PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The Rice Cultures [and Discussion]

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The rice cultures

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Common (Asian) rice was domesticated in the area between north India and the Pacific coast adjoining Vietnam and China. Rice cultivation began when the hunting, fishing, and food-gathering inhabitants near the rivers and along the foothills dropped seeds into low-lying fields. Land preparation, transplanting, and irrigation were largely developed in the Yellow-Han River basins, spreading later to Southeast Asia. As rice culture expanded from the naturally flooded areas into fringe areas where the water was deep or the soil was mesic, human and natural selection greatly accelerated the development of specialized types such as the floating and upland rices. Recognizable races of rice resulted from man's extension of its culture and persistent selection within a geographic region, but rapid changes in predominant varieties occurred within an area due to extensive contacts among the peoples. Such exchanges also resulted in population increases, changes in diet, and predominance of specific draft animals and associated farm tools. While rice cultivars lost their primitive characteristics and acquired wider adaptation, sterility barriers developed and some duplicate loci disappeared. A thrifty and productive plant-type evolved.

1. ORIGIN, DOMESTICATION AND DIVERSIFICATION

Uncertainties or deficiencies in history, archaeology, biogeography, anthropology, philology, and biosystematics obscure the date and place of the first domestication of the cultivated rices (*Oryza sativa* L. in Asia and *O. glaberrima* Steud. in Africa) as well as of many other tropical crops. However, the common ancestral origin of the two cultivated species (figure 1) is quite certain, as indicated by the pan-tropical distribution of their wild relatives in tropical Africa (Harlan 1973; Chang 1976), South and Southeast Asia (Chang 1975), northern Australia (Aldrick, Buddenhagen & Reddy 1973), and Central America, South America and the West Indies (Oka 1961; T.-T. Chang, unpublished). Such a pattern fits the theory of the Gondwanaland continents before they broke up and drifted apart (Chang 1976).

(*a*) *Oryza sativa*

In east India, northern Southeast Asia, and southwest China, alternating periods of drought and temperature variation during the Neothermal age (10000–15000 years ago) favoured the development of annuals at different elevations (Whyte 1972). The annual forms survived better and produced more seeds, thus enabling them to move farther northward than the perennial progenitor. Increasing aridity also forced people to move into more humid areas. The movement of people and the dispersal of plants greatly accelerated ecologic diversification (Whyte 1972, 1974, 1975).

The Asian rice (*O. sativa*) evolved from an annual progenitor over a broad belt that extended from the Ganges plains below the foothills of the Himalayas, across Upper Burma, northern Thailand, and Laos, to North Vietnam and south China (Roschevicz 1931; Ramiah 1937; Chatterjee 1951; Chang 1964, 1976; Morinaga 1967). Domestication could have occurred independently and concurrently at many sites inside or bordering the belt. From this aggregate of centres and non-centres, rice was most likely introduced from the Nepal–Assam–Burma–

Yunnan area into the Yellow River Valley and from Vietnam via a coastal route into the lower Yangtze River basin where the cool-tolerant race (keng or Japonica) became established (Chou 1948; Ting 1949*a*; Ando 1959; Hamada 1956, 1967; Chang, K. 1968; Chang, T.-T. 1976). From China, rice was introduced into Korea and Japan in the third century B.C. (Ando 1951; Anon. 1954; Morinaga 1957, 1967; Hamada 1967). This race could be more appropriately designated as Sinica than Japonica.

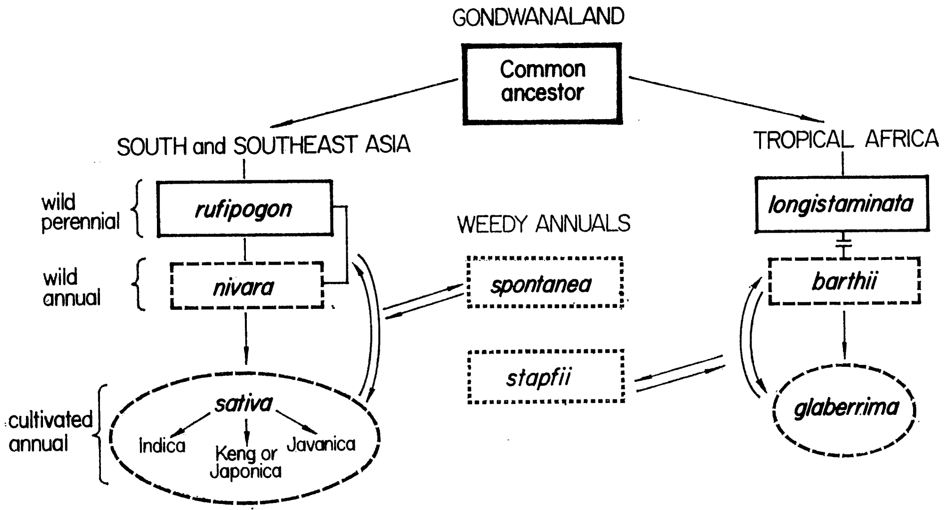

FIGURE 1. Evolutionary pathway of the two cultivated species of rice. Arrows with solid line indicate direct descent. Arrow with broken line indicates indirect descent. Double arrows indicate introgressive hybridization (adapted from Chang 1976).

