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GENETICS OF CEREAL ADAPTATION TO THE MAN-MADE HABITAT

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Abstract
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   The wild progenitor species of all cereals are known with various degrees of certainty. Wild and cultivated taxa of the same species cross and their hybrids are generally fertile. This allows for a study of the genetics of domestication. A survey of the literature, however, reveals few such studies. The adaptation to disturbed habitats is genetically complex, and colonizing ability seems to have been a prerequisite for successful domestication. Natural seed dispersal is controlled by one to several linked genes, and behaves genetically as an overall dominant over loss of efficient seed dispersal mechanisms. Apical dominance, synchronized tillering, and increase in fecundity are complex, recessive genetic traits associated with cereal domestication. Racial evolution resulted from conscious selection by man and involves numerous loci.

1. INTRODUCTION

   Plant domestication involves two distinct, but interdependent processes, harvesting and sowing. Neither harvesting nor sowing will independently lead to domestication. Harvesting enforces wild type adaptations since daughter populations become established from seeds that escaped the harvester. The sowing of harvested seeds differs little in its evolutionary effects from natural seed dispersal. Domestication is initiated when man sows part of what he has harvested in habitats specially prepared for this purpose [1]. Domestication continues as long as seeds harvested from a sown population are again sown in a man-made habitat.

   Weeds and domesticates are adapted to man-made habitats [2]. They differ primarily in that weeds are spontaneous in disturbed habitats, while domesticates depend on man for suitable habitats and seed dispersal. The wild progenitors of cereals are aggressive colonizers. Wild colonizers readily evolve genotypes adapted to man-disturbed habitats, and are readily domesticated. Species adapted to habitats that are not notably disturbed by man are difficult to domesticate; indeed, colonizing ability may be a prerequisite for successful domestication. American wild rice

(*Zizania aquatica* L.) has been an important wild cereal since long before recorded history in North America [3]. The species is not a colonizer and native farmers failed to domesticate this wild rice.

2. CEREAL DOMESTICATION

Food production is a recent innovation in the evolutionary history of man. Archaeological records suggest that some 10–15 000 years ago, in several parts of the world, man abandoned his nomadic way of life to become a food producer. Cereals were among the first plants to be brought into cultivation and the major cereals have become totally dependent on man for survival [4]. They depend on man for suitable habitats as well as for seed dispersal.

The progenitors of domesticated cereals were aggressive colonizers. Some cereals became adapted to man-disturbed habitats before they became domesticated. The archaeological record suggests that oats spontaneously accompanied wheat and barley from West Asia to Europe where it eventually became domesticated [5]. This is also true of several minor cereals [6]. Most cereals were probably forced into cultivation by conscious sowing. Burkill [7] suggests that sowing was initiated when man transported his favourite cereals beyond their natural ranges. Archaeological records, however, indicate that cereals were usually domesticated where their species were, and often still are, particularly abundant. The transition from harvesting in the wild to cultivation was not abrupt and may have involved hundreds or even thousands of years.

Gene exchange between wild and cultivated populations must have been extensive in allogamous species during the initial stages of domestication. As cultivated populations became adapted to cultivated habitats, disruptive selection must have become more effective in preventing introgression. Hybrids between wild and cultivated races rarely are successful in competing with either parent for available habitats.

The genetics of habitat adaptation in cereals is not known in detail. Adaptation is genetically complex and difficult to manipulate. American wild rice has recently been brought into successful cultivation by simulating natural habitats of the species [8]. Overall adaptation to disturbed habitats is genetically dominant over adaptation to habitats that are not notably disturbed by man. Blocks of linked genes seem to be involved and habitat preference is difficult to change.

It is not known when cereals were first cultivated. Barley (*Hordeum vulgare* L.) is among the oldest known domesticated cereals. Wild barley appears in the archaeological records of incipient agriculture in West Asia dating back some 10 000 years. Some one and one-half millennia later, cultivated barley had lost the ability of natural seed dispersal [9]. Barley has become domesticated, in the sense

that cultivated kinds became dependent on man for seed dispersal. Harvesting and sowing by man became an essential part of survival.

