6. Domestication rates in wild-type wheats and barley under primitive cultivation

GORDON C. HILLMAN

Department of Human Environment, Institute of Archaeology, University College London, 31–34 Gordon Square, London WC1H 0PY

AND

M. STUART DAVIES

School of Pure and Applied Biology, University of Wales College of Cardiff, P.O. Box 915, Cardiff, CF1 3TL, Wales

Man's first cereal crops were sown from seed gathered from wild stands, and it was in the course of cultivation that domestication occurred. This paper presents the preliminary results of an experimental approach to the measurement of domestication rate in crops of wild-type einkorn wheat exposed to primitive systems of husbandry. The results indicate that in wild-type crops of einkorn, emmer and barley (a) domestication will have occurred only if they were harvested in a partially ripe (or near-ripe) state using specific harvesting methods; (b) exposure to shifting cultivation may also have been required in some cases; and (c) given these requirements, the crops could have become completely domesticated within two centuries, and maybe in as little as 20–30 years without any form of conscious selection.

This paper (1) considers the possible length of delays in the start of domestication due to early crops of wild-type cereals lacking domestic-type mutants; (2) examines the combination of primitive husbandry practices that would have been necessary for any selective advantage to have been unconsciously conferred on these mutants; (3) considers the state of ripeness (at harvest) necessary for crops to be able to respond to these selective pressures; (4) outlines field measurements of the selective intensities (selection coefficients) which arise when analogous husbandry practices are applied experimentally to living wild-type crops; (5) summarizes the essential features of a mathematical model which incorporates these measurements of selection coefficients and other key variables, and which describes the rate of increase in domestic-type mutants that would have occurred in early populations of wild-type cereals under specific combinations of primitive husbandry practices; (6) considers why very early cultivators should have used that combination of husbandry methods which, we suggest, unconsciously brought about the domestication of wild wheats and barley; and (7) concludes by considering whether these events are likely to have left recognizable traces in archaeological remains.

KEY WORDS:—Domestication rate – agricultural origins – einkorn wheat – emmer wheat – barley – selection pressures – archaeobotany.

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INTRODUCTION

The shift from hunting and gathering to cultivation and pastoralism represents the single most dramatic (and ultimately, perhaps, the most catastrophic) set of changes that human society has experienced since the mastery of fire. The domestication of crop plants played a critical role in these events, if only at a late stage.

Domestication was recognized as an example of accelerated evolution by both Darwin (1859, 1868) and De Candolle (1886), but it was Vavilov (1917, 1926, 1951) who first postulated specific evolutionary pathways for the domestication of cereals such as the wild wheats and barley, and in the secondary domestication of cereals such as rye and oats. Engelbrecht (1917) was developing similar ideas at the same time. Definition of these evolutionary pathways formed an integral part of Vavilov's analysis and identification of centres of origin of cultivated plants (see the review by Harris, 1990 and Hawkes, 1990). Since then, understanding of the possible processes involved has been further extended by the work of, for example, Darlington (1963, 1969, 1973), De Wet & Harlan (1975), Hammer (1984), Harlan (1975), Harlan, De Wet & Price (1973), Hawkes (1969, 1983, 1989), Heiser, (1965, 1985, 1988, 1989), Johns (1989), Ladizinsky (1979, 1987), Pickersgill (1971, 1989), Pickersgill & Heiser (1976), Pickersgill, Heiser & McNeill (1979), Riley (1965), Schiemann (1932), Schwanitz (1937), Wilson & Heiser (1979), and Zohary (1969, 1984, 1989 a, b in press). Research in this field continues apace, and the extent of still unresolved

problems is reflected in the current debate between Ladizinsky (1987, 1989—proposing a model in which domestication of pulse crops such as lentils occurred prior to any cultivation) and Zohary (1989b—arguing that domestication of both pulses and cereals could have occurred only under cultivation).

For the wheats and barleys, the mechanism for domestication outlined in a seminal paper by Wilke *et al.* (1972) (and extended by Harris, 1976) foreshadows what our own studies suggest to have been the probable prehistoric pathway. However, their hypothesis overlooks certain factors necessary for domestication to have occurred at all, and, like most authors, they offer no estimate of the time required to achieve domestication under their proposed system of primitive cultivation. In the few published estimates, the time supposedly required to achieved unconscious domestication ranges from one to 1000 years. However, crop geneticists such as Harlan (1975), Ladizinsky (1987) and Zohary (1969, 1984, 1989b)—with their knowledge of gene-frequency theory and unrivalled field experience of both wild and domestic south-west Asian cereals and pulses—have long recognized that the domestication of such crops could have been very rapid: thus Zohary (1989, in press) suggests that "once the mutation occurred in the population taken into cultivation, mutant lines could have established themselves in a matter of a very few years". Indeed, in 1968, Zohary (in the unpublished discussion following presentation of his 1969 paper) suggested a period of 20 years once the mutant was present), and Ladizinsky (1987) similarly suggests that his proposed 'domestication before cultivation' of lentils could have occurred in about 25 years (although some of his starting assumptions are puzzling). However, in no case known to us have estimates been based on measurements of those selection pressures responsible for domestication in the first place, or on formal mathematical modelling. It was against this background that the present work was begun in 1972.