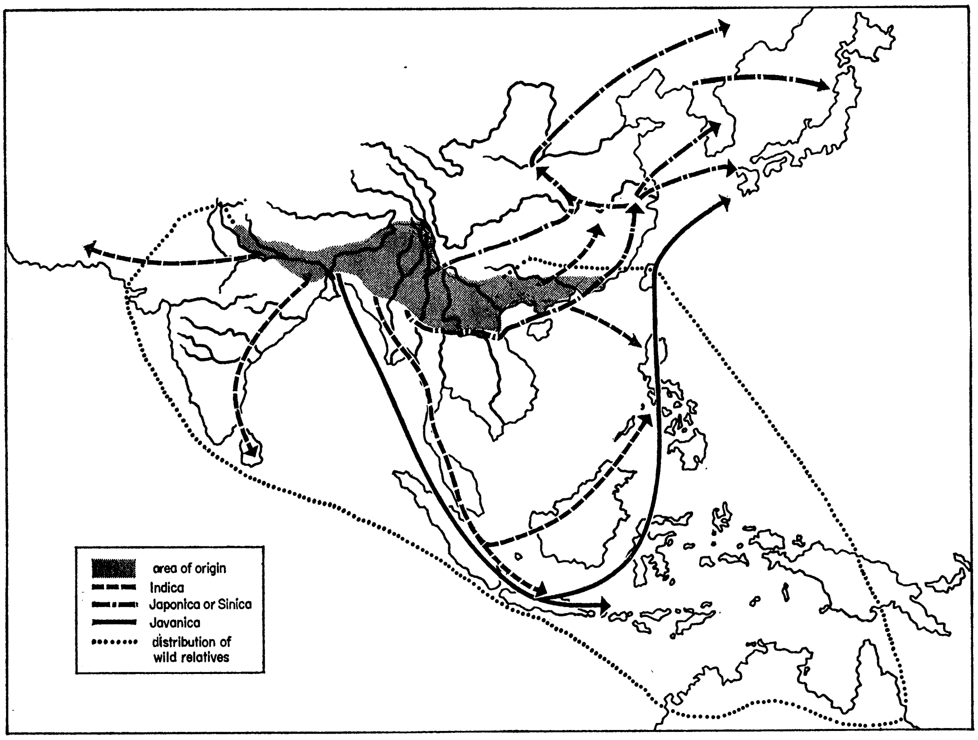

FIGURE 2. Distribution of wild relatives and spread of geographic races of *O. sativa* in Asia and Oceania (adapted from Chang 1976).

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The tropical race (Indica or hsien) spread southward into the Malay Archipelago and northward into central China. Indica rices were grown in the middle Yangtze River basin probably before A.D. 200 and began to spread in the sixth century (Ting 1949*a*).

The tall, large- and bold-grained Javanica race (bulu or gundil) of Indonesia appeared to be a more recent product of selection from the Indica race. Rice was being cultivated in Indonesia around 1084 B.C. (Roschevicz 1931). From there the Javanica race spread to the Philippines, Taiwan, Ryukyus and Japan. Figure 2 schematically shows the pattern of dissemination of the three geographic races in Asia (Chang 1976).

Conversely, the wild races in South America and northern Australia have retained their primitive features, primarily because they have never been subjected to the forces of selection and dispersal that are associated with domestication and cultivation.

(*b*) *Oryza glaberrima*

The African rice (*O. glaberrima*) has its primary centre of diversity in the swampy area of the upper Niger River and two secondary centres to the southwest near the Guinean coast. The primary centre was probably formed around 1500 B.C., while the secondary centres were formed 500 years later (Porteres 1956).

2. Early cultivation

Rice grains were initially gathered and consumed by prehistoric people of the humid tropics who lived near the river estuaries along the wooded foothills where rice grew wild on poorly drained sites. These people also hunted, fished, and gathered other edible plant parts as food. At first, the rice they gathered served as a food supplement. Soon they developed a liking for the tasty cereal and searched for plants that bore larger panicles and heavier grains. This selection accelerated the evolution of the cultivated form. The gathering-and-selection process was more important to people who lived in areas of marked seasonal variations in rainfall or temperature, or both (Hawkes 1970; Whyte 1972), or where the water holes or pans dried up in the dry season.

The cultivation of rice began when men (or, more likely, women) dropped seeds on the soil in low-lying spots near their homesteads, kept out the weeds and animals, and, probably, manipulated the water supply. The sites of cultivation were moved nearer to the homesteads as people found that rice plants responded in yield to the enriched soil near their temporary settlements (Hawkes 1969).

In more hilly areas or where the wet–dry alternation of seasons was less pronounced, rice was probably a secondary or a companion crop to root crops such as taro and yams. Such situations existed in many parts of Southeast Asia until recent times. They have led to the postulate that man learned to plant vegetative parts before he learned to plant seeds, and that rice was a weed in taro gardens (Haudricourt & Hedin 1943, quoted by Sauer 1952). However, the rather recent (*ca.* 2000 B.C.) domestication of the yams (Alexander & Coursey 1969) does not support this postulate.

