it is necessary to restore the entire picture of the complicated history of that crop and of the species of oats associated with it. The polyphyletic origin of oats is an aggravating complication. In this respect, the matter of how cultivated rye was generated is, however, in every sense much simpler. In the Asiatic countries and within the main center of soft wheat, it is still possible to retrace the process of type-formation and to follow the history of rye, in detail, during its dispersal from the south toward the north.

#### EXAMPLES OF THE ORIGIN FROM WEEDS OF OTHER PLANTS

No doubt whole groups of oil-producing cruciferous plants developed from weeds infesting other, more ancient crops. As is well known, the cultivation of flax originated from a multitude of specialized weeds – *plantae linicolae* – the seeds or fruits of which are, as far as their dimensions are concerned, similar to those of linseed, so that they cannot easily be distinguished from the latter when sorting and cleaning the seeds. Some of these weeds are at the same time used as cultivated plants. The garden rocket (*Eruca sativa*) is such an oil-producing plant, grown in Persia, Afghanistan, Bokhara and India (Sinskaya, 1925). This plant, common in Central Asia, is invariably a companion of cultivated flax; under harsher conditions it frequently displaces the flax. Crops can be seen where it is difficult to determine whether flax or garden rocket was sown. The suitability of garden rocket as an oil-producing plant turned it from a weed into a cultivated plant, when grown in areas where flax succeeds badly.

In the Caucasus (especially in Armenia and Georgia) and in Asia Minor as well as the Altai, but also in northern areas, where flax is grown together with garden rocket, the false flax, *Camelina sativa* and *C. linicola*, occur also as specialized weeds and at the same time as cultivated plants, and behave similarly to garden rocket (Tsinger, 1909). The cultivated, large-seeded corn-spurries (*Spergula linicola* and *S. maxima*) have a similar relationship to flax.

In his excellent paper, N. V. Tsinger (1909) investigated in detail the picture of how this group of *plantae linicolae* was selected from flax.

In Transcaucasia (Armenia and Georgia) it is possible to observe clearly the displacement of flax by false flax and colza (*Brassica campestris*; [most likely var. *silvestris*]) in the high mountain areas. There, as hardier and early ripening plants, the false flax and colza displace common flax and become, thanks to the wishes of Man, grown as oil-producing plants. According to the observations made by E. A. Stoletova among the highest mountains of Armenia, the false flax and the winter cress are successful as oil-producing plants, while lower down, in the median belt, flax grows well, while still lower down, in the lowland, sesame (*Sesamum*) and castor beans (*Ricinus*) are preferably cultivated.

A whole series of cultivated species of wild mustard and rapeseed (*Brassica* and

*Sinapis*) are linked to corresponding weedy plants in the crops of various cultivated plants. Tatarian buckwheat (*Fagopyrum tataricum*) is a bad weed in the crops of ordinary buckwheat (*F. esculentum*). In Siberia it occurs as a common weed among the spring wheat. However, at the same time, the Tatarian buckwheat replaces the common buckwheat in the elevated mountain areas of Altai and Kashmir.

The origin of some cultivated leguminous plants is similar: vetches (*Vicia sativa* and *V. pannonica*), possibly also the vetchling (*Lathyrus sativus*), and peas (*Pisum arvense*) originated from admixtures to cereal grasses in the mountain areas of Asia. Narbonne vetch, *Vicia narbonensis*, is a common weed in Spain and in Transcaucasia but is a cultivated plant in Italy.

In the Crimea, einkorn (*Triticum monococcum*) infests, together with oats, the crops of emmer (Barulina, 1925). It is also found in France (Schulz, 1913).

Coriander (*Coriandrum sativum*) occurs as a weed among cereal crops in Transcaucasia and in Asia Minor while being cultivated in the same areas as well as in Central Asia.

In Asia Minor, P. M. Zhukovskiy noted that a common weed among wheat, *Cephalaria syriaca*, was taken into cultivation. When displacing the wheat in the mountain areas, this plant is locally utilized as an oil-producing plant. Wild melons (*Cucumis trigonus*) occur as serious weeds on tilled fields in northern Afghanistan and in Turkestan. Crops of Chinese jute (*Abutilon avicennae*), a common weed in many crops, and hemp-mallow (*Hibiscus cannabinus*) have a similar origin. Wild carrots (*Daucus carota*) occur as common weeds in vineyards and vegetable gardens in Afghanistan and Turkestan, where they practically invited themselves to be cultivated by the local agriculturists.

The number of such examples can, no doubt, be increased considerably if cultivated plants are studied closely. However, we are already able to state that a large group of plants, known to us in the mountain areas and in the northlands and Central Europe as cultivated plants, occur in the south and in the centers of their type-formation as more or less aggressive weeds. Thus, in essence, a direct and natural pathway can be outlined for the provenance of this secondary group of cultivated plants. When advancing into areas with severe conditions, up into elevated mountains, or toward the north, these weeds displace to a considerable extent the original crops, both in the fields and in the vegetable gardens. It could be said that the European lowland is at present covered to a great extent by plants that were once weeds. The two main European crops, rye and oats, are typical representatives of such an origin.

#### PRIMARY AND SECONDARY GROUPS

Thus, it is possible to distinguish two groups of cultivated plants. The first group comprises the basic, ancient cultivated plants, known to Man only in their cultivated state. These we shall call *primary crops*: they are, e.g. wheat, barley, rice, soybeans, flax and cotton. The second group, the *secondary crops*, is no less extensive and comprises all the plants that derive from weeds infesting the primary main crops, especially rye, oats, false flax, garden rocket, large-seeded spurries, Tatarian buckwheat, an number of leguminous plants, American

hemp and so on. The natural pathway for being taken into cultivation independently was, in the case of this secondary group, the transfer of the basic crops from the valleys into localities high up in the mountains, to sites in more northerly areas, into more severe conditions or onto poorer soils. At the same time as the transfer of the crops toward the north, into worsening climates or soils, a natural differentiation took place, selecting the more frost-resistant, earlier ripening, hardier and more tolerant plants. This process was assisted by the wishes of Man. The agriculturalists counted on this process as a fact. Hence both the practical and the scientific interest that should be given such species of field weeds at the main sources of their type-formation and variation can be understood. However, all these have not yet been fully explored by the investigators.

#### CHAPTER 4 MOUNTAIN AREAS AS CENTERS OF AGRICULTURAL CROPS

Representatives of the origin of crops have, in general – just like the basic, major civilizations – been associated with major river systems. In his book, *Civilizations and the great historical rivers*, the geographer Lev Menchikov developed a detailed hypothesis for a link between the major river systems and civilizations. The main civilizations of the Old World were situated mainly in the basins of the Nile, Tigris, Euphrates, Ganges, Indus, Yangtze and Hwang-Ho rivers and, consequently, the idea developed that the cultivation of plants also started in the valleys of these great rivers.

However, during the last couple of years, a closer study of southwestern Asia, Asia Minor and northern Africa has demonstrated that all the varietal diversity of field and vegetable crops is hidden mainly within mountain areas. The mountain regions proved to be where the varietal and racial multiformity of plants is concentrated and, consequently, the hypothesis concerning the beginning of agriculture in the valleys of the great rivers appears to be basically erroneous.

The mountain areas present, of course, optimum conditions for explaining the varietal diversity, the differentiation into varieties and races and for the preservation of all kinds of physiological types. At the same time, the mountains are excellent as isolated areas for the preservation of the varietal wealth. Just as in the case of the wild flora, where the Caucasus, the mountains of Bokhara, mountainous Turkestan, Afghanistan, Asia Minor and Abyssinia, as well as the Cordillera of South America, they appear as 'collectors and guardians' of specific and generic diversity; they are also the 'guardians' of the racial variation of many cultivated plants.

However, it would also be a great mistake to think that the concentration of racial variation in the mountains of southwestern Asia, Asia Minor and Abyssinia is the result of the diversity of ecological conditions only. No doubt, it can also to a great extent be explained on the basis of historical and geographical circumstances, which concentrate the process of type-formation of various Linnaean species just to some particular mountain area.

However varied the conditions for growing plants in Afghanistan are –

ranging from that at the limit up to which crops can be grown in Hindukush to that of the subtropical climate in the areas adjacent to India – some important species of wheat (e.g. *Triticum durum* and *T. dicoccum*) are definitely not found there, although they are common in the mountains of Abyssinia. For historical reasons – mainly proximity to the center of type-formation – Afghanistan is the area where the greatest variety of soft and club wheats is exclusively concentrated, while at the same time the uniformity of barley is striking there. The mountain areas of the Alps and the Pyrenées do not – as far as is known – display any concentration of varietal diversity. The naked-grained oats seem for similar reasons to be concentrated in the mountains of China. An infinite number of such facts can be cited and they all bear witness to the fact that a decisive role in the development of a particular mountain area into a center for type-formation is played by historical circumstances and not only by the diversity of the environment.

