THE PROCESS OF EVOLUTION IN CULTIVATED PLANTS

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One of the most essential factors in understanding the process of evolution in living organisms is the geographical distribution of species and varieties at the present time and in the past.

Several regions of the globe are extremely rich at the present time in numbers of species and varieties of plants and animals. In North and Central America such regions are Southern Mexico, Guatemala and some adjacent small countries to the south. In Europe such regions are the Caucasus, the Balkan States, Italy and Spain. Huge spaces in Northern and Central Asia are on the contrary quite poor in the number of species. On the other hand, Southeastern China, India, Indo-China and the mountainous regions of Persia, Afghanistan, Russian Turkestan and Asia Minor are extremely rich in the variety of existing species of wild animals and plants.

The same applies to cultivated plants and domesticated animals. During the last ten years the INSTITUTE OF PLANT INDUSTRY in the Union of Socialistic Soviet Republics has carried on extensive botanical and geographical investigations of a great number of cultivated plants on a world-wide scale. The principal purpose of these researches has been to ascertain the diversity of varieties of cultivated plants by applying modern methods of differential taxonomy and botanical geography. Separate plants have been subjected to a detailed cytogenetical and biochemical study. In undertaking this work we have been prompted by the actual needs of plant breeding, which is one of the most pressing practical problems in the large-scale socialistic agriculture in our country at the present time. It was evident to us that in order to conduct any rational large-scale work in plant breeding it was necessary to master exhaustively the whole initial varietal potentialities of the world as well as to learn about the nearest wild relatives of our useful plants.

Special attention has been devoted to the regions of the primary origin of cultivated plants, that is, to ancient agricultural countries almost untouched by previous investigators. In this respect the Soviet Union is in an exceptionally favorable condition since a vast initial material of varieties of many of the most important cultivated plants of the Old World is concentrated within the Caucasus and Turkestan, as well as in adjacent oriental countries. Even at present millions of acres of forests may be seen in these regions (especially in the Caucasus) consisting chiefly of wild apples, pears, plums, sweet cherries, wild almonds, and wild pomegranates. Here it is possible to trace the evolution of cultivated plants from wild form step by step.

In conformity with a definite plan, numerous expeditions have been sent to different regions of the Soviet Union, as well as to many of the ancient agricultural countries, including Abyssinia, Afghanistan, Asia Minor, Persia, Western China, all countries bordering the Mediterranean and Mexico, Guatemala, Peru, Bolivia, Columbia and Chile. At present researches are being extensively carried on upon over 300 different cultivated species.

The huge new material on cultivated plants and their wild relatives, collected in all countries of the world and consisting of not less than 300,000 specimens, has been subjected to a detailed study at the stations, and many results were published recently in the form of comprehensive monographs containing a survey of the world diversity of separate crops and showing their distribution over the different regions of the globe as well as the amplitude of their variation in quantitative and qualitative characters. Not only taxonomists are engaged in the study of cultivated plants, but plant breeders, geneticists, physiologists and biochemists have joined in this work. Nurseries have been established containing all varieties collected throughout the world, each nursery in the corresponding climate of the Union of Socialistic Soviet Republics. Exhibits which were sent to the Sixth International Congress of Genetics by our institution will give some idea of the results of these investigations.

The purpose of this brief communication is to formulate on the basis of our studies some general statements which may be distinctly traced in the evolution of cultivated plants.

A SPECIES AS A COMPLEX VARIABLE AND MOBILE SYSTEM

Knowing the great diversity of cultivated plants and of their wild relatives we have been led to conceive of Linnean species as of actually existing real complexes. In our judgment they represent mobile and variable systems embracing categories of different amplitude and connected in their historical development with their habitat and area. At a given geological period and at a given moment of observation, the species have a real existence, some opinions to the contrary notwithstanding. The separation among the species and their divergence are not merely in the investigator's mind. An intrinsic unity of discontinuity and continuity is a characteristic of the evolution of living organisms.

According to a detailed study of a great number of cultivated plants a Linnean species represents a distinct complex and mobile morphophysiological system bound in its genesis to a definite environment and area. Herbarium specimens of species, on the basis of which the present recognized botanical classifications have been drawn up, are only a first approach toward the study of a species. The real species with which the geneticist and the plant breeder have to deal are by far more complicated. Actual investigations of a number of species in their whole varietal diversity and over the whole world have led us to the discovery of great varietal potentialities unknown up to now to the botanist, plant breeder and geneticist.

