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Cytogenetics and evolutionary change under domestication

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Domesticated plants often show more striking variability at and below the species level than their wild relatives. Nevertheless, no unique processes have operated in crop plant evolution.The ultimate source of variation is mutation, which is then exposed to selection, natural or human. The direction of human selection may change through time and can usually be inferred only indirectly from archaeological artefacts. Where a crop is evolving in contact with its wild relatives, disruptive selection may lead to simultaneous divergence of crop and weed races. The crop may then become genetically isolated by change in breeding system, chromosome number or chromosome structure, though these processes are usually arrested short of total isolation or speciation. In crops that are grown on a garden rather than field scale, reproduce asexually, or have a long generation time, gene flow and disruptive selection are less significant, though human selection may be more intense.

Biologists have been interested in evolutionary change under domestication ever since Darwin used domesticated plants and animals to illustrate his theory of evolution. Not only have domesticated plants contributed to an understanding of evolution in wild populations, but recent studies on genetic systems and gene flow in wild species are helping to explain the responses of cultivated plants to domestication (Darlington 1973). As the archaeological record of many crop plants steadily increases, changes in the morphological characters of cultivated plants can be studied through time, thus adding a dimension generally missing from evolutionary studies on wild plants. Furthermore, analyses of the changes that have produced our major crop plants, often from apparently unpromising wild or weedy ancestors, may provide useful models for the development of new crops for industry, for technology, or for agriculture in marginal areas.

The most immediately apparent change under domestication is in morphological characters such as size, shape and colour, particularly of the part of the plant used by man. Other morphological changes involve loss of mechanisms for dispersal of the seed or for protection of the plant from predators. Physiological changes affect characters such as rate and uniformity of seed germination, reaction to day length and length of life cycle. These changes are all well known and have been frequently reviewed (e.g. by Purseglove 1968; Schwanitz 1966), so we do not propose to discuss them further here. We will consider instead the processes by which these evolutionary changes originated and became established in our crop plants.

Up till now, crop plants have not evolved by any processes different from those operating in wild plants. The ultimate source of variability is mutation, though mutations may now be induced artificially as well as occurring spontaneously. The new forms produced are then subject to selection, but in crop plants new variants have to pass the test of human selection as well as, or sometimes instead of, natural selection. The amount of variability actually exposed to selection is affected not only by the rate of occurrence and survival of mutants but also by the breeding system of the crop and by other factors which influence genetic recombination, such as length of generation, chromosome number and chromosome structure. Whether the crop is genetically isolated from its wild relatives is also important, since isolation may prevent new variability becoming incorporated in the crop populations through hybridization. Recent advances in plant breeding, such as improved techniques for producing and raising progeny from wide crosses (Bates & Deyoe 1973), or control of chromosome pairing to incorporate desirable genes from alien species into the genome of a crop (Riley, Chapman & Johnson 1968), have been directed at expanding the potential variability of crops by overcoming their genetic isolation from other wild species. More complex forms of genetic engineering, for example attempts to transfer the ability to fix nitrogen from the legumes to the cereals by techniques such as protoplast fusion (Bajaj 1974), likewise concentrate on producing new combinations of characters, but these characters still originate ultimately by mutation and any new recombinants still have to pass the screen of selection.

Mutation

Domesticated plants differ from their wild ancestors in both qualitative and quantitative characters. Qualitative characters are usually determined by one or a few major genes and show relatively simple patterns of inheritance. Sometimes qualitative changes have greatly influenced the success of certain species as cultigens, for example the change from brittle to non-brittle rachis in the Old World cereals made the timing of harvest less critical, facilitated harvest by reaping and probably increased the proportion of the crop actually harvested (Harlan, de Wet & Price 1973). The change from dehiscent to indehiscent pods in domesticated legumes had similar effects. Most wild gourds (*Cucurbita* and *Lagenaria*) have bitter compounds in the seeds and fruit flesh, so although the fruits could be used for rattles and fish net floats, they could not be used as containers for food or liquid without several months' prior leaching in water. Once a non-bitter mutant was established, containers could be prepared more easily and the fruits could also be used as vegetables (Heiser 1973). Here a single-gene mutation has enabled the crop to be used in a new way. The same seems to be true of tobacco. Most wild species of tobacco contain an enzyme which converts nicotine to nornicotine in senescent leaves, hence dried leaves of these tobaccos have limited or no narcotic properties (Gerstel 1961). Domesticated tobaccos lack this enzyme and their leaves can be smoked. *Nicotiana tabacum* and *N. rustica* arose in areas where there is no archaeological or ethnographical evidence of smoking, and this suggests that they may have been first used green, as a masticatory (Sauer 1950), and that the mutations which produced a smokable leaf occurred after domestication, in a somewhat different area.

