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Origin, Evolution, and Early Dispersal of Root and Tuber Crops

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Tropical root and tuber crops have been domesticated in Southeast Asia, west-central Africa, and tropical Latin America (including the high Andes). The crops belong to different families. Species of the one genus (*Dioscorea*) were domesticated independently in each of the three regions. Species of *Colocasia* and *Xanthosoma* (family Araceae) and *Pachyrrhizus* and *Pueraria* (family Leguminosae) were domesticated in separate regions. Many of these crops have restricted areas of distribution due to physiological requirements and are becoming relict crops.

Roots and tubers are ancient crops, and even today support groups of people who gather them from wild plants. Poisonous, acrid, or bitter qualities were found in the most important crops by early man, who learned how to remove or destroy these undesirable qualities. Most of the root and tuber crops are polyploids, and most of them are vegetatively propagated. Fertility traits are therefore of special importance in their evolution under cultivation, but there is no evidence that clonal propagation has led to sterility. Information on their evolution is extremely scarce as cultural sources, archaeological, linguistic, and historic information is scanty and unevenly distributed. On biological sources, comparative taxonomy, metaphase cytology, and hybridization have given some important clues, but there is still very little information available on the evolution of these species.

Root and tuber crops dispersed slowly between Southeast Asia and Africa. After the seventeenth century a very active interchange occurred especially with the American crops. Since then, there has been a continuous replacement of crop species, especially in Africa. The sweet potato, of American origin, was found in Oceania when the Europeans arrived, but no satisfactory explanation of how it got to Polynesia has ever been made.

Root and tuber crops are thought to be of ancient origin, and are often regarded as relics of primitive agriculture. This concept is based on the important role these crops play in existing primitive societies, and on the rudimentary husbandry they require, particularly vegetative propagation. These crops are easily adapted in the less-advanced agricultural systems because of their high yields, resistance and earliness, and in the dietary pattern by their bulk and taste qualities.

Since the last century, geographers and anthropologists have contrasted root and tuber production, which includes other clonally propagated crops such as bananas, breadfruit, sugarcane, with seed agriculture. Vegetative propagation, developed in tropical regions, is assumed to be a static system, whereas seed agriculture is associated with the development of more advanced societies. Geographers and historians are tempted to associate "civilization" with cereals. In vegetative propagation primitive farmers apply simple husbandry, but the same is true when they grow seed crops. On the other hand, some vegetative crops, such as potatoes, have reached an advanced stage of production and technology, comparable to many other crops. The view persists, however, that vegetative propagation represents a low stage of progress, and a distinguished cytogeneticist in his interpretation of history (Darlington 1969), points to "the fatal abundance of tropical root crops imported from Asia and America" as one of the main factors in the decline of Africa.

The contrasting of agricultural systems based on the differences between seed and clonal propagation is a simplification of a problem that is too complex to be reduced to the duality of planting materials.

The Basic Materials

Roots and tubers are storage organs that are developed in many families of plants, probably as a result of selective pressures in environ-

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ments with varying amounts of rain. The storage organs permit the accumulation of nutrients elaborated by the aerial parts of the plant. By growing underground, they maintain the nutrients with minimal loss. Once the temporary branches or foilage have dried, new shoots develop from the storage organs. By harvesting roots and tubers before the plants have flowered, man has interrupted this process, and has thus kept the plants in a kind of permanent juvenile stage.

Although storage organs may vary in their phylogeny and structure, the nature of their storage tissues is common. These organs are large masses of parenchyma that contain mainly water and starch grains. The parenchyma is intimately connected with the vascular system, which permits easy transport from and to the storage organs. Frequently, there are poisonous, bitter, or acrid substances in the storage tissues, which present an obstacle to the utilization of roots and tubers. However, these substances are a deterrent to animals and therefore play an important role in the survival of plants growing in natural conditions. The quantity of these materials (e.g. raphides or glucosides) varies considerably within the same species, a trait that is mainly determined by inherent factors.

The storage organs may be roots or stems. In roots, such as cassava, the storage tissues may derive from a normal cambium, or as in the sweet potato from tertiary cambiums that develop around vascular elements. Storage stems are of different kinds (e.g. rhizomes, tubers, and corms), and as in roots, the storage tissues may derive from different types of cambium. In most of the root and tuber crops, storage organs are more than carbohydrate sinks. They are also reproductive organs, and this double function has been of foremost importance in their propagation by man.

The common classification of crops by the utilization of certain organs results in artificial groupings. Thus, temperate species utilized for their roots or stems (radishes, beets) are considered as vegetables, whereas tuber crops yielding essential oils (ginger) are included among the spices. The present discussion is limited to tropical and subtropical species used mainly for their starch content as energy foods (Table 1).

Factors in Evolution

The usual sources of biological information on crop evolution — comparative taxonomy, cytological analysis especially at metaphase, and experimental hybridization — have been applied to some of the root and tuber crops. However, as a whole, the information available, with the possible exception of potatoes, is very poor and scattered.

Comparative taxonomy aims to establish the relationships among existing taxa with the cultivated species. The definition of their taxonomic position permits the identification of putative parents and the delimitation, within the genus, of the cluster of species more closely associated with the cultivated taxa. The traditional methods of taxonomy do not work well with root and tuber species. Often foliage is difficult to accommodate in herbarium sheets; flowers are bulky, fleshy, and frequently absent; root and tubers too difficult to preserve. In some genera, like *Xanthosoma*, the taxonomic status is extremely unsatisfactory; the abundant synonymy in the aroids and yams is, in part, a result of studies based on herbarium materials. As in other crops, the identification of a wild population closely related to the cultivated species, raises the question of whether it is an ancestor of the cultivated type or a feral or weedy form. In *Ullucus*, an aboriginal species has been described (Brucher 1962), but this could be only a wild variety. A hexaploid population of *Ipomoea* from Mexico, has been considered as an ancestor species (Nishiyama 1971) or a weedy variety of the sweet potato (Martin et al. 1974).

Cytological studies are interrelated with taxonomy and both have helped to solve some problems. But it is surprising how little is known in this field. Of some of the cultivated species there is no information even on chromosome number. On the other hand, some of the root tuber crops offer technical problems such as chromosome size and high number, which make it difficult to detect possible linkages or identification points.

There is a trend to attribute to interspecific hybridization the origin of most cultivated plants, especially if they are polyploids. In roots and tubers, sweet potatoes (Nishiyama et al. 1975), African yams (Ayensu and Coursey 1972), common potatoes (Dodds 1965), and others have been assigned such origin, and putative parents have been suggested for some of them. Genome identification lends some support to this contention, but it is very difficult to obtain definitive evidence from

Table 1. Tropical and subtropical species used mainly for their starch content as energy foods.

