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Basic Loci in Cultivation of Certain Crops in the Past and Modern Times

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Summary. In 1968 H. Brücher asked: "Gibt es Genzentren?" He proposed a negative answer, but was wrong. The geographical distribution of the majority of crops is not even over all parts of their areas. There are loci of great abundance and regions of small plantations. The abundance of individuals in the large plantation is a factor favouring the display of genetic variability (an increase of the mutation number). The variability of ecological conditions, the antiquity of cultivation and the possibility of interspecific hybridization in such loci promote genetic variability; but a uniformity of ecological conditions and strong selection (natural or artificial) can eliminate new genotypes arising and preserve the homogeneity of the initial populations. Therefore loci of great genetic variability (Genzentren) exist only in conditions favourable for agriculture (with weak natural selection) and in conditions of a primitive consumer agriculture (without strong artificial selection). Loci of genetic variability can be observed in the following regions of a past or existing plantation abundance: in the ancient primary regions of domestication of certain plants; in the regions of ancient large scale cultivation around the primary domestication centers; and in the secondary loci of abundance in conditions favourable for agriculture where certain crops migrated from their primary cultivation regions. Certain loci of abundance (ancient and modern) have no noticeable genetic variability in their different crops, which are relatively uniform there. Such loci of abundance without genetic variability are either disposed at the periphery of the area of the particular crop, with worse natural conditions than in the rest of the area (control by strong natural selection), or are new loci of abundance in conditions of commercial agriculture (control by regular plant-breeding).

All loci of polymorphism (Genzentren) are undoubtedly a temporary historical phenomenon. The absence of regular plant breeding was an indispensable condition for the rise of genetic variability loci in the regions of plantation abundance of certain crops. In modern times plant breeding becomes an inevitable component of commercial agriculture. Thus new loci of abundance have no great genetic variability and ancient centres of polymorphism of different crops now go to ruin, giving place to plantations of the few best varieties. Loci of genetic variability are now a relic of the past, while loci of abundance with the few best varieties conform with the economics of modern world agriculture, which aspires to cultivate each crop in the regions where its production cost will be lower and to avoid areas with an expensive product.

Zusammenfassung. H. Brücher stellte 1968 die Frage: Gibt es Genzentren? Er verneinte sie zu Unrecht. Die geographische Verbreitung von Kulturpflanzen ist im allgemeinen innerhalb ihrer Areale ungleichmäßig. Gebieten mit hoher Anbauhäufigkeit stehen solche mit geringem Anbau gegenüber. Die hohe Individuenzahl umfangreicher Anbauflächen stellt einen begünstigenden Faktor für die Entfaltung der genetischen Variabilität dar (Steigerung der Zahl der Mutanten). Sie kann in diesen Gebieten durch die Vielfalt ökologischer Bedingungen, ein hohes Alter des Anbaues und die Möglichkeit zu interspezifischen Hybridisationen noch gefördert werden.

Durch eine strenge natürliche oder künstliche Auslese können neu entstehende Genotypen eliminiert und dadurch eine genetisch relative Einförmigkeit der Ausgangspopulationen erhalten werden. Daher sind Gebiete mit einer großen genetischen Variabilität (Genzentren) nur dort anzutreffen, wo günstige Anbaubedingungen für die jeweilige Art herrschen (geringe natürliche Selektion) und wo eine primitive Landwirtschaft mit wenig intensiver künstlicher Selektion praktiziert wird. Die Lage derartiger Mannigfaltigkeitszentren kann für eine Art in Zusammenhang mit natürlichen, historischen oder ökonomischen Veränderungen wechseln. Sie waren und sind gebunden an Gebiete der Inkulturnahme von Arten, an diesen benachbarte Regionen mit einer alten und umfangreichen Kultur der Art oder an sekundäre Anbauzentren mit günstigen Anbaubedingungen, in die sich Kulturarten aus den Primärzentren ausgebreitet haben.

Bestimmte alte oder rezente Häufigkeitszentren besitzen bei manchen Kulturpflanzen keine bemerkenswerte genetische Variabilität. Das trifft entweder für die Peripherie des Kulturareals mit ungünstigen Anbaubedingungen und strenger natürlicher Selektion oder für jüngere Anbauzentren zu, in denen die Arten unter regulärer Kontrolle durch die Pflanzenzüchtung großflächig für kommerzielle Zwecke kultiviert werden.