A central assumption

Man's (or more probably woman's) first cereal crops must have been sown from seed gathered from wild stands. These first cereal crops were therefore entirely of the wild type, so it was in the course of cultivation that domestication occurred. (Alternative views are discussed below.) In the case of einkorn wheat, for example, the domestic form (*Triticum monococcum* L. subsp. *monococcum*) emerged from crops of its immediate ancestor—wild einkorn (*T. monococcum* L. ssp. *boeoticum* (Boiss.) A. & D. Löve) which still grows wild in the Near East—mainly in the ecotone between oak forest and steppe (Fig. 1). (Note—throughout this paper, cereals such as einkorn, emmer and barley in their morphologically wild state but growing under cultivation are called 'cultivated wild-type cereals'. The term 'wild cereals' is thus reserved for wild-type populations growing in wild habitats.)

The present paper

The aim of this paper is to present the preliminary results of an experimental approach to measuring domestication rate in crops of wild-type wheats and barley under primitive systems of husbandry. The results indicate that (a)
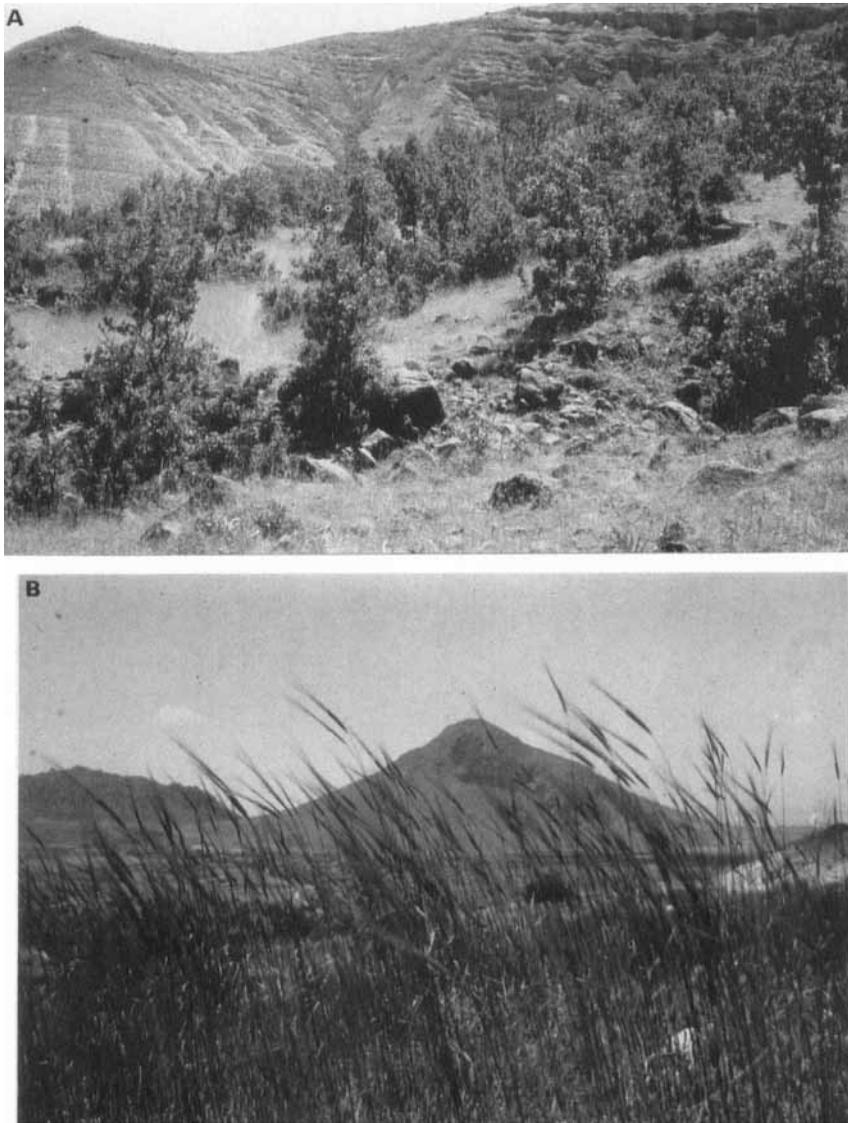
Figure 1. Wild einkorn wheat (*Triticum monococcum* subsp. *boeoticum*). A, Growing in oak (*Quercus cerris*) scrub on the lower S-facing slopes of the Munzur Mts. in eastern Turkey, 1971. B, Growing in the ecotone between oak forest and steppe on the lower slopes of Karadağ in the Konya Basin of central Turkey, 1970. (These were the two locations at which we undertook preliminary field measurements of the selection pressures generated by primitive methods of harvesting wild einkorn.) (Photos: G.C.H.)

