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Theoretical Basis of the Plant Domestication

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Summary. Plant domestication is stimulated by economic demands. Crop plant formation is controlled primarily by natural selection in cultivation; artificial selection is only a useful addition. The ecotypical nature of the initial material has great bearing on the success of domestication. The weeds of a convergent group were well adapted to being cultivated; weeds of a divergent group can be domesticated only with difficulty. Wild plants in nature are extremely varied ecotypically: some can be domesticated easily, others with difficulty. Some wild plants and weeds can be cultivated without genetic change (naturalization), while a genetic transmutation is necessary for the domestication of others (acclimatization). New domesticated ecotypes can be produced: 1. as a result of reconstruction of the initial populations and new ecotype synthesis on the basis of individual genotypes; 2. by means of hybridization of wild or weed initial genotypes with cultivated ones; 3. by use of new mutations in cultivation and further plant breeding.

Key words: Domestication – Acclimatization – Hybridization – Mutations – Domestication – Artificial selection – Naturalization

Introduction

The dawn of agriculture on our globe started about 10,000 years ago. Most of our crop plants arose in these very ancient times. This basic complex of cultivated plants increased slowly and the domestication of new wild plants was a rare phenomenon. Some crop plants appeared mainly as a result of weed domestication under the migration of agriculture in more severe regions. The domestication of wild plants became again an important element in the development of agriculture from the end of the 19th century. It was and is connected with an intensification of agriculture (new forage crops), with the development of industry (the demand for rubber, camphor, new types of plant fibres) and with the rising needs for medicinal remedies (the use of quinine, aloe, domestication of principal medicinal species of European origin). Some of the new experiments in the domestication of wild plants were successful and increased the complex of cultivated plants, whereas some failed. These were only empirical experiments. The theoretical basis of plant domestication is not yet formulated sufficiently well. The author experimented over many years with the domestication of different wild plants (new oil, fibre, forage, rubber, and medicinal plants). He now formulates certain elements of the theory of plant domestication.

Economic and Biological Prerequisites for Plant Domestication

The rise of agriculture and the origin of crop plants obviously had an economic reason: a cultivated plant repays better the labour of man than a collection of plant products in virgin nature. But a new domesticated plant must also be able to compete successfully with its economic rivals among the ancient crop plants, with the industrial manufacturing of such products and their imports.

Thus the successful domestication of the red clover in Central Europe in the 18th century was influenced: a. by the progress in cattle rearing; b. by the absence of cultivated forage hay and pasture plants; c. by the very good red clover forage, the best leguminous species in Central Europe. The domestication of the para rubber tree in Malaya and Indonesia at the end of the 19th century was promoted by such prerequisites as: a. the absence of cultivated rubber plants; b. the better quality of the para rubber and its low price compared with the rubber obtained from other wild plants; c. the presence there of experienced tropical farmers and cheap labour. The fox grape (*Vitis labrusca* L.) was domesticated in the eastern states of the USA at the end of the 19th century as a substitute for the European grape (*V. vinifera* L)

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which suffers in these regions from phylloxera and mildew and cannot grow successfully; the yields of fox grape were then able to compete with imports of European grape and with the products of their processing.

The disregard for economic considerations in the domestication of certain plants was the cause of many experiments which came to nothing.

Examples are the domestication of the kok-saghyz as a rubber plant and of the clove-root plant (*Caluria geoides* Ledeb.) as an eugenol crop plant. These plants are undersized, require very intensive cultivation and cannot compete with imported para rubber from Indonesia and Malaya and clove from Zanzibar. The domestication of wild actinidias (*Actinidia kolomikta* Maxim. and *A. arguta* Planch.) in the Central Chernozem region of Russia failed: the fruits of these species cannot compete with those of cultivated berry bushes usual for this region. Soviet and collective farms now seldom cultivate actinidias and there is no market in the USSR for berries of these species. An analogous case is the prairie dogbane (*Apocynum lancifolium* Russan. and *A. scabrum* Russan.). The wild forms of these plants gave a sufficiently valuable fibre for consumer communes of the Kazakhs, but it was an error to suppose that the cultivated prairie dogbane would be able to compete successfully with such textile plants as cotton, hemp, jute, and rami on the modern world market.

Native wild or weed plants can be mentioned as a more frequent object of domestication. They are already adapted to the climate and soils of their future cultivation, and they must adapt also to the conditions of cultivation. Such cases were known in antiquity and are also often repeated in modern times.

Examples are the camphor tree (*Cinnamomum camphora* T. Nees et Eberm.) in Japan, the tung-oil tree in the basin of the Yantze Kiang, the loganberry (*Rubus loganobaccus* Bailey) and the black raspberry (*Rubus occidentalis* L.) in the Eastern states of the USA.

The domestication of foreign wild plants is also very charteristic of the 19th and 20th centuries. Examples are:

1. the forage species of the European flora e.g. timothy (*Phleum pretense* L.) and sweet clover (*Melilotus albus* Desr.) in North America, where such good forage plants do not exist in the native flora;
2. the quinine (*Cinchona ledgeriana* Moens.) from the high mountainous regions of the tropical Andes which are not fit for quinine plantations; domestication was accomplished in South East Asia which is a region of ancient advanced tropical agriculture;
3. the cashew (*Anacardium occidentalis* L.) from the Amazon jungles which is domesticated in India;
4. the Mediterranean clover (*Trifolium subterraneum* L.) which is domesticated in Australia, where the native flora is very lacking in good forage species.