Alle Genzentren sind zweifelsohne ein temporäres historisches Phänomen. Das Fehlen einer Pflanzenzüchtung war die notwendige Bedingung für ihre Entstehung in den Anbauzentren bestimmter Arten. Heute ist die Pflanzenzüchtung eine unerläßliche Voraussetzung für eine leistungsfähige Landwirtschaft. Daher haben neuere Anbauzentren keine große genetische Variabilität, alte Mannigfaltigkeitszentren werden zerstört und durch den Anbau weniger, hochwertiger Sorten ersetzt. Genzentren sind heute ein Relikt der Vergangenheit, während genetisch verarmte Anbauzentren mit einer geringen Zahl leistungsfähiger Hochzuchtsorten den Bedingungen der modernen Landwirtschaft, die die einzelnen Kulturpflanzen für den Weltmarkt dort erzeugt, wo es aus ökonomischen Gründen optimal möglich ist, entsprechen.

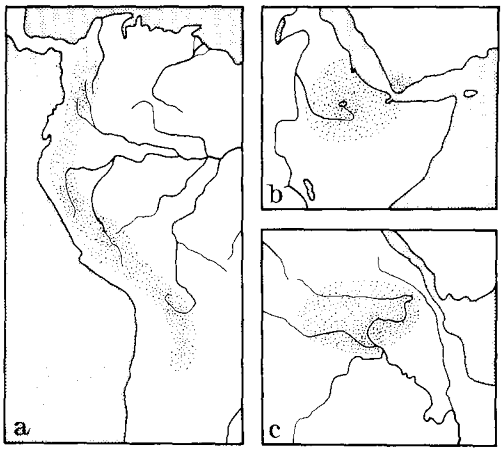

Fig.1. The loci of basic cultivation in the centres of domestication and of ancient agriculture in which the most genetic variability is concentrated.
a - Andean potato (*Solanum andigenum* Juz. *et* Buk.) according to Salaman,
b - Ethiopian oat (*Avena abyssinica* Hochst.) according to Mordvinkina,
c - Jute (*Corchorus capsularis* L.) according to Perevezev and Kul'tiasov

Variation in the abundance of plantations in different parts of the area is a common phenomenon in the geographical distribution of cultivated plants. Certain crops are cultivated chiefly in relatively limited regions of the globe, such as the Andean potato (*Solanum andigenum* Juz. et Buk.) in the Andes, the olive-tree (*Olea europaea* L.) in the Mediterranean regions, the maba (*Abutilon avicennae* Gaertn.) in northern China, the jute (*Corchorus capsularis* L.) in Bangladesh and in eastern India, the date palm (*Phoenix dactylifera* L.) in the deserts of western Asia and of northern Africa. Certain loci of the greatest abundance and concentration of plantations also exist in the areas of widely distributed world crops.

There are principal loci of world production. South-eastern Asia gives 2/3 of the world rice production. America produces half of the world Indian corn output and 5/6 of this American corn production belongs to the "corn belt" of the U.S.A. Half the world's coconut production is harvested in the Philippines and Indonesia. In the area of the sugar-cane there are two principal loci of the greatest production: Hindustan and the islands of the Caribbean Sea. Each of them produces about 1/5 of this crop's world output. More than 4/10 world production of the sweet orange is harvested in the south-eastern and south-western regions of the U.S.A. For cotton, there are three principal loci of the greatest production: southern regions of the U.S.A. (1/3 of this crop's world production), India and China (1/5 of world production in each of them) (Kupzow 1975).

The numerical abundance of certain crops in different countries is a result of economic and geographical conditions. This favours the display of great genetic variability, which can be still further intensified by a long period of continuous cultivation and by a diversity of ecological conditions. But selection (natural or artificial) restricts or excludes completely the possibilities of intraspecific polymorphism in such regions.

The regions of the most ancient agriculture, where the domestication of wild plants and the rise of the first primary crops have occurred, were at one time islands of agriculture in a large sea of vagrant and nomad people. Thus they were the primary loci for the cultivation of certain crops and, therefore, the sites of longest continuous cultivation. Great variability of ecological conditions is characteristic for the majority of the ancient agricultural regions as a consequence of the presence there of vertical zones (Peru, Mexico, Ethiopia, Anterior Asia, Central Asia, Indochina with Indonesia). The climate and soils were favourable for agriculture, so natural selection on the plantations was not too strong. Ancient agriculturists did not know of regular artificial selection, so the most ancient regions of agriculture have become primary loci of crop polymorphism. Certainly this was a temporary historical phenomenon, but its echoes have been well preserved up to the XX century. Many crop species still retain the loci of their greatest variability in the regions of their origin. And certain crops, which have a relatively small area, retain there almost all their resources of genetic variability, e.g., the Andean potato, the Ethiopean oat and jute (Fig.1).