As the early cultivators of rice migrated, they took the grains along and planted the seeds at their new homestead. The introduction of the tropically based race and strains into ecologically different habitats, followed by human selection, led to the rapid increase in ecologic diversity in subtropical areas (T.-T. Chang, personal observation) and also created variants that matured early and escaped drought (Whyte 1972).

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The floating rice evolved as rice cultivators moved from areas of shallow flooding into fringe areas of deep water. These rices branched at the higher nodes, had internodes that elongated rapidly, had adventitious roots at the upper nodes, and location-and-maturity-specific photoperiod sensitivity. The wild perennial race (*O. rufipogon*) may have contributed to the development of the floating rices.

When rice was introduced into areas where the soil had poor moisture retention, the upland type with early maturity and deep-and-thick roots developed.

The marked spectrum of ecotypes of both the Sinica and Indica races found at different elevations in Yunnan and Kweichow provinces of southwest China illustrates the plant's plasticity of environmental adaptiveness (Ting 1961; Hamada 1967).

Ancient India is undoubtedly one of the oldest regions where domestication of *O. sativa* began. The oldest carbonized grains in India date back to around 2300 B.C. (Allchin 1969; Buth & Saraswat 1972; Mehta & Oza 1973; Vishnu-Mittre 1974). The oldest excavation from Mohenjodaro in the Indus Valley of Pakistan dates back to about 2500 B.C. (Grist 1965). Rice cultivation probably began in India at about, or shortly before, the Aryan invasion around the middle of the second millennium B.C. (Candolle 1886). A recent study dated the earliest plantings in Saurashtra and Rajasthan at about 4000 years ago. In Indian states where modern agriculture is practised, such as the Jeypore tract of Orissa, rice-gathering people can still be found (Vishnu-Mittre 1974). Wet rice cultivation began in the middle and upper Ganges (Watabe & Toshimitsu 1974; Grigg 1974), much like in northern China.

Recent excavations from Non Nok Tha in Thailand yielded carbonized rice glumes that date back to 3500 B.C. or earlier (Bayard 1970; Solheim 1972). But the specimens did not clearly indicate whether the rice was a wild relative or the cultivated form (Otsuka 1972).* A more recent glume sample excavated by C. F. Gorman from Banyan Valley Cave and furnished to us by Douglas E. Yen (personal communication) has surface features more indicative of a wild form. This points to the need for both ^{14}C and botanical identification.

The exact date of the glume remains found in Yanshao village of Honan Province in China was a debatable issue several years ago (Watson 1969). Recent dating by the radiocarbon method places the Miao-ti-kou site in Honan at 3280 ± 100 B.C. (Cheng 1974). Several excavations from Anhwei, Chekiang, Hupei, Kiangsu and Yunnan provinces along the Yangtze River produced carbonized husks of more recent age dated between 2750 B.C. and 2000 B.C. (Ting 1959; Treistman 1974; Cheng 1974). Historical records indicate that in the 22nd century B.C., flood control in the Yellow River Valley under Yü was associated with the growing of rice. The Chinese character 'tao' for rice appeared during the Yin (Shang) dynasty, 1766–1122 B.C. (Ting 1949*b*; Yu 1958; Amano 1962). It is not clear, however, if rice cultivation in the middle and lower Yangtze River basin preceded that in north China (Ting 1961; Morinaga 1967; Chang 1968). China's early contacts with India could have dated back to 2200 B.C. (Ando 1951); and with Southeast Asia, even earlier (Aigner 1973). From ecological, geographical, and ethnological considerations, one may assume that the early cultivators in the Han, Huai and the middle and lower Yangtze River basins (Ch'u State) had contributed substantially to cultural techniques such as transplanting and irrigation (Chang 1968; Ho 1969; Grigg 1974; Cheng 1974; Francesca Bray & J. Needham, personal communication). Rainfed lowland

* After the manuscript was submitted, Dr I. Otsuka kindly provided a photomicrograph of the Non Nok Tha rice sample. The author's diagnosis based on the glume surface is that the sample is intermediate between the wild race and the weed race.

culture could have been established in the swampy areas of south China as early as 600 B.C. (Ichikawa 1961), but the cultural practices appeared primitive in the 12th century (Ho 1969).

3. Evolution of agricultural systems based on rice

The historical accounts of rice cultivation in China are sufficiently coherent to permit a reconstruction of the series of developments in rice culture that later influenced rice cultivation in Southeast Asia.

(a) *Evolution of lowland culture in China*

Chinese mythological writings suggest that rice was among the five cereals planted by Emperor Shen-nung at about 2700 B.C. (Candolle 1886; Ting 1949*b*; Ru 1958).

In north China rice was first planted by Lungshanoid farmers who settled in the low plain area of Honan and the central Shensi basin between 3000 and 2400 B.C. (Ho 1956; Chang 1968). The rice fields were sparsely located on marshy but flood-free sites around river bends of the tributaries of the Yellow River in Honan and Shensi provinces, where millet was the predominant crop (Ho 1969). The sites were generally between small rivers and wooded hills (Chang 1968). The total area of rainfed rice was rather small.