Monocotyledoneae		
Agavaceae	*Cordyline terminalis*	Ti, palm lily
Araceae	*Alocasia*	Ape, biga, birah
	Amorphophallus	Suran, elephant yam
	Colocasia	Taro
	Cyrtosperma	—
	Xanthosoma	—
Cannaceae	*Canna edulis*	Achira
Cyperaceae	*Cyperus esculentus*	—
	Eleocharis tuberosus	Water chestnut
Dioscoreaceae	*Dioscorea* (12 species)	Yam
Marantaceae	*Maranta arundinacea*	Arrowroot
	Calathea alluia	Lairen
Taccacaeae	*Tacca leontopetaloides*	Pia, Polynesian arrowroot
Zingiberaceae	*Curcuma angustifolia*	—
	Curcuma zeodoaria	—
Dicotyledoneae		
Basellaceae	*Ullucus tuberosum*	Ulluco
Compositae	*Polymnia sonchifolia*	Yacon
Convolvulaceae	*Ipomoea batatas*	Sweet potato
Cruciferae	*Lepidium meyenii*	Maca
Euphorbiaceae	*Manihot esculenta*	Cassava
Labiatae	*Plectranthus esculentus*	Kafir potato, dazo
	Solenostemon rotundifolius	Hausa potato
	Stachys sieboldii	—
Leguminosae	*Pachyrrhizus* (spp.)	Ahipa
	Psyphocarpus tetragonolobus	Sigarilla
	Pueraria lobata	—
	Sphenostylis stenocarpa	—
Oxiladaceae	*Oxalis tuberosa*	Oca
Solanaceae	*Solanum tuberosum*	Potato
Tropaeolaceae	*Tropaeoleum tuberosum*	Mashua
Umbelliferae	*Arracacia xanthorrhiza*	Arracacha

hybridization work. Often the terms "nobilization" or "ennoblement" are applied to root and tuber crops, meaning improvement by primitive agriculturists. These terms imply a planned hybridization, as in sugar cane breeding, which is not the case in root and tuber crops. On the other hand, information obtained from hybridization aimed at crop improvement is rather incidental to crop evolution.

As a main force in evolution, the impact of recombination is possibly less evident now than in the past. Under original conditions, root and tuber species were closer to their primitive allies and hybridization may have been more frequent. But as man moved them to new environments, not only did the possibility for further crossing and segregation decrease, but the mechanisms of seed setting and sexual reproduction were affected. The practice of vegetative propagation helped to reduce the importance of segregation and increased the role of somatic mutation in the evolution of these crops. However, hybridization in these crops is a potential force of considerable value for further improvement (Abraham et al. 1964).

Polyploidy

As expected in cultivated crops, a good number of root and tuber crops have different ploidy levels. The early cytological studies on potatoes led to the separation of the numerous cultivars included in *Solanum tuberosum* into several species (Juzepczuk 1937), or into one species formed by five groups and two hybrids with other species (Dodds 1962). The cultivated diploids have been derived either from wild diploids, again with no total agreement on the identification of the ancestors, or from a primitive complex in which many diploid species may have taken part (Ugent 1970). The tetraploids may have arisen through allopolyploid or doubling of diploids (Simmonds 1976); the triploids as hybrids of tetraploids and diploids; and a pentaploid group from crosses between a triploid (unreduced gametes) and a tetraploid (Ugent 1970).

Perhaps the group of root and tuber crops in which polyploid is most complex is *Dioscorea*, but here again the studies have been scanty and isolated. In *D. alata*, a survey of chromosome numbers in Indian cultivars has established a series of $2n = 30, 40, 50, 70$ for different clones that do not show phenotypical differences (Sharma and Deepesh 1956). Also polysomaty has been detected in this species and this could be a possible source of new types through vegetative propagation. In *D. bulbifera*, there are morphological differences in the cultivated types of Africa and Asia, the former being considered by some authorities as a distinct species. Cytological counts tend to support such differences. The African cultigens have $2n = 36, 40, 54, 60$ with a basic number *lenta*, $2n = 40, 90, 100$: *D. cayenensis* $2n = 40, 60, 80, 100$ with a basic number of 20 (Martin 1974). Other polyploids are *D. esculenta*, $2n = 40, 90, 100$; *D. cayennensis* $2n = 140$; *D. opposita* $2n = 40$; *D. penthaphylla* $2n = 140$. However, Coursey (1976) points out that in *Dioscorea* polyploidy is not restricted to cultivated species only.

In taro, a general survey of its variability is badly needed, as it is one of the most ancient of the root and tuber crops and one of the most widely spread. Two basic chromosome numbers have been recorded in taro, $X = 12$ and $X = 14$. Clones with $2n = 24$ and $2n = 48$ are reported from India, while clones with $2n = 28$ and $2n = 42$ are found from India to Japan in one direction, and to Timor, New Caledonia, and New Zealand in the other. But east of 180°, that is in most of Polynesia, all clones show $2n = 28$ (Yen and Wheeler 1968).

The most interesting example of polyploidy in root and tuber crops is the sweet potato, a hexaploid, $2n = 90$, which could be derived, as has been proved experimentally, in two ways: (1) by the multiplication of a diploid (*I. leucantha*), or (2) by the duplication of a triploid resulting from the crossing of a diploid (*I. leucantha*) and a tetraploid (*I. littoralis*). The resulting hexaploid, *I. trifida*, is considered a primitive form of *I. batatas* (Nishiyama 1971). As two of the three genomes of the sweet potato show more homology with each other than with the third (Magoon et al. 1970), the second process is more likely to have occurred. Other species showing different levels of ploidy are: *Maranta arundinacea*, tetraploid; *Canna edulis*, triploid; *Ullucus tuberosus*, triploid; *Oxalis tuberosa*, hexaploid; *Tropaeoleum tuberosum*, hexaploid. On the other hand, the cultivated *Xanthosoma* ($X = 13$) are diploids, $2n = 36$ (Plucknett 1976). Cassava, $2n = 36$, has been considered as a diploid (Magoon 1967) and as a tetraploid (Jennings 1976). In the Euphorbiaceae, $X = 9$ is found in *Manihot* and allied genera, and the presence of three nucleolar chromosomes and some chromosome duplication at pachytene, suggest that cassava is possibly a segmental allotetraploid (Magoon et al. 1969; Jennings 1976).

There are several questions to consider in relation to polyploidy. For example, does it have any significance, as in other crops, on the size and quality of the useful parts of the plants. The information is meagre, except on potatoes, and in this crop it is masked by long selection, environmental conditions, and crop protection. There is no information, for instance, of any correlation in size of tubers and ploidy in the *Dioscorea alata* series mentioned above.

In triploids of *Canna edulis*, the starch content is almost three times higher than in the diploid, but there is no information on yield (Mukerjee and Khoshoo 1971). On the other hand, induced polyploids in cassava, assuming that it is a diploid, are not superior in yield to diploids. In *Ipomoea*, wild hexaploids do not show any root thickening, and therefore, the domestication character may result from processes other than polyploidy.

It is well known that most polyploids have a wide adaptability to new conditions. In cultivated polyploids, this characteristic aided by cultural practices, especially crop protection, is a key factor in their success and expansion.

Finally, an important aspect is to consider the possible relationships between polyploidy and vegetative propagation. Through the latter, a not fully balanced allopolyploid, for instance, could be multiplied and meiotic irregularities or gene-determined sterility bypassed. Such polyploids may spread, through clonal propagation, in a way that would be difficult through seed reproduction.