The wild progenitor species of most cereals have been identified with a fair degree of certainty. Cultivated taxa of domesticated species are commonly compatible with their closest wild relatives. This allows for detailed studies of the genetics of domestication. Inflorescence as well as vegetative morphology changed under domestication [1] and these changes are associated primarily with loss of efficient seed dispersal, increase in fecundity, and conscious selection by man to suit his needs and fancies.

3. LOSS OF EFFICIENT SEED DISPERSAL MECHANISMS

Lack of efficient floret or spikelet dispersal generally does not significantly change the inflorescence architecture of domesticated cereals. Appendages such as glumes and bristles are often reduced or absent, but the cereal is still readily recognized as a member of its wild progenitor species. Wild-type dispersal is genetically dominant over lack of efficient dispersal mechanism. Dispersal is generally determined by one to several genes. Mutants preventing efficient dispersal occur in nature, but are selectively disadvantageous and soon eliminated from the population. Only under a regime of harvesting and sowing does selection favour a decrease in seed dispersal efficiency.

Domesticated maize (*Zea mays* L.) differs so significantly from its closest wild relative teosinte (*Z. mays* ssp. *parviglumis* Iltis and Doebley), that these two taxa are frequently treated taxonomically as different species or even genera [10]. Maize and annual teosintes, however, cross and their hybrids are fertile. Genetic compatibility does not prove that teosinte is wild maize [11, 12]. Genetic evidence, however, is overwhelming in favour of maize's being derived from teosinte under domestication [13, 14].

Major morphological differences between maize and teosinte are in the architecture of female inflorescences. In both taxa, terminal inflorescences are generally male, and lateral inflorescences are female, with racemes often tipped by a short section bearing male flowers.

Phenotypic differences between the female sections of lateral inflorescences of maize and teosinte are listed in Table I. Racemes of teosinte are distichous, with solitary female spikelets alternately arranged in cavities of indurated rachis internodes. These cavities are closed by the indurated outer glume to form fruit cases that disarticulate at maturity (Fig. 1(a)). In contrast, the ear of maize is polystichous, with paired female spikelets arranged in whorls of four or more, in shallow cupules along a continuous rachis (Figs 1(b), 1(c)).

TABLE I. MAJOR PHENOTYPIC DIFFERENCES BETWEEN FEMALE INFLORESCENCE BRANCHES OF TEOSINTE AND MAIZE

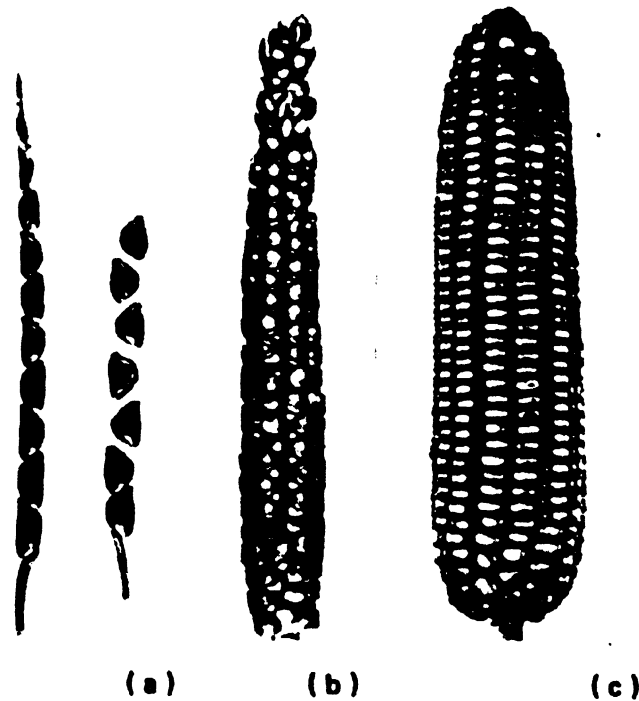| Character	Teosinte	Maize
Female spikelets	Solitary	Paired
Arrangement	Alternate and distichous	Whorled and polystichous
Outer glume	Highly indurated	Less indurated
Rachis	Articulate ·	Continuous
Internode	Laterally compressed	Horizontally compressed
Cupule	Deep	Shallow
Grain	Covered by glumes	Exposed

