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CENTERS OF DIVERSITY AND CENTERS OF ORIGIN

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INTRODUCTION

Nikolai Ivanovich Vavilov is to be credited for first setting the phyto-geographic basis for plant exploration. It is mainly due to him that plant breeders have become aware of the fact that variation in cultivated plants is geographically unevenly spread and that the bulk of genetic diversity in our important agricultural crops is geographically confined to relatively few restricted areas or centers. Since this exposition of centers of diversity by Vavilov in the 1920's, much more information has been gathered, but the general picture remains the same. Centers of diversity are a fact, and intelligent exploration and breeding programs in a given crop should be aimed at collection and full utilization of the genetic variation stored in them.

We frequently confuse the concept of *centers of diversity* with another Vavilovian concept, namely *centers of origin*. When distribution patterns of variation in crop plants became obvious to Vavilov, he also proposed that areas of maximum diversity are places of origin. In fact, in his publications Vavilov uses the term 'centers of origin' instead of 'centers of diversity' and we too frequently follow this tradition. But while centers of diversity are a biological fact, the term 'centers of origin' is only an interpretation. Since its exposition in the 1920's, geneticists and students of cultivated plants have sometimes had heated discussions about the validity of this interpretation. This Chapter aims at a brief survey of the world centers of diversity, and discussion of their origin and nature.

CENTERS OF DIVERSITY

Centers of diversity were recognized and mapped by Vavilov and his group on the basis of the tremendous amount of material which they had collected and brought back to Russia in the 1920's and the early 1930's. Vavilov's collections consisted mainly of cultivated varieties. He had a relatively poor representation of wild species. Historically, perhaps the most significant feature in Vavilov's approach was his ambitious, and successful, effort to 'cover the whole globe'. In crop after crop Vavilov found that over very extensive territories cultivated plants showed relatively few varieties, while in some restricted areas, multitudes of varieties and aggregates of species occurred. Wheat is a classical example to illustrate this pattern.

Over most of Europe, as well as Siberia, wheat cultivation is based on a rather restricted number of varieties, mostly hexaploid bread wheats. But when Vavilov and his colleagues explored the Middle East and particularly Anatolia, Syria, Palestine and Transcaucasia, they were amazed at the multitude of forms and types of wheat grown in these territories. The wide range of variation encountered here is apparent from the taxonomic treatments by Soviet botanists. They recognized here a wealth of 'species', 'subspecies', and 'varieties'—diploid, tetraploid and hexaploid.

In addition to this Near Asiatic center of diversity, Vavilov found that, in wheat, several other variation centers exist as well. In a relatively small and geographically isolated area of the Ethiopian plateau, Vavilov found hundreds of endemic 'varieties' and 'subspecies' of tetraploid wheats. Ethiopia is indeed an excellent illustration of a variation center. The area here is so restricted and the wealth of forms is so conspicuously large!

Other concentrations of wheat variability were found by Vavilov's expeditions in Afghanistan (mainly hexaploid varieties) and in the Mediterranean basin (mainly tetraploid varieties).

Wheat (which was the classical example of Vavilov) serves as an illustration for the patterns of variation and distribution found in scores of cultivated crops. Each agricultural crop shows concentration of genetic variation in one (or relatively few) geographic areas.

Another feature which was immediately apparent to Vavilov is that centers of diversity of different crops often overlap. In other words there is a strong correlation in the distribution patterns of different cultivated plants. Western Asia, for instance, where wheat diversity is so conspicuous is not a wheat center alone! The same area harbours a vast wealth of cultivars of barley, rye, lentil, pea, flax, vines, figs and pistachios. Similar situations are found in other centres. The Andes of South America, for instance, are famous for their richness in potato species and varieties (Dodds, 1956). But this area is also a center of variation in tomato, tobacco, lima bean and several other crops. Based on the really 'colossal' amount of material assembled by numerous collecting expeditions, Vavilov first set up (1926) six main geographic centers for cultivated plants, and later (1935) increased their number to about ten. Since then we have gathered further information which perhaps makes it necessary to somewhat revise boundaries or to lump together some of these centers. Turkey, Syria, Palestine, Transcaucasia, Iran and Afghanistan, for example, should be regarded as a single center of diversity rather than two or three independent ones. But the general notion of centers of diversity remains basically unchanged. The main world centers as proposed by Vavilov (1935, 1951) are enumerated in Table 1 (p. 40) each with a representative list of crops.

CENTERS OF ORIGIN

Vavilov proposed that the centers of diversity are places of origin or *centers of origin* of cultivated plants. In fact, in most of his publications, centers of diversity are referred to as centers of origin. Vavilov's concept in a nutshell is: *The place of origin of a species of a cultivated plant is to be found in the area which contains the largest number of genetic varieties of this plant.* As already pointed out by Stebbins (1950), Vavilov's interpretation of diversity patterns are an elaboration on Willis' age-and-area hypothesis. It is based on the assumption that selective forces of the environment are operating in about the same manner throughout the evolutionary history of a given species or biological group. And thus the longer a given biological entity occupies a given area, the bigger would be the number of variables it would produce.