When contemplating the process of how agricultural crops developed, we must inevitably acknowledge that the period of the great civilizations, uniting a society of many tribal people, was, of course, preceded by a period when people were isolated as tribes and small groups, inhabiting secluded areas. The mountain areas may be considered as excellent refuges for such purposes. The control of the great rivers, the regulation of the Nile, Tigris and Euphrates and the other major rivers, required an ironhard, despotic organization, the building of dams and the regulation of irrigation; it needed organized mass operations such as the primitive agriculturalists could not even dream of. It is, therefore, so much more likely that, just like the centers of varietal diversity, the centers of the first agricultural crops should be found in mountain areas. The regulation of water for irrigation does not require great effort there. Mountain streams can easily be diverted for irrigation by gravity. The areas of the high mountains often provide opportunities for non-irrigated crops as well because of the large amounts of precipitation in the elevated mountain belts. In the agricultural mountain areas of Bokhara it is still possible to observe various primitive stages in the evolution of agriculture, actually preserved unchanged over thousands of years and still illustrating the different stages of the agricultural civilization.

The differentiation of cultivated plants into races was, no doubt, also favored by the mixture of ethnic societies in the mountain areas of southwestern Asia and northern Africa. Ethnological maps of the Caucasus, the mountains of Turkestan, Afghanistan, Bokhara and northern India can be said to also reflect the variety of the racial composition of the plants cultivated in those areas. The mountain areas mentioned represent not only centers of variation of different kinds of cultivated plants but are also foci of diversity of human tribes.

#### Vertical belts and horizontal zones in relation to the differentiation of cultivated plants into races

The interest in mountain areas as centers of varietal diversity is especially important in connection with the fact that the dispersal of varieties in relation to vertical belts in the mountains coincides locally, to a great extent, with their local horizontal dispersal.

In the high mountains of the Caucasus, Bokhara and Badakhshan we found Siberian and Archangelian types of spring wheat and barley, characterized by soft awns, easily threshed grains, low stature and narrow glumes. The people of Pamir call the Siberian and North European strains of sweet peas 'pelyuski'. Flax in the elevated mountain areas approaches the long-staple flax of the northlands with respect to the early maturation and the few, tall stems. Northern strains of cultivated plants are also currently preserved in the Asiatic Cis-Pamir, in areas adjacent to the center of type-formation of a number of plants. In the valleys and the foothills of the mountains, races that are definitely different but typical of extensive territories of southwestern Asia and northern Africa are often concentrated. When descending from the mountains, it is possible to observe an interesting change in types from the extremely early-ripening high-mountain races to late-ripening lowland types, frequently associated with irrigated cultivation.

The maximum amplitude of racial variability is usually concentrated in mountain areas, however, not at the extreme limit of cultivation but considerably lower down, e.g. in the case of soft wheat in southwestern Asia according to our own observations at elevations of 800-1800 m.s.m. When ascending from there, the diversity of varieties and races becomes noticeably reduced with respect to types and kinds of crop. Such a reduction in the variety of plants and races is, as a rule, also characteristic during the advance of the crops from the south toward the north.

The mountain areas of southwestern Asia, Asia Minor, Caucasus and those of northern Africa still display the full range of variability of those types of cultivated plants that are able to populate the enormous territory from Mesopotamia all the way to the Siberian taiga [boreal forest; D.L.] and to the limit of agriculture in northern Europe. In the case of cultivated plants, knowledge of the global geography of type-formation leads to the acknowledgement of the exclusive roles played by the Asiatic, African and South American mountain areas. These act as 'granaries' of different strains and need detailed investigation. Many primitive forms, the cultivation of which was initiated long ago can still be found there and, hence, the enormous interest that they represent both for practical and theoretical investigations of these areas can be understood.

## CHAPTER 5 THE ORIGIN OF CULTIVATED HEMP AND OF CROPS BELONGING TO THE PRIMARY GROUPS OF PLANTS

The origin of cultivated plants that belong to the secondary group is perfectly clear to us. The dynamics of how different plants were taken into cultivation can be traced in minute detail. The problem concerning the origin of the cultivated plants, referred to by us as 'primary', is considerably more difficult. How did the basic crops of wheat, barley, flax, rice and the many leguminous plants become cultivated? The solution of this problem is much more complicated and we may never succeed in solving it completely. In the case of many plants belonging to

this group, the link between the wild and the cultivated forms has already been lost. We are faced only with the result of a clearly expressed selection, executed over thousands of years, and to trace all the historical links requires a lot of more or less believable imagination. However, as demonstrated by the investigations described below, in some cases it is not hopeless and, while not resorting to unnecessary fantasies, the historical process can, in essence, be traced.

During the studies of the botanical complex of hemp, *Cannabis sativa*, in the southeastern parts of European U.S.S.R. and in Asia we were led to pay attention to the problem concerning the origin of this crop as well. Nevertheless, we do not know when, by whom or where hemp was taken into cultivation; however, the natural process of the onset of hemp cultivation turned out to yield to a detailed study and, perhaps, there is no other ancient plant but hemp for which the dynamics of how it became cultivated can be successfully traced with such certainty.

### Wild and naturalized forms of hemp

The wide distribution of wild hemp in the Old World is well known by botanists. Statements concerning observations of such types of hemp are constantly seen in botanical literature.

Until recently, the majority of authors considered this wild hemp to be a form that had escaped from cultivation, i.e. had become naturalized. No essential difference could be observed between the cultivated forms and those not cultivated and all can be referred to the Linnaean species *Cannabis sativa*. The assumption of a wild origin of the thickets of naturalized hemp appeared to be self-evident.

The mass reproduction of the form of wild hemp - in particular under conditions excluding the possibility that it had been sown by man - involuntarily led some authors to reason that, perhaps, this hemp was genuinely wild. However, until recently, there was no definite proof supporting either opinion. Direct observations of hemp that had escaped from civilization indicated the possibility that it had become naturalized. In areas where hemp is grown, it can go completely out of bounds, for instance on vacant land and fallow fields; in other words, it is relatively easily naturalized. Even in America, where hemp was brought by European settlers, it is frequently met with as 'an escape from cultivation' (Britton, 1889). I, myself, was able to collect 'escaped' hemp around St. Paul, Minnesota.

Enormous thickets of 'wild' hemp are known both from European and Asiatic parts of the U.S.S.R. Especially large thickets of hemp occur in ravines in the valleys of northern Caucasus, for instance in the area of Nal'chik, and to the south of Rostov, where harvesting of 'wild' hemp has reached practical importance. Ledebour (1846-1851) mentions hemp in a 'quasi-spontaneous' state all over the southeastern as well as the central and western portions of European Russia, Transcaucasia (at Lenkoran'), in Crimea and along the Don and Ural rivers in the Podoliya area of the Ukraine. Wild-growing hemp is known within the Aralo-Caspian territory as well as the districts of Turgay and Ural

(Bogdan, 1908). S.I. Korzhinskiy mentioned in his 'Tentamen florum Rossiae orientalis' (1898) that hemp occurs in the eastern belt of European Russia in an 'inquinatus' state, i.e. 'dwelling in a place not its own', and was found in the southeastern areas to be 'spontanea videtur' [seen as spontaneous]. It is found in enormous quantities east of the Volga in the Samarskaya and Ufa Governates districts as well as in the Saratov and Astrakhan districts. B.A. Keller observed hemp as a forest plant in the oak-maple forests of the Astrakhan and Saratov districts, especially below Sarepta (Dimo & Keller, 1907). In the Buzuluk woodland, it has long since locally formed almost pure, thick and tall thickets of stalks, although there is no cultivation anywhere in the Yergenyi highlands (Vysotskiy, 1915). It is found there naturalized as well as 'artificial plantations' and in untilled habitats. Dioecious nettles [*Urtica dioica*], black nightshade [*Solanum nigrum*] and thistles [*Cirsium* sp.] are associated with it.

On the Balkan peninsula, 'naturalized' hemp is mentioned from Bulgaria (Velenovsky, 1989) and Serbia (according to Adamovich); it is also found in Hungary and the Banat area (Yanishevskiy, 1924).

In the Asiatic parts of the U.S.S.R. 'wild' hemp is found in enormous quantities as a weed at the Kirgizian camps in Altai, on fallow land, in vacant lots and in vegetable gardens. In addition, weedy hemp grows all over the mountainous area of Altai, reaching up to an elevation of 1440 m.s.m. and, in exceptional conditions, even to 2000 m (at Rakhmanovskiye Springs, according to Sinskaya, 1925). According to a report by A.A. Khrebtov (1926), 'wild' hemp is also found as a distressing weed in fields of spring wheat, barley, spring rye and oats among the mountains of Altai.

According to observations made by E.N. Sinskaya in Altai and by A.A. Khrebtov in western Siberia (in the Semipalatinsk district of the Zaysan Territory, in the Akmolinsk, Omsk and Tobolsk districts, especially the southern parts, as well as in the Tomsk district, etc.) hemp is often seen on steep riverbanks, in valleys and in out-of-the-way corners where, perhaps, man has never set foot but where the thickets of hemp often appear to be of a primary type.