During the migration of a crop and expansion of its area, it is known that the basic abundance of certain crop plantations locates around the primary locus of origin. Some part is played by: genetic-ecological peculiarities of the cultivated species; climatic conditions of the migration regions; and ethnic and cultural character of their inhabitants. Such a situation can be seen in the area of rice (a crop of east Indian origin). The basic abundance of its plantations is located in the monsoon regions of south-eastern and eastern Asia.

During the times before the invasion of European peoples into America, the Indian corn (a crop of Mexican origin) was cultivated there, mainly in regions from Mexico to Peru, which were then the countries settled by agricultural peoples, while other American natives were still at earlier stages of economic development (vagrant tribes). The northern Mediterranean region was probably one of the primary vine-growing regions: now the principal area of vine-growing is situated in western and central Europe, which are the regions of the immediate migration of the vine to the north from its origin locus (Fig.2). The soy-bean (a crop of Chinese origin) had its principal area of ancient cultivation in eastern monsoon Asia as a result of its immediate migration from the origin locus, and it is there that its principal genetic polymorphism is localized (Bazilevskaya and Dagaeva 1937). Up to the XIX century almost all world agriculture had a consumer character, without strong artificial selection. Inauspicious for certain crop regions, the control of natural selection was also relatively weak. Therefore, in the regions of origin and adjacent migration regions, genetic variability was in progress. The ancient area of basic abundance, adjacent to the centre of origin, also became the locus of largest variability of a species, including the formation of different ecotypes and ecoclines and genetic variability among different populations.

Certain crops, during migration far outside their origin region, sometimes invaded a new one more favourable for their cultivation and evolution. There, their genetic variability was better displayed than in the region of primary domestication. Thus the secondary loci of plantation abundance and of polymorphism could be formed. The ecological conditions in the secondary loci of crop evolution usually include: a climate favourable for the species with a certain variability in different regions; an abundance of plantations; and an absence of strong natural or artificial selection. In certain of these loci, an additional factor favourable for genetic variability can be the hybridization of the migrated crop with native wild plants or weeds from its related species. Such hybridization increases combinative variability and stimulates the rise of polyploid genotypes. Thus the secondary loci of genetic variability and of polymorphism in certain crops arose in the secondary regions of their abundance, e.g., in the potato in northern Europe (the crop being of Andean origin, but having in Europe basic evolution and variability of the species *Solanum tuberosum* L. (Hawkes 1944)), in the til in Hindustan (domesticated in Ethiopia), in the sunflower in the steppes of Russia and Ukraine (domesticated in the prairies of north America) (Fig.3).