(a)   (b)   (c)

FIG. 1. *Morphology of* Zea mays *female inflorescences; (a) female spikelets of teosinte are solitary and arranged alternately in fruit cases composed of indurated rachis internodes and outer glumes; fruitcases disarticulate at maturity; (b) female spikelets are paired in maize and occur in whorls of four to form a basic 8-rowed ear; (c) modern maize is mostly 14-, 16- or 18-rowed.*
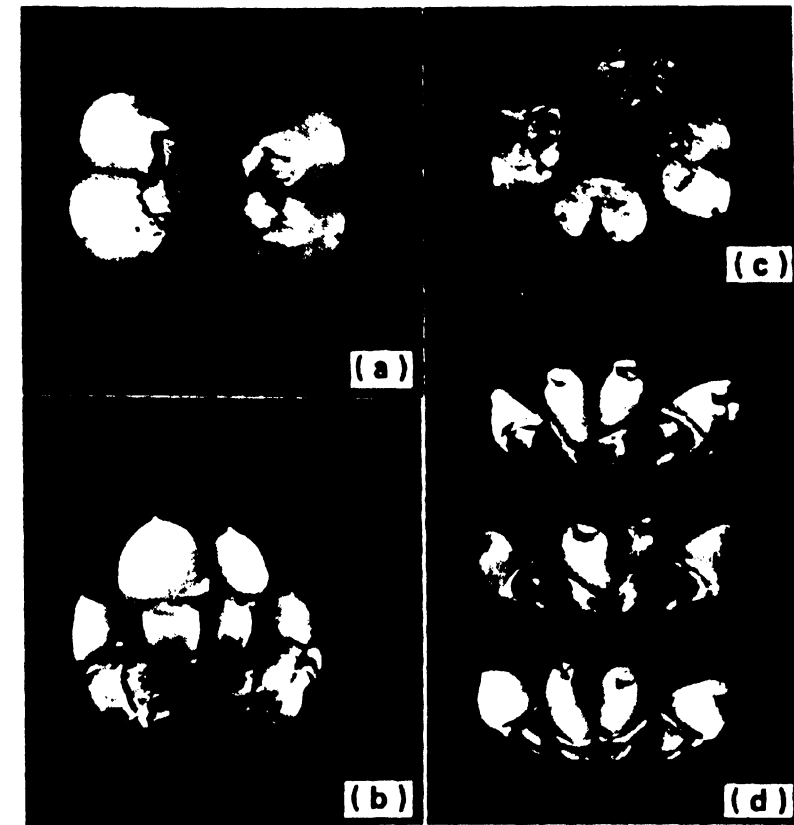
FIG. 2. *Structure of the maize ear; (a, b) female spikelets are yoked into opposite pairs, and arranged to form an ear of opposite spikelet pairs; (c, d) yoked pairs of female spikelets are cross-yoked to form whorls of four, and arranged in 8 rows along a central axis.*

Hybrids between cultivated maize and annual teosinte, both *Z. mays* ssp. *parviglumis* and ssp. *mexicana* (Schrad.) Iltis, are fertile. Hybrid phenotypes indicate that ssp. *mexicana* is variously contaminated with genes from maize. Selected genotypes of Guatemala teosinte (ssp. *parviglumis*) are essentially pure wild-type maize. Phenotypes of hybrids with domesticated maize indicate that the teosinte traits listed in Table I are genetically dominant over their maize counterparts [15–17]. The change from solitary fertile female spikelets at a rachis node in teosinte to two fertile female spikelets in each cupule in maize is associated with selection for increase in fecundity. Fertility is commonly restored to reduced spikelets and florets in cereals under domestication [4, 6]. Reduction in induration of rachis and glume tissues in maize is associated with alleles of the tunicate locus. Mangelsdorf and Galinat [18] suggested that the earliest known cultivated maize must have had soft glumes. The

discovery of a soft glumed teosinte may have led to cultivation of teosinte as a cereal. This mutation facilitates both harvesting and threshing.

