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Physiological Adaptation to Performace as Crop Plants

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Physiological adaptation to performance as crop plants

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Morphological and cytogenetic changes associated with evolution from wild plant to cultivar have been explored for many crop plants, but the physiological adaptations are less well known. Selection for better performance as crops has not been associated with increase in relative growth rate or photosynthetic rate. In fact, photosynthetic rate per unit leaf area has fallen during the evolution of some crops, but this has been counterbalanced by greater leaf area and duration of photosynthetic activity. The capacity to transport assimilates to the storage organs has increased, due mainly to additional phloem differentiation rather than to closer proximity of source and sink organs. Greater size or number of storage organs, together with their more compact arrangement and more synchronous development, have all contributed to their predominance as a sink for assimilates and mobile nutrients towards the end of the life cycle, attracting progressively more substance to the organs harvested by man.

Introduction

Archaeological and cytogenetic studies in recent years have given us a comprehensive, but still tantalizingly incomplete, picture of the course and pace of domestication of several major crop plants. However, the physiological changes which accompanied and contributed to these domestications have only just begun to be analysed in spite of the valuable leads such studies may give as to which avenues are exhausted and which may be further exploited in the search for greater or more stable crop yields.

The physiological changes we shall be concerned with are of several kinds. Some, such as greater speed and uniformity of germination or delayed fruit dehiscence, are important in conferring adaptedness to cultivation, and probably underwent rapid change in the earliest stages of crop domestication. To what extent there was direct selection for these characteristics as against unconscious selection as a result of early sowing and harvesting procedures is difficult to say. Some direct selection for seed retention, e.g. for non-shattering ears of cereals or non-dehiscent pods of legumes, may well have been practised since proto-agricultural man lived close to his domesticated plants and observed them intensely.

Rather later, as crops were introduced to environments different from those of their original hearths of domestication, the responses which controlled the duration and timing of their life cycle had to be modified if the crop was to survive and be productive, particularly when crops of tropical origin spread to higher latitudes. Again, selection for these changes was probably indirect.

More recently, crops have been increasingly subject to direct selection for ability to yield under progressively improved systems of agronomic inputs. Such selection for increased yield potential has not focused on individual physiological characteristics, and the changes we discern in these are due mostly to indirect selection. Now, however, we are entering a phase where direct selection for important physiological attributes, such as rapid photosynthesis, is being urged, although it remains to be seen whether such selection will be more effective than that for yield itself.

Selection of crop plants for better performance has thus passed through several distinct stages, its emphasis shifting from adaptedness to cultivation in the earliest phase of domestication, through adaptation to new environments as crops spread from their original hearths, to increased yield potential with progressively greater agronomic inputs of support energy. As the emphasis has changed, so have the requisite physiological attributes, but no clear line can be drawn between those selected under early agriculture and those modified more recently. Consequently, we should consider here the full range of physiological adaptations to performance as crop plants.

Changes conferring adaptedness to cultivation

The characters under most intense selection in the earliest stages of crop domestication probably bore little relation to yield potential, although they would have influenced actual yield through effects on the efficiency of harvest, as well as adaptedness to cultivation in primitive monocultures.

Selection for non-shattering inflorescences was a crucial early step in the domestication of cereals. Apparently readily achieved in most, its genetic basis is simple (cf. Harlan, de Wet & Price 1973), but its physiological basis has been little studied. Presumably it involves delayed or reduced development of abscission layers at the base of each fruit or inflorescence segment. Delayed dehiscence of pods was an important step in the domestication of many crops such as legumes and crucifers, a step which has been repeated more recently in the domestication of several lupin species in Germany and Australia. Two mechanisms, both simply inherited through single recessive genes, contribute to the desired characters in lupins (Gladstones 1967): sclerenchyma in the pericarp walls are less strongly aligned, so that less rotational torsion develops in the pod during maturation, and sclerenchyma strips tend to fuse across both seams of the pod. Although flower and fruit shedding, and probably fruit dehiscence, are influenced by endogenous growth substances such as abscisic acid, the non-shedding mutants appear to modify anatomical traits rather than hormonal levels.