Domestication is an adaptation of the initial wild or weed plants to cultivation on plantations. This phenomenon is complicated in the case of foreign wild plant domestication where it is necessary to adapt to a new soil-climatic complex. Sometimes this adaptation can be decisive in successful domestication.

Selection for winter hardiness was very important in the domestication of the Australian silver wattle (*Acacia dealbata* Link.) in West Georgia (USSR) and also in the domestication of the Mexican guayule (*Partherium argentatum* Gray) in the Small Caucasus foothills. It may also be the case that the new soil-climatic complex in the region of domestication will be more favourable for the foreign wild plant then that in its native land. This situation is favourable for artificial selection e.g. the kok-saghyz in the Leningrad region had larger roots than in Central Asia.

Plant Ecotypes Grouped According to Their Adaptability to Cultivation

In breeding for domestication, natural selection plays the main part and the genetic character of the initial material is very important. For agriculture the flora is differentiated into 3 basic groups, crop, weed and wild plants.

Crop Plants

Crop plants are adapted to growth in cultivated plantings, to satisfy the demands of their cultivator and to make use of his care. They are ideal ecotypes to which wild and weed plants must aspire through domestication. Water and mineral nourishment of the cultivated plantation is usually more favourable for plant growth than the regime of virgin soils, so that natural selection gives preference to larger individuals from which are formed typical crop plant ecotypes. To satisfy harvest requirements the fruit, in most cultivated plants, ripen over a relatively short time period, and the seeds do not fall readily after ripening, especially in field crop plants. The seeds of field or kitchen garden crop plants have no long dormancy, germinate promptly in favourable conditions, and their seedlings emerge together during a short period of time.

Weeds

Weed plants have also evolved under the control of natural selection on cultivated plantations, but without the patronage of the planter. Weeds are the enemies of the farmer and he aims to eradicate them as rivals of his crop plants. The weeds can triumph in the struggle for life only by adapting to agricultural methods directed towards weakening and eradicating them. This adaptation can take two ways, one convergent with the evolution of the crop plants and the other divergent with this evolution.

Convergent Adaptation

The weeds of the convergent group imitate crop plants. They develop and ripen simultaneously with the crop plant. Their fruit and seeds are not easily shed from their parent plants. In some their ripe dry fruit with many seeds dehisce relatively feebly (in the cockle for instance). Thus the seeds of the convergent group are harvested with those of the crop plant. The seeds or fruit of the weeds of the convergent group are relatively large and are similar to the crop plant seeds in their mobility. They can be separated from crop plant sowing material only with some difficulty and are sown together with it. The seeds of such weeds germinate promptly in favourable conditions, the seedlings emerging more or less simultaneously with those of the crop plant, so that the weeds of the convergent group can be domesticated very easily.

At present the domestication of weed ecotypes of the following species is observed: the blue corn flower plant (as an ornamental flower plant in Western Europe); the sweet clover (*Melilotus albus* Desr.) (as forage plant crop in the USA); the Tatar buckwheat (*Fagopyrum tataricum* Gaertn.), as a substitute for the usual cultivated buckwheat in Eastern Siberia.

Divergent Adaptation

The weeds of the divergent group evolve in the direction which tends to escape the methods of cultivation levelled at weed control. They are not similar to crop plants and have relatively weak shoots with many flowers and fruit. Their numerous seeds are small and ripen and fall earlier then those of the crop plant. Some have a pappus. Many weed species of the divergent group can also multiply vegetatively by means of rhizomes, roots, rooting of stems and other vegetative organs. Germination lasts for a very long time, perhaps several years. These weeds begin to flower earlier than the crop plants and flowering and fruiting last for many weeks. These weeds produce seed very abundantly.

Examples are the yellow foxtail (*Setaria viridis* P.B.), the Canada thistle (*Cirsium arvense* Scop.) and the common chick weed (*Stellaria media* Vill.).

The weeds of the divergent group are very different from the crop plants and their domestication entails many difficulties. The basic obstacles are small seeds, slow and prolonged germination which leads to a plantation heterogeneous for age, with differing times of fruit maturation, accompanied by fruit dehiscence and shedding of seeds or indehiscent fruit. Certain ecotypes of such weeds are adapted to germinating with a covering of the crop and do not sprout when they are sown without this crop plant.

For instance, the treackle erysimum (*Erysimum heiranthoides* L.), which is a common weed of summer grain crop plants in West Siberia, germinates only with a covering of the oat, barley or wheat. When it is sown apart (without grain crop plants) its seeds do not germinate: such small seeds do not survive deep sowing and where embedding is shallow the upper soil layer dries up rapidly, preventing germination. The most successful domestication of the weeds of divergent group is as forage crop plants, where the differences in age of the plants in the planting are less significant, e.g. the white sweet clover, green foxtail, Guinea grass.

Wild Plants

Wild plants are very polymorphous ecologically. Some are adapted to conditions which coincide with some elements of the adaptation to cultivation, for instance, fast and simultaneous seed germination, a positive reaction to sun, and relatively high soil fertility and good humidity. Such wild ecotypes have certain ecological characters usual in crop plants. They have a tendency to anthropophily and often grow near human dwellings. These anthropophilous wild plants resemble the weeds of the convergent group and can be cultivated easily.