Since its exposition in the early 1930's, we are more and more aware of the fact that such an explanation is an oversimplification of the case and that the build-up of variation in the majority of biological entities proceeds at different paces in different places. It is now obvious that the Vavilovian concept of centers of origin should be discarded or at least greatly revised. In the following sections, several aspects pertinent to 'place of origin' and to factors involved in the build-up of variation are presented and discussed.

'PRIMARY CENTERS' VS. 'SECONDARY CENTERS'

Schiemann has to be given credit for pointing out a major difficulty in Vavilov's assumption that a variation center is a place of origin (see review in Schiemann, 1943). In many cases Vavilov found centers of diversity for given crops very far away from the areas in which their wild relatives occur. A conspicuous case is the Ethiopian center. Here wheats, barleys, peas, flax and lentils occur in an extraordinarily rich collection of varieties. Tetraploid wheats, for instance, manifested here according to Vavilov their widest variation. But significantly for all of these crops, they have not a single wild relative in Ethiopia. They therefore could not have possibly been domesticated there. Already Schiemann argued that the wild relatives of these crops, and particularly wheat, are found only in the Middle East, many thousands of kilometers away from Ethiopia. Today, we have sound information to conclude that most, if not all, of these cereals have been domesticated in the Middle East during the neolithic agricultural revolution. They were brought to Ethiopia already as agricultural crops long afterwards, most probably by Hamitic agricultural migrators.

In view of this obvious criticism, Vavilov had to reconsider his concept of centers of origin and to distinguish between *primary centers* (i.e., places where domestication originated) and *secondary centers* which are only explicable in terms of what happened after domestication was achieved.

TOPOGRAPHY AND ITS ROLE

Vavilov was aware of the fact that the centers of variation he encountered occurred mainly in mountainous regions or hilly areas. Such reliefs provide us with much more heterogeneous environment than a flat country does. Furthermore, when you have a dissected country, valleys, plateaux and mountainsides are somewhat isolated from one another spatially and contacts between agricultural communities are less frequent as compared with flat country.

Evolutionists have come to appreciate the role of population structure in relation to divergence. There is a considerable difference in what could happen in cases of continuous large populations as compared with a pattern of clusters of small, partially isolated populations. Already in the 1930's Sewall Wright pointed out that an ideal situation for rapid divergence would be given by a collection of small populations partially isolated from one another, and each occupying its specific niche. Mountain areas with their spatially semi-isolated farming communities and 'cultivation in patches' on the one hand, and with their wide amplitude of climates and soils on the other hand, conform very much with the requirements set up by Sewall Wright's model for rapid evolution. Here apparently lies, at least in part, the explanation for Vavilov's secondary centers of origin. But, this is only part of the story, because one usually finds in these areas enormous diversity in a single cultivated field. There is much more to a center of diversity than a variety of ecological situations.

PLACES OF ORIGIN

A logical and most sound approach to the problem of place of origin would be to find out (on the basis of genetic affinities) which are the wild progenitors of cultivated plants and where they are distributed. If one can plot the distribution of a given progenitor (or more specifically the area where this progenitor occupies primary habitats and is genuinely wild!) one can delimit the area in which domestication could have taken place. Vavilov necessarily based his judgement on variation patterns in cultivated plants. Information on wild plants in his day was much more fragmentary than it is today. Even now genetic and ecological information on wild relatives of most of our cultivated plants is indeed incomplete and in such cases assessment of a place of origin is hard to make. But at least in several crops we have today the necessary information on genetic affinities between wild and tame, on distribution areas and on ecological affinities of the wild progenitors. We thus have the necessary elements for determining the initial place of origin. Furthermore, at least in one or two areas of the world, the newly risen archeological interest in the early development of agriculture makes it possible for us to corroborate our biological finds with archeological evidence. Perhaps the best example for such an approach is the place of origin of the cultivated plants associated with the Old World neolithic agricultural revolution. On combined evidence of genetic affinities between wild and tame, accumulated knowledge on the ecology and distribution of the wild forms and recent analysis of plant remains in archeological digs, we can locate the initial place of origin of at least one dozen of the Old World cultivated plants. Harlan and Zohary (1966) attempted such delimitation of places of origin for wheat and barley. Most of the elements for such an assessment are also already available for rye, oats, peas, lentils, chickpeas, broad beans, vines, olives, figs and pistachios.