More uniform and rapid germination were desirable, to conserve seed and to give denser crop stands, and probably developed in many crops as a result of indirect selection pressures. Reductions in hard seededness and in the content of germination inhibitors were probably involved, coupled with selection for increase in seed size.

Reduced branching or tillering may have been an important component in the early domestication of many crops, such as maize, sunflower (Harlan *et al.* 1973), beans (Smartt 1969) and wheat (Evans & Dunstone 1970). Associated with a more determinate habit and greater apical dominance, it not only adapted the crop to a more suitable habit for growth in monoculture, but also ensured more synchronous ripening and thereby a more complete harvest. Again, such a trend may have been physiologically linked with, and reinforced by, that for greater seed and fruit size.

Adjustment of life cycles

In many wild plants the timing of the reproductive cycle is strictly controlled by daylength and vernalization requirements, most commonly for flower initiation but also during the stage of inflorescence development. These regulatory mechanisms may be relaxed or modified under cultivation. Among many species of rice, for example, Katayama (1964) found a pronounced short day response in most wild forms, but less commonly in cultivars.

In most crops growth of the organs harvested by man is based on carbon assimilated during their growth rather than on reserves accumulated earlier in the life cycle. One path to yield increase, therefore, has been to extend the duration of the grain filling or storage phase. With annual crops in temperate climates this has often involved a corresponding reduction in the pre-flowering phase and, consequently, a relaxation of the daylength requirements which delayed flowering in the wild forms until later in the season. Improved supplies of water and nutrients result in faster early growth and canopy closure, and reduce the time needed for an adequate root system to develop, thereby permitting the storage phase to begin earlier. The most extreme form of these pressures for abbreviation of the pre-flowering phase of the life cycle is associated with the selection of cultivars suitable for multiple cropping in the tropics, such as 3–4 crops of rice each year.

Vavilov's centres of diversity for crop plants were mainly at low latitudes, and in many of them a strict requirement for short days was the usual means for control of the life cycle, whether for the initiation of inflorescences in maize (e.g. Stevenson & Goodman 1972) or of tubers in *Solanum andigena*. Such a requirement did not need much relaxation in the early stages of local domestication, but as crops like maize, potatoes, soybeans, rice and beans spread to higher latitudes a greater relaxation of their photoperiodic responses, sometimes to the point of complete indifference to daylength, was necessary. Response to daylength appears to be readily modified by selection: even *Solanum andigena*, characterized by a very strict short day requirement for tuberization, has had that relaxed under selection in India (Upadhya 1974).

There are also circumstances, however, in which the degree of photoperiodic control may have been enhanced during domestication. As wheat and barley were adapted to higher latitudes, the quantitative requirements for long days among their progenitors were accentuated and have become an absolute requirement in some Canadian cultivars for example. Similarly, the domestication of sorghum in West Africa has involved the development of cultivars with very close adaptation of their flowering to the end of the wet season (Curtis 1968), and some tropical cultivars of rice display extreme sensitivity to daylength. The requirement for vernalization has also been enhanced in order to delay flowering in several crops, such as sugar beet, radish and lettuce.

Increase in size

According to Schwanitz (1966) the most important step in the evolution of wild species into cultivated plants is the transition to gigantism, i.e. to much larger organs, especially those used by man. A substantial increase in seed size has characterized the evolution of many cereal and legume crops (cf. figures 1 and 2), and is apparent from the earliest stages at which wild and cultivated materials can be compared in archaeological studies (e.g. Zohary & Hopf 1973). Several pressures would have favoured the early selection of larger seeds. They are easier to harvest and handle and give rise to larger seedlings (e.g. Evans & Dunstone 1970) better able to compete with weeds, especially when they are also of rapid and uniform germination. In wheat, at least, larger seeds give larger seedlings not because of their larger embryos but because of their larger endosperm reserves (Bremner, Eckersall & Scott 1963), especially of protein (Lowe & Ries 1973). Weeds of crop fields, however, also tend to have larger seeds than their congeners (Salisbury 1974) and may undergo selection for seed size and shape, and also for the duration of their life cycle, in parallel with that for the crop itself. The larger the seed the smaller is the proportion of indigestible seed coat, as shown for the legumes in figure 1. The much greater seed size in grain legumes compared with pasture legumes is evident, as is the increase associated with crop domestication in the comparison between the wild progenitor *Glycine ussuriensis* and the cultivated *Glycine max*. The relatively high proportion of seed coat in *Lupinus cosentini* and *L. angustifolius* may be indicative of their recent domestication.