They include: perennial Kupriyanov rye (*Secale kuprijanovii* Grossh.) growing on the cattle prairies of North-Western Caucasus; wild anthropophilous sunflower (*Helianthus annuus* L.) growing near the dwellings of Indians in the prairies of the USA; the deadly nightshade (*Solanum nigrum* L.), a common plant near peasant dwellings and on melon fields in the Lower Volga region. Certain wild trees and shrubs can be cultivated very easily by planting their seedlings from a nursery or by vegetative propagation. Examples recently domesticated are: para rubber tree (*Hevea brasiliensis* Mull.) in Malaya and Indonesia; tung oil tree (*Aleurites forcii* Hemsl.) in Southern China; fox grape (*Vitis labrusca* L.) in the South-Eastern states of the USA; the high bush blueberry (*Vaccinium corymbosum* L.) in the North-Eastern states of the USA.

Certain wild herbaceous plants and shrubs do not however adapt to growth on cultivated soils with their peculiar biological activity and strong porosity.

Such plants include the mountain cranberry (*Vaccinium vitis-idaea* L.), the tausaghyz (*Scorzonera tsu-saghyz* Lipsch. et Bosse) and the prairie dogbane (*Apocinium lancifolum* Russan. and *A. scabrum* Russan.).

Among the decisive biological characters for successful field culture is simultaneous seed germination. There are 3 basic types of seed germination among wild plants: 1. seeds germinate in favourable conditions relatively rapidly and simultaneously, similar to the seeds of crop plants and weeds of the convergent group (*Secale kuprijanovii* Grossh., *Scorzonera tsu-saghyz* Lipsch. et Bosse, *Plantago psyllium* L.); 2. seeds have a very prolonged germination even in favourable conditions and are similar to seeds of weeds of the divergent group, (*Senecio rhombifilius* Sch.

Bip., *Adonis vernalis* L., *Parthenium argentatum* Gray.); 3. seeds do not germinate without stimulation by certain factors, e.g., low or high temperatures, alternation of humidity and dryness (*Convallaria majalis* L., *Trollius asiaticus* L., *Colchicum autumnale* L.). The wild plants with seeds of the first type can successfully germinate in cultivated soil and, secure in the favourable conditions, can produce a population of similar age. Wild plants with seeds of the second type can be domesticated only with great difficulty and require a change in their germination biology by means of genetic reconstruction or some form of seed treatment. The wild plants with the last type of seed can give a good plantation of similar aged plants only after certain seed treatment; such methods complicate the cultivation of these plants. Transmutation of this seed germination type by genetic means would probably be more rewarding but would entail many difficulties.

The size of seed is an important character in domestication: it affects the exit of seedling shoots from the soil and controls subsequent growth of the seedlings and their development. There is wide variation among the wild plants, from the seeds similar to those of crop plants (*Secale kuprijanovii* Grossh., *Scorzonera tau-saghyz* Lipsch et Bosse, the ginseng, the lily of the valley), to extremely small seeds of weeds of the divergent group (*Digitalis lanata* Enrh., *Polemonium coeruleum* L., *Plantago psyllium* L.). Seed size is important for the crop plants of field culture, but loses its importance when a wild plant is domesticated for market-gardening or forest culture with the use of nursery sowing.

The rates of growth and development are very variable in wild plants. Some grow very slowly in comparison with crop plants, while others develop too rapidly and can be domesticated only by selecting the genotypes with slower development (*Cichorium intybus* L., *Taraxacum kok-saghyz* Rodin). Certain wild plants are characterized by summer dormancy (*Cyclamen persicum* Sibth. et Sm., *Scorzonera tau-saghyz* Lipsch. et Bosse, *Urginea maritima* Baker), which shortens their growth period. The cultivation of such ecotypes outside subtropical zones is absolutely impossible. Their domestication can be based only on selecting the genotypes in which summer dormancy is weakened or quite lacking (Kupzow 1965, 1971a, 1971b).

Naturalization in Culture

The adaptation to new conditions of existence can be accomplished as a result of successful growth and development of the introduced plant in its new region without any genetic change (according to H. Mayr: Waldbau auf naturgeschichtlicher Grundlage, 1925, this phenomenon is called 'naturalization'). In contrast, certain plants cannot be naturalized in the new unaccustomed conditions and their plantations there are unsatisfactory. Some success can be attained there only by genetic transformation of the initially introduced material ('acclimatization', according to Mayr). In the process of domestication there can also be a successful naturalization in cultivation (Fig. 1) or a failure of the naturalization experiments (Fig. 2). The phenomenon of the naturalization of wild and weed plants in cultivation can be observed in many species especially in anthrophilous wild ecotypes and in weeds of the convergent group, but is very seldom observed in the weeds of the divergent group.

The naturalization in culture has been the initial stage in domestication of the following wild plants: para-rubber tree, tung-oil tree, red clover, subterraneous clover, fox grape, wild black plum, loganberry and many others. These wild species formed good planta-

Fig. 1. The wild perennial Kupriyanov rye (*Secale kuprijanovii* Grossh.) cultivated in the Kaluga Botanical Garden. An example of a successful naturalization in culture.