In the second millennium B.C., the area began to spread after Yü initiated flood control measures. Rainfed rice cultivation was well established during the Chou dynasty (1122–255 B.C.). Water works began about 700 B.C. initially for flood control. Irrigation work began in Honan as early as 563 B.C.; in central Yangtze valley, 548 B.C. By 400 B.C. 'rice men' were appointed to supervise the planting and water control operations (Ting 1949*a*; Ru 1958).

The rice crop was directly seeded, probably by broadcasting. The cultivars belonged to the keng race and was of the lowland type (Ting 1949*a*, 1957). The varieties were predominantly awned and were probably early in maturity, insensitive to photoperiod (Ting 1949*a*, 1961), and tolerant to cool night temperature (T.-T. Chang, personal observation). During and after the Warring States (403–222 B.C.), literary works mentioned early and late-season varieties grown in the south (Ting 1961). Because the climate in north China became increasingly arid, rice growing gradually moved east toward the coast and south (Herrmann 1966).

The water buffalo was used as a draft animal since the Shang dynasty. The hoe for cultivation came into use during the Chou dynasty. The iron plough, spade, and scythe came into use during the Warring States (Ting 1961; Chang 1968). The water buffalo was probably imported from Southeast Asia or south China (Ting 1949*b*; Zeuner 1963). Deep ploughing and mid-season cultivation appeared in writing several hundred years before the Christian era. By the Eastern Chou dynasty (255–249 B.C.), rice was already the staple food crop in the middle and lower Yangtze basins (Ting 1961). At about the same time, terraced fields appeared in south-west Yunnan (Chang 1968). Rice cultivation alternated with fallowing and weed control began as early as 700 B.C. (Amano 1962).

Green manuring was practised in the 6th century. Detailed descriptions on the preparation and application of different organic manures appeared in the Sung dynasty (beginning A.D. 960) (Amano 1962).

The term 'glutinous rice' appeared at about 200 B.C. A saline-tolerant variety appeared in writing before the Christian era. The designation of hsien or Indica rice appeared at about A.D. 121 (Ting 1949*a*), though the descriptions were sometimes inconsistent. Manuring became an important part of rice culture more than two thousand years ago (Ting 1961).

Harvesting a second crop from the ratoons was known to be practised in Kiangsu province as early as Western Tsin, A.D. 265–316 (Amano 1962).

The mass migration of people in the north to the Yangtze River basin and to points further south during the Chin and Sung dynasties (A.D. 317–1279) greatly stimulated the expansion of the irrigated rice area in central and eastern China. Demand for the tasty cereal also increased.

During the Chou and Eastern Chin dynasties, all the farm lands were owned and managed by a feudalistic system based on individual families. Private ownership of land began in Sung (beginning A.D. 960) and further increased rice productivity (Amano 1962). Large-scale irrigation projects began in the Wei River basin and in the Red Basin of Szechwan in the third century B.C. (Ho 1969).

Transplanting began in late Han during A.D. 23–220 (Amano 1962; Ho 1969). Its advantages were better weed control in both nursery and field, more efficient use of water during spring shortages, more intensive crop management, and better utilization of land for rice and other crops (T. Nishiyama 1949, quoted by Amano 1962).

Since late Han, farmers south of the Yangtze River burned the weeds before wet ploughing as a means of weed control. Shallow transplanting was urged during Tang (A.D. 618–906). The foot-pedalled water pump came into use in the same period. The spike-tooth harrow and the roller-compactor, which became widely used during the Sung dynasty (A.D. 960–1279), greatly facilitated transplanting (Ting 1961; Amano 1962). The harrow was introduced into Indochina, Thailand, Burma, Malaysia, and the Philippines where it is still widely used (T.-T. Chang personal observation).

Seed selection by relative density, soaking, and incubation to hasten sprouting were described in A.D. 1314. Transplanting of 30-day-old seedlings and straight-row planting were discussed in the 17th century. Mid-season drainage appeared in a book on farming in A.D. 1643 (Ting 1961).

Seed-based agriculture led to the development of a great variety of tools and utensils connected with seed processing and storage (Amano 1962).

The early maturing (100-day or earlier) Champa varieties of central Vietnam were introduced on a large scale into central and south China during the 11th century. This group of Indica rices, including both lowland and upland types, made possible the double rice cropping or the rice-winter crop combination and led to rapid population increases in China (Ting 1949*a*; Ho 1956). The short-season rices made possible intensive multiple cropping and caused the rice area to increase quickly (Ho 1956).