Fertility and Vegetative Propagation

Vegetative propagation is necessary in most root and tuber crops because of their inefficiency in producing seed, a result of natural and cultural factors. Among the natural factors are incompatibility, dichogamy, abnormal seed and seedling development, seed dormancy, and pests and diseases attacking flowers and seeds. Cultural factors are equally important. First, man has taken clonal crops to regions where environmental conditions do not favour seed setting. Second, plants are harvested when the storage organs have reached maturity, which occurs in most cases well before flower initiation. Third, man, by copying the same type (clone) in millions of individuals may have increased the possibilities, if a natural trait limiting fertility is present, to extend it into large populations.

It has been stated often, especially by nonbiologists, that continuous vegetative reproduction leads to sterility. Sauer (1952) stated that cassava reproduction by cuttings has been carried out for so long that it has lost completely its ability to set seeds. Vegetative propagation in itself cannot lead to sterility although, as mentioned above, it may increase the frequency in a population of a trait favouring sterility, or has an indirect effect as it permits the cultivation in environments unfavourable for seed setting. However, some recent work in Nigeria shows that seed production is higher in yams coming from seed-producing plants than those obtained from tubers of continuous clonal propagation (Sadik and Obereke 1975). This could be due to the nature of the samples studied, but is worth further study. Some experimental work in cassava (Jennings 1963) showing different degrees of male and female sterility in hybrids and backcrosses may be partly due to the different materials used and to environmental effects.

As was said before, all root and tuber crops set seed. Reluctant clones are found, but experimental work shows that it may be possible to promote the formation of viable seed by changing environmental conditions or manipulating the flowering process. In cassava, flower induction has been obtained by moving plants to higher altitudes (above 1000 m in Java, Costa Rica, etc.) or in areas with special climatic conditions, such as the coast of central Peru, where most of the clones set seed regularly. In sweet potato, seed setting is reported from many countries (Yen 1974), often outside its natural area (e.g. the Philippines and Papua New Guinea). The scarcity of records of seed production in taro (reports from Papua New Guinea, Raratonga, Philippines) could be due to harvesting practices. In yams, seed setting is often limited by harvesting practices, but with some African species the constraints for sexual reproduction include a large number of male clones, imperfect seed, and dormancy periods. In potatoes, seed reproduction and factors conditioning low setting are well known, but even hybrids of induced haploids can set seeds under special conditions of temperature and air moisture (Subramanyan et al. 1972). All the Andean tubers produce abundant seeds. In oca (*Oxalis tuberosa*), however, seeds are extremely scarce in field conditions, but if protected from wind and frost, which produce abcission of the inflorescences, seed setting is normal (Alandia 1967). In arracacia, seeds are produced the second year but as the root matures in 8–14 months, flowers and seeds are rarely seen.

Vegetative propagation as a cultural practice is very important in the evolution of root and tuber crops. In modern agriculture, it permits the multiplication of superior and uniform materials in large monoclonal plantings. This leads to a continuous replacement of cultivars when superior clones become available, with consequent losses in germ plasm. In addition, monoclonal plantings may be wiped out quickly by diseases or pests. Vegetative propagation materials may become sinks of viruses and mycoplasma, and are subject to physiological degeneration also requiring clonal replacement. Under systems of primitive agriculture the effect of changes in planting materials is of less importance, as the standard practice is to plant several clones in the same plot, mixed or separated. Frequently the planting material is the edible part, and in time of scarcity or famine the "seed" has to be eaten. This double utilization made it possible for the Polynesians and possibly Incas to propagate as crops what they had brought as food for their long sea journeys.

As a whole, vegetative propagation, especially in monoclonal plantings, is an important restriction in increasing variability. In species of imperfect evolution, sexual reproduction is a second best choice in their reproductive system (Martin 1967).

The Role of Mutation

In root and tuber crops, evolution through chromosome or gene recombinations is limited by the predominance of vegetative propagation. Therefore, somatic mutation plays a very important role. However, any new type has to be carefully evaluated before determining if it is a bud mutation or a chance seedling. There is no survey of somatic mutations in root and tuber crops to determine mutation rates. In primitive populations of sweet potato, changes in the skin colour of the root — from white or cream to orange or purple — have been recorded roughly at 1:1000 (Yen 1974). In more reduced samples of improved clones, mutation rates vary from 0 to 2.9% (Hernandez et al. 1964). The frequency of mutation may give an indication of the age of the crop, although it is mainly determined by the number of individuals. Because mutations change only certain characters, the original population could be recognized. The mutants form "groups of varieties" (e.g. in taro and other tuber crops). Within a mutant population not all the individuals are alike (e.g. potatoes). Some may produce subclones that differ in important characters such as yield and resistance to disease.

The same mutation may appear in different places, and this is one of the reasons for the high number of repetitions in collections. However, two mutations phenotypically alike may be different in their physiological responses. Most mutations do not have any agricultural value and in an advanced system of agriculture, where uniformity is highly desirable, they are immediately eliminated. But in primitive systems of agriculture, farmers like to maintain as many types as possible, as a kind of agricultural asset. It is likely that the "magic gardens" of the taro growers of Polynesia are collections of aberrant clones. A similar situation occurs in the mixed agricultural system in the Andes. Primitive farmers have learned by experience that some of these new types may show special resistance and become an important resource when the common clones are wiped out by disease and pests.

Somatic mutations affecting the whole plant are known in few cases. Brachytic types are found in cassava and sweet potato and the main difference between wild and cultivated *Ullucus* is internode length.

Several instances are known in sweet potato in which a normal branch produces others with leaves of different shape (Yen 1974). Characters like the "piko" in taro (a deep cut of the leaf up to insertion of the petiole, often blotched), or the branching in the corms of *Xanthosoma* and *Colocosia*, could also be attributed to somatic mutations. Colour changes due to mutation were mentioned above in roots of the sweet potato and a characteristic feature of somatic mutation, sector colouring, is found in the petioles of many taro and *Alocasia* clones. Quite common are chimeras affecting colour or structure of the outer layers in tubers and corms. In potatoes and *Ullucus*, buds coming out of areas of different colour give rise to different clones. In potatoes, it is common to find purple areas in white tubers. In *Ullucus*, there is a group of clones with tubers either completely yellow or magenta or with large areas of both colours. In this crop, as in potatoes, russeting is common and types with this kind of skin are recognized as different clones. It is very likely that the ornamental cassava has a similar origin. As mutation rate is a function of population size, it is quite likely that in the relict crops so common among root and tubers, this force is decreasing its effects and therefore reducing crop diversity.

Somatic mutation is probably the most important factor in the evolution of root and tuber crops under cultivation. It is probably easier to find a bud mutation than a chance seedling. However, gene and chromosome mutation, although less well-documented and with far less chances of occurring, may have contributed considerably to the diversity of these crops, especially when they were grown under more natural conditions and seed setting was more frequent.