The rate at which an original wild-type condition is replaced by a new major gene mutant under domestication will depend in part on the breeding system of the crop and on whether the mutant is dominant or recessive, as well as on the intensity of selection for the new mutant. In inbreeding crops such as wheat or barley, a recessive mutant soon becomes expressed as a homozygote, and phenotypic selection of such homozygotes immediately produces a line which will breed true as long as crossing with the dominant wild type does not occur. In contrast, a desirable dominant mutant in an inbreeding crop is more difficult to establish in a true-breeding condition, since phenotypic selection will retain both homozygotes and heterozygotes and the latter will segregate some of the undesirable recessive homozygotes in each generation. In outbreeding crops such as maize, if a desirable recessive mutant occurs in the cultivated population and the recessive homozygote is selected as seed parent for the next generation, the chances are that it will have been pollinated by pollen carrying the prevailing dominant allele and hence will not breed true for the mutant character. On the other hand, a dominant mutant in an outbreeder will produce progeny at least half of which will show the mutant character, and selection in later generations will lead to a further decrease in the number of homozygous recessives. In the early stages of domestication of most plants, man is likely to have practised at most a fairly crude form of phenotypic selection and this might then be expected to favour establishment of recessive mutants in inbreeding crops and dominant mutants in outbreeders. The wild-type brittle rachis is dominant to non-brittle in wheat and barley, while in the major-gene characters by which maize differs from its closest wild relative teosinte (e.g. paired versus single and 4-ranked versus 2-ranked female spikelets), the maize condition is dominant. In the archaeological record, one might expect the inbreeders to become incontrovertible domesticates, devoid of wild-type characters, more rapidly than the outbreeders, which would continue to produce wild-type segregants over a number of generations. Few data are available, but the earliest archaeological maize, though undoubtedly maize and not teosinte, does include a few cobs with the 2-ranked arrangement of spikelets found in teosinte (Galinat 1971), though this character disappears in later levels.

There are, of course, exceptions to this tentative correlation between breeding system and the dominance relationships of the mutants distinguishing domesticates. Sunflower and rye are two outbreeding crops in which mutants that were presumably important in domestication are recessive, not dominant. However, both are crops which seem to have been domesticated from weedy ancestors outside the natural range of their truly wild relatives. In such weedy plants the 'founder effect' may lead to new populations being composed of genetically related individuals and outcrossing among such individuals is equivalent to a certain degree of inbreeding, so establishment of recessive mutants might be less difficult than in genetically more broadly-based populations of outbreeders. Chili peppers are self-compatible but outcross to varying extents. Domesticated peppers have non-deciduous pendent fruits which may be various colours other than red. Pendent fruit is dominant to wild-type erect, while non-deciduous fruit and fruit colours other than red are recessive to the wild-type condition. These varying dominance relationships may reflect the fact that under peasant agriculture peppers are grown in very small populations, so either dominant or recessive mutants could presumably be fixed relatively easily.

Quantitative differences between wild and domesticated plants, such as size and many of the other components of yield, are usually influenced by a number of genes whose individual effects can be analysed only in favourable cases. Crosses between wild type and domesticate show intermediate values in the F_1 hybrid, and selection under cultivation for increased yield produces a gradual response, continuing over a long period, e.g. seed size in *Capsicum* (Pickersgill 1969), fibre diameter and seed size in cotton (Stephens & Moseley 1974), unlike the more rapid changes in qualitative characters.

Non-lethal mutations usually involve a change in the functional efficiency of a particular gene (e.g. suppression of capsaicin formation in non-pungent chili peppers, reduction in the amount of red pigment in fruits of orange or flesh-coloured peppers) rather than development of a totally new function. However, when a gene is present in duplicate, as a result either of polyploidy or of segmental duplication, then the opportunity exists for the duplicated gene to develop a new function. Such evolution by gene duplication has been considered extremely significant in the origins of new taxa (Ohno 1970) and is, theoretically, one way in which cultivated plants might diverge from, and display greater variability than, their wild counterparts. However, there is little evidence that this has in fact occurred.

Bread wheat is probably the best known cytogenetically of the polyploid crop plants, and here the homoeologous chromosomes in the three genomes (A, B and D) have remained sufficiently similar throughout the millennia since hexaploid wheat originated that deficiency for one pair of chromosomes may be compensated by addition of an extra pair of homoeologues of the missing chromosomes. Furthermore, many characters of bread wheat are still determined by three pairs of genes located one on each of the homoeologous chromosomes, for example red grain colour is determined by genes on chromosomes 3A, 3B and 3D; coloured coleoptile by genes on chromosomes 7A, 7B and 7D; alcohol dehydrogenase by genes on chromosomes 4A 4B and 4D, etc. (see data in McIntosh 1973). In tetraploid wheats, some genes affecting chlorophyll production may have been 'diploidized' but few essential genes have been affected in this way and there is little evidence that such diploidization has involved divergence in function rather than loss of the duplicated loci (Morris & Sears 1967). Tetraploid cotton and tetraploid tobacco also show two-factor control of many of the traits that have been genetically analysed, though in cotton there is some evidence that at least two of the homoeologous genes do differ slightly in function and that these differences do not occur in the diploid ancestors of the tetraploids (Stephens 1951).