(*b*) *Cultural systems in Southeast Asia*

Information is fragmentary on the history of lowland rice culture in Southeast Asia. Recent excavations at sites in Thailand have advanced the beginning of pebble stone culture to 10000 B.C. and that of plant domestication to 3000 B.C. or earlier (Solheim 1967). Prehistoric contacts between the peoples of China and of Southeast Asia mainland, particularly between the Hoabinhians and the people in the lower Yangtze, are well established (Aigner 1973; Treistman 1974). There is a controversy between one school which claims an earlier Southeast Asian rice culture (Sauer 1952; Solheim 1970, 1972; Aigner 1973) and the other school, which opts for earlier Chinese rice culture (Chang 1968, 1970; Ho 1969). This could be resolved if one visualizes Southeast Asia as an early site of plant and water buffalo domestication, with some of the domesticated rices brought to the seed-based early cultivators in east and central China, while the technology of transplanted culture (Ho 1969) and the iron farm implements were exported from China to Southeast Asia through the migration of people (Chang 1970).

One should also visualize that before the advent of the iron tools, Southeast Asia was largely occupied by hard-wood forests with occasional savannah-like areas (Hanks 1972). Iron implements were required to clear land on a large scale (Whyte 1972). North Vietnam could have both dryland and lowland rice cultures on terraces as early as 2000 B.C. (Spencer 1963), but such an early date of lowland culture appears doubtful (Wheatley 1965; Hill 1973). The agricultural technology in Vietnam was more primitive than that of China at 111 B.C. (Wheatley 1965; Grigg 1974).

Transplanting in Vietnam began about 1000 A.D. (Hanks 1972). The ancestors of today's Malays, Indonesians, and Filipinos spread lowland rice cultivation to northern Philippines, west Sumatra, west Java, and south Sulawesi sometime after 1500 B.C. (Spencer 1963). In many hilly areas of Southeast Asia, shifting cultivation based on a combination of rice and other crops is still practised. When cultivators build terraces and impound the rainwater, the transplanted rice culture replaces the upland planting of rice, or other cereals such as millets and sorghum, or the root crops.

A recent case study of Bang Chan, a town on the central plain of Thailand only 35 km by highway from Bangkok, clearly showed that rice cultivation on the annually flooded plain developed from shifting cultivation (probably by the dibbling method of seeding), to broadcasting, and then to transplanting. In the sparsely populated community, the evolution from shifting cultivation to transplanting took 85 years (1850–1935). The interrelationships among the types of culture, energy requirements for each cultural type, field size, human population density, and input/output ratios were revealed by a study of this community (Hanks 1972). Improvements in rice culture obviously progressed faster when the community as a whole exercised control over a large portion of the rice cultivators in the area, as it did in north China during Lungshan period (Chang 1968) and in Japan during the Jomon period (Kagawa 1973). Such an integrated adaptation of crops, livestock, and men to the new environment parallels the development of agriculture in the 'nuclear zone' of Anatolia, Iran and Syria (Darlington 1969).

In areas where the water level is more than 1 m deep during the peak monsoon period, cultivators in Southeast or South Asia resorted to either the double transplanting of relatively tall and late varieties or the broadcasting of floating varieties before rains began. When they found that water could be controlled by dykes and ditches (for flood control) or canals and levees (for irrigation), they resorted to transplanting.

The spike-tooth harrow drawn by the water buffalo greatly facilitates puddling of the heavy clayey soils and the levelling of the field for transplanted rice. This practice originated in China and is popularly used in a long arc that extends from Burma (Watt 1891) to Malaysia and the Philippines. It is less popular, however, in Indonesia, where Indian influence probably is relatively greater. The less widespread use of the harrow in India is partly reflected by the relatively larger area of the direct-seeded crop (Ghose, Ghatge & Subrahmanyan 1960).

(*c*) *Upland culture*

Upland culture is probably almost as old as the lowland culture. Cultivars with red seedcoats predominated during ancient times in mountainous regions of Southeast Asia (Ichikawa 1961; Spencer 1963). Primitive tribes in many parts of Southeast Asia today use wooden sticks and

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axes to dig holes in the ground, into which they drop seeds of rice and other grains. This widespread dibble culture probably led Hamada (1949), Sauer (1952), and Solheim (1967) to postulate that upland rice culture or vegeculture is older than lowland rice culture. Varieties adapted to upland culture, however, generally have early maturity (a drought-escape mechanism), low tillering ability, thick and deep roots, long panicles, non-shattering habit, and heavy grains (Chang, Loresto & Tagumpay 1972, 1974) and in some instances, glabrous leaves and glumes – features which indicate a more advanced form. Moreover, all of the wild and weed races are found in poorly drained sites and have rather weak root systems.

In areas where initial showers in the rainy season are insufficient to puddle the soil, rice is often broadcast or drilled as a dryland crop and the plants later ripen in a flooded field. This is called semi-arid culture in India (Ghose *et al.* 1960) and gogo rantjah culture in Indonesia. Some of the cultivars adapted to this kind of culture, however, appear to be of the lowland type (T.-T. Chang, personal observation).

In the shifting type of upland rice culture, the cultivators often mixed their plantings of rice, other cereals (corn, millet, or sorghum), grain legumes, vegetables, fibre crops, and root crops (Huke 1953; Freeman 1955; Conklin 1957, 1967; Spencer 1966; Sasaki 1970). This pattern of intercropping can still be found in upland areas of South and Southeast Asia. Such an influence is also indicated by the gogo tegalan culture in the highlands of Sumatra where farmers intentionally mix-plant morphologically distinct varieties of similar maturity in permanent upland fields. Under the shifting scheme, the farmers also mix-plant different rice varieties.