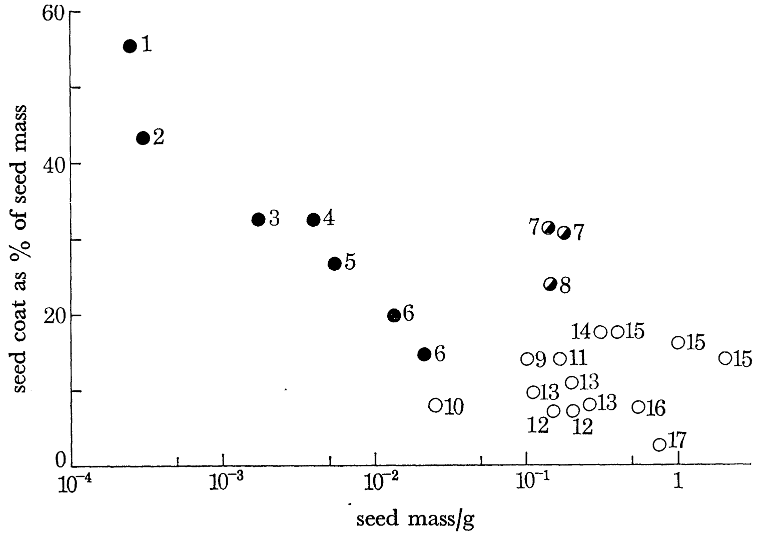

FIGURE 1. Relation between legume seed size and the proportion of seed dry mass represented by the coat (i.e. all layers external to the embryo). Data for the pasture legumes (1–5) are from Grant Lipp & Ballard (1969); those for the grain legumes are from measurements on samples of 20 seeds. The species represented are 1, *Lotononis bainesii*; 2, *Trifolium glomeratum*; 3, *T. pratense*; 4, *Desmodium uncinatum*; 5, *Trifolium subterraneum*; 6, *Glycine ussuriensis*; 7, *Lupinus cosentini*; 8, *L. angustifolius*; 9, *Cajanus cajan*; 10, *Lens culinaris*; 11, *Cicer arietinum*; 12, *Glycine max*; 13, *Pisum sativum*; 14, *Lupinus albus*; 15, *Vicia faba*; 16, *Phaseolus vulgaris*; 17, *Arachis hypogaea*.

Certain disadvantages may attend increase in seed size. Larger seeds are more susceptible to predation, less easily dispersed, and may have greater difficulty imbibing sufficient water for germination (Harper, Lovell & Moore 1970). Along with a reduced proportion of seed coat they may also have a smaller proportion of protein, as in the wheats (Dunstone & Evans 1974). Without increased vasculature in the grain, the greater path length for diffusion of sugars and amino acids may limit the rate of starch and protein synthesis in them. And the large seedlings they give rise to may encounter too much resistance to emergence in heavy soils, as in soybeans (Edwards & Hartwig 1972). Consequently, there may well be an optimum seed size, although this will vary among species and conditions. Where cool temperatures favour a long period of grain growth, for example, potentially large seeds may be an important component of heavy yields, as in the high altitude Cuzco race of maize in which the seeds weigh about 1.25 g.

Although selection pressure in grain crops may have been focused on seed size, parallel increases in the size of other organs have occurred. This is illustrated in figure 2 for wheat and its wild relatives, in which a twentyfold range in grain size is matched by a comparable range in the area of leaf blades. A close relation between leaf and seed size is evident in other crops, such as beans (Duarte & Adams 1972) and soybeans (Burris, Edje & Wahab 1973). With sugar cane, in which sugar content (as a percentage of fresh mass) is closely related to stem diameter, this latter has increased over a twentyfold range from *Saccharum spontaneum* through *S. robustum* to modern forms of *S. officinarum* and so has the area of the upper leaves (Bull 1965, 1967).

