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Aspects of unconscious selection and the evolution of domesticated plants

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Summary

Unconscious selection may be defined as non-intentional human selection. The term was introduced by Darwin and its modern concept was developed by C.D. Darlington. Unconscious selection, or automatic selection as it is sometimes called, could have been responsible for most of the differences that distinguish domesticated seed crops from their wild progenitors, including loss of natural dispersal mechanisms, even and rapid seed germination, larger propagules, simultaneous ripening, and loss of mechanical protection as well as changes in the breeding system. Some differences, such as those in seed or fruit colors, may have developed from conscious selection at an early time. For unconscious selection to operate in the development of domesticated plants there would have to have been a deliberate planting of seeds by people.

Unconscious selection

Darwin mentions 'a kind of selection which may be unconscious' in *The Origin of Species* (1859) and later develops the subject more fully in *The Variation of Animals and Plants under Domestication* (1868, 1875). There he states that the principles of selection may be conveniently divided into three kinds.

> *Methodical selection* is that which guides a man who systematically endeavours to modify a breed according to some predetermined standard. *Unconscious selection* is that which follows from men naturally preserving the most valued and destroying the less valued individuals, without any thought of altering the breed; and undoubtedly this process slowly works great changes. Unconscious selection graduates into methodical, and only extreme cases can be distinctly separated; for he who preserves a useful or perfect animal will generally breed from it with the hope of getting offspring of the same character; but as long as he has not a predetermined purpose to improve the breed, he may be said to be selecting unconsciously. Lastly, we have *Natural selection,* which implies that the individuals which are best fitted for the complex, and in the course of ages changing conditions to which they are exposed, generally survive and procreate their kind. With domestic productions, natural selection comes to a certain extent into action, independently of, and even in opposition to, the will of man.

Further along in the same chapter he tells us more about unconscious selection.

> It is difficult to offer direct proofs of the results which follow from this kind of selection; but the indirect evidence is abundant. In fact, except that in the one case man acts intentionally, and in

> the other unintentionally, there is little difference between methodical and unconscious selection. With plants, from the earliest dawn of civilisation, the best variety which was known would generally have been cultivated at each period and its seeds occasionally sown; so that there will have been some selection from an extremely remote period, but without any prefixed standard of excellence or thought of the future.

Following Darwin, the first person known to me to expand upon the concept of unconscious selection was Darlington (1956). He maintains that natural or unconscious selection through the activities of man led to changes in the plants-tillage conditions leading to the selection of larger forms, sowing conditions leading to selection of forms with rapid and even germination, harvesting conditions leading to forms with nondehiscent fruits, and that changes of habitat led to changes in the breeding systems. Earlier Darlington had pointed out that the distinction between artificial and natural selection was arbitrary, stating that 'most artificial selection is natural to the extent of being unconscious.' The discussion of unconscious selection is little changed in the second and third edition of the work (Darlington, 1963, 1973) except for introducing the term 'operational selection' for this particular class of unconscious selection. In another work (Darlington, 1969) he further develops the concept of unconscious selection and points out that it was unconscious selection that gave agriculture its start.

The most thorough treatment of unconscious selection is that of Harlan, de Wet & Price (1973). In their paper all of the examples are drawn from the cereals, but Harlan (1978) later gives examples from other domesticated plants. In these discussions the term 'automatic selection' is used. There is no mention of unconscious or operational selection, nor, for that matter, of Darwin or Darlington.

Although Darwin introduced unconscious selection, he did not understand it in the way it is presently used. The reason is probably that he did not have the advantage of knowing the wild ancestors of many domesticated organisms and hence was not aware of some of the most fundamental changes that occurred with domestication. The use of values in the explanation can no longer be accepted. Unconscious selection today may be considered as selection resulting from human activities not involving a deliberate attempt to change the organism. Unconscious selection, operational selection and automatic selection are more or less equivalent, but the oldest term is probably preferable, and moreover it is already in wider use than the others. Unconscious selection, of course, still contrasts with methodical selection which is conscious selection. The term artificial selection, usually used to embrace all of human selection, was introducted by Tait & Stewart in 1879 (Anom., 1971). There might be an advantage in limiting it to methodical selection, for, as pointed out above, unconscious selection hardly differs from natural selection whereas methodical selection is human-contrived.