In an economic essay about southern Altai, N.N. Oganovskiy (1922) also mentions 'wild hemp' when speaking of the utilization of natural resources of that territory and, particularly, of its wild flora. According to his calculations, 'the fibers and the seeds of the wild hemp can easily furnish a profit of up to 150 000 rubles a year' in this area. V.F. Semenov (see Krylov, 1909) reports on a distribution of hemp along the right-hand bank of the river Irtysh in the northeastern part of the Omsk district. 'Wild' hemp is also noted from the Semipalatinsk (B.A. Keller) and Syr-Daryan districts (Knorring & Minkovitz, 1912).

As far as the weedy/naturalized hemp is concerned, it was observed in the former Manchuria by V.L. Komarov, K.I. Maksimovich and L.I. Litvinov (cf. Komarov, 1903). It was noted by V.E. Pisarev also in northern Mongolia.

E.L. Regel (1892) mentions hemp in a 'naturalized state' in the Ussuri territory around houses, in weedy hollows and in sites where yurts [nomad felt-tents; D.L.] have stood, but also secluded along river banks.

Boissier (1879) indicated that hemp in the Himalayan region was 'subspontaneous'. Hooker (1890) called the hemp in northeastern Himalaya a wild plant. We have found 'wild' hemp in northern Persia (at Mazanderan), in Kafirstan and Afghanistan in areas where hemp is definitely not cultivated. Belts of 'black hemp' emanating from crops of maize and other cereals stretch along the Kunar river (on the border between Afghanistan and India) from Chekhosarai to Djelalabad for a distance of 150–200 verst [100–125 miles; D.L.].

The very abundance of hemp found independent of crops of other plants has made botanists suspect that it has a 'wild nature'. However, prudently and in view of the lack of any differences between it and the cultivated form, the authors prefer to call it 'quasi-spontaneous' (Ledebour), 'subspontaneous' (Boissier), 'seemingly spontaneous' (S.I. Korzhinskiy) or 'erratic' (Erndtelio).

### Studies of wild hemp

While studying hemp cultivated in the Saratov and Astrakhan districts in 1920, we turned our attention also to the wild, naturalized or weedy hemp. During a close study thereof, it was revealed that the wild or weedy hemp represented forms sharply different from the cultivated ones as far as the seeds are concerned and, most of all, with respect to how the seeds are shed when ripe.

For a long time we did not succeed in collecting a sufficient quantity of seeds from this kind of hemp. Mature plants of 'wild hemp' habitually do not hold on to their seeds. After careful examination, it turned out that the majority of the plants belonging to this kind of hemp had seeds with characteristic, prolonged formations at the base of the seeds, reminding one of the shapes of the 'horseshoes' [actually, elaiosomes] of wild oats. The disarticulation and shedding of the seed when ripe occurs along this formation. The cell membranes covering the seeds of wild or weedy hemp turned out to be thicker and to have an appendix at the base. The 'wild' seeds are also considerably (ca. 1½ times) smaller than those of the cultivated hemp. Unexpectedly, it was revealed that, just as in the case of wild cereal grasses, the weedy or naturalized hemp had peculiarities of the flowers that favor the self-pollination and self-dispersal of the seeds.

In particular, germination of the ripe seeds of weedy hemp is extraordinarily slow and uneven, a fact reported by V.F. Antropov and T.Ya. Serebryakova in the case of crops on our experimental fields. After being harvested and sown during the fall, the seeds of wild hemp rest for some weeks, even several months, without germinating, while, under similar conditions, those of the cultivated hemp germinate very nicely within a few days of being sown. During normal spring seeding, the germination of the wild seeds is also peculiarly slow and exceptionally uneven. Out of 100 seeds, usually a few dozen will germinate and, occasionally, only individual seeds of different plants.

In other words, this kind of hemp has peculiar biological characteristics common to many wild and weedy plants and is sharply distinguished from those of the corresponding cultivated plants, e.g. the rapid and even germination of the seeds of the latter. The attributes revealed with respect to the wild

plants made us bravely consider the weedy and naturalized hemp as a genuinely wild plant, similar, e.g., to wild barley, *Hordeum distichum* var. *spontaneum*. We suggested therefore that it should be likewise distinguished as a special variety, *Cannabis sativa* var. *spontanea* (Vavilov, 1922).

In 1924, D.E. Yanishevskiy published an interesting paper on the wild hemp in southeastern Russia for which he suggested the name *Cannabis ruderalis* when providing it with a Latin diagnosis. He studied the fruits thoroughly and it was revealed that the essential peculiarity of the fruits of wild hemp was to be found in the membrane covering the seeds and developed from the perianth. It remains on the seed after it is shed. In the case of the cultivated form, no perianth remains on the seed, only traces of it hang on as occasional scraps of a membrane. In the case of the weedy (wild) hemp, the perianth covers the seeds as a thick membrane and makes them appear multicolored or marbled and very hard, because of the pericarp covering them. Due to the development of the pericarp there is, according to D.E. Yanishevskiy, a certain similarity to the same structure of the seeds of hops, *Humulus lupulus*, where the perianth also completely envelops the ripe fruits.

D.E. Yanishevskiy described in detail the characteristic of the seeds of the wild hemp called 'horseshoes' [elaiosomes]. Anatomical studies revealed the development of a special, thick tissue with cells rich in oils and inclusions. This tissue develops between the site where the perianth is attached and the site of the carpels. The observations made by Yanishevskiy soon made it clear that this thick tissue attracts the attention of a red bug, *Pyrrhocoris apterus*, to the seeds shed by the weedy hemp, particularly when the bug is at the stage of young individuals. The bug carries off the seeds, piercing its proboscis into the appendix at the base of the hemp seed, where the thick tissue is opened. *Pyrrhocoris* is able to carry the seeds of the weedy hemp over long distances and to bury them. Since they live around fences, hedges and barns, these bugs bring the hemp seeds there, due to which, perhaps, the frequent occurrence of hemp around dwellings can be explained. It was also revealed that other insects are attracted to this thick tissue at the base of the seeds of the weedy hemp. The basal part of the seeds of the wild hemp, thus, has much in common with the so-called elaiosomes, studied by Sernander in the case of various other plants, the dispersal of which is due to their seeds or fruits being carried away by ants (myrmecochory).

The marbled or patchy dark color of the seeds is advantageous for wild hemp and makes them, according to the observations by Yanishevskiy, barely visible on the ground. Indeed, it plays a role of a 'homochromatic' color.

D.E. Yanishevskiy was also able to establish the length of the rest period necessary for weedy hemp seeds in order to favor germination only during the spring; with such a type of germination, weedy hemp does not risk being subjected to winter frosts.

Thus, according to the old botanical scheme for understanding the genesis of cultivated plants alongside the typical cultivated forms, which are deprived of the characteristics of self-fertilization and shedding of seeds, such genuine forms of what is indisputably wild hemp can be acknowledged, in which we can also of course see the ancestors of cultivated hemp.

## FORMS OF WILD AND CULTIVATED HEMP

Investigations made in our laboratory by V.F. Antropopov and T.Ya. Tsingerling-Serebryakova and also field tests of a large number of samples of cultivated, weedy and wild hemp have revealed a great diversity of various forms.

Cultivated hemp is represented by a complicated mixture of strains with a wide range of variation and is regularly distributed in the Old World from the Equator to the Polar Circle. The length of the vegetative period in relation to branching increases toward the south. The northern forms in the Archangelsk and similar districts differ considerably by their short (ca. 35–50 cm tall), non-branching stalks, small fruits, small flowers and anthers half the size of those of hemp from the Orlov and Kursk districts, as well as a short vegetative period (Serebryakova, 1927–28). They ripen a month earlier than hemp in Central Russia. The late-maturing Chinese and Far Eastern races do not ripen even in the black soil belt of the European U.S.S.R. but reach enormous proportions (3 m and more tall), are strongly branched and differ by big leaves with broad leaflets, large flowers and seeds three times heavier than those of the small-seeded northern races.

The Central Russian hemp (from Orlov or Kursk) occupies an intermediate position with respect to their characteristics and differs from the northern ones by taller growth, more branches, a medium-long vegetative period and medium-sized seeds. Toward the south and southeast of Asia, the large-seeded and much-branched forms increase, while in the Khibinskiy Oasis, Turkestan and Afghanistan hemp, growing lower than in eastern Asia also occurs, although branching types are found as well.

Under uniform conditions at the Steppe Station (in the Voronezh district) the north Yakutian and Archangelsk forms ripen in 80 days, those from Tambov and Tul' require 105 and those from Ukraine 111 days, while the races from Persia and Bokhara never ripen under the conditions there. The northern races have narrow and ordinary leaves, the southern ones larger leaves with many more leaflets when grown under the same conditions. The geographical regularities in relation to the distribution of the races of hemp are just as evident as those of flax.

There is a wide variation with respect to seed color in the case of cultivated hemp. Besides the predominant type with light-colored pericarp, we know of races with brown and almost black perianths. As a rule, the cultivated forms so far studied are without a pericarp, although the presence thereof is typical of wild hemp.

As could be expected, cultivated races are on the whole characterized by seeds that are not easily shed but there are striking differences in the case of various strains.