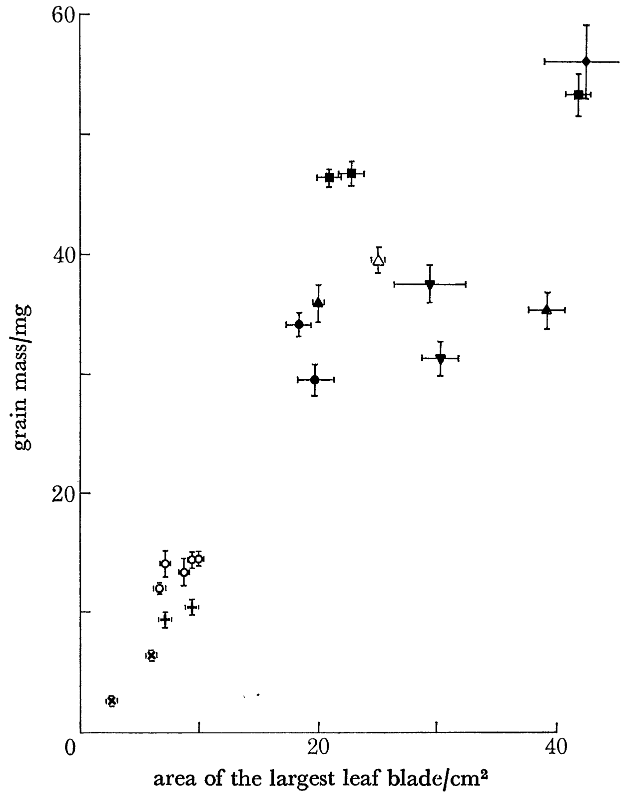

FIGURE 2. Relation between grain size and area of the largest leaf blade among 21 lines from various stages of the evolution of wheat (Evans & Dunstone 1970): *Triticum boeoticum*, ○; *T. monococcum*, ●; *T. dicoccoides*, △; *T. dicoccum*, ▲; *T. durum*, ▼; *T. spelta*, ◆; *T. aestivum*, ■; *Aegilops speltoides*, ×; *A. squarrosa*, +.

Such parallel increases in the size of several organs throughout crop evolution suggest that a common basis, such as increasing cell size, might be involved. However, the magnitude of the increases seems too great for changes in cell size alone to accommodate them. Also, whereas leaf area would increase in proportion to the square of cell dimensions, fruit and seed volume could be expected to increase in proportion to the third power. Consequently, if increase in cell size was the only mechanism involved, storage capacity would soon outrun the assimilatory capacity of the crop, especially as larger leaves confer no photosynthetic advantage to crops once the canopy is fully light-intercepting.

Kranz (1966) found an increase in the size of palisade cells in the leaves of wheat with increase in ploidy from diploid to tetraploid, and with selection for cultivation at the diploid but not at the tetraploid level. We found a significant, but weak, correlation between the areas of mesophyll cells and of leaves at all stages in the evolution of wheat (Dunstone & Evans 1974).

The cross-sectional area of aleurone cells (but not of endosperm cells) was significantly and positively correlated with that of mesophyll cells on the one hand, and with grain size on the other. However, the increases in cell size accounted for only a small part of the increases in leaf area or grain size in the course of evolution, and contributed very little to the substantially greater leaf and grain sizes in *Triticum monococcum* compared with *T. boeoticum*. With sugar canes from all stages of evolution of the crop, Bull (1965) found the volume of internode cells, which are the main sites of storage, to increase as internode volume increased. The increase in cell volume largely accounted for the increase in internode volume in the wild species *Saccharum spontaneum*, but for only a small part of it in *S. robustum* and *S. officinarum*.

Thus, in at least two crops increase in cell number rather than in cell volume has presumably been the major component of increase in organ size during domestication. This confers the advantage that selection specifically for increase in the size of the harvested organs is easier than when most of the increase in organ size is due to increased cell size. Increase in cell size has, nevertheless, played a role in the evolution of crop plants, as emphasized by Schwanitz (1966). Among the grain legumes like pea and broad bean cell volume in the cotyledons increases throughout the period when storage proteins are synthesized, and the ability to form large cells is an important component of increased storage capacity.