Domestication

The process of domestication in root and tuber crops, including potatoes, has not been widely studied. Domestication of grain crops in arid lands has been studied, but the results are of little value in explaining root and tuber domestication. The archeological evidence has considerable limitations. Evidence depends on preserved plant materials, from which we can determine the structure of the organs and environmental conditions. However, because of the fleshy tissues of roots and tubers, they are easily destroyed by fungi, bacteria, and insects. As well, most grow in wet regions and the materials preserved are very scarce and irregularly distributed. The presence of plant remains in dry areas, like the coast of Peru, provides secondary clues often of great importance, as in the case of the sweet potato, but not the fundamental information on original places and processes. Even less helpful is the indirect evidence derived from tools and pottery. Historical evidence is most important but, like archeology, it provides an irregular picture. Africa has been the foremost meeting place of root and tubers, however its early written history is very fragmentary. A similar situation occurs in southeast Asia and tropical America.

Plant domestication was initiated to answer the needs of primitive man for food, clothing, body painting, medicines, and poisons. It could have been carried out in areas where materials for domestication were abundant but also under the pressure of scarcity (Harlan and Zohary 1966). The common concept that plant domestication led to the establishment of sedentary human communities is open to some questioning. Burkill (1960) suggested that fishing people, who were rather sedentary, after a period of gathering may have started domestication and cultivation of yams. However it may have been a different process for each species, and it is extremely important not to generalize.

Some domestication characteristics common in root and tuber crops are: (1) large size of edible parts; (2) earliness; (3) low content of poisonous or acrid substances; (4) attractive shape and colour; (5) shallow underground growth; (6) sugar content. Other characteristics, such as resistance to disease, may come in more advanced stages of agriculture. The size of the useful parts, like the corms of aroids, and the shape and colour (e.g. Andean tubers) may have attracted the attention of gatherers. In the transition from gathering to cultivation, the main obstacle was the presence of bitter or poisonous substances in the edible parts. The discovery of techniques to eliminate these substances played a decisive role in domestication. The processes differed according to species. One special technique was washing the roots or tubers for many hours to remove poisonous principles. In the Andes this method permitted the use of bitter types of potatoes, mashuas (*Tropaeolum*), and oca (*Oxalis*). This also led to the preparation of "chuño," a dry mass easier to store and transport than the whole tubers. Roasting or washing methods were developed in Polynesia to remove the acrid substances from the stems of aroids. The Polynesians also learned to prepare a taro mash ("poi"), which was more nutritious and easier to keep than the fresh product. The extraction of glucosides in cassava required the development of special techniques and tools.

The planting and cultivation practices and tools are less complicated than those used in preparing the crop for meals. The digging stick of the yam gatherers can be easily transformed into a planting tool. In Hawaii a very simple instrument was developed to cut the upper part of the taro to obtain propagation material (Buck 1964). Evidently early man learned simple cultural practices, such as providing support for yams and piling earth on the base of the plants to supply better and looser soil to the growing tubers. The processes of domestication of roots and tubers, particularly the development of practices and instruments for their preparation as food, were far more difficult than for fruits or grains. Also in selecting less poisonous or acrid clones and developing cultural practices, primitive man showed such ingenuity that Burkill (1951) said they must have "already graduated in horticulture." Out of simple management practices, man evolved more complex systems of agriculture. In southeast Asia, terracing was developed for taro cultivation, which eventually was adapted for rice production. In the Andes, the most complex system was developed to cultivate tubers and other crops, including terracing, fertilization, irrigation, and food storage. This development was far superior to any agricultural system in western Europe or elsewhere in the world in the fifteenth century.

Geographical Origin and Early Dispersal

Root and tuber crops were domesticated independently in three regions: (1) southeast Asia and its geographic continuation — the Sunda Islands, Papua New Guinea, Oceania; (2) Africa — Madagascar; (3) Tropical America. A few species were domesticated in southern China and Japan. The three regions were active centres of domestication of animals as well. Agricultural systems were developed independently but they have many common features because of similar environments. Prior to the 1500s there were no exchanges of materials and techniques between the Old and the New Worlds. The sweet potato was the only known root crop in tropical America and Oceania.

Southeast Asia

The Indo-Malayan region, the land between the Deccan peninsula and the South China Sea, could be considered as a primary agricultural hearth because of its domestication of plants and animals, the development of systems of agriculture typical to the region, and the invention or changes in the utilization of plant materials for food and other uses. The region is limited by natural barriers to the north (the Himalayas but in its northeast corner is open towards China) and to the west (the Indian Desert). The rest of the region is surrounded by water. The larger Sunda Islands and Papua New Guinea could be considered as a natural continuation of the region. The Indian section comprises mainly the coastal areas of the Deccan peninsula. In Indochina, the relief is quite complex, and is determined mainly by three major mountain ranges, which run from northwest to southeast with narrow valleys and alluvial plains in between. Its western side, towards the Bay of Bengal, from the foot of the Himalayas to the tip of Malaysia and farther on to Sumatra, Java, and Borneo, is a "tropical rainy" area (over 2000 mm per year). Towards the centre, there are large areas with "tropical rainy" or "wet and dry" climates with savannas and open forests. The vegetation is one of the richest in the world and decreases in number of species from west to east. The conditions in the region are not favourable for the preservation of plant remains, and archeological surveys have been sporadic.

There were five racial groups in this region belonging to the Negrito stock who, up to this century, lived only by gathering roots and tubers. These were the Andamanese in the Andaman Islands; the Semang in North Malaya; the Kadar and the Chenchu in the Western Ghats in India, and the Veddas in Sri Lanka (Burkill 1953; Coon 1974).

The gathering practices of these groups give a picture of how man lived before agriculture. Even today, small groups of food gatherers in this region collect yams and aroids which are abundant in the rain forest. Because of their reduced numbers and the availability of other food sources, they have survived in the same areas for many centuries.

The Negrito stock settled in the region some 25 000 years ago, but was pushed eastwards by other immigrants and is represented today only by enclaves. The new arrivals, Australoid and Mongoloid, came in successive waves from different regions. They mixed together and the resulting population, to which the names of Indo-Malays or Malays have been applied, was possibly the group that started plant domestication. Burkill (1953) says it is likely that root and tubers were the first domesticated crops in this area.

As was stated earlier, the development of more efficient techniques in food preparation may have been as important in domestication as the development of crop husbandry. Yams gathered in India and Malaya are roasted or cooked. The removal of poisonous substances or acrid materials in yams and aroids is done by pounding, washing, and heating. Thus, through a combination of simple practices and tools, it was possible in this region to start an agricultural system based on the production of tuber crops. The region is extremely rich in other foods, especially fruits — mangoes, durian, rambutan and others — which grow wild in the forests. Fish and wild animals supplied the necessary protein. The later domestication of rice in the region started a new pattern of agriculture.

The most important expansion of root and tuber crops from the Southeast Asian region was eastward, carried out by a mixed group, the proto-Malays, which moved from the continent first to the Great Sunda Islands and then to Papua New Guinea, about 3000 years ago. The first expansion occurred about 2000 years ago with the settlement of Polynesia when the Malays from Samoa and Tonga reached the Marquesas to the east, Tokelau to the north, and the Ellice islands to the northeast. Previously, Micronesia had been settled by other immigrants from the Sunda and Philippine islands. The second expansion occurred before 500 AD when the Polynesians starting from the Marquesas reached the extremes of the Polynesian triangle (i.e. Hawaii, Easter Island, New Zealand). There are no written records before 1500, and linguistic and archeological evidence is not strong enough to support the view that in Oceania there was a pre- and post-Polynesian stage in agriculture.