Fig. 2. The wild tau-saghyz (*Scorzonera tau-saghyz* Bosse et Lipsch.) cultivated in the Atabaevo experimental station (Southern Kazakhstan). An example of an unsuccessful naturalization in culture.

tions their seeds were sown or their seedlings planted. The growing of seedlings of certain arboreous and shrub wild species in special nurseries, with more intensive agrotechnics than on commercial plantations, and the subsequent planting of such seedlings in the usual plantations, was a good method favouring the naturalization in culture of these species. Thus successful cultivation of the guayule became possible only by using irrigated nurseries where the seeds were sown and seedlings grown. The sowing of this wild plant directly onto the soil of a semidesert without irrigation was ineffective.

In some cases wild plants can be cultivated by grafting onto better growing stocks. The modern culture of *Cinchona ledgeriana* Moens. is based on the grafting of this species onto the stocks of *C. succirubra* Pav.

It is possible to modify certain climatic factors during the domestication of foreign wild plant species by using agricultural methods such as irrigation, warming during certain developmental stages (including growing seedlings in special nurseries or propagating frames) and special seed treatments (scarification, stratification, warming up, alternate soaking and drying). Annual culture of some perennial wild plants is also possible, e.g. the domestication of the kok-saghyz.

The experimental domestication of the guayule in the foothills of the Small Caucasus was also attempted by cultivating the plant on the open ground only during one summer: the seedlings, from special irrigated nurseries were transplanted in spring, after their first wintering, onto the commercial plantations and were harvested in the autumn for rubber extraction. There was also an attempt to domesticate the cinchona tree (*Cinchona succirubra* Pav.) in the West Transcaucasus by cultivation during only one summer, following transplantation in spring of cuttings rooted during the previous summer and wintered under glass. In the autumn they were harvested for alkaloid extraction. Both these attempts have been abandoned as uneconomic.

Even with relatively successful naturalization of wild or weed plants in cultivation, the modern plant breeder who knows their geographical distribution must solve the problem of which of the existing wild or weed populations from different regions would be the best for experimental domestication. The selection of distinct genotypes inside certain populations of wild or weed ecotypes must also be decided. When certain interesting characters are variable depending on the surrounding conditions, such selection can be executed only by testing in the culture conditions in the regions where naturalization of these species occurs.

The study of ecologic differentiation in the valerian (*Valeriana officinalis* L.) in the USSR showed that the best ecotypes for root production and pharmacological quality were those from the forest-steppe of the Ukraine. Investigations on the wild populations of the guayule from its natural area in northern Mexico and the South-West of the USA showed that the best for domestication in the USSR are the populations from Texas, which have a higher rubber content. In the tau-saghyz, whose natural area is in the mountains Kara-Tau (Southern Kazakhstan), the ecotypes of Jelagan-Ata (central part of the range) showed the best productivity in the irrigated plantations of Central Asia and on the forest-steppe of the Ukraine.

But certain characters of plants are sufficiently stable not to change very greatly when the wild ecotypes are naturalized on cultivated plantations.

Thus, differences in the colour and taste of drupes of individual trees in the wild populations of myrobalan plum (*Prunus divaricata* Ledeb.) are retained by grafting such individuals on the usual plum stocks and also, but to a lesser degree, in their seedlings in culture. Thus the variants with differing drupe colour (yellow, red) and taste (more or less sour or sweet) from the wild ecotypes of myrobalan plum in the Caucasus and Central Asia can be preserved on cultivated plantations in these countries. Among wild populations of the almond tree (*Amygdalus communis* L.) in Central Asia, there are very rare individuals with sweet kernels. They are obviously destined for selection and domestication by grafting or sowing. It is also possible to select from the wild populations and adopt for culture the mutants with differing colours of flower (white, rose, red) in such species as *Galega orientalis* Lam., *Polemonium coeruleum* L., *Nerium oleander* L., and *Digitalis purpurea* L. These recessive mutants, as experiments have shown, are poorer in pharmacological constituents but can be used as ornamental plants.

It is necessary to take into account the fact that the conditions of naturalization of wild plants in culture produce new phenotypes of their genotypes, and that during subsequent cultivation under the same conditions these modifications must be kept.

The wild tau-saghyz in its natural area in Kara-Tau reaches a root diameter of no more than 1 cm and has scarcely begun to bloom at the age of 10 years; in culture this plant forms a thicker root and begins to bloom at the age of 2 - 3 years. The wild ginseng (*Panax schinseng* Nees.) blooms only by the age of 10 - 12 years of even later in the forests of the Soviet Far East, but in culture it blooms at the age of 3-4 years both in that region and in the European region of the USSR. The conditions of seed ripening in nature control, at times, the process of slow prolonged seed germination. The seeds of a plant formed in culture are larger and have a shorter period of germination. Some seeds (25-35%) of the kok-saghyz in its natural area in Tian-Shan have a period of dormancy; this is probably the result of low temperatures during the period of ripening. In the wild kok-saghyz of the plantations in Burnoe (a high point in the mountains of Southern Kazakhstan with low night temperatures in summer), 30% of the seeds show dormancy; in the irrigated oases of Central Asia and in different regions of the European part of the USSR (with milder climates) only 2-7% of seeds of the kok-saghyz from cultivated plantations have a period of dormancy. In one experiment with *Delphinium elatum* L. only 5% of seeds gathered in the wild in the region of Novosibirsk showed rapid germination, the rest having a long period of dormancy. The first reproduction of this population on the plantations near Moscow already showed a seed germination of 58%, with a large decrease in seeds with dormancy.