Rates of growth and photosynthesis

Although larger seeds give larger seedlings, the relative growth rates of the seedlings may not differ. Indeed, the relative growth rate for leaf area is remarkably similar among wild relatives and cultivars from all stages of evolution in wheat (Evans & Dunstone 1970), a conclusion that may also be deduced from the data of Kranz (1966). In the experiments of Khan & Tsunoda (1970*b*) the wild diploid progenitors tended to have higher relative growth rates than the modern wheats. Among tomatoes, likewise, highly productive modern cultivars have relative growth rates no higher than their wild progenitors (Warren Wilson 1972). Similarly, among 22 races of maize and teosintle, ranging from ancient and pre-Columbian varieties to modern hybrids, Duncan & Hesketh (1968) found only a very small range in relative leaf growth rates.

The relative leaf growth rate is an important determinant of the time taken for a crop to develop a fully light-intercepting canopy. Once the canopy has closed, however, the rate of photosynthesis per unit leaf area and the structure of the canopy become the main plant determinants of crop photosynthesis. Canopy structure may be modified in many ways, by reduced branching and by changes in the shape, size, inclination, horizontal arrangement and vertical spacing of leaves. Watson & Witts (1959) have suggested that selection for more upright inclination of leaves has occurred during the domestication of sugar beet, but the role of changes in canopy structure in the evolution of other crops has yet to be established. So too has the role of change in photosynthetic rate which might be expected to have increased in the course of crop evolution. Comparisons of photosynthetic rate are not easy to make. Not only must the rates be measured under standard environmental conditions, but the leaves must be comparable in age, in ontogenetic rank, in the conditions under which they are grown, and in the demand on them for the products of photosynthesis. For example, differences in the photosynthetic rate of leaves of wheat from various stages of evolution become more marked in successively formed leaves, and are more pronounced in plants grown under high intensity light (Dunstone, Gifford & Evans 1973). For these reasons they were missed by Belikov, Motorina & Kurkova (1961).

From their comparisons of 22 races of maize and teosintle Duncan & Hesketh (1968) concluded that 'improvement in maize over the centuries was not associated with marked improvement in net photosynthetic rates'. Likewise there appears to be no consistent difference in photosynthetic or net assimilation rate between the wild and cultivated forms of sorghum (Downes 1971), sugar beet (Watson & Witts 1959) and sugar cane (Bull 1971). Among species of *Gossypium*, the fastest rates of photosynthesis measured by El-Sharkawy, Hesketh & Muramoto (1965) were in several wild species. Among wheats, the wild diploid progenitors display the fastest light-saturated rates of photosynthesis (Evans & Dunstone 1970; Khan & Tsunoda 1970*a*). Maximum photosynthetic rate seems to have fallen progressively in the course of evolution in wheat, even in the step from the wild diploid *T. boeoticum* to the cultivated *T. monococcum*, as illustrated in figure 3. The superiority of the primitive wheats in this respect is more pronounced the higher the light intensity under which the rates are measured and the plants are grown. Reduced resistance to CO_2 transfer through both the stomata and the mesophyll cells is involved. In fact, there was a close relation between gas phase and residual resistance to CO_2 exchange among most of the lines of wheat examined, although the residual resistance was of greater magnitude (Dunstone *et al.* 1973). Khan & Tsunoda (1970*a*) associate the slower photosynthetic rates of modern wheats with thinner leaves of lower nitrogen content per unit leaf area. Although the maximum rates of photosynthesis by flag leaves of wheat are greatest in the primitive wheats and least in modern cultivars, this ranking is reversed when photosynthetic rates are measured several weeks after anthesis, due to earlier cessation of grain growth and more rapid senescence of flag leaves in the more primitive wheats.