Towards the west, the expansion of crops was prevented by the dry and desert areas in northeast India. Only one species (*Colocasia esculenta*) may have followed a land route, either through Syria or by the Sabean Lane to Egypt.

To the northeast, taro and some yams

moved into the subtropical areas of China and from there to Japan.

From the background of roots and tubers, new crops and techniques were developed in Southeast Asia and Malaysia, thus creating a large agricultural complex. Rice was the main crop on the continent and the large islands, alone with bananas, sugar cane, breadfruits and many other minor crops. The oldest archeological date for rice in India is 4300 BC. By that time other cereals such as wheat and sorghum had been introduced and were already in cultivation (Rao 1974).

Aroids

Alocasia macrorrhiza (A. indica). This is a very primitive crop, possibly domesticated in India (Assam, Bengal), or in Indochina; in India other species (e.g. *A. cucullata*) are cultivated and wild *Alocasia* is used as food. Its large trunk contains a fine starch, but because of the high oxalate content, it must be cut and baked on hot stones, or boiled. In Java and Tonga some cultivars are used only for their leaves. *Alocasia* spread only to the east towards Melanesia and Polynesia. It is of some importance in Tonga and Samoa and to all of Micronesia, especially the Marshall Islands, and was introduced into Brazil in the last century as cattle feed.

Amorphophallus campanulatus. This plant is found from India to Polynesia but with no clues as to the area of domestication. It is an ancient plant, low-yielding, and difficult to prepare for eating, with the result that it is being grown less and less. It is cultivated from India to Malaysia, and in Java as a backyard crop (Sastrapradja 1970). In Polynesia, it grows wild and is occasionally gathered, but is unknown in Micronesia (Barrau 1962).

Colocasia esculenta. This species is found wild from India to Southeast Asia, and has spread throughout the tropical world and to the fringes of the temperate regions.

Towards the east, the plant was spread by the Malayans and Polynesians to all the islands of Oceania, including Hawaii, Easter Island, and New Zealand. In this vast area, some hundreds of clones are known, but there is no complete survey of its diversity. From chromosome counts, it has been established that there are two types, $2n = 28$ and $2n = 42$, with the former the predominant type from India to Japan and Polynesia. Type $2n = 42$ occurs in India, New Zealand, and the Philippines and seems to have originated in India. It has spread eastward in recent times, but is not found in Polynesia (Yen and Wheeler 1968).

It reached China and the Lower Yangtze valley and is mentioned in literature towards 100 BC. From China it moved into Japan. The introduction into the Philippines came possibly through the Sunda Islands.

The spread of *C. esculenta* to the west is poorly documented. It reached Egypt around 100 AD, either through Syria (and there is some linguistic support for this, Tackholm and Dar 1950), or through the Sabean Lane, since it is found in Yemen from where it may have originated. From Egypt, it went through North Africa to Morocco and then to Spain and Portugal. It spread also from Egypt to Italy and to Cyprus, where it is an old and important crop.

When, where and by whom Southeast Asian crops were transported to Africa is still open to question. Indians or Indonesians settled south of Ethiopia around 500 AD, leaving instruments and practices, like certain types of boats along the coast of Zanj and the lakes, and they brought in their crop plants from Malaysia. Madagascar is culturally linked with Indonesia, and many of the words for crops like *Tacca*, coconut, taro, are the same in the two areas. The Malay sailors may have reached the coast of Africa with the favourable winds during the monsoon season. Propagation material of roots and tuber crops, brought in these trips, may have remained viable for weeks and very likely were established in Africa after many failures. Taro, bananas, greater and lesser yams, and sugar cane were adopted by the Bantu people and other tribes on the continent. Either by the geographic spread of the former ethnic group, or through diffusion into different tribes, these crops reached central Africa and later on west Africa. Taro was already in cultivation in Gambia and San Thomé around 1500 (Mauny 1953).

Taro was taken from west Africa to tropical America, probably in the early 1500s. However, it is difficult to establish its arrival because early descriptions confuse it with *Xanthosoma*. By the end of the 18th century it had spread from the Caribbean to Brazil, and early in this century to the southern coast of the United States. Again, very little is known of its diversity in this area. Superior clones, called "dasheen," are recent introductions but the native *Xanthosoma*, being more productive and resistant, has prevented the expansion of *Colocasia esculenta* in the American tropics.

Cyrtosperma chamissonis. This aroid was not domesticated on the continent since it is not cultivated in India and Malaysia. Its range extends from Indonesia to the north side of New Guinea; in Melanesia, the Solomons and Fiji, but not in New Caledonia; in Polynesia, in the central part as far as the Marquesas, but not in Hawaii or Southeast Polynesia; throughout Micronesia, as it grows well in the low atolls (Barrau 1962).

Yams (Dioscorea)

Six species of *Dioscorea* were domesticated in this region: *D. alata*, the "greater yam," originated in the area occupied by Burma and China where the rivers Irrawaddy, Salween, and Mekong ran closely and parallel to each other (Burkill 1951). This is a mountainous area with alternate seasons. Two wild species, closely allied to *D. alata*, and many primitive cultivars are found here. These yams grow large rhizomes deep in the soil to survive the dry season, and this characteristic may have attracted the attention of man since early times.

The greater yam was taken first to the Sunda Islands, to the east, quite possibly only as clones with shallow-growing tubers. Many mutants were concentrated or appeared in these islands, differing in tuber shape and size, and in other characteristics, and this area has the highest diversity of the species. It spread also to the Philippines and to all parts of Oceania, including New Zealand. Toward the west, it extended to west India, stopped by the Great Indian Desert. It spread toward Africa, maybe taking the same route as taro, banana, and other Southeast Asian crops. It spread to East Africa and Madagascar, and later to central and west Africa. In the latter region, however, it did not become important because there were already native yams under cultivation. An historical expansion took place after 1500, when the Portuguese brought it to the west coast of Africa. It became the main food in the slave ships and was marketed widely as "Lisbon yams," especially from San Thomé. With the slaves, the greater yam arrived quite early, around 1530, in the Caribbean and Brazil, but in the New World its expansion was checked again by the African yams.

Dioscorea esculenta, the "lesser yam," was possibly domesticated in the same area as *D. alata*. Wild types have been reported from India and Guam. Before the arrival of the Europeans, it had spread from Southeast Asia to the Philippines and into Oceania but not beyond Tahiti, and north to China, where it is mentioned in the literature around 200 and 300 AD. It was taken by the Portuguese, along with *D. alata*, around the Cape to west Africa. By selection, superior clones with larger and fewer tubers and less thorny stems have been obtained in Southeast Asia and Oceania. Recent collections suggest that this species has a greater potential than previously realized (Martin 1974b).

Dioscorea bulbifera was independently domesticated in the region, and the Asiatic clones show morphological and cytological differences from the African cultivars. It is found from India to north Australia (only wild types on this continent) and all over Oceania. Asiatic clones have recently been introduced to tropical America (Martin 1974a).