The wild and weedy forms, which in essence cannot be distinguished from each other are, apparently, represented by no less complex races than cultivated hemp, although the former have not yet been adequately studied. The different forms can be distinguished by the speed with which the seeds germinate, by the dimensions and colors of the seeds, and by the length of the vegetative period.

The common European and Asiatic wild and weedy hemp has well developed pericarps, giving the seeds a mosaic of colors.

When, in 1924, we traveled along the Kunar River between Chekhosaray and Djelalabad in Afghanistan, we discovered among the wild hemp a peculiar race with light-colored, small seeds, thin membranes, slightly splitting and transparent pericarps (f. *afghanica* Vav.). The seeds of this race are very small (1000 seeds weigh 2.1–2.7 g), ca. 10 times smaller than those of the Far Eastern large-seeded races (1000 seeds – 26.0 g); 1000 seeds of the ordinary, central Russian races (from Orlov and Kursk) weigh ca. 17–19 g.

All the forms of wild hemp, collected along the Kunar River, approach the cultivated type with respect to seed color and the slightly splitting pericarp but differ by shedding their seeds and in the development of 'horseshoes' [elaiosomes; D.L.]. When sown, the seeds germinate very slowly and unevenly, i.e. these plants display attributes of wild plants as well.

The wild races of hemp in eastern Afghanistan have even more new characteristics. The leaflets, of which the compound leaf is composed, differ from those of the ordinary wild and cultivated hemp by having a narrow, obovate shape such as so far not observed by us among the European, Siberian or Turkestani forms. Just as in Afghanistan itself, these races differ when sown in our experimental fields at the Steppe Station (in the Voronezh district), by medium-tall growth and having many branches, which is typical also of the common Turkestani forms.

The wild Afghani races, with light-colored and easily splitting pericarp, from the areas adjacent to India (they have, indeed spread into northern India as well), thus turned out to constitute a morphological link between the wild and cultivated races of hemp with respect to the most important differentiating characteristics.

#### Characteristics of wild and cultivated hemp

A number of forms of cultivated and wild hemp, including all the diversity of the strains so far studied and listed in Table 9, demonstrate clearly a gradation of characteristics approaching each other. The 'cultivated type' of the wild, Afghani, small-seeded hemp with thin, transparent and slightly splitting pericarp appears to be a clear example of such an intermediate. Some races of wild hemp from Altai and Lower Volga have only slightly developed 'horseshoes' [elaiosomes; D.L.], which in this respect approach those of the cultivated form. As far as the rapid germination of the seeds and their dimensions is concerned, there is also a gradation of types. With respect to the dimensions, the small-seeded Yakutian cultivated form yields to the wild Altaian and Saratovan hemp. As far as the quantitative and qualitative characteristics are concerned, whole series of intermediate forms can be described that link the cultivated types to the wild ones. Only the extreme variants differ sharply from each other, e.g. as the Far Eastern cultivated hemp does from the small-seeded Afghani race with slightly splitting pericarps.

#### Hybridization between cultivated and wild forms

Although typical wild and cultivated forms of hemp show a gradation of characteristics, by their series of races, this phenomenon becomes so much more evident when studying the commonly occurring hybridization that takes place in areas where cultivated and wild forms occur together. It is possible to observe a mixture of typically intermediate forms in the vegetable gardens in Altai, in addition to the cultivated forms with light-colored seeds, no 'horseshoes' [elaiosomes; D.L.] and no perianth, as well as comparatively few branches. According to the observations made by E.N. Sinskaya (1925) in Altai, all the stages of transition from wild to cultivated hemp can be seen there. In comparison with typical hemp, the intermediate forms in the vegetable gardens of Altai have mostly dark-colored seeds; when compared with genuinely weedy forms, the seeds are larger and the 'horseshoes' less well developed. Among the weedy hemp in Altai, plants are occasionally seen with weakly developed 'horseshoes' but such forms with light-colored seeds have not been found. Some Caucasian forms of cultivated hemp remind one of the intermediate Altaian forms. A hybrid origin of these strains is highly likely since the main types occur together in the Caucasus. The occurrence of male and female flowers on different hemp plants makes it very easy to hybridize the races. The morphological borders between the hemp appearing as a field weed and completely wild plants are hard to draw; the forms can hardly be distinguished from each other as far as the characteristics of the seeds are concerned.

#### The ecology of wild, weedy and cultivated hemp

As far as cultivated hemp is concerned, it displays an exceptional requirement for well-manured soil. No other plants exhaust the soil as hemp does. It is only necessary to look at crops of hemp in order to see how well they react to changes in the fertility of the soil. A shortage of manure reduces the growth sharply and makes the green color of the plants paler; on the other hand, when increasing the amount of manure, stalks and leaves develop vigorously.

In practice, hemp is sown on special plots, 'hempfields', provided with large amounts of manure. Hemp prefers in particular manure rich in potassium. Because of this biological peculiarity, cultivated hemp is a plant of well-fertilized soils.

Genuinely wild and weedy hemp has the same preference for well-fertilized soils. According to our observations, wild and weedy hemp in Asia and in the European parts of the U.S.S.R. grows mainly along hedges and in ravines and hollows as well as, between harvests, on rich fallow soils. When looking at several examples of habitats of wild and weedy hemp, it can be seen that hemp has a tendency toward selecting fertilized soils and colonizing only sites where there is an accumulation of humus and manure.

The nomadic camps around the lower Volga and in Altai appear to be typical sites for an abundant and splendid growth of hemp. The cattle manure the soil



Table 9. Series of forms of cultivated hemp, Cannabis sativa, and wild hemp, C. sativa var. spontanea (C. ruderalis)

Characteristics	Cultivated hemp <i>C. sativa</i>				Wild hemp <i>C. sativa</i> var. <i>spontanea</i>	
	RSFSR	Yakutia	Far East Primor'e	Altai	Lower Volga (Saratov, Samara, Astrakhan)	Afghanistan
<i>Vegetative</i>						
<i>Stalks</i>						
Height						
Tall (> 150 cm)	-	-	+	-	-	-
Medium (60-150 cm)	+	-	-	+	+	+
Short (35-50 cm)	+	+	-	-	-	-
Diameter						
Thick	-	-	+	-	-	-
Medium	+	-	-	+	+	+
Thin	+	+	-	-	-	-
Branches						
Many	+	-	+	+	+	+
Few or none	+	+	-	-	-	-
<i>Leaves</i>						
Dimensions						
Large	-	-	+	-	-	-
Medium	+	-	-	+	+	+
Small	-	+	-	-	-	-
Leaflets						
3-5	-	+	-	-	-	-
5-7-9	+	-	-	+	+	+
9-11-13	-	-	+	-	-	-
Shape of leaflets						
Ordinary European, spool-shaped	+	+	-	-	-	-
Broad, spool-shaped	-	-	+	-	-	-
Narrow, spool-shaped	-	-	-	+	+	+
Narrow, obovate	-	-	-	-	-	+
<i>Generative</i>						
<i>Seeds</i>						
Dimensions						
Large (4-5.5 mm)	-	-	+	-	-	-
Medium (3-4 mm)	+	+	-	+	+	+
Small (2.7-3 mm)	-	+	-	+	+	+
Color						
Light	+	+	+	-	-	+
Dark	+	-	-	+	+	+
Shape						
Roundish	+	+	-	-	-	+
Spherical	-	-	+	-	-	-
Round-ovate	-	-	-	+	+	+
Elaiosomes						
Present	-	-	-	+	+	+
Absent	+	+	+	+	+	+
Mosaic (presence or absence of perianth)						
Present	-	-	-	+	+	+
Absent or slightly cracked	+	+	+	-	-	+
<i>Flowers</i>						
Dimensions						
Large	-	-	+	-	-	-
Medium	+	-	-	+	+	+
Small	-	+	-	-	-	-
<i>Biological</i>						
<i>Vegetative period</i>						
Short	-	+	-	-	-	-
Intermediate	+	-	-	+	+	+
Long	-	-	+	-	-	-
<i>Germination of seeds</i>						
Rapid, even	+	+	+	-	+	+
Fairly slow, uneven	-	-	-	+	+	+

around the camps during the winter. Weedy hemp thrives especially well in vegetable gardens. When driving around the villages in the Astrakhan district, one can see from afar the thickets of weedy hemp around dump sites, in backyards and around small patches of trees. In Altai and northern Caucasus hemp frequently grows also in gorges, which are hard to penetrate and far from any dwellings; there it mainly occupies depressions and ravines where there is an accumulation of dung and excrement of wild animals, or habitats receiving something like natural manure (Sinskaya, 1925).

The ecological aspect of wild and weedy hemp is determined mainly by its infestation of rich, manured soils, which are not compacted and lying fallow. This is typical of ruderal plants.

### Genesis of cultivated hemp

Common wild and weedy hemp appears to be a 'camp-follower' of nomads. Because of its biological peculiarities, wild hemp has, thus followed Man and with his knowledge accompanied the camps, seeding itself on dumps and manured sites.

When considering all the facts mentioned above, the multitude of forms of wild and weedy hemp and the very process by which it became cultivated becomes eminently clear.