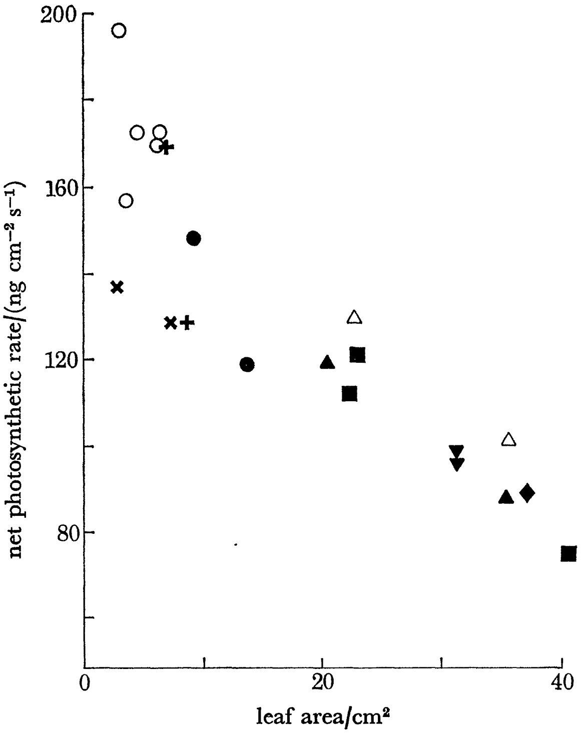

FIGURE 3. Relation between area and net photosynthetic rate of flag leaf blades (at 21 °C, 300 parts $CO_2/10^6$, under a visible light flux of 266 W m^{-2}) among 21 lines of cultivated wheats and their wild relatives (Evans & Dunstone 1970). Species and symbols as in figure 2.

Comparison of photosynthetic rates among soybean cultivars suggests that selection for greater yield may be associated with faster rates (Shibles, Anderson & Gibson 1975), but in maize, sugar cane, sugar beet and sorghum there is no evidence that photosynthetic rate has risen in the course of domestication, while in wheat and cotton it appears to have fallen. Yet treatment of crops with additional CO_2, thereby increasing their photosynthetic rate, often increases yields. Why then has selection for greater yield not led to an increase in photosynthetic rate?

One explanation may reside in the negative correlation between leaf area and photosynthetic rate evident in figure 3, and also found among modern wheat cultivars (Gale, Edrich & Lupton 1974), maize (Hanson 1971), soybean (Burris *et al.* 1973), lucerne (Delaney & Dobrenz 1974) and several other crops. In several of these studies yield and leaf area were positively correlated, and therefore yield and photosynthetic rate are unlikely to be so. But why larger leaves tend to have slower rates of photosynthesis is not clear. El Sharkawy & Hesketh (1965) found a negative correlation between photosynthetic rate and mesophyll cell size among 15 species of plants, including several crops. Wilson & Cooper (1969) found a similar negative relation among genotypes of *Lolium perenne*, which they suggested could be due to a decreased surface:volume ratio in the larger cells. However, chloroplasts usually occur in a single parietal layer, and their area and number bear a close relation to cell surface area (Butterfass 1966; Kranz 1966; Honda, Hongladarom, Kwanyuen & Wildman 1971). Thus chloroplast volume per unit leaf area will fall as cell size increases only if leaves of greater area tend to be thinner, with fewer layers of mesophyll cells. It is perhaps for this reason that we found a negative correlation between mesophyll cell size and photosynthetic rate among species of *Triticum* (Dunstone & Evans 1974). Wilson & Cooper (1970) have shown that selection for smaller size of mesophyll cells within a population of *Lolium perenne* can lead to increased mass of shoot and seed. This suggests that the frequently negative correlation between leaf size and photosynthetic rate in crops could be broken by selection.

Shifts in the partitioning of plant weight

Increase in yield can be obtained without any increase in the rates of crop growth and photosynthesis if a greater proportion of plant substance is distributed to the harvested organs. In the domestication of many plants these organs have undergone a disproportionate increase in number or, more commonly, in size. Perhaps the most striking examples are to be found among flower and vegetable crops, as in the cabbage-kale-collard-kohlrabi-Brussels sprout-cauliflower-broccoli complex. Such shifts have been less obvious and varied in agricultural crops, but very important nevertheless. In the course of evolution in wheat, for example, there has been an increase in the proportion of photosynthate which is translocated from the leaves to the grain at the expense of tillers and roots (Evans & Dunstone 1970). This increases yield not only directly but perhaps to an even greater extent indirectly in that stored starch requires far less respiratory maintenance than do the additional roots, stem and leaves that would otherwise have been formed. Thus a small shift in the initial allocation of assimilates for storage can be amplified in time to a substantial increase in yield.