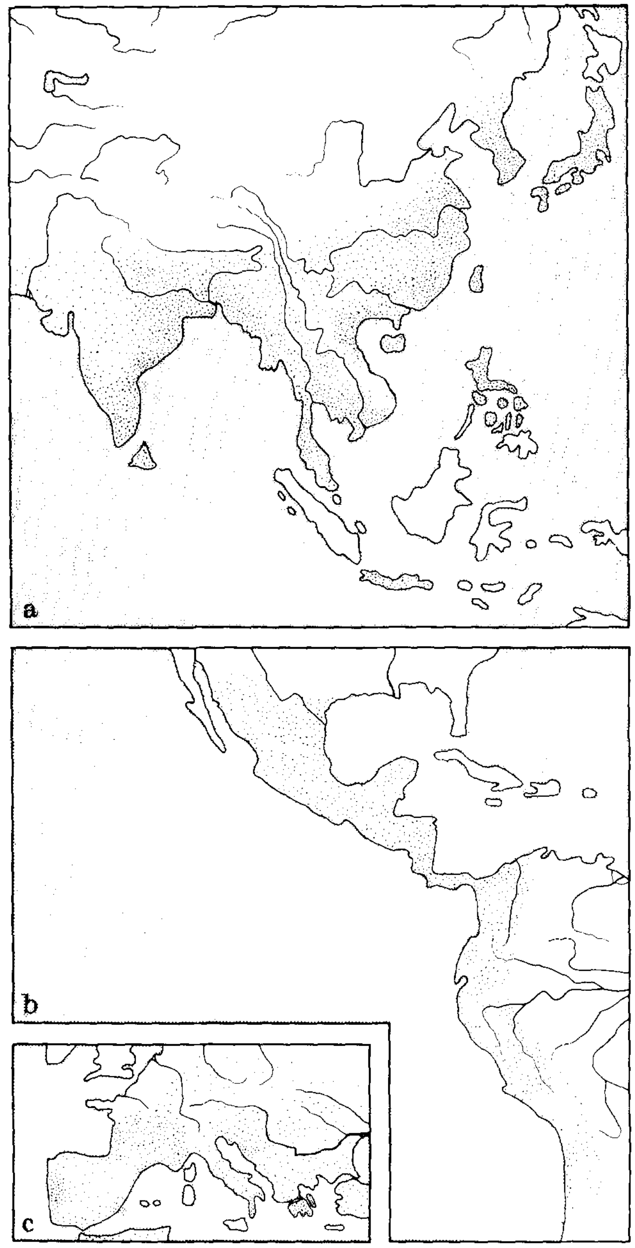

Fig.2. Loci of basic ancient cultivation and of the greatest polymorphism in the regions around the primary domestication centres.
a - rice in south-eastern and eastern Asia, according to Van Royen,
b - maize in ancient America, according to Weatherwax,
c - vine in Europe, according to Van Royen

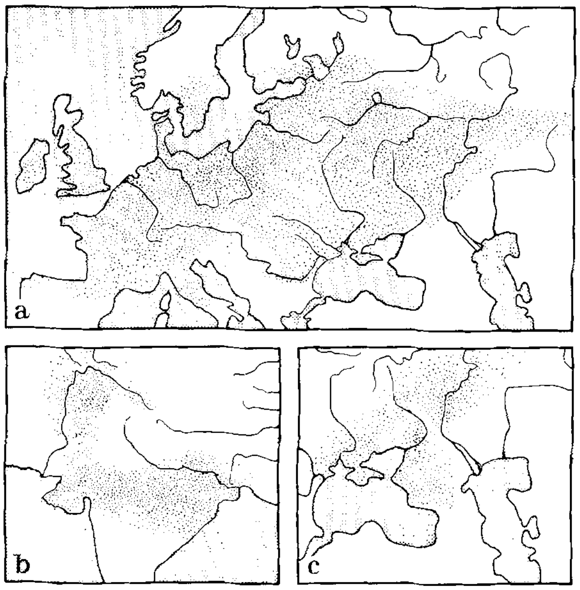

Fig.3. Secondary loci of abundance and of large genetic variability.
a - potato in Europe, according to Van Royen,
b - til in Hindustan, according to Hiltebrandt,
c - sunflower in the XIX century in Russia and Ukraine, according to Wenclawowicz

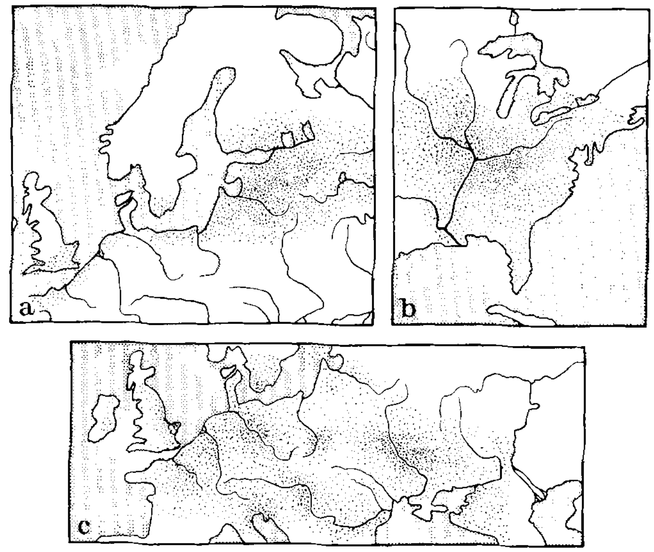

Fig.4. Loci of a large but not very ancient cultivation, without great genetic variability.
a - fibre flax in northern Europe, according to Elladi,
b - soy-bean in the U.S.A. according to Bazilevskaya and Dagaeva,
c - Sugar beet in Europe, according to Van Royen

The hybridization of diploid wheats with *Aegilops speltoides* Tausch. in the territory of Anterior Asia was a cause of the rise here and in Ethiopia of powerful loci of genetic variability in tetraploid wheats. The ensuing hybridization of such tetraploid wheats with *Aegilops squarrosa* L. in Central Asia was a basic factor in the origin of hexaploid wheat and in the formation there of the locus of greatest variability (Vavilov 1935). New Guinea was probably the mother country for cultivated sugar-cane (a derivative of *Saccharum robustum* Brandes *et* Jeswit.). During its migration to the north-west this crop coincided on the territory of Indonesia and Indochina with the wild *Saccharum spontaneum* L. The result of this meeting was extensive interspecific hybridization and the rise of great variability in a background of abundant cultivation (it is the secondary locus of sugar-cane evolution) (Artschwager and Brandes 1958).