domestication will have occurred only if the wild type crops were harvested in specific ways, (and in certain circumstances, may also have required shifting cultivation); (b) the crop had to be harvested when at least partially ripe (and not while still green as evidenced archaeologically for some early cereals); and (c) given these requirements, the crop could have become completely domesticated within two centuries, and maybe in as little as 20–30 years, without any form of conscious selection.

Figure 2. Near-ripe ears of wild einkorn from which the upper spikelets have already been spontaneously shed. The ears would originally have had 20–26 spikelets. Hills above Aşvan in eastern Turkey, 1971. (Photo: G.C.H.)

More specifically, the paper (1) considers the possible length of delays in the start of domestication due to early crops of wild-type cereals lacking domestic-type mutants; (2) examines the combination of primitive husbandry practices that would have been necessary for any selective advantage to have been unconsciously conferred on these mutants; (3) considers the state of ripeness (at harvest) necessary for crops to be able to respond to these selective pressures; (4) outlines field measurements of the selective intensities (selection coefficients) which arise when analogous husbandry practices are applied experimentally to living wild-type crops; (5) summarizes the essential features of a mathematical model which incorporates these measurements of selection coefficients and other key variables, and which describes the rate of increase in domestic-type mutants that would have occurred in early populations of wild-type cereal crops under specific combinations of primitive husbandry practices; (6) considers why very early cultivators should have used that combination of husbandry methods which, we suggest, unconsciously brought about the domestication of these wild cereals; and (7) concludes by considering whether these events are likely to have left recognizable traces in archaeological remains.

The field measurements of selection coefficient used crops of wild-type einkorn, and the mathematical model also uses this species. However, Daniel Zohary (personal communication, 1988) has stressed that our results are equally valid for emmer wheat and barley, as the wild types of all three have parallel wild adaptations, and have closely similar pollination systems, 'domestication syndrome', and early prehistory. On his advice, therefore, we have extended the terms of reference of our paper to include all three of the Near Eastern 'founder crops'.

DEFINITIONS OF DOMESTICATION

For the purpose of this paper, we adhere to the narrow, classical definition of domestication, rather than its all-embracing application advocated by Rindos (1984: 152–166, 1989). 'Domestication' is thus applied to that process which causes populations of cultivated plants to lose features (especially reproductive features) necessary for their survival in the wild in primary habitats; i.e. that process which renders crop populations dependent on human intervention for their reproduction. Such a process involves genotypic changes (which are only tardily reversible) in entire populations, rather than fully reversible (plastic) changes in the phenotypes of individual plants of the sort which apparently distinguish wild and cultivated forms of *Dioscorea* yams in Africa and which have recently been reproduced experimentally by Chikwendu & Okezie (1989).

DIFFERENCES BETWEEN WILD AND DOMESTIC FORMS OF WHEAT AND BARLEY

In cereals such as wheat, even the most primitive domesticated forms today differ from their wild progenitors in a number of polygenically determined grade characters such as awn robustness, glume rigidity, grain size, numbers of fertile florets, tillering tendency, uniformity of grain ripening, photosynthetic rate and the abundance of barbs and hairs on the rachis and glumes (see for example Darlington, 1963, 1969; De Wet, 1977; Evans, 1976; Hammer, 1984; Harlan, 1975; Heiser, 1988; Miller, 1986, in press; Percival, 1921; Schiemann, 1948; Schwanitz, 1966; Sharma & Waines, 1980; Zohary, 1969, 1984, 1989a, b, in press). However, all these authors note that the most critical adaptive differences involve loss of wild-type seed dormancy and rachis fragility, and, of these, only rachis fragility is readily apparent morphologically.