THE GEOGRAPHICAL PRINCIPLE IN EVOLUTION

DARWIN in his researches devoted much attention to the geographical principle in evolution. A mere knowledge of general boundaries of the habitat of a species with which the botanist and the geographer usually have to deal does not satisfy either the plant breeder or the geneticist. For us it is quite important to know the localization of the definite genotypes within the limits of a species and the geographical distribution of genes within the area of a species. It has become at once evident that this principal factor in the understanding of the evolution of cultivated plants had practically been left out of consideration. Even in regard to the most important cultivated plants the botanist, the plant breeder and geneticist have had to content themselves with isolated specimens of species, without knowing the sum total of the varieties constituting the species. A study of one plant after another has led us to the discovery of regions characterized by a striking intraspecific diversity, hitherto never suspected by the botanist or the plant breeder, to say nothing of the geneticist.

Even for such plants as wheat we have discovered regions containing quite exceptional riches of new varietal character up to now unknown to the plant breeder. Thus little Abyssinia has proved to contain more than half of the varietal diversity of cultivated wheat found in the world.

As a result of our investigations of field and truck crops, as well as of fruit trees and shrubs, a new immense primary diversity of varieties has been found. Moreover, for a series of cultivated plants this study has led to the discovery of a great number of new Linnean species. Thus during the past five years we have succeeded in discovering five new wheat species each represented by a great diversity of forms. These species were found in Transcaucasia and in Abyssinia.

Expeditions of the INSTITUTE OF PLANT INDUSTRY sent out in 1926 to Mexico and to Central and South America, which worked there for three years, have revealed that up to the present we have had no real knowledge of the potato. It has been proved by morphological and physiological methods and by cytogenetical analysis that instead of fragments of one species—*Solanum Tuberosum*—known to plant breeders, there exist not less than

14 good species of the cultivated potato grown by the natives of Peru, Bolivia, Chile and Columbia. The whole series of polyploid species with 24, 36, 48, 60 and 70 chromosomes was discovered. These species are well differentiated, each characterized by a different number of chromosomes, by their crossability, their morphological and physiological qualities and their area of distribution. Very likely there are even more than these 14 species of potato in the regions of the Andes. The whole group of wild species of potato in Mexico and Guatemala proved to be immune to *Phytophtora infestans.*

Similar facts have been established for several fruit trees in Transcaucasia.

Such an extension of our knowledge of species naturally will create a new basis for the comprehension of evolution and make us alter our own conceptions of the species themselves.

A detailed analysis of the geographical localization of evolution has not received due attention up to this time. The predominant influence of the methods of archaeology and history in the study of the process of evolution is responsible for the fact that the biological substance in this process has been ignored. A wide field of new, interesting work, full of practical purpose, opens before the geneticist and will lead him to a better knowledge of evolution.

The detailed study of the varietal diversity of cultivated plants and their wild relatives has enabled us to establish for a majority of them the regions of their origin. These regions have proved to be confined to comparatively small territories concentrated mainly in the mountains and at the foothills in the subtropics and tropics.

At the Fifth International Congress of Genetics in Berlin the author outlined five principal world centers in which the most important cultivated plants have originated. On the basis of a large amount of supplementary data obtained during the last five years, we have been enabled to locate more exactly the regions of the origin of cultivated plants. We distinguish at present seven principal world centers of the origin of cultivated plants:

1. Southwestern Asia including Transcaucasia and the northwestern portion of India originated soft wheats and rye as well as many grain Leguminosae, alfalfa, Persian clover, etc. Here, especially in the western part of this area, is the home of the most important fruit trees.

2. India is the native country of rice, sugar cane and many tropical plants.

3. The mountains and foothills of Eastern China are the home of many fruit trees, truck crops and the soybean. The vast regions of Central Asia,

investigated by us in detail in 1929, have proved alien to the primary process of form origination. In spite of some former botanical suppositions, Central Asia and Siberia have had no influence upon the origin of cultivated plants.

4. Abyssinia, though economically a country of no particular importance with its cultivated area of only several million acres, shows a striking concentration of the diversity of the genes of wheat, barley and many leguminous grain crops.

5. Certain countries bordering the Mediterranean are the home of the olive tree, the carol tree, a series of original forage plants and Egyptian clover.

The sixth and seventh centers must be sought in America. In the New World the primary process of form origination is narrowly localized; the regions showing a striking species and varietal diversity occupy comparatively small territories concentrated in Southern Mexico and Central America as well as in Peru and Bolivia. The home of corn and of the upland cotton in all probability is Mexico and Central America, whereas that of the potato is in Peru and Bolivia.

These seven centers have developed on the basis of an extremely rich wild flora. Here we find conditions especially favorable to the development of species and varietal diversity. These regions have proved equally favorable to civilizations and of course it is no accident that the map showing the distribution of the chief sources of food plants essentially coincides with that of the distribution of the first agricultural civilizations.