If one examines the differences between domesticated plants propagated from seed and their nearest wild relatives, it becomes apparent that unconscious selection could have been responsible for most of the changes – the *Domestikationssyndrom* of Hammer (1984). A comprehensive list will not be attempted here and other examples can be found in Harlan et al. (1973) Hawkes (1983) and Murray (1984). A number of examples of the changes that have occurred with domestication is also given by Schwanitz (1966), although he does not comment on whether these arose through conscious or methodical selection. Zohary (1984) has discussed the changes in breeding systems that have occurred through unconscious selection, and I shall not repeat them here.

1. Loss of natural dispersal mechanisms. Although not found in all domesticates (Pickersgill & Heiser, 1976), this is one of the most common differences between domesticated plants and their wild ancestors. It is also one of the most fundamental, perhaps often triggering some of the other differences. The non-brittle rachis in cereals, non-dehiscent pods in pulses and the non-dehiscent berries in chile peppers are examples. Zohary (1969) has given a good account of how this change took place in the cereals. When wild stands are harvested, grains

from the less brittle plants have a better chance of being gathered by people whereas the more brittle plants contribute more seed for the next generation in the wild. 'Mere collection of wild stands would therefore actively select for quick-shattering forms.' On the other hand, planting of seeds by people would bring about selection in the opposite direction, for the non-brittle mutants now have the advantage. 'Thus under domestication, one should expect establishment of non-brittle cereals whether or not the cultivator is conscious of this trait.'

2. Even and rapid seed germination. One might expect the first plants to germinate to have an advantage over the later germinating seeds in producing more vigorous plants which in turn would furnish more seeds for the next planting. Once weeding was practiced the later germinating plants might also be eliminated by man.

3. Larger propagules. Although the relation between seed size and seed vigor is not always a simple one (Marshall, 1986), there is some experimental evidence (Lush & Wien, 1980) to indicate that larger seeds give more vigorous seedlings than do smaller seeds and that larger seeds will germinate better after deeper planting. Thus unconscious selection would favor larger seeds. When man began to cover seeds after sowing and when conscious selection of larger seeds for planting was initiated is impossible to say. It could be that when unusually large seed appeared, some prehistoric gardeners might have saved them for planting; thus conscious selection could have operated at times.

4. Simultaneous ripening. Any plant having most of its seeds or fruits mature at the time of harvesting would furnish more seed for the next planting. Thus after a time this character could have been fixed.

5. Loss of mechanical means of protection. One might postulate that man could collect more fruits or seeds from plants without armature so that its loss would follow the same development as those characteristics previously listed. However, I think it likely that it often resulted from conscious selection. The domesticated species of section *Lasiocarpa* of *Solanum* (*S. quitoense,* etc.) lack prickles or have highly reduced ones compared to the wild species. Some of the wild species occasionally produce plants with few or no prickles. Perhaps the original cultivation began with one of these. Presence or absence of spines is frequently under the control of a single gene so the establishment of unarmed plants would have been relatively simple.

6. Color changes in the fruit or seed. The great variability of colors in the propagules of many domesticates is most striking. Moreover, in some domesticates white or light-colored ones have replaced the darker colored ones of the wild type, e.g., quinua (*Chenopodium quinoa*), chocho (*Lupinus mutabilis*) and *Amaranthus spp.* These changes probably at many times resulted from conscious selection. The early farmer would have given special attention to color variants, and perhaps attached religious significance to them. This would be particularly true for those crops in which the seeds were planted individually as opposed to being broadcast. Witness the great variation in the grains of maize contrasted to those of other cereals. With the change of propagule color there may have been correlated changes in other characters, perhaps those leading to a more rapid germination or a loss of toxic substances. It has been shown (Elias et al., 1977) that black and red beans have higher levels of tannins than do white ones; the tannins react with protinase to decrease the digestibility. Thus the selection of lighter colored seeds may have unconsciously resulted in an improvement of their nutritive value. However, at the same time this may have had disadvantages, for it has recently been shown (Powell et al., 1986) that white bean seeds have a lower seed emergence and less vigorous seedlings than do black and brown ones. The seeds of quinua have lost, or virtually lost the testa, although it must be admitted that archaeological seeds of *Chenopodium berlandieri* that have a highly reduced testa are still black in color (Smith 1985a, b). The domesticated sunflower differs from the wild sunflower in lacking an armored layer in the achene, a change almost certainly associated with germination. If more rapid germination re-

sults from a change in seed colors then the former would be an indirect result of conscious selection.