(*d*) *Rice cultures in Africa*

Records are lacking concerning the evolutionary process of rice cultivation in Africa. The cultural methods used today are probably similar to the early practices.

In West Africa, the cultivated species (*O. glaberrima*) was most likely domesticated from the wild annual *O. barthii* (formerly known as *O. breviligulata*); the latter is primarily adapted to water holes in the savannas and secondarily adapted to the forest zone (Harlan 1973). Rice cultivation is probably not more than 3500 years old (Porteres 1956).

In West Africa, *O. glaberrima* is the dominant crop grown in deep-water areas of the Niger and Sokoto River basins; it is broadcast on hoed fields. On parcels of land flooded shallowly, a rainfed lowland crop is either directly sown by broadcasting or dibbling or transplanted. About 75% of the land planted to rice in Africa is grown under upland culture, largely under the bush fallow or grass fallow systems (Jordan 1964). *O. glaberrima* seeds are broadcast or dibbled after the ground had been hoed (Oka & Chang 1964; Anon. 1968). Many African farmers still use axes, hoes, and knives in land preparation (Anon. 1968).

In most fields, *O. glaberrima* is grown in a mixed stand with *O. sativa*. Sometimes the mixed stand appears to have resulted from mechanical mixtures during harvesting and drying. In some cases a 1:1 mixture appears to be intentionally provided by the farmer. *O. barthii* is also frequently found in *O. glaberrima* fields.

The Asian species *O. sativa* introduced into West Africa in the 17th century, is rapidly spreading in rainfed lowland areas formerly grown to *O. glaberrima*. In irrigated areas and in mangrove swamps, only *O. sativa* is grown (Oka & Chang 1964).

The slow improvement of cultural practices in the growing of African rices in West Africa since civilization began is associated with relatively low population density, a narrow north-to-south distribution of the cultivated species and the annual weed race, a relatively flat

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topography, and a dearth of iron farm implements. Although the rate at which progressive rice culture evolved was slower in Africa than in Asia, the stepwise process was the same: shifting cultivation, to broadcasting or dibbling in permanent sites, to transplanting in bunded fields.

4. Evolutionary changes under domestication and cultivation

The rice plant has changed markedly from the time the wild-growing annual was domesticated. It underwent further changes when it was widely disseminated by cultivators from the tropical environment to subtropical zones where the greatest diversity is found today (T.-T. Chang, personal observation). Further spread and selection led it into temperate zones as far north as 53° latitude (Ting 1961).

(*a*) *Changes under domestication*

The evolutionary trend in *O. sativa* from its wild progenitor consists of a number of changes in morphology and physiology: larger plant size in terms of leaf size, culm length and diameter, and panicle length; higher leaf number and rate of leaf development; more extensive root system; increased rate of seedling growth and tillering capacity; increased synchronization of tiller development and panicle formation; slightly higher net photosynthetic rate of individual leaves; more secondary branches on a panicle; shorter anthers; smoother glume surface; larger grain dimensions and mass; thicker grain; and a longer period of grain filling.

Concurrent with the above changes were gradual losses or decreases in pigmentation, rhizome formation, ratooning ability, ability to survive deep water, pubescence, awning, shattering, duration of grain dormancy, photoperiod response, or sensitivity to cool temperatures (Chang 1975*b*). The trend in such adaptive changes is similar to that of other cereals (Harlan, de Wet & Price 1973).

The cultivator's efforts in preparing land, weeding, planting, and harvesting seeds (Oka & Morishima 1971) accelerated the loss of primitive traits and the increase in self-fertilization.

Plants were also selected by early cultivators for their ability to grow in habitats other than continuously flooded conditions and to withstand short periods of water stress. The upland type evolved, with early maturity and low tillering ability, quick stomatal response to water stress, and long and thick roots (Chang *et al.* 1972, 1974).

The cultivated species appear to have acquired a more asymmetrical karyotype at the pachytene stage than their wild relatives (Shastry 1964*a*).

(*b*) *Changes under cultivation*

As the early cultivators in Asia carried the tasty and productive cereal to new habitats, the travel was largely along a latitudinal cline (figure 2) or involved changes in elevation. In central and south China, farmers experimented with double cropping when the growing season permitted a second crop of an early maturing variant. In tropical monsoon Asia, the dry season crop was added to the wet season crop at sites where water was available in the spring. In the lower Ganges River delta, cropping patterns involving as many as three crops (winter, summer, and autumn) could fit into varying water and temperature regimes. Deliberate human selection in a disruptive manner, along with contributions from the weed races, led to enormous diversity among rice cultivars in adaptiveness to climatic factors (mainly temperature and photoperiod), water regimes (deep, shallow, dryland, and various intermediaries), and edaphic conditions (saline, alkaline, acid, cold, etc.) – figure 3. The extent of variation in climatic adaptiveness is indeed remarkable for a tropical species (Chang & Oka 1976).