Mutations that changed the distichous female inflorescences branch of teosinte into the polystichous ear of maize are associated with loss of natural seed dispersal. Recessive alleles at at least three tightly linked loci seem to determine loss of natural seed dispersal in maize. The recessive allele at one locus yokes alternate fruit cases into opposite pairs (Figs 2(a), 2(b)). A second recessive allele cross-yokes paired fruitcases and compresses them into whorls of four (Figs 2(c), 2(d)). A third recessive allele unites whorls of four fruitcases, through the prevention of abscission callus, into the basic 8-rowed maize ear (Fig. 1(b)). The female inflorescences of teosinte and maize are phenotypically distinct, but are genetic and phylogenetic alternative structures. Iltis [19] proposed that a catastrophic sexual transmutation transformed the male inflorescence of teosinte into a female inflorescence. Such a postulate certainly is not necessary. Selection pressures associated with harvesting and sowing could have led to the origin of the maize ear from a female inflorescence of teosinte [14].

4.   INCREASE IN FECUNDITY

Spectacular changes in inflorescence morphology, owing to domestication, are not unique to maize. In other cereals, selection for increase in fecundity, rather than increase in percentage of harvestable seed, produced spectacular phenotypic changes. Harvesting selects for synchronized tillering or apical dominance, two heritable traits that are recessive in nature. In cereals such as rice and wheat, inflorescences mature simultaneously because tillers are all of the same age. Apical dominance initially reduces overall seed production because the number of tillers as well as number of inflorescences per tiller are reduced. Increased inflorescence size and restored fertility in reduced florets and spikelets, however, compensate for this initial drop in seed production. Three examples will suffice to demonstrate changes associated with an increase in fecundity.

Green foxtail (*Setaria italica* L.) ssp. *viridis* (L.) Thell. (Fig. 3(a)) is difficult to recognize as the wild progenitor of foxtail millet (ssp. *italica*) with its often gigantic inflorescence (Fig. 3(b)). Yet, these two taxa cross to produce fertile hybrids, and cultivars are grown in South Asia that differ little from their wild progenitor except in efficiency of natural seed dispersal [20]. Inflorescence size and shape are determined by elongation of the central axis, increase in number of secondary branches and an increase in number of spikelets on tertiary branches [21]. The number of alleles determining these traits is not known.

Pearl millet (*Pennisetum glaucum* (L.) R. Br.) is characterized by cultivars with solitary spike-like inflorescences up to 200 cm long, while the several inflorescences of wild pearl millet are 2–20 cm long [22, 23]. Fecundity in pearl millet is

FIG. 3.   *Inflorescence morphology of* Setaria italica: *(a) cultivated foxtail millet from China, (b) wild foxtail millet from China, the progenitor of the cultivated cereal.*

further increased through an increase from one or rarely two functional spikelets per involucre in the wild, to as many as nine fertile spikelets per involucre in cultivated kinds.

Changes in inflorescence morphology, owing to restored fertility in spikelets, are particularly obvious in barley. Wild barley (*H. vulgare* ssp. *spontaneum* (C. Koch) Thell.) is two-rowed [24]. The central spikelet at each rachis node is fertile, while the lateral spikelets of each triad are sterile and reduced in size and structure. Cultivated barley includes two-rowed, four-rowed and six-rowed kinds. In six-rowed barley all spikelets of a triplet are fertile, although in some cultivars isospiculate and heterospiculate triplets occur in the same spike. Spontaneous six-rowed barley occurs in Western Asia [25, 26], and it is often assumed that six-rowed spontaneous barley was independently domesticated to produce race hexastichon [27]. It seems more likely, however, that six-rowed spontaneous barley represents derivatives of crosses between wild two-rowed barley and cultivated six-rowed kinds [28, 29], and that six-rowed cultivated barley was derived from two-rowed cultivated barley under domestication [30]. Alleles at several loci determine the number of fertile spikelets at each rachis node.