Dioscorea hispida extends from west India, where it is sporadically cultivated, to Malaysia and Papua New Guinea. In Java it is planted as a minor crop. The cultivated types are often as poisonous as the wild plants.

Dioscorea nummularia is a relict crop, found from the Philippines to Borneo, Celebes and Papua New Guinea and Tahiti, but is not cultivated in Java, Sumatra, or New Caledonia.

Dioscorea pentaphylla grows wild in India, southern China (to 22°N), Philippines, Indonesia, and all over Oceania; cultivated types have been selected in separate localities in Malaysia and Oceania.

Other minor root and tuber crops originating in this region

Cordyline terminalis is found wild in Southeast Asia, Australia, and most of Oceania; a clone with green foliage extensively planted for the fleshy roots that contain levulose (Ezumah 1970). *Curcuma augustifolia* is planted in south India as a source of starch, "East Indian arrowroot," and *C. zeodaria*, used for the same purpose, is cultivated mainly in north India and Sri Lanka (Kundu 1967). *Tacca leontopetalcides* is planted sporadically from Southeast Asia, Philippines to eastern Polynesia as a source of starch, the "Tahiti arrowroot." It was possibly domesticated by Polynesians, who developed several ways of preparing it for food or starch, but it is now losing importance. It was taken by Malays to

Madagascar but it is likely that the African cultivars found from west Africa to Ethiopia may have an independent domestication. It has not improved as has the Malaysian crop. *Pueraria thunbergiana* (*P. lobata*) is cultivated in the highlands of Papua New Guinea for its fleshy roots. *Psophocarpus tetragonalobus* is cultivated from India to Polynesia, especially in Burma, for the fleshy, sweetish roots. Its origin is unknown, though it could be traced to Africa. The recent interest in this crop is due to the protein value of the seeds. It is widely planted as a vegetable for its green pods.

Root and tuber crops in the Far East

Several species have been domesticated in China or Japan but they have not spread much outside this region. In the last decades in China, both native and introduced root and tuber crops have had a large expansion in area and production. These far eastern species include: *Dioscorea opposita*, the "China yam," is possibly derived from *D. japonica; Amorphophallus rivieri*, or "bonjac," is found in Japan, China, and possibly Vietnam. Its origin is possibly south China, with quite a complex utilization in Japan; *Eleocharis dulcis*, the "water chestnut," is assumed to be the cultivated form of *E. tuberosa*, a wild species widely distributed in the Asiatic tropics; *Sagittaria sagittifolia* is cultivated mainly in China for its tubers, and was introduced by the Chinese to Polynesia and *Stachys sieboldii*, which is referred to in the Chinese literature of the fourteenth century, is also grown in Japan. It was introduced into Europe at the end of the nineteenth century and became quite popular in France.

Africa

In Africa, more than in any other continent, we see a full range in the gradual transition in utilization of root and tuber crops, from gathering of wild materials to well-established cropping systems. The African root and tuber crops were domesticated south of the Sahara, some in the savanna region, others in the Guinean forest. Africa is also the meeting point for Asian and American roots and tubers, and nowhere else has there been such drastic replacements in these crops. Among the Asian roots and tubers, taro (*Colocasia esculenta*) was the first.

Several African crops were taken to Asia by the Malays or Indians. Among the root and tubers, *Plectranthus tuberosus* was introduced to India and Indonesia. Perhaps the two cultivated species of *Psophocarpus*, if they are African, followed the same route.

From tropical America the introductions are more recent and important: cassava, sweet potato *Xanthosoma*, and potatoes have drastically changed the agricultural systems and food habits in west and east Africa. The Guinean yams were taken very early to the Antilles and the coast of Brazil, during the slave trade, and are now the most important yams in the region.

Yams

The main contribution of Africa in root and tuber crops is the domestication of the Guinean yams *Dioscorea cayenensis* and *D. rotundata*. These have been considered one species with *D. rotundata* as a subspecies of *D. cayenensis*, but the recent trend is to keep them apart, partially based on anatomical characters (Coursey 1967). The Guinean yams are especially important in West Africa, and were probably domesticated in this area 5000 BP. (Coursey 1976; Ayensu and Coursey 1972).

Dioscorea cayenensis, the "yellow yam," which is less important than the white yam, is a polyploid of unknown origin, although it may derive from *D. minutiflora* or other closely related species. It grows wild throughout West Africa, and was probably domesticated in the Guinea coastal area, spreading through the Guinean region in areas of high rainfall. Thornless clones have been introduced into tropical America.

Dioscorea rotundata, the "white yam," is supposed to be a hybrid between *D. cayenensis* and *D. praehensilis* (Ayensu and Coursey 1972). It is more widely adapted to moisture conditions, and its cultivation is most intense in Nigeria. It has spread from Senegal to south Ethiopia, including parts of the savanna area, and to Uganda, Angola, and Northern Rhodesia. It is also cultivated in the Comores and Madagascar. The primitive types have thorny roots which provide good protection, but through selection of mutants, thornless clones have been established and were taken to tropical America during the slave trade where it has become the most important yam.

The following yams are of lesser importance. *Dioscorea bulbifera*, which was mentioned before, is found in Southeast Asia and Polynesia.

There are differences between the Asian and the African clones, the latter being less advanced in their domestication. Some clones do not produce underground tubers. It grows roughly between 10°N and to 10°S lat throughout west Africa and from the Nile valley near the Ethiopian border to Southern Rhodesia. The clones in tropical America seem to belong to the African group. *Dioscorea dumetorum* is cultivated particularly in the border of the yellow yam plots, and is found wild through Africa from 15°N to 15°S (Ayensu and Coursey 1972). Other species cultivated are *D. abyssinica*, *D. colocasiifolia*, *D. hirtiflora*, *D. praehensilis*, *D. quartininiana*, and *D. sansibarensis*. In Madagascar a number of local species (*D. antaly*, *D. ovinala*, *D. soso*, the latter with very sweet tubers) have been domesticated but their cultivation is being reduced by cassava and sweet potato.

The African tuberous Labiatae

In the mint family (Labiatae) the formation of tubers is not uncommon, as was mentioned under *Stachys sieboldii*. Two African species have been domesticated. One was taken some centuries ago to India and Indonesia, and has become a regular crop in these countries (Chevalier 1905).

Plectranthus esculentus (*Coleus dazo*, *C. esculentus*, *C. langouassiensis*, *C. floribundus*), the "Kafir potato" is native to west and central Africa, though its origin and variability are unknown. The plant produces many elongated tubers, arising from the central stem.

Solenostemon rotundifolius (*Coleus dysintericus*, *C. rotundifolius*, *C. coppini*, *Plectranthus tuberosus*, *P. ternatus*), the "Hausa potato" is cultivated in west and central Africa to Transvaal and Madagascar. The plant produces spheric to ovoid tubers, dark red and white. It is an old introduction to India ("koorkan"), Malaysia, Indonesia, and recently to the Philippines.