Surely it should be possible, during the reproduction of wild populations on cultivated plantations, to create a combination of the phenotypical influence of the new environment with the action of natural selection for genotypes better adapted to cultivation. The role of the first factor is undoubtedly very important. The more favourable conditions for growth and development on cultivated plantations compared with virgin nature usually produce a shortening of the period of dormancy. Such seeds sprout more rapidly and give larger seedlings; this favours naturalization of the wild ecotypes in culture.

The problem of domesticating wild species outside their natural area arises as the global problem of naturalization. Usually cultivation facilitates the struggle for existence for a domesticated plant and favours its wider diffusion.

The wild pear tree (*Pyrus communis* L.) in the woods of the European part of Russia does not spread north of latitudes of 50°, while in culture it grows successfully in Leningrad and further north. The wild opuntias of Mexico grow excellently as cultivated plants or weeds on the northern coasts of the Mediterranian Sea. Many xerophilic species can be domesticated successfully in regions with adequate moisture. Plant ecotypes demanding water can be cultivated in arid regions on irrigated plantations. Sometimes it is enough to provide inter-row hoeing of soil. Thus the fig (*Ficus carica* L.), almond (*Amygdalus communis* L.) and pistachio (*Pistacia vera* L.) can be cultivated in the semideserts of Kopet-Dag (Central Asia) without irrigation.

The success of naturalization depends on a positive reaction by the naturalized plant to the new conditions of cultivation. It is not decisive that the climates of the areas of origin and of introduction should be similar.

The fruit trees of the genus *Citrus* originated in tropical South-Eastern Asia but are chiefly cultivated in subtropical regions both humid and arid (with irrigation of the latter). The winter crop plants of the Mediterranean Sea region, such as cabbage, beet and onion, are successfully cultivated in the taiga region of Europe and Siberia. The lilac (*Syringa vulgaris* L.) grows wild in the woods of the Near East, the Balkan peninsula and Central Europe and is cultivated in all taiga regions of Europe and Siberia. In the tropical zone of Africa certain wild and weed grasses of temperate climates, such as the Bermuda grass (*Cynodon dactylon* Pers.) and the Bahia grass (*Paspalum dilatatum* Poir.), are new successfully domesticated as forage crop plants.

The naturalization of wild and weed ecotypes in culture can, however, be only a temporary stage in the process of domestication. These ecotypes can never be completely adapted to cultivation as crop plant ecotypes. The wild or weed populations naturalized in culture undergo an inevitable genetic change under the control of natural selection in the new conditions of the cultivated plantation. Thus the naturalization in culture is a temporary phenomenon which can last for several years, but cultivation involves subsequent genetic changes in the domesticated ecotypes, and naturalization is replaced gradually by acclimatization in culture with the formation of complete crop plant ecotypes. (Kupzow 1971b, 1973, 1975).

Acclimatization in Culture

The phenomenon of acclimatization is the adaptation of a plant species to new environmental conditions by means of genetic changes in the composition of its populations or by the advent of new genotypes and their subsequent selection.

Choice of Population

The transformation of wild plants or weeds into cultivated ones depends on the choice of their best populations as the initial material for subsequent domestication. In accordance with the use envisaged for the new crop, it is necessary to orient domestication towards the initial populations most similar to the projected ideal.

For instance the Altai ecotypes of the orchard-grass (*Dactylis glomerata* L.) are more productive as forage crop and ripen earlier than the European wild populations of this species. Most wild populations of the German chamomile (*Matricaria chamomilla* L.) have a sufficiently high content of chamazulen in their calathides, but their ecotypes from West Siberia (Novosibirsk region) have no chamazulen, and can not be domesticated as a future medicinal crop. From the populations of the wild perennial rye only *Secale kuprijanovii* Grossh., which originates in the North-West Caucasus and reaches a height of more than 2 m, can be recommended as the initial material for domestication as a forage crop. Assessment of the wild common *Valerian* species leads to the conclusion that the best for domestication as a medicinal crop will be the ecotypes of *Valeriana cardamines* M.B. from the Great Caucasus. The guayule populations from Texas (USA) are the best for domestication for rubber; they consist only of individuals of the variety *angustifolium* Nic. which has a high rubber content and vigorous production of stems and roots. The Mexican guayule populations are inferior.

The next step is the analysis of the initial wild populations on the cultivated plantation. The study of wild ecotypes in their natural environment makes it possible to select certain interesting genotypes, and this selection begins the first tests of such populations under the conditions of cultivation.

Thus in the wild populations of the almond in Kopet Dag, occasional individuals are found having kernels without amygdalin. Among the ecotypes of the European birdcherry (*Padus racemosa* Gilib.) in Narym (West Siberia) are found individuals with early flowering (before the opening of leaf buds) and with late flowering (after leaf bud opening). This makes it possible to breed two different ornamental varieties. Among the ecotypes of the aspen (*Populus tremula* L.) in the woods of Narrbotten (Sweden) and Novosibirsk (West Siberia), triploid forms were found, which, being bigger and faster growing, had a higher potential as cultivated genotypes for the production of workable wood.

Selection

The subsequent transformation of wild initial populations must be accomplished by the breaking up and recombination of their genetic components. The most important role in this process of domestication belongs to natural selection through which the initial wild populations adapted to their new habitat under cultivation. In this way the struggle for existence corrects the results of artificial selection.