7. Lose of toxic or bitter properties. At first thought it might seem obvious that this change resulted from intentional selection, and well it has in recent times, but if it did develop in prehistoric times it may have been from unconscious selection. Once people began using plants with toxic or unpleasant-tasting substances they devised ways of eliminating these substances so that there was probably no premium placed on plants with less bitter compounds. Moreover the people would unlikely be aware if such a change occurred. So in all probability if some crops experienced a loss or reduction in these substances, it was correlated with some of the other changes discussed above. For example, some toxic compounds are known to inhibit seed germination (Bewley & Black, 1985) so that with development of rapid germination they may have been eliminated. Such is not known, however, for either saponins or alkaloids so we would have to look for other explanations for the loss of these. The loss of toxic compounds would also likely mean greater predation of the crops by animals; therefore, until methods were devised for the control of predators, there would have been a disadvantage for selecting the non-toxic mutants.

Thus far the discussion has considered selection operating on seed-propagated plants. In plants propagated vegetatively, 'selection is absolute and its effects immediate (Harlan, 1975).' Thus from the very beginning we might well expect that there may have been conscious selection in that preference may have been given to certain clones over others. The future variation, of course, would not be limited to the cultivated clones for the primitive vegetatively-propagated crops were also capable of reproducing sexually and starts from spontaneous seedlings might also be incorporated in future plantings (Hawkes, 1969).

From the foregoing discussion it can be seen that much of the evolution of seed propagated crops could have occurred without methodical selection. The idea that agriculture developed unconsciously is not a new one, having been mentioned by both Englebrecht (1917) and Vavilov (1926), as Darlington (1963) points out. Recently this position has been championed by Rindos (1984). He, in fact, sees no difference in the domestication of certain fungi by ants and the domestication of plants by man – there was no intentionally on the part of man. However, he overlooks one important point. Unconscious selection did not operate in the evolution of the domesticates until man deliberately planted seeds. This was a conscious act on the part of man to secure more plants – either directly, or indirectly as an appeasement to the gods to ensure bountiful harvests in the future (Heiser, 1985). The plants, unconsciously selected by man but not planted, became weeds, some before and some after domestication occurred. Some of the weeds later became domesticated after deliberate planting. Anderson (1939) in his classification of weeds and weed-like plants makes a clear distinction between cultivated plants, 'plants intentionally grown by man,' and weeds, 'plants unintentionally grown by man.' For our purposes weeds may be defined as plants that are adapted to habitats disturbed by man or his domesticated animals (Heiser, 1949). Domesticated plants are also adapted to disturbed areas, but we would have only weeds had not man exercised a deliberate act in the beginning of their domestication.

If we concede that the early evolution of seed-propagated domesticated plants was guided by unconscious selection, we may ask how early methodical selection began.

> In attributing so much importance to the selection of animals and plants, it may be objected, that methodical selection would not have been carried on during ancient times. A distinguished naturalist considers it as absurd to suppose that semi-civilized people should have practised selection of any kind. Undoubtedly the principle has been systematically acknowledged and followed to a far greater extent within the last hundred years than at any former period, and a corresponding result has been gained; but it would be a greater error to suppose, as we shall immediately see, that its importance was not recognized and acted on during the most ancient times, and by semi-civilized people. (Darwin, 1868).

There is little to add to Darwin's comments, for the archaeological record has not provided clear-cut answers, nor is it likely to. However, it would probably be erroneous to assume that the earliest farmers did not have a fairly sophisticated knowledge of plants. As pointed out above, color variants may have been the subject of special attention from near the beginning of seed planting.

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Postscript

Since the above was written I have seen the paper by P. Hanelt, Pathways of domestication with regard to crop types, p. 179–199, in C. Barigozzi (ed.), The Origin and Domestication of Cultivated Plants; Elsevier, Amsterdam, 1986. His discussion is pertinent to a number of points that I make.

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