Until we are more sure of the mechanism of translocation we must remain uncertain as to what controls the partitioning of photosynthetic assimilates. The pattern of vascular connections influences the pattern of assimilate distribution, and proximity of source leaf and sink organ is also important. Inflorescences and fruits tend to be supplied predominantly by the leaves and bracts subtending them, as in cotton or beans. Indeed, Canny (1973) includes this observation among his arguments for translocation by accelerated diffusion and concludes that plants which produce fruit remote from leaves tend to have small fruits. Only over very short path lengths between source and sink, less than 10 cm, could specific mass transfer rates of 3–4 g cm^{-2} phloem per hour be maintained according to his calculations. Were this so, there should have been a pronounced tendency during crop domestication for source leaf and harvested sink organ to be closer together.

'Condensation' of the inflorescences has certainly occurred during the domestication of cereals such as maize, sorghum and millet, and in other crops such as sunflower and castor bean (Harlan *et al.* 1973), but this may have been for other reasons. In most cereals, even in the semi-dwarf small grains, the path from flag leaf to grain is at least 40–50 cm, yet even with paths of this length modern wheats can sustain transport of photosynthetic assimilates through the culm at a rate of 3–4 g cm^{-2} phloem h^{-1} (Evans, Dunstone, Rawson & Williams 1970). Some of the assimilate required for grain growth comes from sources close to the grains, such as glumes and awns, but even in the awned modern wheats this is a smaller proportion than in the primitive wheats (Evans & Dunstone 1970). For this reason, and because of increased plant stature, the mean path length from source to harvested sink has actually increased during the domestication of wheat and other cereals, and probably in potatoes, sugar cane and several other crops too.

One of the striking features of successful crop plants is that there is apparently no preferred position for the dominant sink; it may be a terminal inflorescence as in wheat, a mid-stem axillary inflorescence as in maize, the whole stem itself in sugar cane, or a potato tuber or sugar beet root. Distance from the upper, most actively photosynthesizing leaves appears to be less important than the predominance of the harvested sink organ.

In some recent experiments with wheat plants, Miss M. G. Cook and I have been examining the effects of relative size and geometry of sinks, and their distance from source leaves, on the ability of ears to compete for a limited supply of ^{14}C-labelled assimilates. Figure 4 illustrates the effect of the relative size of the two sinks on their import of ^{14}C-labelled assimilates from a symmetrically placed source leaf, the flag leaf of the main stem. This was the only source of current assimilate remaining on the plants, whose reserves had also been depleted by prior defoliation and spraying with an inhibitor of photosynthesis, 3-(3,4-dichlorophenyl)-1,1-dimethyl urea. Although the sink ears on the two tillers were matched in every way other than the number of grains in them, the relative distribution to the ear with more grains increased approximately in proportion to the square of its size relative to that of the ear with fewer grains. Thus, once a particular sink begins through selection to predominate over others, further selection may rapidly enhance its advantage in securing assimilates. Hence, for example, the increase in grain growth at the expense of root and tiller growth in the evolution of wheat.

Given the competitive advantage of a predominant sink organ in securing assimilates, what limits its further enlargement? Transport capacity does not seem to do so because, in both wheat (Evans *et al.* 1970) and sugar cane (Bull 1965), phloem area and the number of vascular bundles serving the major sink have increased in proportion to the size and needs of the major storage organ. The real limit to the development of the harvested sink organ is imposed by the level of agronomic control, which determines the extent to which crop plants can concentrate their substance in the organs harvested by man at the expense of others required for survival under natural selection. With the provision of water by irrigation and of nutrients by fertilizers less investment in root growth is required. Weed control makes investment in tall stems and large light-excluding leaves less necessary. Control of pests and diseases reduces the need for storage of reserves to support recovery. With each agronomic advance, a greater proportion of crop dry mass is freed for investment in the organs of interest to man without endangering crop survival, and selection can shift in this direction.