Natural selection can be directed against the breeder's efforts, so the effects of the struggle for existence need to be suppressed by the action of careful artificial selection. Certainly the suppression of natural selection and the choice, in spite of it, of economically valuable characters diminish some characters of adaptive importance. Cultivated plants are usually more fastidious and less easily withstand unfavourable conditions than do their wild ancestors. The necessity for better care has to be compensated by increased yield. This loss of certain adaptive characters in the process of domestication can sometimes be conducted consciously. The evolution in culture of perennial wild plants as future root-crops is directed towards selecting individuals with larger roots, which are usually biennial, so that the cultivated beet and chicory lose their longevity.

In the domestication of the tau-saghyz and kok-saghyz the loss of longevity and transformation into biennial root-crops were envisaged in the breeding plan. During domestication of the guayule, the simple reproduction of its Mexican populations on the plantations, without any artificial selection, resulted in a large reduction in the rubber content of later generations, since the genotypes with a high rubber content have achenes with very resinous coatings and low germinating ability. Genotypes with an abundance of well germinating seeds and low rubber content (2-3%) therefore triumphed in the struggle for existence.

In certain cases of the favourable action of natural selection on the plantations, the necessity of its corroboration by artificial selection can be doubtful. The struggle for existence on the cultivated plantations within wild populations can be so strong that only a few individuals survive there. Such results of natural selection are not inferior to the results of a stringent artificial selection.

For instance, no more than 20-30% of tau-saghyz seedlings survived on the plantations in the third year of life and only 10-30% of them flowered at this age, so that the yield of seeds was equivalent to the selection of 1-6% of seedlings. The result of such natural selection was a large decrease in seedling death on plantations, an increase of mean root diameter by almost $1\frac{1}{2}$ times and a 2-5 fold rise in the numbers of individuals flowering in the third year of life (fig. 3). Even a severe artificial selection does not produce such good results, especially in cross-pollinated species. The problem of domesticating *Acacia dealbata* Link. on the Black Sea coast of Georgia was solved basically by natural selection which has destroyed a huge number of genotypes in its wild populations from New Zealand (perishing from frost) and retained only single individuals (the most frost-resistant in culture conditions).

When natural selection is very hard the necessity for additional artificial selection initially falls away (and at times so does its possibility). But if a sufficient number of individuals survive in the struggle for existence on the plantations, the development of mass artificial selection considerably accelerates the evolution of wild ecotypes towards domestication.

Sometimes the result of natural selection on plantations depends on cultivation methods accepted there. Thus the populations of the kok-saghyz, wild beet and wild carrot evolve inevitably with a prevalence of small individuals flowering rapidly during the first year of life when their reproduction is based on seed collection from the plantations of the first year. When collection is accomplished on the plantations in the second year natural selection conducts evolution towards a predominance of genotypes with larger roots which flower only in their second year. Therefore, during the domestication of kok-saghyz, its reproduction on the seed-growing plantations was based only on seed collections from the 2-year-old plantations, as a method helping to domesticate the best genotypes of this plant. A knowledge of the correlations which exist in the initial wild populations, and study of the struggle of their components among them, are necessary for the breeder to determine his attitude to natural selection: whether to utilize it as his ally, to struggle against it as his enemy or to be able to regulate it and turn it into an ally.

Even the most stringent natural selection on the plantations usually retains sufficient individuals for the development of individual artificial selection on their basis. The limited number of these individuals underlines the necessity for individual selection rather than the mass one.

Mass selection occupies a peculiar position in the pro-

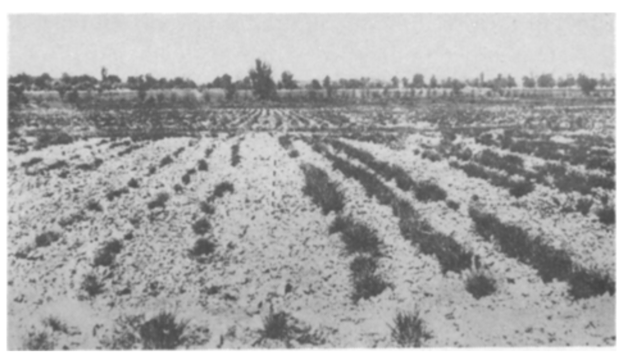

Fig. 3. The tau-saghyz cultivated in the Kaunchi experimental station (near Tashkent). Left: the plants from the seeds collected in a natural association; right: the plants from the seeds ripened on the specimens grown on cultivated plantations. A result of natural selection and prolonged modification in culture.

cess of domestication. It is able to give improved material quickly and in significant amounts before more perfect varieties are created through individual selection. To use this advantage during the first stages of domestication it is necessary to be guided by the laws of an inner differentiation which act inside populations and on this basis to choose the most favourable direction of mass selection. Mass selection should be orientated not towards the greater number of easily estimated characters but towards the improvement of some of their complexes. By such methods the process of mass selection can be accelerated and can be extended to the volume of the breeding work.

The correlation of economically important characters, which are difficult to estimate, with easily visible morphological peculiarities is very important for such selection.