INTROGRESSION AND THE BUILD UP OF VARIATION

In the last twenty years introgressive hybridization in plants has received more and more attention from evolutionists (see reviews by Anderson, 1953; Anderson and Stebbins, 1954). A considerable amount of information is already available to indicate that introgression operates as a major evolutionary factor in plants, particularly when areas are drastically disturbed by man or when new habitats are being opened up. In fact, some of the best illustrations of introgression and its consequences are provided by cultivated plants and their closely related weeds.

The annual sunflowers of North America can serve as a demonstration for what actually happens when introgression operates in full force. Here, as Hieser so beautifully demonstrated, one species, i.e., *Helianthus annuus*, considerably expanded its geographical distribution and ecological amplitude by 'absorbing' genetic variation (through interspecific hybridization) from at least half a dozen other *Helianthus* species. As a result of this process, *H.annuus* presents us today with a vast polytypic complex and an extraordinarily large gene pool. All indications point out that the build-up of genetic variation by introgression here is recent. It apparently all happened in the last 100–200 years when man drastically churned up the landscape across the North American continent. 'Donations' of genes from *different* species situated in *different* locations and adapted to *different* environments enabled *H.annuus* to rapidly expand over the *entire* area and successfully and *continuously* occupy the vast climatic and edaphic range on which it is now found.

H.annuus thus serves as a model for what apparently happened in many of our crop plants. There is a great deal of accumulated evidence to indicate that introgression is responsible for rapid build-up of variation in many of our crops. A well cited case is introgression from *Tripsacum* to maize. But today we have sufficient information to assume that introgressive hybridization played a major role in the build-up of variation in *Triticum-Aegilops* (Zohary, 1965), rye (Zohary, unpublished), oats (Ladizinsky, unpublished), tomato (Rick, 1958), sorghum (Doggett, 1965), and various other crops.

I am willing to risk my neck and emphasize the role of introgression even more strongly. It seems that introgression in cultivated plants should be regarded as a rule, not as an exception. Everywhere when I have had a chance to examine places of contact between cultivated plants and their wild relatives, I have found indications for hybridization, and introgressive hybridization patterns could be detected. We should strongly suspect a full scale operation of this process in all cases where initial domesticates expanded their distribution with the help of men and came into contact with new wild races or additional wild species of their genera.

Introgression, of course, complicates the whole concept of a definite 'place of origin'. Instead of an exactly delimited area of a single progenitor, we are faced with blurred boundaries. Harlan (1956, 1961) already suggested the term *diffuse origin* for such situations.

POLYPLOIDY AND PLACE OF ORIGIN

A large proportion of our cultivated plants are polyploids, and polyploidy has its own complications for the concept of place of origin. In a few cases polyploidy actually provides us with a real advantage for determining places of origin. When faced with simple allopolyploidy, we can pinpoint the origin of the polyploid entity by finding the area of contact between the two involved diploid donors. Such examples are often cited in literature, but they present us with rather simple and rare text book models. In many plant groups, and in cultivated crops in particular, the nature of polyploidy is much more complex. Instead of simple cases, we are faced with *polyploid complexes*. At the base of such a complex we have ecologically and morphologically easily definable 'diploid pillars'. Superimposed on them is a 'polyploid superstructure' with a wide range of continuous or almost continuous variation which combines and fuses the separate gene pools found in the diploid level. Only a few polyploid complexes have been satisfactorily analyzed. These include, for example, *Dactylis* (Stebbins and Zohary, 1959), *Triticum–Aegilops* (Zohary, 1965), and blue stem grasses (Harlan, 1963). In many other cultivated crops, such as potatoes, alfalfa, oats, sugar cane, rice, apparently similar compound situations exist.

The crux of the matter in polyploid complexes is that the formation of polyploids is not an end by itself. It is an effective means to fuse gene pools of numerous independent sources and to rapidly build up variation. The polyploid level serves as a buffer; it facilitates hybridization and introgression. It makes possible the fusion of gene pools which are fully isolated between diploids. In polyploid complexes, the polyploid superstructure can be compared to a sponge that sucks variation from numerous sources. Thus the problem of place of origin in polyploid complexes is again vastly complicated, even more than in cases of simple introgression in diploid plants. Diffuse (or may we say 'confused') origin is the proper term here.

TABLE 1. *World Centers of Diversity* (Centers of Origin *Sensu* Vavilov) *of Cultivated Plants* (after Vavilov, 1951.)

1. THE CHINESE CENTER

Avena nuda, Naked oat (Secondary center of origin).
Glycine hispida, Soybean.
Phaseolus angularis, Adzuki bean.
Phaseolus vulgaris, Bean (Recessive form; secondary center).
Phyllostachys spp., Small bamboos.
Brassica juncea, Leaf mustard (Secondary center of origin).
Prunus armeniaca, Apricot.
Prunus persica, Peach.
Citrus sinensis, Orange.
Sesamum indicum, Sesame (Endemic group of dwarf varieties. Secondary center).
Camellia (Thea) sinensis, China tea.