A mixture of strains of wild hemp, represented by a multitude of morphological and physiological types ranging from genuinely wild ones with elaiosomes around the small seeds, which germinate slowly and carry pericarps, to the typically cultivated, large-seeded ones with thin seed-membranes, rapid germination and non-shedding seeds, accompanied Man during his wanderings and migrations throughout the Old World. Hemp must have caught the eye of the primitive inhabitants of the Old World, when it followed in their heels and amassed around their dwellings at the same time as it was useful.

During times of hunger, when turning to collection of seeds and fruits, Man naturally selected the races of hemp with large seeds that were not easily shed. Unconsciously, just the 'cultivated type' with less easily shed seeds and rich in fats was selected from the mixture of races of wild hemp; thus, the cultivation of hemp developed, in essence, by the will of Man.

Such a picture of a gradually developing cultivation of hemp can still be observed in Altai. According to reports by E.N. Sinskaya from Altai in 1925, it was at that time still possible to observe the following stages: 1. plants in an entirely wild state; 2. an initial colonization by these wild plants of habitats on dump sites and around dwellings; 3. the utilization of the weedy hemp by the inhabitants; and 4. intentional cultivation of hemp.

The inhabitants of Altai usually collect seeds for their crops from hemp in their vegetable gardens but, frequently, when there is a shortage of seeds, they take them also from wild plants; consequently, one can occasionally even now witness the initial stages of an introduction of hemp into cultivation.

It seems that the cultivation of hemp arose for the sake of the seeds; the process of introduction into cultivation was a natural and unconscious development.

The transition toward cultivation of hemp for the sake of its fibers was more complicated. However, it did not demand special inventiveness: in Turkestan, in the Khibinskiy Oasis, we were able to observe a direct separation of bundles of bast from hemp stalks by grinding the dried plants without first retting them.

The utilization of hemp for hashish did not even require special creative efforts on behalf of Man. When burning stalks and leaves over a wood fire, the humans could certainly not avoid noticing the stupefying effect of the hemp. The quantity of the narcotic substance increases toward the south, where the utilization of hemp for hashish is concentrated.

While not representing a major discovery, the utilization of hemp seeds for their fat content apparently took place during a comparatively late historical epoch. With respect to the wild plants, i.e. a mixture of hereditary strains, there are indications of a widespread colonization associated with humans, who brought the hemp along with them from the Equator to the Polar Circle. As demonstrated by observations concerning the segregation of hybrid forms, many characteristics of 'cultivated' hemp, such as the lack of a perianth and the thin seed-covering, associated with it, as well as the lack of elaiosomes, are apparently recessive characteristics, the selection of which was intentionally correlated with the cultivation of hemp.

It is extremely hard to tell when the cultivation of hemp was initiated and what people were instrumental in this. There is no objective information concerning its cultivation in the Nile Valley (Buschan, 1895). During the investigation of the tombs in ancient Egypt, no traces have been found of hemp fibers. Hemp is not mentioned in the Bible. All the information available, both historical and botanical, indicates that hemp is a plant of Asia. Its maximum variation is concentrated there, including the above-mentioned peculiar form which is endemic in Afghanistan. Large-seeded, late maturing races are typical of Manchuria, the Far East and China. Hemp is known as cultivated from time immemorial in China and India. Epithets for hemp exist in Sanskrit. De Candolle's suggestion that hemp was brought to Europe by Scythian nomads and their camps is not at all unlikely. Herodotus (from the 5th Century B.C.) mentioned that hemp was not known in the ancient Greco-Roman world before 484 B.C. Varro, Columella, Plinius and Dioscorides furnish information about the cultivation of hemp for its fibers. [Herodotus was a Greek historian; Marchus Terentius Varro (127-116 B.C.) was a Roman author, among others of books about agriculture; Columella published books about agriculture, *Rei rustics libri XII*, in 65 A.D.; Plinius (23-79 A.D.) was a Roman scholar making lots of observations concerning daily life; and Dioscorides (the 1st century, A.D.) was a physician and herbalist, whose methods were used well into the Middle Ages: D.L.]

It is more likely that the cultivation of hemp arose simultaneously and independently at several sites. The diversity of the geographical races of cultivated hemp indicates this as does the introduction of wild hemp at present taking place under our own eyes in Altai and northern Caucasus and, most of all, the ecological peculiarity of hemp making it a 'camp-follower' of nomads and leading to its cultivation.

## CHAPTER 6 ECOLOGICAL PRINCIPLES FOR THE ORIGIN OF CULTIVATED PLANTS

Using hemp as an example, it was possible to see with one's own eyes that ecological peculiarities could determine the introduction of plants into cultivation. Engelbrecht (1916) justly pointed out the intensified requirement of many kinds of cultivated plants for increased fertilization and, consequently, the link associating these with human inhabitation. When studying cultivated plants and the wild species closely related to them and the varieties thereof in Turkestan, Persia and Afghanistan, we were able to point out a number of facts that, in our own opinion, to some extent clear up the very process toward the introduction of primary plants into cultivation.

When considering a number of primary plants and the wild species known to be close to them and when comparing their ecological peculiarities with each other, some very important facts can be noticed, i.e. that in general the closer the wild species or varieties are related to cultivated plants, the more often they belong to similar ecological groups.

We shall consider some of the examples we studied. Let us start with barley.

### Species of *Hordeum*

Enormous stands of wild barley (*H. spontaneum*) can be found in northern Afghanistan, in the Transcaspian district (Turkmenistan) and in the Syr-Daryan district (Uzbekistan) as well as in Bokhara. Already, a quick glance shows that this group of wild types, which are close to cultivated barley, thrives on cultivated soils, along borders between fields, around water and on loose, uncompacted soils. For instance, in the Syr-Daryan district, wild barley (*H. spontaneum*) very often invades fallow fields. Such fallow land occasionally looks as if it had been purposefully sown with wild barley. According to the ecological nature of *H. spontaneum*, it is in all its forms a plant that has been essentially pre-adapted to cultivated conditions and to cultivated soils.

In Turkestan and Afghanistan, large quantities of the genetically somewhat more distant species of the genus *Hordeum* can also be encountered: *H. crinitum*, *H. maritimum*, *H. murinum*, *H. bulbosum* and *H. brevisubulatum*. The first of these grows on dry slopes and the last one, *H. brevisubulatum*, on wet soils; *H. maritimum* grows in saline habitats. This means that these three species are characterized by specialized ecological requirements, sharply different from those of *H. spontaneum* and *H. sativum*.

*H. bulbosum* and *H. murinum* grow along the banks of irrigation ditches in foothills, thus, ecologically approaching *H. spontaneum*. They all belong to a special ecological group.

In other words, the closer a group is to wild barley (*H. spontaneum*) the closer it correspondingly approaches to cultivated conditions and to conditions found on cultivated fields, and the easier is the introduction into cultivation by Man of the non-brittle forms associated with him.

### Species of *Aegilops*

A still more obvious picture of the differentiation into ecological types, paralleling the differentiation into genetical types, is revealed by a number of wild species of *Triticum*, referred by some authors to the genus *Aegilops*, a group very close to wheat. The following species are known from Turkestan and Afghanistan: *T. triunciale* (L.) Gren. & Godr., *T. crassum* (boiss.) Hackel., *T. aegilops* P.B. and *T. cylindricum* Cesat.

*Triticum triunciale* constitutes a special group genetically, as demonstrated by our investigations concerning its resistance to parasitic fungi (Vavilov, 1918). The other three species, *T. crassum*, *T. cylindricum* and *T. aegilops*, are, on the other hand, close to soft wheat, hybridize comparatively easily with it and are characterized by similar reactions with relation to specialized parasites. In conformity with this, the four species are ecologically differentiated in such a manner that *T. triunciale* grows mainly on more compact soils and on dry slopes, while, on the other hand, the other three species, infesting wheat and barley crops, thrive along boundaries between fields, and remind one of the ecological aspects of the common wheat.

### Other species

Wild oats, *Avena fatua* and *A. ludoviciana*, hybridize easily with ordinary oats, *A. sativa*, and thrive under conditions close to cultivated ones, around water, and on uncompacted soils. As weeds, they invade fields of wheat, barley and oats, and show a tendency for being associated with cultivated oats.

Wild lentils, *Ervum orientale*, bitter vetch, and *E. ervilia*, which is close to the cultivated forms of *Ervum*, grow in Uzbekistan on loose, uncompacted soils, around fields and not far from water.

Ecologically, wild melons (*Cucumis trigonus*), which hybridize with ordinary melons, are weeds of rotating crops such as corn, melons and cotton. In the ecology of these plants, which are genetically close to cultivated melons, there are characteristics associating them with loose soils, closeness to water and rotating crops.

The wild carrot (*Daucus carota*) usually invades gardens, vineyards and vegetable plots, as well as borders between fields, just as if inviting itself to be cultivated.