One of the important characters in the evolution of domesticated bread wheat seems to have arisen as a result of segmental duplication of a particular gene. All the true bread wheats carry the squarehead factor Q on chromosome 5A. The recessive allele q produces a brittle rachis and hulled grain, and it has been suggested that Q evolved as a consequence of selection under domestication against the reappearance of wild-type characters introduced from *Aegilops squarrosa* (MacKey 1966). Increasing the number of q alleles in the genotype to four has no effect on the phenotype, but addition of a fifth q allele produces a phenotype identical to the Q phenotype of the domesticated hexaploids. Q is therefore probably a duplication of q not a new mutant allele (Muramatsu 1963). Again the duplicated genes have not diverged in function: the striking effect on the phenotype results instead from a dosage effect of the products of q to which each allele appears to contribute equally.

Recent work on DNA contents of various plants has shown that related species often differ considerably in the amount of DNA per nucleus that they contain. The onion (*Allium cepa*) has 27% more nuclear DNA than the related *A. fistulosum* (Jones & Rees 1968); *Vicia faba* (broad or horse bean) has more nuclear DNA than any other species of *Vicia* (Chooi 1971). The nature of the additional DNA in species with high DNA content is not entirely clear, but it seems to consist of longitudinal replication ('amplification') of particular nucleotide sequences (Rees 1972). There is no evidence that this 'amplified' DNA has any genetic effects *per se*, though it has been suggested that it may alter recombination percentages between linked genes or affect pairing of homoeologous chromosomes (Rees 1972). Certainly increased DNA content does not seem to be a factor behind the increased variability of cultivated plants. The wild C genome cottons of Australia have higher DNA contents than the domesticated A genome diploids (Edwards, Endrizzi & Stein 1974); amongst the diploid species in the wheat group cultivated einkorn does not have a higher DNA content than its wild or weedy relatives (Rees

& Walters 1965). The high DNA contents of onion and broad bean compared to wild species in their respective genera are probably a reflection of differences established prior to domestication rather than a consequence of domestication.

These negative findings (that duplicate genes in polyploid crops have not diverged significantly in function, that small-scale duplications of chromosome segments do not appear to have created new characters under domestication, and that DNA content per genome has not altered significantly with domestication) fit with observations that most cultivated plants have not in fact diverged very far from their wild ancestors. Superficially striking though many of their differences are, taxonomically many crops belong to the same species as their closest wild or weedy relatives and no crop is generically distinct from its putative ancestors (at least, not since revised taxonomic treatments have provided wild species in *Zea* and *Lagenaria*). Evolution under domestication, operating over a mere 10000 years or so, has produced mainly variations on established themes and has created no new genera and few new species despite the introduction of new and sometimes intense selection pressures not encountered by wild plants.

Selection

Cultivation, the first step towards domestication, begins, for the seed crops, with planting by man of harvested seeds to provide a new crop. The harvested seeds represent a selected sample of the total variability, biased towards those components of the population particularly attractive to man and/or having the least efficient mechanisms for seed dispersal. Seed planted by man is to some extent protected from pressures of natural selection and this, together with changes in the population size, will lead to changes in variability of the crop through time. Gene flow from related wild or weedy forms growing in the same area also contributes to variability in the crop and creates a situation where disruptive selection can operate, producing further cytogenetic changes in the crop.

(*a*) *Conscious and unconscious human selection*

To explain the morphological changes which have become established in domesticated plants we need to know the selection pressures exerted on them throughout their history. Human selection has not always acted in the direction expected on a present-day standpoint. For example, crops grown for their seed are usually assumed to be subject to fairly intense selection for loss of seed dispersal mechanisms. But sesame has been grown as a crop of peasant agriculture in Asia for centuries and harvested by the simple method of cutting the stem when the lowest capsules are mature, bunching the cut stems and inverting them over a blanket so that as the capsules dry out and open the seeds rain down and are collected (Haarer 1950). Under these conditions the farmers would regard an indehiscent mutant as undesirable, since it would necessitate an additional process, threshing, in the handling of the harvested crop. Indehiscent mutants were favoured only when sesame was grown in developed countries and harvested mechanically.

Similarly, we assume that early cultivated wheat and barley were grown as grain crops and harvested by reaping. Human selection would then favour large, naked, free-threshing grain and tough rachis. However, Bohrer (1972) has suggested that these cereals were first cultivated as winter fodder for domestic animals and that the grinding implements, etc., associated with early agricultural sites in the Middle East were used to grind acorns and/or pistachio nuts rather than cereals. If the cereals were originally cultivated for fodder, human selection would not be directed at grain characters. Furthermore, even cereals grown for grain can be harvested in a variety of ways other than by reaping at maturity. Whole plants may be uprooted (Bohrer 1972), which would disturb the soil and favour new stands of weedy cereals and weedy legumes which could be further exploited by man. The grain could also be harvested by beating, or by tying the awns together so that the seeds fall as a bundle (Clark 1967). Neither of these methods would favour evolution of a tough rachis. Jarman (1972) suggested that brittle-rachis cereals could be reaped successfully if the ears were harvested immature. However this, like reaping at maturity, would probably favour evolution of tough rachis, since the most viable seeds for producing the next crop would be the most mature seeds, derived from ears in which shattering had longest been delayed. There are some indications that 'cultivated wild' cereals were widely grown (at Tell Mureybit and Beidha, for example: van Zeist & Casparie 1968; Helbaek 1966), possibly for several centuries, without developing tough rachises. This suggests that man was not selecting intensively for this trait.