The mountain and foothill regions in the subtropics are the most remarkable places for comprehending the evolution of cultivated plants as well as of many wild species.

In these seven regions the beginnings of the evolutionary process manifest themselves in a salient way especially when we compare the evolution of different species and genera. The existence of such group evolution of different species and genera facilitates greatly an understanding of the evolutionary process.

THE LAW OF HOMOLOGOUS SERIES IN VARIATION

The phenomenon of parallel variation, that is, of the regular repetition of series of characteristics in varieties in different allied species and genera, is quite general. In our studies we have found thousands upon thousands of examples of this parallelism in different species belonging to the same genus, or in different genera belonging to the same family. Such a parallelism is remarkable, for example, when we compare the varietal diversity of wheat, barley and rye, or of peas, chick peas, lentils, vetches and horse beans. Every month brings new evidence of this astonishing parallelism which can not be neglected in the study of the evolutionary process. The author has named this parallel variation, "The law of homologous series in variation" (*Journal of Genetics,* 1922). This law is actually a development of the idea of evolution and helps considerably in the study of the varietal diversity and of the same process of evolution. Of course, this parallelism should not be taken as something absolute. But on the whole it is quite general and manifested by all groups of cultivated and wild species studied by us in detail. For a great majority of the plants we can speak only about phenotypical parallelism, but there are already known many cases of experimentally established facts of genotypical parallelism.

A great majority of varietal links missing in the species were found in the primary seven centres of the origin of cultivated plants.

REGULARITIES IN THE DISPERSION OF CULTIVATED PLANTS FROM THEIR PRIMARY REGIONS

The above described primeval regions are characterized by a vast potentiality of genes and not infrequently (though not always) by a great diversity of forms. A study of the genetical diversity of the most important cultivated plants in such primeval regions has divulged the presence of a great number of the dominant genes along with the recessive ones. Many dominant forms have been revealed by us for the first time in these primary regions of the origin of a given plant. Thus, for instance, dominant violet-grained, almost black-grained wheats have been found only in Abyssinia. The regions of Abyssinia, the region enclosed between the Hindu-Kush and the Himalaya, as well as Asia Minor, Southern Mexico and Guatemala are characterized by an extremely great number of dominant forms of cultivated plants. Central Peru is distinguished by an enormous diversity of cultivated potatoes and especially by the presence of dominant genes. An actual investigation has shown that during the spreading of the species toward the boundary of a region chiefly recessive forms are singled out and survive. As we withdraw from the primary regions, a decrease of dominant forms and a predominance of recessive forms are observed.

The process of the separation of recessive forms is evidently connected with frequent mutations toward recessiveness which, as is well known, usually take place. For instance, ERWIN BAUR and his collaborators have established about 300 different mutations in *Anterrhinum Majus,* among which only 9 or 10 are dominant, and all others are definite recessives. To a considerable degree this separation of recessives in the process of intra-species evolution is also a result of inbreedings. The spreading out of forms, their geographical isolation, is particularly favorable for the singling out of recessives. The trend of evolution within a species toward recessives is a common phenomenon. In peas, corn, rice, sweet peas and barley, mostly studied from a genetical point of view, the mutations are almost exclusively recessive in relation to the wild Cilician forms. In maize, far from its Mexican primary centre, we have found exclusively new recessive types like ligules, waxy and ramose varieties as well as forms with glossy seedlings (N. KULESHOV).

The opposite process, that is, the singling out of dominant forms, though observed is of very rare occurrence. Quite frequently it manifests itself in a peculiar way. Thus for example the appearance of such a dominant beardless barley is observed in Eastern Asia and in Japan, far away from the principal centres of the origin of cultivated barley in Southwestern Asia and Abyssinia. The dominant hornless varieties of cattle are known in great numbers in the extreme north of European and Asiatic Russia. Biologically such forms are unquestionably secondary ones, as hornless cattle, awnless barleys, and awnless wheats may exist only under conditions of cultivation.

The dominant vegetative mutations occur frequently in the potato (T. V. ASSEJEVA). It is possible to say that as a rule cultivated types of plants are mostly recessive.

A series of peculiar, as if synthetic, forms have been found in a number of cultivated plants in primeval regions. These forms show an absence of the divergence of characteristics and combine the qualities of different species, showing thereby that this phenomenon is without relation to hybridization.

Such forms are of considerable interest in the study of the process of evolution. Thus, for instance, wheats of Abyssinia combine the properties of soft and of durum wheats.