The subtropical region embracing Nepal, Sikkim, northeast India (Assam), and Upper Burma, along with the high-elevation areas of Laos, Thailand, and Yunnan, provide the richest spectrum in varietal diversity and ecological specialization, on the basis of the 35000-accession collection conserved at the International Rice Research Institute (I.R.R.I.) (T.-T. Chang, personal observation) and the pattern of esterase isozyme distribution among 776 cultivars (Nakagahra, Akihama & Hayashi 1975).

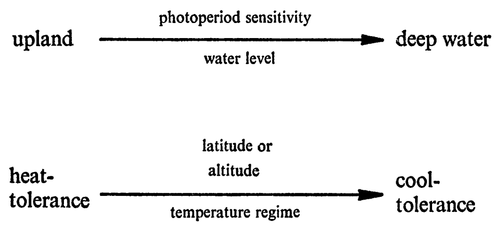

FIGURE 3. Ecologic diversification in rice following dispersal and selection.

Earlier, on the basis of F_1 fertility or grain dimensions, Japanese researchers postulated that the aus varieties of the Indian subcontinent (Morinaga 1955; Nakao 1957), the bold-grained varieties of the Himalayan region, and the glabrous varieties of Laos (Morinaga 1968) were the progenitors of the lowland varieties of Japan. Many such short-grained varieties are not typical of keng or Sinica, however, in ecological characteristics, shattering habit, thickness of the grain and chemical composition of the endosperm starch (T.-T. Chang, personal observation). Only those short-and-thick-grained ecotypes that could tolerate cool night temperatures were the likely prototype of keng.

Recent studies on ancient rice glumes imprinted in bricks show that the evolutionary trend in South and Southeast Asia was from a short and bold grain type to a longer and more slender type. A survey by Japanese explorers also indicates that within a broad ecologic region, one grain type could replace another within 5–10 centuries (Watabe, Akihama & Kinoshita 1970; Watabe & Toshimitsu 1974). But it took a relatively longer time to move rice cultivation further northward in Japan when the crop had approached its marginal area of climatic adaptation (Kihara 1969).

The Javanica race evolved when Indonesian farmers persistently selected for cultivars with long panicles, fully exerted panicles, non-shattering habit, and heavy, bold grains.

Other forces that rapidly increased varietal diversity were religious beliefs (Watt 1891; Freeman 1955; Conklin 1967), the need for different maturities or grain qualities for household uses, morphological peculiarities to serve as markers (Harlan *et al.* 1973), reputed differences in nutritive or medicinal values (Watt 1891), and linkages between morpho-agronomic features and adaptiveness to primitive or progressive agriculture. Many farmers of tropical Asia still grow on a small farmstead several varieites that differ in maturity and quality features. Under human selection, a number of duplicate loci related to primitive features such as pigmentation and awning disappeared from the more elite forms (Chang 1964, 1976). Meanwhile, genetic polymorphism within cultivars was retained despite rigorous selfing and selection.

Intervarietal hybrid sterility developed as a result of geographic and spatial separation. Sterility occurs in both inter- and intra-racial crosses (Engle, Chang & Ramirez 1969). A variety of pre-zygotic mechanisms – genic, chromosomal, and genic imbalance – are associated with sterility (Oka 1964; Shastry 1964*b*; Henderson 1964; Demeterio, Ando, Ramirez & Chang 1965; Dolores, Chang & Ramirez 1975). Post-zygotic mechanisms ranged from hybrid inviability, to breakdown, to weakness (Oka 1964).

As the cultivars gained a wider range of geographic adaptiveness, the loss in photoperiod- and thermo-sensitivity was accompanied by a reduction in plant height, a more determinate tillering habit, more synchronous heading among tillers, a longer grain-ripening period, and a weaker ratooning ability (Chang & Oka 1976). A more thrifty and productive plant type – but one that was less competitive with weeds – evolved in the temperate regions.

Because *O. glaberrima* had not been subjected to widespread dispersal or to intense natural or artificial selection, these African rices have never attained a degree of diversity comparable to that found in *O. sativa* cultivars. Populations of *O. barthii* are also less genetically diverse than the Asian wild race, *O. nivara* (T. T. Chang, personal observation).

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Discussion

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Our business in these discussions is with early agriculture, but the essential reason why this common theme has brought together so diverse and distinguished a body of participants is that it is a component of the general cultural history of mankind. Of course settled societies with advanced cultures have existed, and indeed still exist, which do not raise crops (for example in certain communities which depend on the harvest of the sea), but early agriculture was associated with cultural changes so widespread and diverse that we are bound to regard it as one of the most significant elements in our cultural evolution.

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Perhaps we might attempt to order our discussions under four main headings – when, and where, did agriculture begin to be important as a cultural element, what sort of people began to practise it, and with what biological and environmental resources?