Maize is another crop that has been used in various ways. The immature ears may be chewed green, as in present-day sweet corns, or the grain may be popped, parched, made into hominy by treatment with lye, ground into meal, etc. If teosinte is the ancestral form of maize, then primitive maize must have had a strongly indurated rachis and glumes. If maize was first consumed green, selection against induration in the mature cob would not have been particularly intense, but as soon as the mature grain was used, man would presumably select for grains which were easily shelled off the cob, i.e. for reduction in the size and induration of the glumes. Hard endosperm is a prerequisite for grain which is to be popped, but undesirable in grain which is to be hand-ground for meal. Conversely, the soft, easily-ground endosperm of Amerindian flour corns renders the kernels more liable to attack by pests and diseases, hence undesirable where losses from these causes severely limit yield. In maize, as in most other crops, understanding the changes which have taken place under domestication requires a study of the archaeological specimens, not in isolation, but in their archaeological context, with all the supplementary evidence about diet, processing, storage pests etc. that can be obtained from coprolites, artefact inventories and the like.

(*b*) *Changing variability of crop populations through time*

Although there is no evidence that the mutation rate increases as a result of cultivation, apart from exceptional circumstances such as unequal crossing-over in hybrids heterozygous for small-scale structural changes in the chromosomes (maize; Mangelsdorf 1958) or selection in favour of unstable, 'ever-sporting' genotypes (sweet pea; Darlington 1973), a mutant's chance of survival varies considerably at different stages of the domestication process and in different types of crop. A crop grown on a field scale, such as the grain crops and many legumes, goes through an early expansive phase of development when the number of individuals is increasing dramatically. The plants selected as seed parents are contributing large numbers of progeny to the next generation, pressures of natural selection are relaxed since the plants are grown in the artificial environment of a cultivated field with reduced competition from natural vegetation, human selection for 'trueness to type' is not yet intense, so conditions are ideal for the survival of mutants and/or rare recombinants. New World coffee passed through this phase comparatively recently. Although coffee was spread to the Americas by both the French and the Dutch, the introduced plants were all progeny of a single plant brought from the East Indies to the Amsterdam Botanic Garden (Purseglove 1968). Despite the very limited genetic base, more mutants have been described in the New World than in all the coffee-growing regions of the Old World combined.

Most crops completed this initial phase of their evolution in prehistoric times, but it may be detectable archaeologically as an increase in variability in the early stages of cultivation. The maize recovered from Coxcatlan levels of caves in the Tehuacan valley of Mexico was considered wild maize because it was less variable than maize from succeeding levels in which there was clear evidence of agriculture (Mangelsdorf, MacNeish & Galinat 1967). Galinat (1974) has now suggested that these early cobs came after all from domesticated or semi-domesticated plants, but they were a relatively unimportant component of the total plant remains from this period and the subsequent increase in variability correlates with the increasing abundance and dietary importance of maize in a way that suggests that the maize populations were expanding during the post-Coxcatlan periods.

After an initial increase in variability, selection partitions the variability between different lines, the basis of our modern cultivars or land races. Hulled wheat has to be parched to free the grain from the investing glumes, naked wheat will thresh free without parching; because of these differences in processing there would be a tendency to grow and handle the different types separately. Environmental conditions, selecting for adaptation of the crop to local conditions, will produce phenotypically homogeneous local races. In northern Nigeria, in areas with a marked dry season, the principal cereals are short-day forms of sorghum and bulrush millet, very precisely adapted to local variation in day length so that they flower at times related to the average date of the ending of the rains. Further north, where both the start and the duration of the rains are uncertain, day-neutral forms of sorghum and bulrush millet, which will produce their harvest in the shortest possible time, are favoured (Bunting 1973). Sometimes the uniform phenotypes created by stringent selection for a particular type of plant adapted to a particular set of environmental conditions may mask a considerable degree of genetic heterogeneity. In perennial ryegrass, the Welsh-bred cultivar 'S 23' initiates its inflorescences on a uniform date when grown in the field in Wales, but when grown under different temperature and day length in California the same cultivar appears extremely heterogeneous, some plants remaining completely vegetative, others initiating inflorescences on a variety of dates (Cooper 1965).