2. THE INDIAN CENTER

Oryza sativa, Rice.
Eleusine coracana, African millet.
Cicer arietinum, Chick pea.
Phaseolus aconitifolius, Math Bean.
Phaseolus calcaratus, Rice bean.
Dolichos biflorus, Horse gram.
Vigna sinensis, Asparagus bean.
Solanum melongena, Egg plant.
Raphanus caudatus, Rat's tail radish.
Colocasia antiquorum, Taro yam.
Cucumis sativus, Cucumber.
Gossypium arboreum, Tree cotton, 2x.
Corchorus olitorius, Jute.
Piper nigrum, Pepper.
Indigofera tinctoria, Indigo.

2a. THE INDO-MALAYAN CENTER

Dioscorea spp., Yam.
Citrus maxima, Pomelo.
Musa spp., Banana.
Cocos nucifera, Coconut.

3. THE CENTRAL ASIATIC CENTER

Triticum aestivum, Bread wheat.
Triticum compactum, Club wheat.
Triticum sphaerococcum, Shot wheat.
Secale cereale, Rye (Secondary center).
Pisum sativum, Pea.
Lens esculenta, Lentil.
Cicer arietinum, Chick pea.
Sesamum indicum, Sesame (One of the centers of origin).
Linum usitatissimum, Flax (One of the centers of origin).
Carthamus tinctorius, Safflower (One of the centers of origin).
Daucus carota, Carrot (Basic center of Asiatic varieties).
Raphanus sativus, Radish (One of the centers of origin).
Pyrus communis, Pear.
Pyrus malus, Apple.
Juglans regia, Walnut.

4. THE NEAR EASTERN CENTER

Triticum monococcum, Einkorn wheat.
Triticum durum, Durum wheat.
Triticum turgidum, Poulard wheat.
Triticum aestivum, Bread wheat (Endemic awnless group. One of the centers of origin).
Hordeum vulgare, Endemic group of cultivated two-rowed barleys.
Secale cereale, Rye.
Avena byzantina, Red oat.
Cicer arietinum, Chick pea (Secondary center).
Lens esculenta, Lentil (A large endemic group of varieties).
Pisum sativum, Pea (A large endemic group. Secondary center).
Medicago sativa, Blue alfalfa.
Sesamum indicum, Sesame (A separate geographic group).

Linum usitatissimum, Flax (Many endemic varieties).
Cucumis melo, Melon.
Amygdalus communis, Almond.
Ficus carica, Fig.
Punica granatum, Pomegranate.
Vitis vinifera, Grape.
Prunus armeniaca, Apricot (One of centers of origin).
Pistacia vera, Pistachio (One of the centers).

5. THE MEDITERRANEAN CENTER

Triticum durum, Durum wheat.
Avena strigosa, Hulled oats.
Vicia faba, Broad bean.
Brassica oleracea, Cabbage.
Olea europaea, Olive.
Lactuca sativa, Lettuce.

6. THE ABYSSINIAN CENTER

Triticum durum, Durum wheat (An amazing wealth of forms).
Triticum turgidum, Poulard wheat (An exceptional wealth of forms).
Triticum dicoccum, Emmer.
Hordeum vulgare, Barley (An exceptional diversity of forms).
Cicer arietinum, Chick pea (A center).
Lens esculenta, Lentil (A center).
Eragrostis abyssinica, Teff.
Eleusine coracana, African millet.
Pisum sativum, Pea (One of the centers).
Linum usitatissimum, Flax (A center).
Sesamum indicum, Sesame (Basic center).
Ricinus communis, Castor bean (A center).
Coffea arabica, Coffee.

7. THE SOUTH MEXICAN AND CENTRAL AMERICAN CENTER

Zea mays, Corn.
Phaseolus vulgaris, Common bean.
Capsicum annum, Pepper.
Gossypium hirsutum, Upland cotton.
Agave sisalana, Sisal hemp.
Cucurbita spp., Squash, Pumpkin, Gourd.

8. SOUTH AMERICAN (PERUVIAN-ECUADOREAN-BOLIVIAN) CENTER

Ipomoea batatas, Sweet Potato.
Solanum tuberosum, Potato.
Phaseolus lunatus, Lima bean.
Lycopersicum esculentum, Tomato.
Gossypium barbadense, Sea Island Cotton (4x).
Carica papaya, Papaya.
Nicotiana tabacum, Tobacco.

8a. THE CHILOE CENTER

Solanum tuberosum, Potato.

8b. BRAZILIAN-PARAGUAYAN CENTER

Manihot utilissima, Manioc.
Arachis hypogaea, Peanut.
Theobroma cacao, Cacao (Secondary center).
Hevea brasiliensis, Rubber tree.
Ananas comosa, Pineapple.
Passiflora edulis, Purple granadilla.

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