Selection according to indirect morphological characters has been very successfully utilized during guayule domestication in the Eastern Transcaucasus. The analysis of wild populations of this species led to the conclusion that their components, which have been distinguished as different varieties, differ strongly in rubber content. Some of them are also very stable because of the predominance of apomictic seed formation (pseudogany). Var. *angustifolium* Nic. was the most valuable of the widely distributed varieties but f. *argentata* N. Kult., which is relatively rare, was even more valuable. This has allowed mass selection to be oriented to choosing these genotypes according to their morphological characters, thus creating the first Soviet cultivated varieties of the guayule: Uzkolistnaya (var. *angustifolium* Nic.) and Pioneer of Karabakh (f. *argentata* N. Kultiasov). These varieties had a rubber yield of 1 metric centner from 1 ha on the first year plantations. This yield was 1,5 times higher than the productivity in culture of the intitial Mexican populations where the var. *brevifolium* Nic. is predominant; and the mean yield of populations resulting from simple reproduction of wild populations without any artificial selection was 2-4 times lower.

During the utilization of mass selection for one single character one must not forget the possibility of diverting the process of change in an undesirable direction. The first Soviet varieties of the guayule created by mass selection had a considerably increased rubber content and rubber yield, but their seed production and seed germination ability were sharply diminished compared with initial wild populations. The wild population in culture had a seed germination ability (which is very low in guayule in general) often of 50% or even more. In the variety Uzkolistnaya it has fallen to 20-30%. Of course such lowering of the seed germination ability was not catastrophic in the cultivation of the guayule, with the transplantation of seedlings, and later this defect was eliminated through individual selection.

It is necessary to know that the existing correlations reflect the principles of genetic differentiation of the initial and selected populations. They can be changed by altering their composition and environmental conditions. The correlations in the ecotypical differentiation of certain species cannot conform to the correlations which act inside separate ecotype populations.

The ecotypes of the tau-saghyz which develop more slowly and delay flowering are characterized by larger plant dimensions (including thicker roots). But inside their separate populations the individuals with earlier flowering (at the age of 2-3 years) possess the biggest roots. The breaking down of the initial population to its elementary genotypes often reveals new correlations which did not exist in the initial intact population. The initial wild populations of the tau-saghyz have no negative correlation between root dimensions and rubber content, but this correlation becomes visible during the mass selection of plants possessing large roots, and grows clearer with each new round of selection and with greater levelling of the populations according to root dimension.

The choice of the best wild ecotypes, natural selection on plantations and artificial mass selection are based on the already present differentiation of the initial material, but, to create good cultivated varieties, genotypes which break the laws of such differentiation and the correlations existing in the initial material are often necessary. These can be identified by individual selection.

Mass Selection in Guayule and Tau-Saghyz

In the guayule, mass selection resolved the problem of the economic advisability of cultivation in the Eastern Transcaucasus, but in the semideserts of Turkmenistan cultivation without irrigation can be based only on the extremely xeromorphous genotypes which are very rare in the guayule populations. The individual selection of the guayule in Kara-Kala (South-Western Turkmenistan) uncovered the lines which preserved their green leaves and flowered during the whole summer, while all other forms of the guayule were dormant during this dry hot period. It is evident that the successful cultivation of the guayule in Kopet Dag is practicable only on the basis of varieties without summer dormancy. Their yield of stems and roots there was more than twice the yield of the best lines with summer dormancy. The lines with summer dormancy had 4,2% of rubber and the best lines without summer dormancy 4,5%.

It was then necessary to improve the first Soviet varieties of guayule as a product of mass selection by increasing their seed germination ability and the ratio rubber: resin (it was 0,73 in Pioneer of Karabakh). By means of individual selection in the Eastern Transcaucasus new varieties of the guayule were created with seed germination ability of 24-25% and a ratio of rubber: resin of 1,31.

Mass selection could not create varieties of the kok-saghyz with a high content of rubber because, among the roots which had a top diameter of more than 2,5 cm, a negative correlation between root dimension and rubber content was apparent. The first Soviet cultivated varieties of the kok-saghyz were created by means of individual selection based on correlation-breakers which had an average root weight of 7,5 g (in the initial population it was 5,9 g) and a rubber content of 5,9-7,6% (in the initial population it was 5.5%).

Some effect of individual selection was also observed in the domestication of the tau-saghyz, although it was relatively small compared with the effect of natural and mass selection. The best families of the tau-saghyz in Kaunchi (near Tashkent) were characterized by an increase in root yield of no more than 4 metric centners per ha, in comparison with the material improved by natural or mass selection with an almost invariable rubber content and also with an invariable percentage of individuals flowering during the third year of life (39-46%).

Wild plants have one very advantageous moment during their domestication: it is a sharp positive asymmetry of their curves of variations in a series of their economically valuable characters. Thus the breeder can rely on the variants greatly deviating from the mode. Also, the first cultivated varieties created on the basis of acclimatization in culture usually are greatly improved in comparison with the initial wild material. The one mass selection increased the rubber content of guayule 2-3 times. Each of the first rounds of mass selection in the tau-saghyz increased by 2-3 times the numbers of individuals flowering in the third year of life. In the kok-saghyz, family 485, a product of three family selections, decreased by 3 times the percentage of individuals flowering during the first year of life, increased the yield of roots from one ha almost $1\frac{1}{2}$ times and raised the rubber content in them more than 15%. For the ancient crop plants such improvements are inconceivable.

Populations of wild plants and weeds are usually sufficiently polymorphous to offer advantageous subjects for selection. This is concerned with the characters which are visible and also with the hidden recessive ones, which will be inevitably revealed after some generations in cultivation. Mutations in nature often produce genotypes which are not adapted to their habitat and are eliminated by natural selection when their harmful characters become visible. When these genes are recessive, they can be kept in the population in a hidden condition and become visible and not harmful in some new conditions. Domestication can be very convenient here through the mitigation of natural selection.