The non-taxonomist is usually struck by the wide range of infraspecific variability in cultivated plants; by the fact that, for example, kale, cauliflower, cabbage, Brussels sprouts and kohlrabi are all variants of a single species, *Brassica oleracea*, whereas wild species apparently vary far less. The overall variability of most cultivated plants is however made up of numerous relatively invariable races closely adapted to local usage and local growing conditions. A field of a modern cereal cultivar in fact shows less variation in characters such as height, number of nodes per stem, time to ear emergence, etc., than a comparable-sized population of a wild grass.

(*c*) *Disruptive selection*

Many crops have remained in genetic contact with their wild or weedy ancestors, at least during the early stages of their domestication. The distinctive characters of the crop and wild populations are maintained despite the gene flow between them by the action of disruptive selection: the crop populations are subject to human selection for large seeds or other parts, loss of dispersal mechanisms, uniform germination, etc., while natural selection in the wild populations maintains small seeds or fruits, efficient seed dispersal, irregular staggered germination, etc. Theoretical considerations and laboratory experiments indicate that disruptive selection will produce either polymorphism, with tight linkage of the characters of adaptive value in the two subpopulations, or isolation between the subpopulations (Mather 1973). Recent studies on crop-weed relationships suggest that examples of both can be found.

Maize and its closest wild relative, teosinte, are sympatric throughout most of the range of teosinte, cross readily and produce fertile hybrids. This gene flow has a heterotic effect on the maize crop and enhances the ability of teosinte to survive in maize fields by mimicking the crop (Wilkes 1967, 1970). Nevertheless, maize and teosinte remain morphologically distinct despite considerable hybridization. This seems to be due mainly to chromosomal rearrangements which have increased the linkage between the genes differentiating maize and teosinte. In Guatemalan teosinte, which is not a weed of maize fields and does not hybridize naturally with maize to any extent, genes affecting morphology of the female inflorescence are located on most of the ten chromosomes, whereas in Mexican weed teosinte, which hybridizes extensively with maize, these genes are restricted to just a few of the ten chromosomes, most notably chromosome 4, which carries closely linked factors affecting development of the fruit case, induration of the outer glume, development of abscission layers in the rachis and inclination of the female spikelets (Galinat 1971). The restriction on recombination imposed by this tight linkage may be further enhanced by linkage between the 'chromosome 4 complex' and a gametophyte lethal which causes one-way cross-sterility and, in at least some forms of Mexican teosinte, by an inversion affecting chromosome 4 (Galinat 1971). 'Polymorphism' for maize versus teosinte inflorescence morphology is thus maintained in interbreeding populations.

Genetic isolation between domesticate and weed can be achieved in a variety of ways. In inbreeding crops which are derived from inbreeding ancestors, crop and weed populations are adequately isolated by breeding system alone. The cultivated lentil (*Lens culinaris*) and its putative ancestor *L. orientalis* have small, usually cleistogamous flowers. *L. orientalis* occurs in primary and secondary habitats in an area where lentils have been cultivated since about 7000 B.C. but the distinctions between the two species are only occasionally blurred (Zohary 1972). Wheat and barley and their wild relatives are also predominantly self-pollinated and Zohary (1969) has already suggested that the isolation thus imposed pre-adapted them to domestication. In the wheat group, isolation due to self-pollination has been further reinforced by polyploidy. Cultivated tetraploid potatoes are likewise partially isolated from their diploid progenitors by the difference in chromosome number.

In insect pollinated plants, studies on wild plants have shown that differences in height (Levin & Kerster 1973), corolla colour (Levin & Kerster 1967) or corolla form (Levin 1969) may be sufficient to produce assortative mating between like forms and hence a degree of isolation between unlike forms. Bateman (1951) carried out experiments which showed that honey bees discriminated not only between cabbage and swede, which are closely related species, but also to some extent between cultivars of either cabbage or swede. Floral differences between crop and weed races are likely to be at least as great as those between cultivars and may hence provide an adequate basis for assortative pollination, but the published data are too scanty to furnish any convincing examples of isolation developing by this means.

Disruptive selection may also lead to isolation through differences in flowering time. Paterniani (1969) showed experimentally that selection for parental type white flint and yellow sweet cobs in a freely intercrossing population of maize reduced the percentage of intervarietal crossing from about 40 % to about 4 % after 5 generations. This was achieved by a change in the number of days to flowering such that one variety became earlier and the other later.

Presumably equivalent differences in flowering time could be equally easily and equally rapidly established in sympatric populations of crops and their weedy relatives, but examples are not easy to find. Radishes are self-incompatible outbreeders pollinated by various insects. The domesticated radish (*Raphanus sativus*) and a related weedy species *R. raphanistrum* are sympatric in parts of Europe and North America and will produce viable hybrids. In California, and presumably in other parts of their ranges, *R. raphanistrum* flowers about a month earlier than *R. sativus* (Panetsos & Baker 1967), but it has not been shown that this is the outcome of disruptive selection in an originally interbreeding population.

Changes in chromosome structure impose a degree of isolation, since hybrids heterozygous for translocations or inversions are at least partially sterile. *Raphanus sativus* and *R. raphanistrum* differ by one reciprocal translocation, which is sufficient to reduce pollen fertility in the F_1 to about 50%. The genes affecting flowering time and root structure (swollen versus slender) in the two species are closely linked and carried on the chromosomes involved in the translocation (Panetsos & Baker 1968). This must further help to maintain the morphological integrity of the two species.