THE INCREASE OF THE SIZE OF SEEDS, FRUITS AND FLOWERS IN A DEFINITE GEOGRAPHICAL DIRECTION

In the geographical evolution of cultivated plants interesting general facts have been observed. Thus one of the most noteworthy relationships is a regularly observed, gradual increase in the size of seeds, fruits and flowers from the Himalaya region toward the Mediterranean. In extreme cases, the linear dimensions are consistently increased several times.

The varieties of flax which originated in Morocco, Algeria and Cyprus are twice as large as those of Persia and Afghanistan. In the Mediterranean countries the seeds of beans, lentils, and chick peas exceed in size several times those of Indian forms. At any rate the fact of accumulation in the Mediterranean region of exceptionally large-fruited and large-seeded forms of cultivated as well as of certain wild species is incontestable.

Perhaps these are extreme cases of recessives, or they may be results of hybridization. At any rate the genetic nature of this increase in size is as yet unknown, but the fact itself must be taken into consideration by the plant breeder.

Another regularity in regard to cereals has been observed in Eastern Asia, where an apparently simultaneous development of naked oats, naked millet and naked barley has taken place.

Some regions are characterized by a number of species showing a definite trend toward some particular variation which is of great importance to those in search of initial material for the purposes of plant breeding. As an illustration, Peru and Bolivia are characterized by many tuber-bearing species and genera, such as oca, Tropaeolum, Ulluco, etc., besides potatoes.

SEPARATION OF ECOLOGICAL GROUPS

The process of differentiation of particular ecological types under the influence of a definite environment may be convincingly established by studying various geographical groups within the limits of a species. A knowledge of such ecological groups allows one to comprehend the process of geographical evolution, so important for the mastery of the diversity of types by the plant breeder. Not infrequently such groups of plants are characterized by a large number of features in common. Such groups doubtless are determined by a great number of genes. In the long historical process of the migration of species from the primary regions this crystallization of specific ecological types may be discerned clearly.

THE RÔLE OF NATURAL SELECTION

Doubtless an important rôle in the evolution of cultivated plants has been played by natural selection. Thus, for instance, some of the most important European crops, such as rye and oats, have been forced irrespective of man's will into cultivation as a result of natural selection. It may be observed in the Caucasus even now that a weed rye gradually supplants wheat. By way of natural selection, as cultivation of wheat moves northward into more severe climatic conditions, rye from a weed gradually becomes an independent useful crop. Northern countries cultivate now chiefly the former weeds, namely rye and oats.

In certain specific cultivated plants, for instance flax, the formative rôle played by natural selection may be clearly seen. We have ascertained for flax that the decisive factor in the geographical distribution of this crop is the length of the vegetative period. Due to a shorter vegetative period in the North, earliest forms were selected for cultivation there. The character of earliness in flax is to a considerable degree correlated with the length of its stem, in the sense that earlier varieties grow taller and *vice versa;* hence, it is in the North that the bulk of long-stemmed fiber flaxes were selected. As a consequence flax is grown for fiber in the North and for oil in the South. This example is quoted to show that a differentiation of the crop has been above all a result of natural selection.

THE RÔLE OF MAN IN THE EVOLUTION OF CULTIVATED PLANTS

Undoubtedly an important rôle in the evolution of plants has been played by man. The destiny of many cultivated plants is intimately connected with the history of human civilizations and migrations of peoples. In some plants in particular the rôle played by man in their modification has been quite conspicuous. The influence of such great sedentary ancient civilizations as that of China and the Mediterranean on the modification of initial primitive plants was extremely great. Giant forms have been obtained by selection of extreme recessives and mutations, not infrequently surprising in their contrast with wild primitives.

It is interesting to note that some of the most peculiar cultivated types were selected by agriculturists of high, old civilizations. Varieties of rice, barley, cabbage, fruits, and radishes indigenous in China, Japan and the Mediterranean countries indicate considerable creative work on the part of plant breeders. The same is noticeable in some European types of cultivated plants. On the other hand, in the majority of cases cultivated varieties of plants of India and Afghanistan as well as Bolivia and Peru do not differ greatly from the corresponding wild forms. Numerous transitional forms may be readily observed.

A systematic study of quantitative variation in a vast material affords facts for the comprehension of the range of differences of the extreme types. Thus the best European pear reaches a weight of seven pounds, while the fruits of wild pear trees in Caucasus weigh but one gram. All quantitative transitions may be traced in certain cultivated plants. Some of the extreme cases biologically are cultivated monstrosities, not vital under natural conditions. It suffices to mention different seedless varieties of fruits and double flowers.