Tuberous Leguminosae

Two species of possible African origin, *Psophocarpus palustris* and *P. tetragonolobus*, are cultivated widely in tropical Africa and Asia for their fleshy, sweet roots and for the green pods. The second species, by far the most important, is intensively cultivated in Burma for its tuberous roots. The origin of these species is unknown. *Psophocarpus* is found from tropical Africa to Papua New Guinea.

Sphenostylis stenocarpa, one of the "yam beans," of African origin possibly from Ethiopia, is cultivated in east Africa and the Guinea area for its spindle-shaped tubers and dry seeds.

Tacca leontopetaloides
(T. involucrata, T. pinnatifida)

This species is found wild from Senegal to East Africa and also in Southeast Asia and Oceania. In Africa it is seldom cultivated. The tubers require careful preparation to remove the toxic principles; in some places they are used as a source of starch.

Tropical America

The three most important root and tuber crops — potatoes, cassava, sweet potato — come from Tropical America. Other crops, like *Xanthosoma*, are of high potential value and several minor crops offer limited possibilities due to their physiological requirements.

The American root and tuber crops have two main areas of domestication — the high Andes and the lowlands in northern South America, and a secondary area, Middle America. The Andean crops include potatoes, oca (*Oxalis tuberosa*), mashua (*Tropaeolum tuberosum*), ulluco (*Ullucus tuberosum*), and maca (*Lepidium meyeni*) that were domesticated in the Peruvian-Bolivian altiplano, above 300 m, and two crops native to the northern section of the Andes (i.e. Colombia), at lower elevations (1000–2500 m), arracacha (*Arracacia xanthorrhiza*) and yacon (*Polymnia sonchifolia*). In the Andes, other root and tuber crops were early introduced from lower areas and became an important part of the agricultural complex: sweet potato, achira (*Canna edulis*), ahipa (*Pachyrrhizus* sp).

The second source of root and tuber crops is the lowlands of northern South America including the Antilles, an area of very imprecise limits, in which *Xanthosoma* spp., arrowroot (*Maranta arundinacea*), lairen (*Calathea allouia*), *Pachyrrhizus tuberosus*, and possibly cassava and sweet potato were domesticated. Middle America, which is so rich in native crops, has contributed few and unimportant crops: jicama (*Pachyrrizus erosus*) is the most outstanding and has spread to Asia and Oceania. In pre-Colombian times and even today in remote localities, some plants are gathered for their tubers or corms: *Bomarea edulis*, *Dalechampia* spp., some beans (*Phaseolus*), *Tigridia pavonia*, and *Dahlia* spp. The last two species are now grown as ornamentals but were once used for their corms and fleshy roots respectively. *Sechium edule* is planted for its fruit though it also yields edible roots. The early introduction of cassava and sweet potato to Middle America probably prevented the domestication and expansion of the local tuber crops.

Cassava

Cassava (*Manihot esculenta*), known only under cultivation, is a complex of clones showing the widest morphological diversity in the Paraguay – South Brazil area. Clusters of closely-related species to cassava are located in both North and South America (Rogers and Fleming 1973), but no wild species have been suggested as a possible ancestor. The time and place of domestication are unknown. The most important trait for the use of cassava as a food is the HCN content in the roots, which has a wide range from high (bitter cassavas) to very low (sweet cassavas). There is a clear correlation in the geographic distribution of the two kinds: sweet cassavas occur in the western side of South America, Central America – Mexico, while bitter clones are planted mainly in the eastern side of South America and the Antilles, with an overlapping area in between (Renvoize 1972). Archeological evidence is very scarce. The remains of cassava leaves have been identified in caves in Mexico dated 2500 BP, and tubers in coastal Peru from about the same age. Indirect evidence, such as the presence in early times of grinding stones in Colombia and Venezuela assumed to be used for grinding cassava roots, is not very convincing. It is also assumed that cassava flour was an important article of commerce in northern South America in the second and third millenia BC (Jennings 1976). What is clear is that cassava was more intensively used in South America than in Middle America. In the former area, the artefacts for the preparation of flour were far more developed, and other uses, such as the utilization of leaves as vegetables or for the preparation of sauces, are typical of South America. Archeological information, such as representations in ceramics and early historical information, gives additional support to a more intensive use in South America. Its role in the Mayan agriculture is still open to discussion (Bronson 1966; Cowgill 1971), but it is unlikely that cassava could have been a very important food source in the conditions of Yucatan and Petén. All this may point to a South American domestication and the fact that its spread towards the north was restricted to the sweet varieties. On the other hand, Humboldt suggested that the sweet types may have been domesticated first and that later on man learned how to utilize the bitter varieties.

Cassava was introduced early to Africa by the Portuguese. The first published report by Barré and Thevet is dated 1558 (Mauny 1953). Further spread inside Africa was determined by its adoption first as a vegetable and later as a flour source in the Kingdom of Congo, which was an advanced state that influenced the rest of tropical Africa. The spread apparently was rather slow, but was favoured by the resistance of cassava to locusts (Jones 1959).

Cassava was introduced to India and Southeast Asia late in the nineteenth century.

Sweet potato

Sweet potato (*Ipomoea batatas*) was the only food crop common to Tropical America and Polynesia before the Discovery. As such, it has raised a long discussion on which of the two regions is its place of origin and on how its early dispersal occurred (Yen 1974). The recent discovery in coastal Peru of sweet potato tubers dating from 10 000 BP (Engel 1970) settles the question of the origin, as this date by far antedates any agricultural development in Polynesia. However, it should be considered that, like all other plants cultivated in the coastal region of Peru, sweet potato was introduced from elsewhere, possibly from the north, the coastal area of Ecuador and Colombia, where close wild types have been found (Martin et al. 1974), or from across the Andes, like *Canna edulis* and other crops.

At the arrival of the Europeans, the sweet potato was known in all Tropical America, with an important area of diversity around the Caribbean. Oviedo, writing in 1530, reports that several varieties he had seen in the early days of the Conquest were already disappearing.

The spread of the sweet potato to the Old World was quite rapid; it was introduced in Spain, after several failures, as living plants before 1550. It is not known how it reached Africa, whether from Spain or from tropical

America. A report that sweet potato was grown in San Thomé in 1520 seems doubtful (Mauny 1953). More reliable information shows that it was widely cultivated by the end of the seventeenth century in West Africa, and a century later all over the tropical areas of the continent.

The introduction to Polynesia, as discussed above, has not been properly explained. It could have been accidentally transported in one of the Peruvian rafts lost in the Central Pacific, which reached Polynesia where the crop was established by Indo-Americans and developed later on by Polynesians. It has been proposed also that the sweet potato may have been taken to Polynesia by one of the Spanish expeditions that visited the area starting from Peru in the sixteenth century. It was taken to China in 1594 and after a famine in Fukien, it later became an important crop. Sweet potato was introduced early to Japan from Okinawa and cultivated and adopted in the southern region up to 35°N.

Xanthosoma

The identification of the species of *Xanthosoma*, cultivated for the corms, is still not clear. The "species" described vary between themselves like the clones of taro which is now considered to be one species. The genus is found from Mexico to Brazil, but the cultivated "species" are centred around the Caribbean. There is no information on the evolution of this crop. It is superior to taro in yield, resistance to disease, adaptability, and taste, and therefore it is not surprising that this species is replacing taro all over the tropics. *Xanthosoma* was introduced to Africa by the middle of the last century, where the replacement is most active.