5.   RACIAL EVOLUTION UNDER DOMESTICATION

Domestication not only leads to phenotypic differentiation between wild and cultivated complexes of domestic species, but also to rapid evolution within cultivated complexes. Relatively simple recessive or, more rarely, dominant mutations are involved. Man transports domestic species beyond their natural ranges, often necessitating changes in adaptation that are reflected in inflorescence morphology. Farmers further select genotypes to suit their individual fancies and needs, resulting in rapid shifts in gene frequencies and changes in phenotype. An example is *Sorghum bicolor* L. (grain sorghum). This species is widely distributed in Africa. It occurs spontaneously in open habitats of the African tropical forest, is common across the savanna from Mauritania to Ethiopia and South Africa, and extends into the desert along the floodplains of the Nile and its tributaries. Sorghum cultivation started some 5000 years ago in the savanna of West Africa [9]. During its relatively short evolutionary history, grain sorghums evolved into a phenotypically and ecologically variable complex of cultivated taxa that are variously classified by taxonomists. They are recognized as 28 species with 156 varieties by Snowden [31]. These Snowdenian species, however, are genetically conspecific, and are recognized as five ecogeographic complexes by de Wet [32].

Racial evolution within cultivated complexes is associated with ecogeographical adaptation, and racial distinction is maintained by a combination of habitat preference and spatial isolation. Variation within races results from conscious selection by man of genotypes to serve his particular needs. More efficient isolating mechanisms,
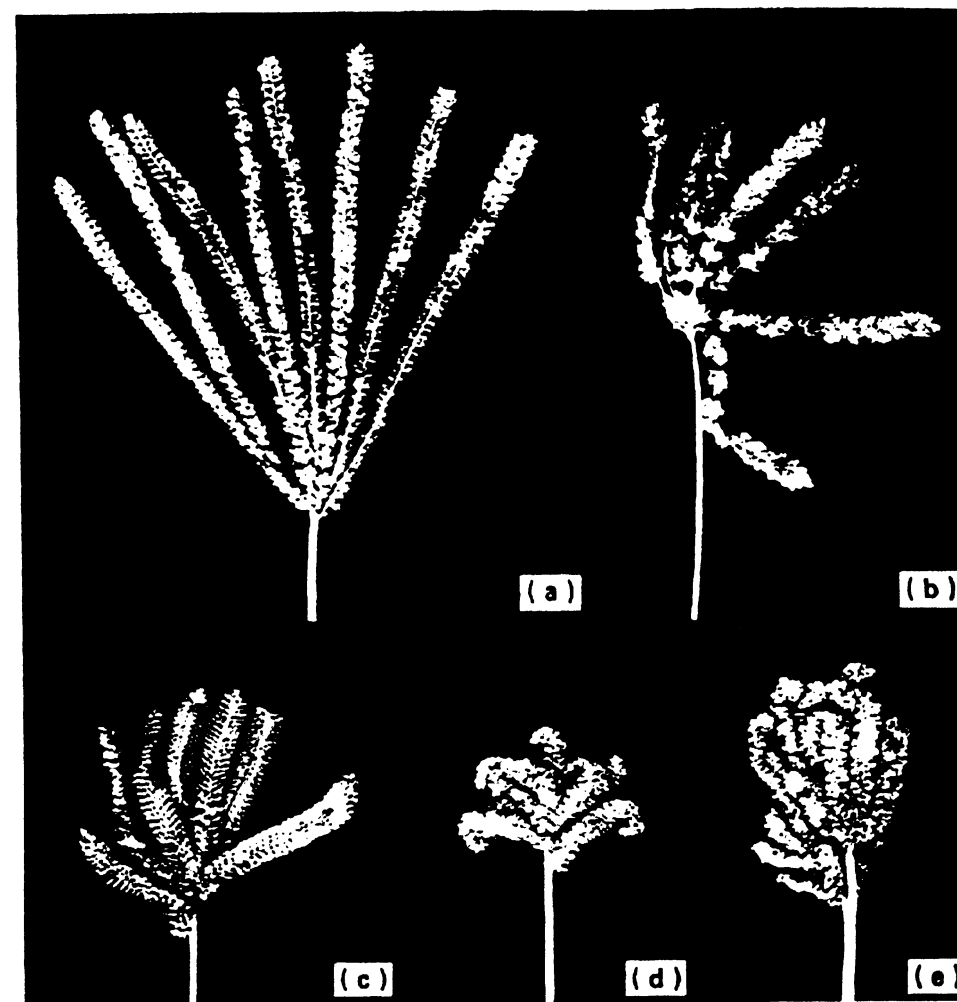