In the evolution of certain crops, however, there can be observed a phenomenon in which the economic situation provokes abundant cultivation of a certain crop at the periphery of its area, in climatic conditions sufficiently favourable for only a few ecotypes. They are controlled here by strong natural selection which may be supplemented with artificial selection for adaptation to the claims of the agriculturist. In such loci strong selection does not permit noticeable genetic variability to be manifested, in spite of an abundance of plantations. This can be observed in North-European fibre-flax. Forms with a long stem and without branching were strongly selected by the struggle for life here, and therefore formed a relatively homogeneous complex of fibre-flax ecotypes, with weak variability in the composition of different populations. Later, such natural selection was supplemented by artificial selection and plant-breeding. Thus in northern Europe the locus of abundance of fiber-flax (with about 1/10 world flax seed production) arose without considerable polymorphism. Soy-beans have been cultivated in the basin of Missouri and Mississippi since the beginning of the XIX century. Their cultivation was stimulated by economic development of the U.S.A., and now they have become more wide-spread there than in their ancient area in East Asia. The climate of this basin is colder than in the basic area of soy-beans: only ecotypes of soy-beans from Manchuria can grow sufficiently well in these regions of the U.S.A. They were introduced and then evolved under the strong control of natural selection and subsequently of regular plant breeding. Poor initial material, cultivation over a relatively brief space of time, lower variability of climatic and ecological conditions in the north-east of the U.S.A. than in East Asia, and strong natural selection followed by regular plant breeding were the causes of relatively little variability of the soybeans in their locus of abundance in North America. The locus of sugar-beet in Europe also belongs to this type of abundance locus. Culture of the sugar-beet arose in Europe at the beginning of the XIX century. This was the northern periphery of the world beet area. As initial material for sugar-beet breeding there, some white forms of northern vegetable beet were utilized (probably a hybrid of the cultivated vegetable beet with a northern ecotype of *Beta maritima* L.). The ecological conditions under which sugar-beet culture was developed were not very variable and the evolution of this crop was controlled by regular plant breeding. Therefore the locus of sugar-beet in Europe has very abundant plantations and gives more than 65 % of the world sugar-beet root production, but its genetic composition is relatively homogeneous, being represented by the few best local-bred varieties (Fig.4).

A similar situation of poor genetic variability in the locus of abundance is observed in the rose-bush in Bulgaria (Eastern Rumelia). This is a world centre for the production of rose essential oil with large plantations of this crop. Commercial cultivation is very ancient here, stimulated by proximity to such great religious centres as Constantinople and Athens. Permanently severe artificial selection accompanied rose-bush cultivation in Eastern Rumelia and the genetic variability of this plant (rose of Kazanlyk) is very weak here, in spite of the great antiquity of its culture and its large plantations (Zander 1928). A similar phenomenon can also be seen in the area of cotton, where its new locus of abundance in the southern U.S.A. (arisen in the XVIII century) is not a centre of polymorphism. Cotton cultivation arose here from the introduction of a few good commercial varieties and genetic variability was permanently controlled by regular plant breeding (Mauer 1954).

The relatively new loci of abundance, situated far from the centres of origin, are observed in the world distribution of many crops. This abundance, however, is not accompanied by propitious and varied ecological conditions, the cultivation of certain crops is not very ancient, and natural and artificial selection is not very weak. In such loci of secondary plantation abundance, considerable variability of these crops, can be observed, but lower than in their centres of origin. An example is the distribution of the wheats (mainly the area of the soft wheat - *Triticum aestivum* L.). There are 3 principal loci of abundance: the steppes of the U.S.S.R. (about 1/4 of the world production), the prairies of the U.S.A. (1/5 of the world production) and central and western Europe (1/10 of the world production). All these 3 loci had a relatively poor set of wheat varieties at the beginning of the XX century and then it is even more limited to a few of the best varieties. The basic genetic variability of the wheats is now conserved in the loci of their origin, in Anterior Asia, Central Asia and Ethiopia, where agriculture is very ancient but primitive, of a consumer character and without regular plant breeding (Flaksberger 1935).