Tubers of the high Andes

A group of tuber crops was domesticated in the high Andes, above 3000 m, where they are now intensely cultivated (Léon 1964). The most important are the potatoes, which at present are considered as one species, *Solanum tuberosum*, including: (i) two tetraploid groups, *Tuberosum* and *Andigena*; (ii) a triploid, *Chaucha*; (iii) two diploids, *Phureja* and *Stenotomum*; (iv) two intersperific hybrids, × *juzepozukii*, triploid, a cross between *S. tuberosum* × *S. acaule*, and × *curtilobum*, resulting from *S. tuberosum* × *juzepozukii* (Ugent 1970).

In spite of its importance, very little is known on the domestication and early dispersal of the cultivated potato, but the complexity of its structure as a species shows that it has a long history. The oldest tubers are dated 200 BP (Ochoa, personal communication) and potatoes are represented in ceramics of the third century BC. Although very little is known of the domestication process, the early spread to Europe and other continents is fairly well documented (Dodds 1966; Hawkes 1967).

Other root and tuber crops of the highlands are: *Oxalis tuberosa*, or "Oca", of which no wild ancestors are known. It has a large number of clones differing in size, colour, and shape of the tuber, plant size, foliage colour, and heterostyly. Clones with bitter tubers are used to prepare "chuño." The oca was introduced into Mexico during colonial times ("papa extranjera"), into southern France, and last century to New Zealand where it is called "yam." *Ullucus tuberosus* has slimy tubers which are not as attractive as ocas, but they are consumed even in the large towns. Wild or ancestor types grow in the highlands of Peru and Bolivia. Two main groups of clones are known: in the northern extreme of the range (Colombia), with trailing branches and large, red tubers; and in Peru and Bolivia, erect, short branches, with multi-coloured tubers. The ulluco was introduced into southern Europe but it is not planted. *Tropaeolum tuberosum* grows in the same area as oca. No wild relatives are known, although some other South American species are reported to form large tubers. Two main groups of clones are known: in Colombia, tubers are slim, white, with deep eyes from which emerge fine rootlets; and in Peru and Bolivia, the tubers do not have rootlets and the predominant colours are yellow with purple lines or fine points. The mashua grows often at altitudes where only bitter potatoes are produced. *Lepidium meyeni* produces a radish-like root, sweet, yellow or dark purple in the highlands of Peru, above 400 m. It is a relict crop that is rapidly disappearing.

Other Andean root and tuber crops

At lower elevations in the Andes, between 0 and 3000 m, several root and tuber crops are grown: *Arracacia xanthorrhiza*. "Arracacha" is especially important in Venezuela and Colombia; no wild types are known and it seems to be of ancient cultivation. Several clones are known to differ in shape and size of the roots, foliage, colour, etc. It has been introduced into Middle America, Brazil, East Africa, India; *Canna edulis* is possibly native to the eastern part of the Andes, and was brought to the coast of Peru where it has been cultivated since 4000 BP; diploid and triploid types are known (Mukherjee and Khoshoo 1971); cultivated in Australia ("Queensland arrowroot"), Hawaii, India, Polynesia; *Polymnia sonchifolia* is cultivated from Venezuela to Argentina, and according to Bukasov (1930) grows wild in Colombia. The tuberous roots are fleshy, contain sugar (10%), and were used in colonial times on long sea trips; introduced to southern Europe as a forage crop; *Pachyrrizus* sp. are ancient crops in the Andes, probably introduced from the Amazonian lowlands.

Minor tropical American root and tuber crops

The West Indian yam (*Dioscorea trifida*) is the only species of the genus domesticated in the American tropics, although other species are gathered, particularly in Brazil. The species has the highest diversity in the area between the Guianas and Brazil and selected types are planted in the Antilles. Its domestication was, of course, independent of the Asiatic and African yams (Alexander and Coursey 1969).

Arrowroot (*Maranta arundinacea*) was, around the middle of the eighteenth century, used mainly to cure the wounds from poisoned arrows, and also started to be used in the Antilles as a source of starch (the "St. Vincent arrowroot" — Stutervant 1969).

Lairen (*Calathea allouia*) was intensively cultivated at the time of the Discovery in the Great Antilles and the Continent. The ovoid tubers are now used for food mainly in Venezuela.

Several species of jícamas (*Pachyrrhizus* spp.) are cultivated in South America, and are particularly important in Mexico and Central America. From Mexico the plants went, by the Acapulco–Manila connection, to the Philippines and subsequently spread to Southeast Asia and Oceania. Plants of the same "species" offer such a variability in size, shape of leaves, and tuberous roots that the specific limits are difficult to recognize.

Conclusion

In considering the evolution of root and tuber crops, the roles of polyploidy, mutation, and vegetative propagation give some clues to the general process. Some outstanding research in sweet potatoes has established the possible transition stage of the wild diploids to a complex hexaploid, and has recognized wild populations which may have had a role in the development of the crop. But in sweet potato, and even in the common potato, there is an appalling ignorance as to how domestication traits occurred. Today there are increasing doubts among anthropologists and botanists about the capacity of primitive man to have carried out crop selection. Primitive farmers profited from the presence of edible organs in certain species. However, it is quite difficult to explain how he could carry on the improvement of inherent traits without knowledge of the rules of genetics and the help of permanent records. On the other hand, primitive man exchanged planting materials with his neighbours, and in vegetative crops he introduced superior clones and thus eventually contributed to their hybridization. At the same time, by moving crops to new areas, he restricted the possibilities of further crossing with the species of its native habitat. Man-made isolation has been, therefore, an important factor in the evolution of crop species. Man has also executed an important action in taking plants to new habitats. This is seen more clearly in relation to the selective impact of diseases and pests, such as the attack of cassava viruses in Africa.

Roots and tubers are ancient crops and primitive man independently domesticated species of the same genus (*Dioscorea*) or of allied species (*Colocasia* and *Xanthosoma, Pachyrrhyzus* and *Pueraria*) in different parts of the world and at different times. Many of these crops, due to physiological constraints or lack of acceptability, have not spread farther than their native habitat, and in fact many are now becoming relicts in old agricultural systems. Their spread, particularly after the Discovery, has led to competition among themselves and to the eventual replacement of some species, a process that continues today.

Root and tuber crops are associated with primitive systems of agriculture. A duality has been established between seed agriculture, which is supposed to be a dynamic process characteristic of advanced communities, and vegetative propagation which is supposedly maintained by more primitive communities. The fact is that in the tropics there is no such difference, and root and tuber crops as the only source of energy food are found only in a few isolated communities. Grains and tubers are integral parts of most agricultural systems in which they have different not antagonistic roles. Perhaps the best answer to the academic problem of seed versus vegetative culture lies in the ceramics of the Trujillo valley in Northern Peru. On one of these ceramics dating from around 1500 BP an Indian farmer is shown holding, at the same level, a corn plant in one hand and a cassava plant in the other.

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