FIG. 4.   Inflorescence morphology of cultivars of Eleusine coracana *(finger millet); (a) race* elongata *from Malawi; (b) race* elongata *from Sikkim; (c) race* plana *from Malawi; (d) race* vulgaris *from India; (e) race* compacta *from India.*

however, are selectively advantageous and an autogamous breeding behaviour is common. In *Eleusine coracana* (L.) Gaertn. *(finger millet)*, a range of phenotypes (Fig. 4) are often sown together or occur sympatrically without losing their phenotypic identity [33].

6.   DOMESTICATION AND SPECIATION

Speciation describes that stage in the evolution of a population when all members of a daughter population acquire mechanisms that either prevent crossing with members of the parental population or result in hybrid sterility or weakness when mating does occur. Selection pressure for genetic isolating mechanisms to become established is absent among cultivated races that are spatially isolated from one another or from their close wild relatives. Isolating mechanisms that do exist among allopatric races are probably relics of mechanisms that originated during an earlier period of sympatric evolution, or they arose as incidental consequences of differential adaptive evolution. In cultivated races that evolved sympatrically, and in those that evolved sympatrically with their wild progenitors, mechanisms that prevent or restrict gene flow among populations are selectively advantageous.

Isolation can be achieved through saltational mutations such as chromosomal rearrangements, or through gradual allelic substitution associated with changes in adaptation [34–36]. Efficient reproductive isolating mechanisms are rare in domestic species, even among races that remained sympatric for thousands of generations. Isolation among sympatric cultivars is effectively achieved by man through spatial separation and selection. Among differently adapted wild and cultivated races, disruptive selection is the principal mechanism that restricts gene flow.

The most common mechanisms isolating sympatric races of domestic species from one another are differences in flowering time and gametophytic or sporophytic systems that prevent cross-fertilization. Linked blocks of genes that determine racial phenotypes and racial habitat preference also occur in domesticated cereal species. This is well demonstrated in maize. Chalco teosinte is a weed of maize fields in the Valley of Mexico [37]. The weed is more or less seasonally isolated from the maize it accompanies, but hybrids do occur in many fields. Chalco teosinte resembles the Chalqueno maize it accompanies as a weed in vegetative traits, but maintains a teosinte female inflorescence morphology. Cytological studies reveal that Chalco teosinte differs more significantly in chromosome knob constitution from Chalqueno maize than from other races of maize with which it is not sympatric [38]. Since chromosome knobs are known to reduce adjacent genetic crossing-over [39], strategically placed knobs may help to maintain allelic combinations that determine the female inflorescence phenotype of Chalco teosinte. The selective advantage of maintaining a teosinte phenotype is that it allows for efficient natural seed dispersal.

More efficient isolating mechanisms became established among races of rice. Cultivated fields of African rice (*Oryza glaberrima* Steud.) are commonly invaded by populations of its wild relatives (*O. barthii* Chevalier). Hybrids between wild and cultivated taxa are common and fully fertile, but hybrid derivatives are weak, and introgression is rare. Dominant alleles of two complementary weakness genes determine adaptability of these hybrids [40]. One dominant allele is carried by *O. barthii* and the other by *O. glaberrima*. Modifier genes affecting the expression of these weakness genes also occur, with the result that derivatives of hybrids between *O. barthii* and *O. glaberrima*, although fully fertile, are poorly adapted for survival in competition with either parent. Cultivated races of *O. sativa* L. in Asia are also more or less isolated from sympatric races of wild *O. rufipogon* Griff. by genetic sterility barriers [41]. Hybrids between wild and cultivated *O. sativa* display a range of fertility, with sympatric populations often effectively isolated by hybrid sterility. Similarly, hybrids between some cultivars of the tropical ecotype (race *indica*) and temperate ecotype (race *japonica*) of rice show reduced fertility.