LYSSENKO'S DISCOVERY

The remarkable discovery recently made by T. D. LYSSENKO of Odessa opens enormous new possibilities to plant breeders and plant geneticists of mastering individual variation. He found simple physiological methods of shortening the period of growth, of transforming winter varieties into spring ones and late varieties into early ones by inducing processes of fermentation in seeds before sowing them. LYSSENKO's methods make it possible to shift the phases of plant development by mere treatment of the seed itself. The essence of these methods, which are specific for different plants and different variety groups, consists in the action upon the seed of definite combinations of darkness (photoperiodism), temperature and humidity. This discovery enables us to utilize in our climate for breeding and genetic work tropical and sub-tropical varieties, which practically amounts to moving the southern flora northward. This creates the possibility of widening the scope of breeding and genetic work to an unprecedented extent, allowing the crossing of varieties requiring entirely different periods of vegetation.

THE PROBLEM OF GIANTISM IN THE EVOLUTION OF CULTIVATED PLANTS

The study of the quantitative range of the vast world material has established the limits of hereditary variation for many species of cultivated plants. Several of these species show a striking variability. Thus in cucurbits, in root crops, hereditary variation in regard to the size of fruits and roots may be a hundred- and even a thousandfold.

A tendency toward giantism in the evolution of cultivated plants, as well as of animals, may be traced quite distinctly. For comprehending the evolution of cultivated plants, this is one of the most important points on which so far very little genetic research work has been done.

The evolution of many cultivated plants essentially consists in an increase of the size of fruits, seeds, and roots. An important rôle in this process has been played evidently by crossing different species and different geographical races. This most important quantitative factor in the evolution of cultivated plants and domesticated animals demands an immediate careful genetical study. Experimentally it can be tackled. This study will undoubtedly do much to further breeding work.

PHENOTYPES AND GENOTYPES

In studying evolution, the chief attention of investigators was up to now concentrated on phenotypes. So far the immense diversity of species and varieties has not yet been embraced even by systematic genetic study. A boundless sea of experimental work opens before the geneticists. We have mastered to a certain degree knowledge concerning evolution in space and time, as it finds expression phenotypically. The following stage is the genetics of this phenomenon.

An important rôle in evolution has been played by the process of hybridization, by mutation and by inbreeding. Interspecific hybridization has played a great part in the genesis of some cultivated plants. The study of the primary regions of the origin of species has revealed a number of facts pointing to the presence of interspecific hybridization in nature, even among the wild relatives of those species. This is particularly obvious in different fruit trees and shrubs, the pear, the almond, and the blackberry. Some species of cultivated plants are evidently the result of interspecific hybridization.

Recent studies conducted in the Union of Socialistic Soviet Republics have proved how great is the rôle of hybridization of distant species in the origin of several cultivated plants. A natural crossing on a large scale was established between wheat and rye, between wheat and different species of Aegilops and between several species of Agropyrum and wheat. European plums very likely originated in this way. Such might be also the origin of *Triticum Persicum*. In this way too, very likely, originated tobacco which is unknown in wild nature.

The phenomenon of amphidiploidy of sterile hybrids proved to be rather frequent. Hence the fertility of these distant hybrids. At Saratov recently many amphidiploids were found among hybrids of wheat and rye. Several cases of amphidiploidy were produced in hybrids of wheat and Aegilops.

Artificially produced tetraploidy in cabbage as was recently shown by KARPETCHENKO in our institute, increases the crossability of distant species. Cabbage and mustard, for instance, can be crossed.

The crossing of distinct geographical races is in many instances responsible for an increase in size and for a change of many quantitative as well as qualitative characteristics. This crossing of distant geographical races affords vast possibilities for the improvement of the existing varieties. The combination of genes of geographically distant races makes it possible to transcend the limits of the ordinary types.

GENERAL CONCLUSIONS

An experimental study of the process of evolution in cultivated plants throws a light on many phases of breeding work. The range of this study is exceptionally wide, as the number of cultivated plants already amounts to not less than twenty thousand. The growing needs of civilized man and the development of industry make the introduction of new plants necessary. The vast resources of wild species, especially in the tropics, have been practically untouched by investigation.

Our studies have made it clear that in order to control evolutionary processes in cultivated plants, preliminary research should be done on a world-wide scale. In order to understand evolution and to guide our breeding work scientifically, even in application to our principal crops such as corn, wheat and cotton, we must go to the oldest agricultural countries, where the keys to the comprehension of evolution are hidden.

An actual mastery of the processes of evolution which is the chief aim of genetics can be accomplished only through the combined efforts of a strong international association and through the removal of barriers impeding research in those most remarkable regions of the world. Let us hope that this time is not far off. We are only at the start of our work in this direction and an enormous field lies ahead of us. There is enough work for all of us.