With respect to the ecological aspect of wild forms close to cultivated species, characteristics can, in general, be perceived, that pre-adapt a given plant to cultivation and to tilled soils. Consequently, the introduction into cultivation of various primary plants can be understood. Elements already existed in the wild flora that were attractive to the farmer and that, to a great extent because of the farmer's wishes, became introduced into cultivation.

Hypotheses (cf. Aaronsohn, 1910; Cook, 1913) suggesting that mountain forms of *T. dicoccoides*, growing on slopes in Syria and Palestine, should be the ancestors of cultivated wheat, correspond little to the truth just like that

hypothesis, which is far from the truth, that the ancestor of cultivated rye should be the perennial mountain rye (*Secale montanum*). Although some stands of *T. diccooides* are found in Syria and Palestine in mountain ravines and in fissures in the rocks on soils rich in lime, humus and adequate amounts of manure are at the same time available there. Statements by Aaronsohn concerning the companions of wild emmer (e.g. *Hordeum spontaneum*) and the description by Cook of local observations already indicate the character of the habitats of the distichous wheat. Just like its companion, *H. spontaneum*, *T. diccooides* is, in essence, a plant pre-adapted to cultivated conditions.

The closest wild and ancestral forms of plants are necessarily found in conditions with habitats similar to those of the cultivated ones, as our direct observations of the wild ancestral types of many cultivated plants have demonstrated. This fact explains to a great extent how primary plants became cultivated. We do not doubt that in the case of the original species of wild plants and in mixtures of races which represent ancestral groups, an ecological tendency is already found in Nature that compelled Man to utilize a given plant species. It is quite obvious that Man took what came easily to him. In the case of many plants, both secondary and primary ones, the process of introduction into cultivation occurred to a great extent thanks to the will of Man.

## CHAPTER 7 GEOGRAPHICAL REGULARITIES IN THE TYPE-FORMATION OF CULTIVATED PLANTS

During the geographical analysis of hereditary forms of flax, hemp and millet, we discussed above a number of regularities concerning the dispersal of the races from the south toward the north.

The data concerning the general direction of the type-forming processes, typical of different groups of plants in different regions, are even more interesting.

### Non-ligulate rye and non-ligulate wheat

Above, we could see that non-ligulate rye was found just where the non-ligulate varieties of soft wheats are established, i.e. in Badakhshan and the mountains of Bokhara. The relationship between the geographical centers of origin of both these groups through some stages explains, in the given case, the coincidence between the habitats of these similar types.

### Naked-seeded races

The differential-geographical method makes it possible to establish that the center of type-formation of naked-grained barley appears to be eastern and southeastern Asia, i.e. China and the areas adjacent to it. However, what is especially significant is that at the same time southeastern Asia seems to be the center of type-formation also of the large- and naked-grained oat, *Avena nuda*.

What is even more remarkable is that races of paniced millet, *Panicum miliaceum*, with narrow, easily disarticulating glumes corresponding to those of naked-grained oats and barley, are also concentrated in southeastern Asia as far as type-formation is concerned.

We do not know what causes such coincidences in the provenance of naked grained oats, barley and millet from eastern Asia; in any case, the similarity of the landscapes alone cannot explain the existence of similarities as far as type-formation of these very different genera of grasses is concerned.

### Regularities of type-forming processes in southwestern and southeastern Asia and in the Mediterranean Region

As regards the centers of type-formation, we drew the conclusion that the cultivation of many plants originated initially within two centers: Asia and the Mediterranean region.

Wheat, barley, flax, peas, lentils, horse beans and castor beans have such origins. A detailed investigation of numerous samples from the Mediterranean region and from Asia unexpectedly revealed a regularity in the type-forming process, which, after a detailed scrutiny, turned out to be a general phenomenon. It demonstrated that while there is a tendency toward formation mainly of large-fruited, large-seeded and large-flowered types within the Mediterranean regions, the areas of southwestern Asia – Afghanistan, Turkestan, Bokhara and India – are characterized by a corresponding formation of mainly small-seeded, small-fruited and small-flowered forms.

Let us consider a number of concrete examples:

As we could see above, southwestern Asia seems to be where flax is concentrated, both in the form of linseed and fiber flax, but mainly the small-flowered, small-fruited and small-seeded types. On the other hand, Spain, Algeria, Tunisia, Egypt and Palestine produce flax with seeds 2–3 times heavier than those of the other European and Asiatic kinds and, similarly, with very large flowers and capsules.

The tendency to small-seeded leguminous plants in the Indian area is particularly strong. On the other hand, within the Mediterranean area, the corresponding kinds of legumes appear gigantic with respect to their flowers, pods and seeds. The horse beans of coastal Asia Minor, Smyrna, Sicily, Tunisia and Egypt have beans up to 3 cm long while the horse beans collected by us in Afghanistan (in the vicinity of Djelalabad) remind us of small peas. Large, disk-shaped lentils are typical of the Mediterranean coasts, while on the other hand, we found very small-seeded races with small leaves, low growth and black seeds, similar to those of peas, with respect to their dimensions, in India and southeastern Afghanistan.

The same can be no less clearly outlined as far as green peas (*Pisum*), sweet peas (*Lathyrus sativus*) and chickpeas (*Cicer arietinum*) are concerned.

We have compiled some tables illustrating the striking differences with respect to type-formation within the two different areas (Tables 10–14).

Table 10. *Lentils* (*Ervum lens*)

Provenance	Length of pod (cm)	Diameter of seed (mm)	1000-seed weight (g)
<i>The Mediterranean coastal area</i>			
Algeria	1.7	8.0	88.0
Italy	1.8	8.0	82.5
Spain	1.7	7.8	90.0
Tunisia	2.0	7.8	64.0
<i>Southwestern Asia</i>			
Mountains of Bokhara	1.2	4.5	26.0
Persia	1.1	4.7	37.0
India	1.1	3.6	20.0
Afghanistan (Mazar-i-Sharif)	1.2	4.0	26.0
Afghanistan (Djelalabad) <sup>1</sup>	0.7	3.0	7.5

Notes:

<sup>1</sup> Black-seeded.

Remark: Statistics by E.N. Barylina

Table 11. *Horse beans* (*Vicia faba*)

Provenance	Length of pod (cm)		Diameter of bean (mm)	1000-bean weight (g)
	Min.	Max.		
<i>The Mediterranean coastal area</i>				
Tunisia	9.4	2.4		171
Spain	9.9	2.3		150
	9.3	2.4		200
Italy	15.2	2.1		130
<i>Southwestern Asia</i>				
Persia	5.8	0.8		30
Bokhara	5.5	0.9		38
Pamir	5.7	0.9		32
Afghanistan (Herat)	5.6	1.1		40
Afghanistan (Kabul)	4.6	0.7		20
India	4.9	0.7		20

Note:

Remark: Statistics by V.S. Muratova

Table 12. *Chick peas* (*Cicer arietinum*)

Provenance	Length of pod (cm)	Diameter of pea (mm)	1000-pea weight (g)
<i>The Mediterranean coastal area</i>			
Spain	2.7	12.0	470
Italy	3.0	9.5	369
	2.3	8.4	280
France	2.2	8.5	331
<i>Southwestern Asia</i>			
Persia	1.7	7.7	110.0
Afghanistan	1.7	7.5	113.5
Turkestan	1.8	7.6	127.0
Bokhara	1.8	7.8	114.0
Pamir	1.8	7.8	128.2
India	1.7	6.4	94.3

Note:

Remark: Statistics by K.G. Prozorova

Table 13. *Peas* (*Pisum*)

Provenance	Length of pod (cm)		Diameter of pea (mm)		1000-pea weight (g)	
	Min.	Max.	Min.	Max.	Min.	Max.
<i>The Mediterranean coastal area</i>						
Italy	4.5	6.5	0.65	0.95	18.0	40.0
Spain	5.5	6.0	0.75	0.83	21.7	—
Africa	5.9	7.3	0.7	0.89	24.0	38.0
Mean	5.3	6.6	0.7	0.89	21.2	39.0
<i>Southwestern Asia</i>						
India	3.0	5.2	0.65	0.65	5.2	23.0
Afghanistan	2.9	4.5	0.4	0.6	5.0	26.5
Khiva	4.9	—	0.5	0.5	6.5	8.5
Pamir	3.2	5.6	0.5	0.7	8.5	22.0
Mean	3.5	5.1	0.47	0.65	6.3	20.0

Note:

Remark: Statistics by V.S. Fedotov

Table 14. *Vetchling* (*Lathyrus sativus*)

Provenance	Length of pod (cm)	Diameter of pea (mm)	1000-pea weight (g)
<i>The Mediterranean coastal area</i>			
Africa	4.3	1.0	24
France	3.9	1.4	60
<i>Southwestern Asia</i>			
India	2.9	0.4	6
Pamir	4.0	0.6	12
Afghanistan	3.8	0.5	15
Mountains of Bokhara	2.9	0.7	18

Note:

Remark: Statistics by K.G. Prozorova

The differences in type-formation of leguminous plants within the two areas affect both the vegetative characteristics (dimensions of stems and leaves) and the generative ones. In Asia, small dimensions are typical, in Africa large ones.