The modern locus of abundance of maize cultivation in the U.S.A. ("the corn belt", south from the Great Lakes in the basin of Missouri-Mississippi) has relatively poor genetic variability. It is the northern periphery of the maize area in high latitude and natural selection does not allow tropical and subtropical late ecotypes to grow there. From the end of the XIX century commercial culture of maize prevailed with the cultivation of the few most advantageous varieties (Humlum 1942). An analogous situation is found in the sugar-cane in the islands of the Caribbean Sea, where this crop also has no great genetic variability (Rosenfeld 1956).

Still more homogeneity of genetic composition can be observed in the newest regions of large commercial culture of certain crops. It is the result of very poor initial material and of strong artificial selection. The para-rubber tree is now represented in its basic world plantations in Malaysia and Indonesia by the few best bred varieties. Brazil, which gives over 1/2 of world coffee production, has a very poor composition in its cultivated *Coffea arabica* L. This is the result of the origin of the Brazilian coffee plantations from one tree introduced in 1727 (Purseglove 1965) and of subsequent strong artificial selection. The subterranean clover is a sufficiently polymorphous species in Europe. Its European populations were introduced into Australia at the end of the XIX century. Now there are found all 3 subspecies native to Europe, but the subsp.

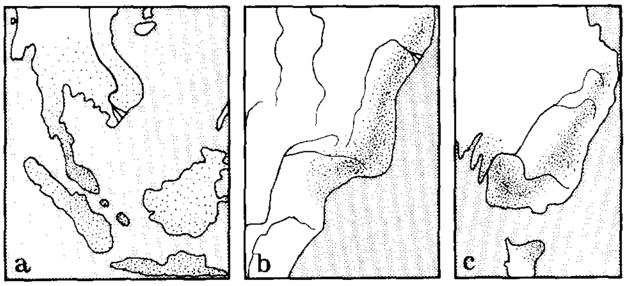

Fig.5. Modern loci of large cultivation with weak genetic variability.
a - para-rubber tree in Malaysia and Indonesia, according to Polhamus,
b - coffee tree in Brazil, according to Wickizer,
c - subterranean clover in Australia, according to Morley and Katznelson

subterraneus (from north-west Europe) prevails very strongly, so that the variability of the subterranean clover cultivated in Australia is relatively low. It may be the result of strong natural and artificial selection in the new cultivation region (Fig.5).

The cocoa tree is also extremely uniform in Ghana and other tropical African countries, which produce over 60 % of world cocoa yield. This is also the result of the introduction of limited genetic resources followed by strong artificial selection (Purseglove 1965).

The alteration in genetic variability of the quinine tree in its basic region of domestication and principal cultivation in Indonesia is very interesting. The genus *Cinchona* has many species in the Andes. Some of them were domesticated in south-eastern Asia. Now, as a result of strong artificial selection, only one of them, *C. ledgeriana* Moench., is a producer of quinine there and it is represented by a few best bred varieties (Kupzow 1975).

The variability of the clove tree, a crop of Indonesian origin is also very poor in Zanzibar, which is now a basic world producer of the clove: all its clove tree plantations have a commercial character and the genetic variability is controlled by strong artificial selection.

At the present time, it is very characteristic that a certain crops cultivation is concentrated around the centres of processing industry, which utilize its production. Thus, southern France and Italy are a base for the French parfumer industry. Concentrated here are plantations of many parfumer crops, such as rose, hyacinth, tuberose, carnation and lavender, and especially the species with flowers utilized for the "enfleurage". All these plants are represented by their best varieties and have no noticeable polymorphism, being controlled by strong artificial selection. A similar situation can be observed in the south-eastern regions of the U.S.A., which is the base of that countries parfumer industry. The development of the European pharmaceutical industry stimulated the domestication and widespread cultivation in Central Europe of medicinal plants from European flora, such as the valerian, foxglove, belladonna and lily-of-the-valley. A similar large-scale cultivation of European medicinal plants can also be observed in the north-eastern regions of the U.S.A., where the American pharmaceutical industry is concentrated. All plant species cultivated for the pharmaceutical industry have no noticeable genetic variability and are represented in the plantations by their best varieties, under strong control by artificial selection. For the forage crops, loci of plantation abundance are observed usually in the regions where large-scale milk stock-raising has developed, as in north-western Europe and north-eastern U.S.A. There are large plantations of different forage crops, but they are represented by their best varieties, without noticeable genetic polymorphism.

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