Although disruptive selection favours the development of barriers to gene exchange in an originally panmictic population, few crops are completely isolated genetically from their wild relatives. On genetical as well as morphological grounds, domesticated and wild populations are often conspecific. We may therefore enquire why evolution of these barriers should be arrested at an intermediate stage, in which some gene exchange remains possible. Laboratory experiments on disruptive selection in *Drosophila* suggest one answer. Millicent & Thoday (1961) found that the ultimate divergence between two subpopulations subjected to disruptive selection was just as great when there was 25% gene flow (random interbreeding) as when there was no gene flow (complete isolation) and they suggested that complete isolation may in fact limit divergence by preventing alleles from migrating into the subpopulation where they will be favoured by selection. Selection pressures on cultivated plants are continually changing with changing agricultural technology and changing usage of the crop, so continual, although limited, gene flow from its wild relatives may be advantageous in giving the crop the genetic flexibility to respond to these changing selection pressures. Anderson (1961) and Harlan (1965, 1970), in particular, have stressed this role of weed races in crop evolution.

Migration

Isolation between a crop and its wild relatives is also affected, of course, by the activities of man. As a particular crop becomes more widespread it may become geographically isolated from its wild ancestors, or it may move into the ranges of other wild species with which it can hybridize, stimulating further evolutionary changes.

Galinat (1974) suggested that teosinte has had a braking effect on the evolution of maize in areas where the two are sympatric. As kernel size in maize increased, he considered that modifiers reducing kernel size would develop in teosinte to counterbalance the deleterious effects of gene flow from maize. Gene flow in the reverse direction, from teosinte to maize, would in turn restrict the development of yet larger kernels in maize. Only when maize moved out of the range of teosinte were some of its most striking variants able to develop: the enormous kernels of 'Cuzco Gigante' and the greatly reduced cupules of 'Confite Morocho' in South America; the increased pollen grain size of 'Longfellow Flint' in North America.

Hutchinson (1974) has given examples of the converse situation, in which gene exchange between a crop and a formerly allopatric wild species has led to further extension of the range of the crop. In northern India sugar cane (*Saccharum officinarum*), originally domesticated in southeast Asia, came into contact with a local wild species, *S. spontaneum*. Gene flow from *S. spontaneum* into *S. officinarum* enabled sugar cane to become established in cultivation outside the tropics. Similarly, the domesticated sunflower seems to have acquired genes for adaptation to different environmental conditions by hybridization with local wild species as it expanded its range in cultivation (Heiser 1965).

Evolutionary change in crops which are not propagated by seed and/or not grown on a field scale

Most discussions of crop plant evolution, this one included, have concentrated on crops which are propagated by seed and grown on a field scale. These crops are usually annuals or short-lived perennials and the short generation time, large populations and sexual reproduction combine to facilitate rapid response to selection. However, a number of important crop plants, particularly the starchy root crops, reproduce asexually or are propagated vegetatively in cultivation. Asexual reproduction is analogous to inbreeding in that any phenotype selected by man can be immediately maintained. However, unlike inbreeding, asexual propagation can conserve heterozygous as well as homozygous genotypes, and some successful cultivars in vegetatively propagated crops are in fact highly heterozygous hybrids. The lemon, like other species of *Citrus*, reproduces in part asexually by means of nucellar embryos which usually suppress the sexual embryo in the seed. Biochemical, genetical and geographical evidence suggest that the lemon is a stabilized hybrid between the citron and the lime (Scora & Malik 1970).

Since the opportunities for reassortment and recombination of characters afforded by sexual reproduction are mostly absent under asexual reproduction, asexually propagated plants should show greater homogeneity within selected lines than seed propagated plants and may thus be less responsive to changing selection pressures. However, few if any crops reproduce entirely by asexual means. Under primitive agricultural conditions crops such as potato, sweet potato, manioc and pineapple produce volunteer seedlings from sexual reproduction which contribute to the variability of the cultivated populations, and plant breeding programmes in all these crops use sexual reproduction to produce an array of recombinants for subsequent selection. In most vegetatively propagated crops sexual reproduction is predominantly by outbreeding, achieved by cross-pollination by insects (potato), *S*-allele systems of self-incompatibility (sweet potato, pineapple), or unisexual flowers (manioc, yams) combined with protogyny (*Colocasia*, *Xanthosoma*). When sexual reproduction does occur, it thus maintains heterozygosity and releases considerable variability through reassortment and recombination.