The castor beans (*Ricinus persicus*) of Persia and Afghanistan are distinguished from the African varieties by small beans, low growth, small leaves and small inflorescences (Popova, 1926).

The same is the case also with respect to major field crops: wheat, barley and oats. Both oats and wild oats in the Mediterranean coastal regions are characterized by a tendency toward the formation of large grains and long paleas and glumes. Some African races of *Avena sterilis* are astonishing with respect to the size of their spikelets, which exceed by two and a half times those of ordinary wild oats.

*Avena byzantina*, a species cultivated in some Mediterranean countries, is distinguished from *A. sativa* by the large dimensions of its spikelets and the lengths of its paleas and glumes in all its races. Small-grained oats, *A. sativa*, and wild oats, *A. fatua* and *A. ludoviciana*, are typical of Transcaucasia, Afghanistan and northeastern Persia.

Similar low-growing, small-grained and small-spiked forms of wheat are typical of India and Afghanistan. The centers of type-formation of *Triticum sphaerococcum* and *T. compactum* are located there. On the other hand, gigantic dimensions, long awns and large grains become increasingly more common toward the Mediterranean coastal areas. In Spain, Morocco, Tunisia, Algeria, Sicily, Egypt and Palestine *T. turgidum*, *T. polonicum* and *T. durum* are grown, the many strains of which can without exaggeration be called gigantic in comparison with the typical compact forms found in southwestern Asia.

In China and Japan, low-growing races of naked-grained barley are typical; even under the best of conditions they do not exceed 40–50 cm in height (e.g.

var. *japonicum* and some forms of var. *coeleste*). All the naked-grained Asiatic races of barley differ in general by their low stature when compared with the African races of hulled barley.

A comparison between the type-formation of Asiatic millet, *Panicum miliaceum*, and its gigantic analog in Africa, the sorghum, *Andropogon sorghum*, practically suggests itself.

It is quite possible to suggest similar differences with respect to type-formation within other genera as well. However, the facts presented are adequate for describing the general character of the regularity that clearly demonstrates that it can be utilized for practical purposes.

In southwestern Asia, the center of type-formation of soft wheat and many leguminous plants, such characteristics that approach those of the small-seeded wild forms are in general typical. On the other hand, the Mediterranean areas are characterized predominantly by crops of large-fruited species and races that undoubtedly are of great interest for practical utilization as far as the European crops are concerned.

### Species of *Phaseolus* in the Old and the New Worlds

A similar kind of regularity can be found when comparing the species of *Phaseolus* in the Old and New Worlds. The Asiatic species, *Ph. aureus*, *Ph. radiatus* (*Ph. mungo*), *Ph. calcaratus*, *Ph. acutifolius* and *Ph. angularis*, are, as far as type-forming processes are concerned, characterized by small seeds, small flowers and small, cylindrical pods, a strongly developed pubescence, broad stipules and long, linear bractlets. The American species, *Ph. lunatus* and *Ph. acutifolius* var. *latifolius*, differ by their extreme diversity of large seeds, large flowers and short bractlets. (This problem was worked out in detail at the Institute of Applied Botany by N. R. Ivanova, who prepared it for publication under the title *The Peculiarities of the Type Formation Among the Species of Phaseolus in the Old and the New Worlds*; it will appear in 1928.) As demonstrated also by other studies by G.M. Popova and N.R. Ivanova at the Institute of Applied Botany, the variability of the American and the Asiatic species of *Phaseolus* is at the same time definitely subject to the law of homological series.

It was especially interesting to compare the process of type-formation of some plants cultivated in the Old World with species of the same genus grown in the New World. There are rather many such genera. It is enough to mention the cottons of the Old and the New Worlds, *Gossypium herbaceum*, *G. hirsutum* and *G. barbardense*, or the many species of cultivated fruits and berries belonging to such genera as *Vitis*, *Ribes*, *Rubus*, *Malus*, *Prunus* or *Fragaria*, typical of both the Old and the New Worlds.

Just as in the case of *Phaseolus*, studies of the genus *Gossypium* made by G.S. Zaytsev revealed a striking parallelism of type-formation concerning the Asiatic and the American cotton species.

The reason for the different tendencies with respect to type-formation is still not completely understood. A correlation with the landscape hardly constitutes a condition since, when grown under similar conditions, the Mediterranean

racess remain sharply different from the races from southwestern Asia. To relate them to the great antiquity of agriculture in the Mediterranean area and the more primitive agriculture of southwestern Asia did not appear correct either. We have no definite or uncontestable data indicating that the crops of the Mediterranean coastal areas should be older than those of Mesopotamia. Corresponding differences affect not only the cultivated races but also the wild species close to them just as could be seen, e.g. in the cases of wild peas, oats and wheats (e.g. the dimensions of the grains of *Triticum dicoccoides*).

### GENERAL CONCLUSIONS - BASIC GLOBAL CENTERS OF ORIGIN OF CULTIVATED PLANTS

During the evolution of the variety of cultivated plants, general characteristics, i.e. parallelism, definitely occurred. A number of forms of wild and cultivated races can be united into Linnaean species - i.e. whole series of hereditary forms, ranging from typically wild ones with brittle inflorescences and seeds with elaiosomes to such with dehiscent capsules, repeat themselves within different genera and even families. We can find similar formations in the cases of wheat, oats, millet, barley, rye, buckwheat and hemp. Analogous cycles are displayed within the type-formation of many specialized weeds (Thellung, 1925).

The general regularity allows us, in essence, to construct a system of type-formation and to predict the whereabouts of some particular form, whether cultivated or not, and, at the same time, to simplify the problem of its origin.

#### General centers of type-formation of cultivated plants

There can be no doubt that a detailed study of the centers of type-formation of a large number of cultivated plants will very likely also establish centers common for whole groups of cultivated plants, and help us succeed in approaching in earnest the recognition of universal centers of origin.

Considerable efforts will be needed in order to bring such a work to completion. However, as a result of preliminary investigations of some dozens of plants, it is already now possible to outline five basic centers with respect to the most important field crops, vegetables and garden plants (Fig. 13):

1 *Southwestern Asia*, comprising India, southern Afghanistan and the adjacent mountain areas of Bokhara and Kashmir, Persia, Asia Minor and Transcaucasia; this center initially gave rise to soft and club wheat, rye, small-seeded flax, small-seeded vetches, lentils, horsebeans and other beans, vetchlings and chickpeas as well as a number of vegetables and, in addition, to Asiatic cotton (*Gossypium herbaceum*, *G. arboreum*), etc.

2 *Southeastern Asia*, comprising the mountain areas of China, Japan, Nepal and adjacent areas; this is the center of type-formation of naked-grained oats, naked-grained barley, millet, soybeans, many cultivated cruciferous plants and a number of endemic species of fruit trees.

3 *The Mediterranean focus*, comprising all the coastal areas of the Mediterranean including northern Africa (Egypt, Algeria, Tunisia), Palestine and Syria,