In the soybean (*Glycine max* (L.) Merr.), cultivars are known that differ from their wild progenitor *G. soja* Sieb. & Zucc. by one or two chromosomal inversions [42], and in *Phaseolus vulgaris* L. developmental abnormalities in hybrids effectively isolate different cultivated complexes [43]. Saltational chromosome rearrangements, as well as genic mutations, contribute to reproductive isolation among races of domestic species. Races which are adaptively distinct and isolated by hybrid sterility or weakness are well on their way to true speciation.

REFERENCES

[1]   HARLAN, J.R., DE WET, J.M.J., PRICE, E.G., Comparative evolution of cereals, Evolution 27 (1973) 311-325.

[2]   DE WET, J.M.J., HARLAN, J.R., Weeds and domesticates: Evolution in the manmade habitat, Econ. Bot 29 (1975) 99-107.

[3]   FORD, R.I., BROSE, D.S., Prehistoric wild rice from the Dunn farm site, Leelanau County, Michigan, The Wisconsin Archaeol. 56 (1975) 9-15.

[4]   DE WET, J.M.J., "Principles of evolution and cereal domestication", Broadening the Genetic Base of Crops (ZEVEN, A.C., VAN HARTEN, A.M., Eds), Centre for Agricultural Publishing and Documentation (PUDOC), Wageningen, Netherlands (1979) 269-282.

[5]   HARLAN, J.R., "The origins of cereal agriculture in the Old World", Origins of Agriculture (REED, C.A., Ed.), Mouton Press, The Hague (1977) 357-384.

[6]   DE WET, J.M.J., Species concepts and systematics of cultivated plants, Kulturpflanzen 29 (1981) 177-198.

[7]   BURKILL, I.H., Habitats of man and the origins of the cultivated plants of the world, Proc. Linn. Soc. London 164 (1952) 12-24.

[8] DE WET, J.M.J., OELKE, E.A., Domestication of American wild rice (*Zizania aquatica* L., Gramineae), JATBA 25 (1979) 67–84.

[9] HARLAN, J.R., Agricultural origins: centers and non-centers, Science 174 (1971) 468–474.

[10] RANDOLPH, L.F., Contribution of wild relatives of maize to the evolutionary history of domesticated maize: a synthesis of divergent hypotheses, Econ. Bot 30 (1976) 321–346.

[11] MANGELSDORF, P.F., Corn, Its Origin, Evolution and Improvement, Belknap Press of Harvard University, Cambridge, MA (1974).

[12] MANGELSDORF, P.F., ROBERTS, L.M., ROGERS, J.S., The probable origin of annual teosintes, Bussey Inst. of Harvard University Publ. 10 (1981) 39–68.

[13] BEADLE, G.W., The ancestry of corn, Sci. Amer. 242 (1979) 112–119.

[14] GALINAT, W.C., The origin of maize as shown by key morphological traits of its ancestor, teosinte, Maydica 28 (1983) 121–138.

[15] COLLINS, G.N., "The Metamorphosis" of *Euchlaena* into maize, J. Hered. 16 (1925) 348–380.

[16] LANGHAM, D.G., The inheritance of intergeneric differences in *Zea-Euchlaena* hybrids, Genetics 24 (1940) 88–107.

[17] ROGERS, J.S., The inheritance of inflorescence characters in maize–teosinte hybrids, Genetics 35 (1950) 541–558.

[18] MANGELSDORF, P.F., GALINAT, W.C., The tunicate locus in maize dissected and reconstituted, Proc. Natl. Acad. Sci. 51 (1964) 147–150.

[19] ILTIS, H.H., From teosinte to maize: the catastrophic sexual transmutation, Science 222 (1983) 886–894.

[20] DE WET, J.M.J., OESTRY-STIDD, L.L., CUBERO, J.I., Origins and evolution of foxtail millets (*Setaria italica* L.), JATBA 26 (1979) 53–64.