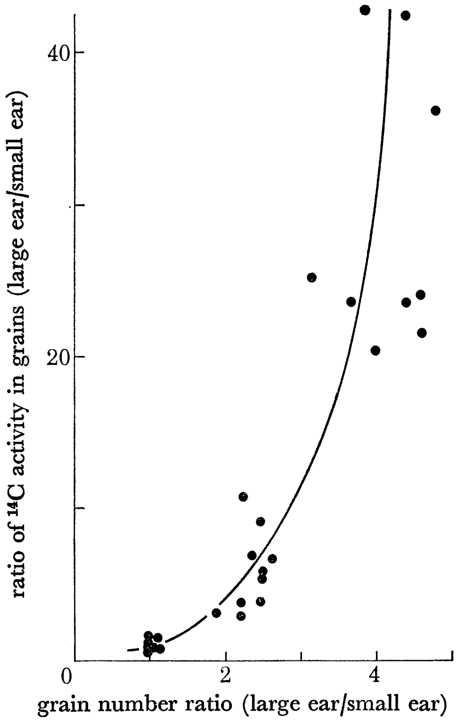

FIGURE 4. Effect of relative sink size (i.e. the relative number of grains in the ears of the first two tillers) on the distribution of ^{14}C-labelled assimilates from the flag leaf of the main stem to grains in the ears of the two tillers of wheat plants, two days after exposure to $^{14}CO_2$.

CONCLUSIONS

The evidence reviewed above has indicated the range and variety of modification of crop plants achieved under the impulse of domestication. The length of the life cycle, the proportion given over to its various phases, and the degree of environmental control over these have all been changed. Growth habit has been modified to suit monoculture in various ways, by the reduction of branching or by more upright leaf inclination. The size of organs, particularly those harvested by man, has been increased substantially, or specifically reduced when this confers agronomic advantage, as in the shortening of cereal stems. The capacity for transporting assimilates to the various organs has also been increased as required. Morphological correlations have undergone major changes, the cabbage and its relatives being a striking example, especially the Brussels sprout with its enlarged axillary buds. The composition of plants has also been modified profoundly, some components such as sugar in beet and cane being increased, others such as bitter and toxic principles decreased.

In fact, so susceptible to selection are some crops that it has often proved easier to modify an old crop for new purposes than to develop a new one with the required characteristics, as

Engelbrecht first noted in 1916: 'Man hates to look beyond the familiar plants of his immediate surroundings. He uses the cultivated plant in so many ways that it serves entirely different purposes...' (Zeven 1973). This raises the question of what characteristics, particularly what physiological ones, confer the striking adaptedness to performance as crops of the few major domesticates, a question we have only partly answered.

Also, in view of the range and variety of changes made in the major crop plants, why has photosynthetic rate per unit leaf area not increased? Although it is difficult to select for faster rates directly, they would surely have been selected for unconsciously unless there are counter-productive features associated with faster rates of photosynthesis. Some of these have been discussed above, but it is one of the major challenges before crop physiology to identify such counter-productive features more surely. Modifications to growth habit – to the size, shape, inclination and arrangement of leaves for example – may also increase the rate of crop photosynthesis, but it is surprising that these have not been coupled with increase in the rate of photosynthesis per unit leaf area in some crops at least.

Increase in size of the harvested organs and in the proportion they represent of total plant mass has been a striking feature of the domestication of many crops. In fact, the evolution of cultivated plants has been primarily the evolution of the 'sink' organs useful to man. Translocation experiments suggest that the effective limit on this trend is likely to be imposed by agronomic rather than genetic art. In the cereals, for example, further increase in harvested mass as a proportion of the whole crop will depend on the extent to which agronomic control – in the form of increased input of energy from fossil fuels – permits reduced investment in roots, stems, reserves and even leaves.

However, most of the physiological changes involved in the early stages of domestication, the subject of this meeting, probably conferred better adaptedness to agriculture rather than greater yield potential, which has increased only relatively recently. For example, the grain yields harvested by Zohary (1969) from mixed stands of the wild progenitors of wheat, barley and oats in the Middle East are comparable with the yields of wheat crops in England and of rice crops in Japan in the Middle Ages. Only in this context, surely, could Charles Darwin have written in *The variation of plants and animals under domestication*, 'Although the principle of selection is so important, yet the little which man has effected, by incessant efforts during thousands of years in rendering the plants more productive or the grains more nutritious than they were in the time of the old Egyptians, would seem to speak strongly against its efficacy'.

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