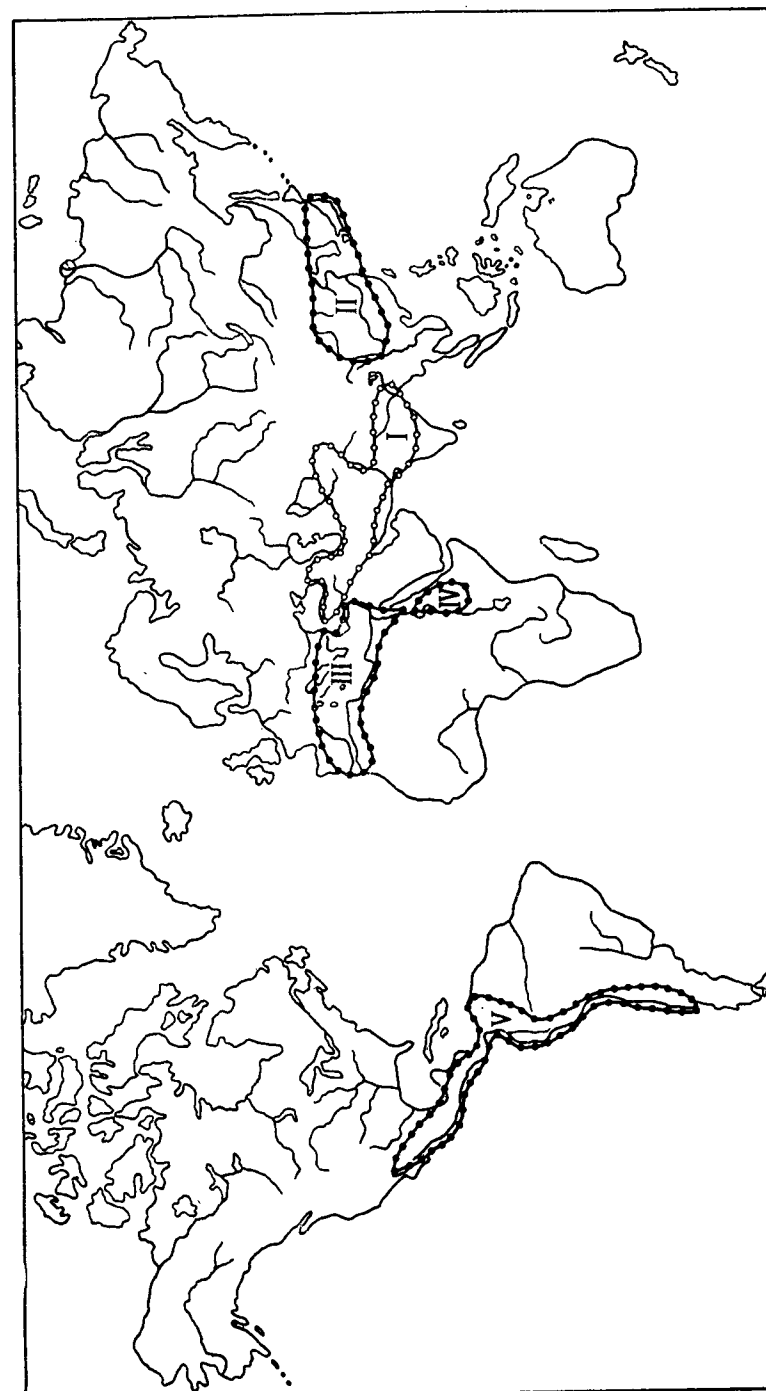


Fig. 13. Basic centers of origin of the most important cultivated plants in the Old and the New Worlds. 1. Southwestern Asia; 2. southeastern Asia; 3. the Mediterranean area; 4. Abyssinia and Egypt; 5. mountain areas of South America and Mexico.

Greece and its archipelago, Spain and Italy and a portion of Asia Minor; the centers of origin of a large number of cultivated plants are concentrated there, such as hard wheats (*sensu lato*) including all the group with  $2n=28$  chromosomes, a number of cultivated strains of oats belonging to *Avena byzantina*, large-seeded flax, large-seeded vetches, vetchlings, horsebeans and lentils as well as sugar beets and many vegetables in addition to fruit trees.

4 In northern Africa, an independent center can be observed in *Abyssinia* and the areas adjacent to it; in that area unusual formations of the types of many cultivated plants are concentrated. Globally, the Abyssinian focus stands out by the formation of such types as hulled barley, peculiar races of leguminous plants and oats and a number of other cultivated plants.

5 As far as it is possible to judge from the data available, it is possible to distinguish a focus of primary agriculture in the New World and a center of type-formation in *Mexico and Peru* and the mountain areas adjacent to them. The type-formation of potatoes, maize, species of *Phaseolus*, tobacco, sunflowers, American cotton and many other species and even specific genera of cultivated plants and fruit trees is concentrated in those areas.

The first two Asiatic foci are, apparently, adjoined toward the south by an independent island focus, including both the Philippine Islands and the so-called East Indian islands (e.g. the Sunda islands). In order to single out this focus we can refer to a number of endemic groups of cultivated plants found only there: the basic group of Philippino rice, *Coix*, waxy types of maize, etc. The plants cultivated within this focus are still badly studied from a botanical point of view and therefore we have not yet included this area as a basic center of origin of cultivated plants.

In addition to the above centers, we will, in the future, certainly be able to outline a number of secondary centers and to specify more exactly the actual geographic centers; at the same time, it is necessary to keep in mind that a number of plants such as hemp and rye were introduced into cultivation simultaneously in many places.

As can be seen, the areas of origin and type-formation of the most important cultivated plants which, at the same time, are the foci of a wealth of types, belong mainly to the mountain areas of Asia (Himalaya and its system), the mountain systems of northeastern Africa and the mountain areas of southern Europe (the Pyrenées, the Apennines and the Balkans), the Cordilleras and the southern spurs of the Rocky Mountains. In the Old World, the original areas of cultivated plants belong mostly within a belt between  $20^{\circ}$  and  $40^{\circ}$  N. latitude.

These mountain areas are bordered by the deserts of Central Asia and by the Sahara and, with respect to their diversity of climate and soil, they offer optimal conditions for explaining type-forming processes. In those areas there is a gradation with extreme variants in the amounts of precipitation, temperature and soil types.

The diversity of conditions – from those of deserts to those of oases, from soil lacking in humus to those rich in nourishment – promoted a concentration and formation of an exceptional variety of vegetation in the upper and middle belts of the mountains.

The abundance of water for irrigation from melting snow and ice, the ease

with which this water can be utilized for irrigation by means of gravity, the opportunity for cultivation even of imperfect crops in areas with high amounts of precipitation, the isolation of the fields and their defense from attacks, all contributed to the development in those areas of a primary kind of agriculture.

So far, the mountains of Asia and Africa represent globally just the kind of areas where people would settle. This fact has recently become even more evident. More than half of the world's people (ca. 900 million) inhabit such mountain areas, which constitute a very small portion of the total area of the world's surface (less than  $1/20$ th).

To a traveler in southwestern Asia, the unusual utilization of every inch of soil and the crops in remote areas are astonishing. If the infertile deserts and waterless mountain areas, slopes inaccessible for crops, rocky screes and areas with a permanent snow cover in Persia, Afghanistan and Bokhara were disregarded and if the density of the population in relation to the accessibility to crops were taken into consideration, a population density exceeding even that of the cultivated areas of Europe would result.

#### Centers of origin of cultivated plants and foci of human civilizations

The elucidation of the centers of type-formation and the origin of cultivated plants allow us to approach objectively the establishment of basic foci of agricultural civilizations. Arguments about whether the Egyptian civilization is autonomous and has not adopted elements from Mesopotamia and vice versa or the questions about the independence of the autonomy of the Chinese and Indian civilizations can be objectively solved by studying their kinds of crops. Plants and their varieties are not easily dispersed from one area to another; in spite of the many thousands of years of wandering about by peoples and tribes, it was, as we have seen, not difficult to establish the basic foci of type-formation of the majority of cultivated plants. The presence in northern Africa and southwestern Asia of large groups of endemic plants, both species and varieties of cultivated plants, on the basis of which independent agricultural civilizations arose, can solve the problem of autonomy of these civilizations also from an historical point of view.

The history of the origin of human civilizations and agriculture is, of course, much older than the documentation in the form of pyramids, inscriptions and bas-reliefs or tombs can tell us. A close acquaintance with cultivated plants and with the multitude of types and their differentiation into geographical groups as well as their frequently sharp physiological isolation from each other compel us to refer the very origin of cultivated plants to such remote epochs, where periods of 5–10000 years such as concern archeologists represent but a brief moment.

When studying the foci of type-formation in detail with respect to the most important cultivated plants, the botanist is in a condition to introduce essential corrections into the hypotheses launched by historians and archeologists.

On the map surveying the primary civilizations, compiled by Smith and Perry (1925; cf. chapter VIII, 'Anthropology', written by G. Elliot in the book, *Evolution . . .*, 1925) on the basis of all kinds of archeological, anthropological



and historical data, the following areas appear as the basic foci of human civilizations: Egypt, Italy, the Balkan Peninsula, Asia Minor, Mesopotamia, Persia, Afghanistan, a portion of Turkmenistan, Uzbekistan, Transcaucasia and the areas of the ancient Scythians. We do not in the least doubt that, based on the botanical studies of cultivated plants, also India, the mountains of China, Mexico and Peru and the areas adjacent to these should be included among the number of initial areas in addition to those mentioned.

A very large number of endemic, cultivated plant species and varieties in India, China, Mexico and Peru appear to have been the objects of ancient agriculture, as has been demonstrated for these countries. In spite of the lack of corresponding archeological documentation (because of which these areas were not included by Smith among those with primary civilizations), these areas should be included among the ancient centers of agricultural civilizations.

Thus, a phytogeographical analysis of cultivated plants allows us to introduce additional evidence for solving the problems of history concerning human civilizations in general and those of agricultural civilizations in particular. The most recent discoveries in Punjab, the Sunda islands and China of archeological documentation contemporary with the ancient Mesopotamian civilization, support our phytogeographical opinion.

Apart from the spontaneous and utilitarian importance of mastering the sources of a multitude of plant types, the ultimate objective of the investigations discussed is to try to approach, in earnest, the general biological problem of speciation. Evolution occurs both in space and time. It seems to us that only by earnestly approaching the geographical centers of type-formation and by establishing all the links connecting the species will it be possible to find the way to the establishment of a system of Linnaean species and to understand the latter as a system of forms. The geneticist can consciously approach the selection of forms for hybridization and the solution of the problem of experimental phylogenetics only by understanding taxonomy and geography. Hence, the very problem of speciation becomes a problem concerning the evolution not only of the different races, which, according to the Darwin's hypothesis, were isolated into basic species, but also of the origin of the complicated system within which the present Linnaean species developed.

As a result of all that has been said above, the solution of the problem of speciation lies in a synthesis of a far-reaching investigation of various groups of plants, while using the methods of differentiating taxonomical phytogeography for the purpose of establishing centers of type-formation, and the methods of genetics and cytology. The way to grasp the integrity of the species can only be found in a synthesis of taxonomy, differentiating geography, genetics and cytology.

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