[21] KRUSE, J., Beitrag zur Morphologie der Infloreszungen von *Setaria italica* (L) Beauv., Kulturpflanzen 19 (1972) 53–71.

[22] BRUNKEN, J.N., DE WET, J.M.J., HARLAN, J.R., The morphology and domestication of pearl millet, Econ. Bot. 31 (1977) 163–174.

[23] BRUNKEN, J.N., A systematic study of *Pennisetum* sect. *Pennisetum* (Gramineae), Am. J. Bot. 65 (1977) 161–176.

[24] HARLAN, J.R., ZOHARY, D., Distribution of the wild wheats from the Near East, Science 153 (1966) 1074–1080.

[25] BAKHTEYEV, F.K., Studies on barley: present problems of the origin of barley, Folia Quaternaria Krrkow 46 (1975) 73–81.

[26] WITCOMBE, J.R., Two-rowed and six-rowed wild barley from the western Himalaya, Euphytica 27 (1978) 601–604.

[27] BELL, G.D.H., "Comparative phylogeny of the temperate cereals", Essays on Crop Plant Evolution (HUTCHINSON, S., Ed.), Cambridge University Press, Cambridge (1965) 70–102.

[28] ZOHARY, D., Studies of the origin of cultivated barley, Bull. Res. Council Israel 9 (1960) 21–42.

[29] MURPHY, P.J., WITCOMBE, J R., SHEWRY, P.R., MIFLIN, B.J., The origin of six-rowed 'wild' barley from the western Himalaya, Euphytica 31 (1982) 192.

[30] HARLAN, J.R., Barley, "*Hordeum vulgare* (Gramineae-Triticinae)", Evolution of Crop Plants (SIMMONDS, N.W., Ed.), Longman, London (1976) 93–98.

[31] SNOWDEN, J.D., The cultivated races of sorghum, Adlard and Sons, London (1936) 274 pp.

[32] DE WET, J.M.J., Systematics and evolution of *Sorghum* sect. *Sorghum* (Graminaea), Amer. J. Bot. 65 (1978) 477–484.

[33] DE WET, J.M.J., PRASADA RAO, K.E., BRINK, D.E., MENGESHA, M.H., Systematics and evolution of *Eleusine coracana* (Gramineae), Am. J. Bot. 71 (1984) 557.

[34] PATERSON, H.E.H., More evidence against speciation by reinforcement, So. Afr. J. Sci. 74 (1978) 369–371.

[35] GOULD, S.J., Is a new and general theory of evolution emerging?, Paleobiology 6 (1980) 119–130.

[36] STEBBINS, G.L., AYALA, F.J., Is a new evolutionary synthesis necessary?, Science 213 (1981) 967–971.

[37] WILKES, H.G., Hybridization of maize and teosinte in Mexico and Guatemala and the improvement of maize, Econ. Bot. 31 (1977) 254–293.

[38] SMITH, J.S.C., GOODMAN, M.M., A comparison of chromosome knob frequencies between sympatric and allopatric populations of teosinte and maize, Am. J. Bot. 68 (1981) 947–954.

[39] GALINAT, W.C., "The origin of corn", Corn and Corn Improvement (SPRAGUE, G.F., Ed.), American Society of Agronomy, Madison, WI. (1977) 1–47.

[40] CHU, Y.E., OKA, H.I., The distribution and effects of genes causing F1 weakness in *Oryza breviligulata* and *O. glaberrima*, Genetics 70 (1972) 163–173.

[41] HINATA, K., OKA, H.I., A survey of hybrid sterility relationships in the Asian forms of *Oryza perennis* and *O. savita*, Jap. J. Genet. 37 (1962) 314–328.

[42] AHMAD, Q.N., BRITTEN, E.J., BYTH, D.E., Inversion heterozygosity in the hybrid soybean — *Glycine soja*, J. Hered. 70 (1979) 358–364.

[43] SHII, C.T., MOK, M.C., TEMPLE, S.R., MOK, D.W.S., Expression of developmental abnormalities in hybrids of *Phaseolus vulgaris* L., J. Hered. 71 (1980) 218–222.