In thinking about the 'when' question, I have concluded that there is less interest than I once thought in attempts to identify precise points in space and time at which agriculture 'began' or 'was invented'. Though, in a particular time sequence at a particular place, remains of apparently cultivated plants may appear suddenly, it seems likely that the deliberate sowing and tending of useful plants went on alongside gathering and hunting and fishing for a long time and over substantial areas. In Britain, where our agriculture is as advanced as any in the world, we gather blackberries and many other wild plants, and we hunt several species of wild birds and mammals for food. It may well be sufficient to think of the time between around 10000 and 5000 B.C. as an extended period during which the deliberate sowing and tending of useful plants emerged in at least two distinct regions of the earth. Long after the end of this period Herodotus described a world in which the raising of crops was still far from universal, and in which nomadic herders ranged over what are today settled agricultural regions.

As to where, we recognize that the first stirrings of crop production began at much the same time in Middle America and southwest Asia, with no evidence of any connection between them, and with quite different plants, drawn in each case from more or less identifiable elements of the local flora. I feel today that I must be prepared in future to encounter yet other independent origins of crop raising, at the same or at other times. But one cannot but be tantalized by the approximate coincidence in time of the separate seminal events in the two continents – coincidence, communication, how are we to enquire?

The question about what sort of people poses itself for me as a question about how people lived before they began to tend crops. The social-evolutionary interpretation of events in the Tehuacan valley is intellectually satisfying to me – but perhaps it is so because it spells out what my preconceptions lead me to expect. I hope we shall continue to acquire more and more comparable information – not from single sites alone, but from the 'territories' (in the sense in which students of social organization in animals use the word) of early human social–economic units.

About environmental resources it is not easy to feel sure. Zeuner felt that the climate of the Middle East had not changed in any important way since the apparently cultivated plants were first deposited in the archaeological record, and this may be true of Tehuacan also; but there is ample evidence in Anatolia and elsewhere of changes in terrain associated with erosion and deposition. The tells in the region along the southern margins of the Sahara, where there is clear evidence of long-term swings in climate over several hundreds of kilometres during some tens of thousands of years, may provide sensitive evidence of the cultural and agricultural consequences of climatic variation on this scale.

We are on rather surer ground with the biological resources, where we can call in the aid of taxonomy, including its newer biochemical and phytochemical tools, some of which have been fascinatingly displayed in papers presented to this meeting, and of genetical and evolutionary studies. Indeed it must be an important part of the study of early agriculture to reconcile the archaeological and genetical evidence – a task as important for our understanding of the evolution of cultivated plants as for our description of cultural history. In all of this the related wild forms are particularly important – provided we recognize that they too have evolved over 10000 years, especially where selection by man and reciprocal gene flow may well have influenced evolution in the wild forms as profoundly as in their cultivated relatives. I am bound here to refer to the work of the recently constituted International Board for Plant Genetic Resources, of which I have the honour to be a member, which will seek to ensure that all relevant elements of the wild-cultivated spectrum are collected, conserved and made available for use in future crop improvement as well as in evolutionary studies.

Our tasks are made both more difficult and more fascinating by the continually shifting background of human migration and communication. Man is an insatiable wanderer, over both land and water. Evidently many cultigens moved, with or without the human societies that used them, over very considerable distances in ancient times. They changed as they went, partly because mutation and recombination threw up new variants which could become adapted by selection, not all of it unconscious, to new places and new purposes, and partly because they encountered new wild relatives, as sorghum seems to have done in West Africa. In this way we have come to regard southwest Asia as a primary centre from which crops were dispersed to the Mediterranean, the Nile Valley, Arabia and Ethiopia, to India, along the ancient communication routes north of the mountains to Afghanistan, central Asia and China, to the Russian plains and the Danube Valley, and in the end to northwest Europe. Along the way new species, some of which may previously have been weeds, or plants gathered for food, were domesticated. For me, the Indian Ocean has always appeared as a great lake of early domestication, around the margins of which, from Southeast Asia and the Pacific to the African coast, crops moved far and wide at a time when Britain was a misty offshore island inhabited by wild cave dwellers who knew nothing of crops, trade or cities.

In all this, our speculations can be greatly illuminated by studies of the traditional farmers, nomadic herders, and hunting and gathering peoples of our own time. I first read about some of them in Daryll Forde's *Habitat, economy and society*; and in much of Africa, and no doubt elsewhere, we may talk to such people and see them at work. In the Northern Sudan, twenty years ago, you could buy a new quern for fifty piastres – as I was told, a trifle condescendingly, when I proudly bore home an ancient one, worn and broken, from the plinth of a small hill on the research farm at which I worked. The main food resources of the farming people of parts of the forest region of Eastern Nigeria appear in earlier times to have come largely from about six indigenous tree species (including the oil palm), and a few non-African old world perennials (including coconut, banana/plantain) which are deliberately cultivated as well as protected, together with a single vegetatively reproduced indigenous annual crop, the yam, which is planted amongst them. Since 1492 this ecologically complex tree-cropping system has been reinforced by the American crops maize, cassava and cocoyam (*Xanthosoma sagittifolia*). The indigenous species, between them, provide some food in every month of the year, but the American additions have made the system more diverse, more intensive and more securely productive, so that it can carry many hundreds of people per square kilometre if necessary.

The field we have gathered to discuss has many dimensions and brings together many disciplines. To the extent that this meeting has advanced this multivalent mode of thought, the Royal Society will, I hope, feel that its welcome initiative has been amply rewarded.

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