Mutation may be a more significant source of variability in asexually propagated crops than in seed crops, simply because the chances of a mutant surviving are greater. In seed propagated crops mutations must be incorporated in the cells of the germ line if they are to be passed on to the next generation, but in vegetatively propagated crops somatic mutants may be transmitted also. Some cultivars of potato are chimaeras in which cells of the outer and inner layers of the tuber differ in genotype. This mixture of tissues may be perpetuated from asexual generation to asexual generation, as in the cultivar 'Golden Wonder' which actually has a core of the variety 'Langworthy' (Crane & Lawrence, 1956) .Or a somatic mutant may give rise to a mutant sector on the parent plant, propagation of which may produce a new variety. The potato cultivar 'Red Craig's Royal' arose from 'Craig's Royal' in this way, and the pink-fleshed grapefruit originated as a somatic mutant of the normal grapefruit.

In some vegetatively propagated crops it has been suggested that extra-nuclear genes can supplement nuclear genes as sources of variability enabling the population to respond to selection. Breese (1966) found that long-lived varieties of perennial ryegrass, which maintained themselves by continual tillering, showed considerable maternal control of mature plant characters. Selection over a number of generations of asexual reproduction could induce differences within a clone greater than those between clones at the start of the experiment. However, this work has not been duplicated in other vegetatively propagated crops.

In crops which are not grown on a field scale, population size is much smaller and this, like asexual reproduction, may slow down the rate of evolution under domestication. It takes relatively few bushes of chili pepper to supply the year-round needs of a household addicted to even the hottest foods. Each bush therefore leaves very few descendants in the next generation and the chances of survival for rare mutants or recombinants are greatly reduced. Gene exchange with sympatric wild or weedy races is also decreased. Chili peppers are self-compatible but visited by pollinating insects. Most pollen is probably transferred from flower to flower on the same plant (effectively self-pollination) but some cross-pollination also occurs. Field observations suggest little if any modification of domesticated chili peppers by sympatric weedy forms or vice versa, presumably because the few seedlings which establish are unlikely to be the low-frequency hybrids, and if a hybrid does establish it will in turn leave very few descendants, so extensive hybrid or backcross swarms are not formed. These effects may be counterbalanced by more intensive selection by man, in that any variant that does occur is more likely to be noticed and, if advantageous, propagated, where population size is small. Certainly the domesticated chili peppers are as variable as most field crops. Similar effects may occur in other cultigens in which relatively few individuals are required to supply the needs of the community, for example many of the tree fruits (in which small population size combines with long generation time to retard further the rate of change) and possibly some of the cultivated cucurbits.

CONCLUSIONS

The cytogenetic and evolutionary changes which take place under domestication are now well understood, at least in general outline, but there is considerable scope for cooperation between archaeologists and botanists in filling in the details. The archaeological record is always and inevitably incomplete, even under the most favourable conditions of preservation, but now that techniques of recovery and analysis are advancing so fast, more might be done to pool the data from macroscopic plant remains (including, where possible, data on insect or fungal attack: the recent recovery of an archaeological cotton boll with boll weevil still inside (Warner & Smith 1968) shows that this may be possible), coprolite analysis (to provide data on food processing and consumption) and associated artefacts (which may provide information on the handling of the crop) to reconstruct at least partially the sorts of selection pressures operating at different stages in the evolution of the crop.

Not only do reports on botanical specimens from archaeological contexts frequently appear divorced from the supplementary information that would enable one to build up a picture of the technology of harvesting, processing and utilizing the crop concerned, but such reports are frequently limited to a record of presence or absence of particular crops in the various levels of a stratified sequence. There is seldom any information on the homogeneity of the samples, which would enable one to study replacement of primitive by improved forms, variability of the crop at different stages of domestication and in different parts of its range, rate of response to selection in crops with different breeding systems or markedly different population sizes, etc.

However, it does not behove botanists to be too critical. The increasing interest of archaeologists over the last 20 years in the subsistence of prehistoric cultures has added immensely to our knowledge of evolution under domestication, confirming conclusions from cytogenetics in some instances, causing them to be re-examined in others. New advances in the recovery and analysis of plant remains hold out the possibility of obtaining new types of information, as well as information on crops not hitherto represented archaeologically, so that the next 20 years promise to be equally challenging.

In preparing this paper we have become very much aware that many of the points which we wished to discuss have been made previously by other authors. We have, of course, tried to give credit where credit is due and cite these earlier papers, but we should like to express our gratitude here to all those whose writings on evolution under domestication have been assimilated into our thinking to such an extent that they have become victims of our unconscious plagiarism.

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Discussion

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In their excellent paper Barbara Pickersgill and Charles Heiser referred to ways in which variations in techniques of harvesting cereals (and wild grasses) might have differential selective effects on the taxa undergoing domestication. I would like to stress the significance of this aspect of human or cultural selection because it can contribute to our understanding of why cereal-based agriculture emerged in some parts of the world but not in others. The ethnographic record affords many examples – such as the Indians of the Great Basin of western North America (see Steward 1941) and various Australian Aboriginal groups (see, for example, Allen 1974) – of 'hunters and gatherers' whose subsistence depended in large part upon the seeds of wild grasses and forbs. It is relevant to ask why cereal agriculture based on domesticated grasses did not develop among such groups. Part at least of the answer is suggested by study of the harvesting methods employed.