Flower Mutations

The appearance of individuals with white flowers in species which in nature have coloured flowers is very well known in the process of domestication. Apparently these white-flowered mutants are less viable than the initial forms with coloured flowers. Individuals with white flowers in the cultivated populations of Jacob's ladder (*Polemonium coeruleum* L.), purple foxglove (*Digitalis purpurea* L.), oleander (*Nerium oleander* L.) and sun-dial lupin (*Lupinus polyphyllus* Lind.) have a lower chlorophyll content in their leaves, poorer respiratory enzyme activity (catalase and peroxidase), a slackening of the growth process and a decrease in the synthesis of physiologically active compounds (saponines, steroid glucosides, alkaloids). During tau-saghyz domestication it was very characteristic that single gigantic individuals appeared, without summer dormancy and which could grow during the entire summer in conditions of sufficient soil moisture; they were inevitably doomed in the natural area of this species in Kara Tau (Southern Kazakhstan) with an inclement summer drought. A seedling with large fruit arose in the cultivated population of wild ground cherry (Cerasus fruticosa Pall.), and it became the predecessor of the new cultivated variety 'Griot grushevidnyi' of I.V. Michurin.

The artificial transformation of natural genetic resources (hybridization and experimental mutagenesis) can also take place. During domestication interspecific hybridization is usually used earlier than the intraspecific type, because the rational utilization of the latter is possible only after careful study of the variability laws inside the initial wild populations of the interesting species, and of the resources of genetic elements which are desirable for the future crop plant and are present in its congener species.

Interspecific Hybridization

In the past an interspecific hybridization was very important in the domestication of the banana, sugar cane, wheat, plum and strawberry. However, failures are also possible. The hybrids of the guayule with the mariola (Parthenium incanum HBK.) gave by segregation a complex of guayule forms already existing in the natural populations of the *Parthenium argentatum* Gray. In the domestication of the subsequently bred apomictic pseudogamous forms with a facultative amphimixis, it should be possible to recommend as a prospective method the hybridization of the best amphimictic forms with apomictic ones, to attain the combination of the complex of economically and agronomically valuable characters with apomixis.

At times interspecific hybridization can help a wild species in adapting to cultivation conditions and domestication. Many very valuable ornamental species of the genus *Sarcochilus* (Orchidaceae) are represented in the virgin flora of Australia, but almost all of them do not naturalize in culture. Only one, *S. hartmanii* F. Muell., can be successfully cultivated. Apparently the hybridization of the other wild species of the *Sarcochilus* with *S. hartmanii* F. Muell. can be utilized as a method of obtaining new interesting forms of different *Sarcochilus* species adapted to cultivation.

Polyploidy

Artificially induced tetraploidy is probably a very valuable method in the process of domestication. In most cases the tetraploids of wild plants and weeds differ from their initial diploid forms in having larger seeds (this facilitates the shooting of seedlings through the seed covering) and larger underground and aboveground organs (which facilitate care of the plants and help to improve yield) (fig. 4 and 5). In many cases the tetraploids have a higher content of certain chemical combinations (e.g. rubber in the guayule,

Fig. 4. The ordinary diploid weed Tatar buckwheat (*Fagopyrum tataricum* Gaertn.)

Fig. 5. The experimental tetraploid Tatar buckwheat.

hyoscyamine in the jimsonweed dature, quinine in the quinine tree, chamazulon in the German camomile). Among the vegetatively reproducing plants the experimental triploids are also of great interest for domestication, for instance the Caucasian pyrethrum – Pyrethrum roseum M.B. Many ancient cultivated plants are represented by their polyploid forms.

Use of Mutants

The utilization of gene mutants in the process of domestication is not, as yet, studied. It is known that in the wild strawberry (*Fragaria vesca* L.) experimental mutagenesis produced mutants with one simple leaf blade, mutants with very rapid development which bore fruit during the first year of life, and mutants without creeping stems. The appearance of characters obviously adaptive to cultural conditions as a result of experimental mutagenesis has not yet been described.

It is possible that the methods of experimental variability, including hybridization, polyploidy, and gene mutagenesis, will find their place in plant domestication. Certainly they will develop as a factor in widening the basis of individual selection after the analysis of initial wild populations and after the identification of the existing genetic resources of the wild or weed species introduced into culture. Only against this background can be revealed the perspectives of subsequent enrichment by means of combinative and mutagenic variations. Vavilov's law of homologous series in genetic variability will be a good guide in the choice of direction in selection and in the goals of hybridization and experimental mutagenesis (Kupzow 1971a, 1971b, 1973, 1975).

Literature

Kupzow, A.J. (1965): Dinamika estestvennogo otbora pri perekhode v kul'turu dikikh rastenii. Genetika 1, 150-160

Kupzow, A.J. (1971a): Osobennosti iskusstvennogo otbora pri vvedenii v kul'turu dikikh i sornykh rastenii. Geneticheskic osnovy selektsii rastenii. pp. 200-223. Moscow

Kupzow, A.J. (1971b): Elementy obshchei selektsii rastenii. Novosibirsk

Kupzow, A.J. (1973): Ekologicheskie usloviya vozdelyvaemykh plantatsii kak faktor evolyutsii flory zemnogo shara. Problemy ekologii 3, 43-51

Kupzow, A.J. (1975): Vvedenic v geografiyu kul'turnykh rastenii. Moscow

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