In a recent paper Wilke, Bettinger, King & O'Connell (1972) pointed out that among groups such as the Indians of the Great Basin, who traditionally harvested wild grasses by beating the ripened seeds into baskets, there was no cultural selection in favour of plants with poorly shattering inflorescences, such as does occur when seeds are harvested by hand picking or with a sickle. Thus harvesting could continue indefinitely without producing 'domesticated' forms with non-shattering inflorescences. Even among those Indian groups in the Great Basin who sowed as well as harvested wild grasses and forbs (Steward 1941, p. 218), there would have been no *inherent* cultural selection of plants with non-shattering inflorescences as long as seed-beating remained the normal mode of harvest. On the other hand, if wild grass seeds are harvested by sickle or by hand and a proportion of the harvested seed is re-sown, then selection of plants with poor natural seed dispersal is automatically favoured. Harlan, De Wet & Price (1973, p. 315) suggest that 'mutants toward nonshattering probably occur in all large populations of wild grasses'. If so, then sustained exploitation of wild grasses by hand picking or sickle harvesting combined with re-seeding will ultimately result in 'domestication' (in so far as establishment of a non-shattering population is regarded as a criterion of domestication). Other morphological changes, such as suppression of lateral seed-bearing branches, increases in the size of inflorescences and of seeds, and more uniform maturation (Harlan *et al.* 1973), also result from long continued hand or sickle harvesting and re-seeding. All these changes are advantageous to the cultivator and their combined effect is to increase yields (by comparison with those obtained by seed beating) and thus to favour the emergence of cereal cultivation as a system of food procurement.

I do not imply that harvesting method is the only variable that accounts for the prehistoric rise of cereal agriculture in areas where hand or sickle harvesting was practised, such as Southwest Asia and Mesoamerica, and for its failure to emerge in other regions where wild grass seeds were intensively exploited. Clearly the development of other techniques, such as grain storage in pottery vessels or underground pits and the use of grindstones for seed processing, is likely to have amplified the role of cereal cultivation in overall subsistence (leaving aside consideration of non-technological variables such as demographic change and the social regulation of food procurement). But through the comparative study of techniques of grain harvesting, storage, processing, and seeding it is possible to develop archaeologically testable hypotheses capable of refining our understanding of the emergence of cereal cultivation and other systems of seed-crop agriculture (Harris 1976).

Thus, in addition to the differential selective effects of variations in harvesting methods, comparative investigation of seeding techniques throws light on the contrasted patterns of seed-crop domestication and cultivation that developed in different regions of the world. One of the most striking contrasts is that between Southwest Asia, where cultural selection evidently favoured grasses, legumes, and other annuals such as species of *Triticum*, *Hordeum*, *Pisum*, *Lens*, *Cicer* and *Linum*, which bear many small seeds per plant, and Mesoamerica, where larger-seeded forms were selected, especially of *Zea*, *Phaseolus* and *Cucurbita*. Traditional seeding techniques also contrast strongly in the two regions. Shallow broadcast sowing is characteristic of Southwest Asia whereas in Mesoamerica the hand planting of individual seeds is traditional. Broadcast sowing, and the setting aside of (often mixed) seed stock that precedes it, is a relatively indiscriminate method which does not encourage the sower to focus his attention on minor variations in the size, form, and colour of individual seeds; whereas with hand planting the selection of variants is likely to be more intensive and discriminating. Furthermore, as in Mesoamerica, hand planting is often associated with deeper burial of seeds in holes or mounds than occurs when seeds are broadcast. This practice favours the selection of larger-seeded variants which tend to germinate and compete as seedlings more successfully than smaller-seeded forms.

These contrasts in seeding as well as in harvesting techniques go some way to explain the different courses that seed-crop domestication followed in Southwest Asia and Mesoamerica; and it is tempting to ask whether, if broadcast sowing and sickle harvesting had developed in Mesoamerica, small-seeded cultivars of genera such as *Zea* and *Phaseolus* might have emerged as dominant crops. Perhaps this line of argument could account for the failure of the *Setaria* sp. abundant in the El Riego phase at Coxcatlan Cave in the Tehuacan Valley (Smith in Byers 1967, p. 249, Callen in Byers 1967, pp. 287–8) to become domesticated and established as a crop, and it may also enhance understanding of the selective factors that led to the emergence of domesticated maize from its smaller-seeded wild progenitor(s), (whether teosinte or wild maize).

Study of comparable contrasts in traditional techniques of seeding and harvesting helps to explain the pathways towards seed-crop domestication and agriculture followed in other parts of the world, such as interior West Africa, highland Northwest Ethiopia, the Huang-ho Valley of North China, and mainland Southeast Asia (Harris 1976), but sufficient has been said to underline the relevance of such an approach to study of the early history of agriculture. It is to be hoped that the systematic study of cultural selection will develop and complement the cytogenetic approach to domestication so well exemplified in Dr Pickersgill's and Professor Heiser's paper.

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