Differences in rachis fragility

In the wild wheats and barley, the mature rachis disarticulates between each of the fertile spikelets, thereby allowing them to be shed spontaneously. Disarticulation occurs from the top of the ear downwards (Fig. 3A). The arrow-like morphology of the spikelets with their smooth points, springy awns, long straight glumes and backward-pointing barbs and hairs thereafter ensures that they quickly penetrate any surface litter and wedge themselves in cracks in the ground where at least a proportion of them remain relatively safe from birds, rodents and seed-eating ants. In the Near East where wild wheats and barley are native, pressure from these predators is intense. By contrast, in even the most primitive of the *domesticated* wheats and barleys, the rachis fails to disarticulate spontaneously, and the ear remains intact until the crop is harvested and threshed (Fig. 3B). (Note—in domestic emmer and einkorn wheats, the relatively tough rachis nevertheless disarticulates when the ear is threshed, and it is therefore termed 'semi-tough'. However, this semi-tough rachis is not to be confused with the *fully* tough rachis of, for example, bread and macaroni wheats which remains intact when threshed, as it does in all the domestic barleys (see pp. 73–74 below).
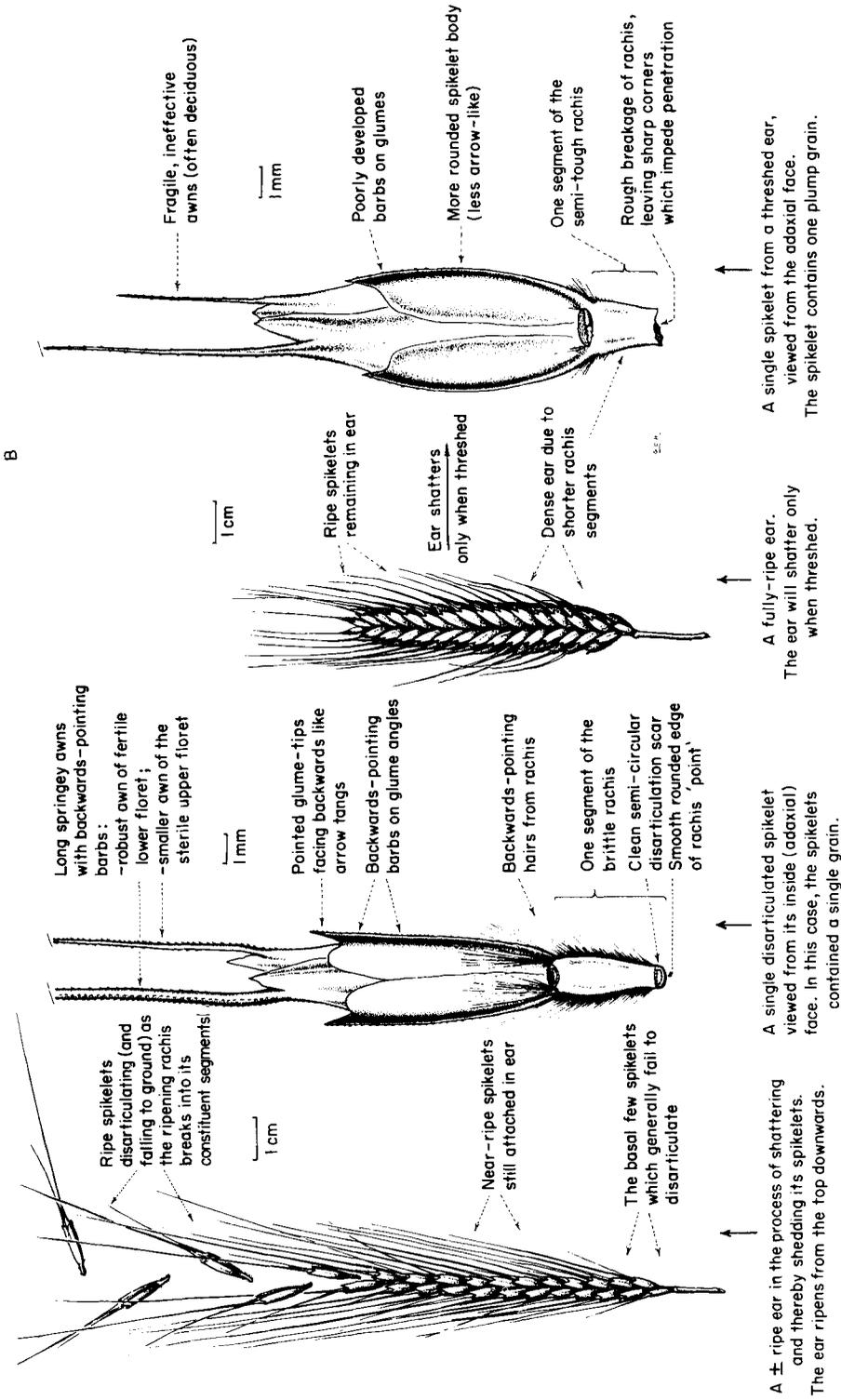
Figure 3. Diagrams showing the features affecting seed-dispersal and spikelet-implantation which distinguish the wild and domestic forms of einkorn wheat. A, Wild einkorn (*Triticum boeoticum*) showing brittle-rachised ear and arrow-shaped spikelets adapted for penetrating surface litter and cracks in the ground. B, Domestic einkorn (*T. monococcum*) showing semi-tough rachised ear and plumper spikelets which have lost some of the key features necessary for self-implantation. (Drawings: G.C.H.)

If sown in the wild, these domestic plants are unable to reproduce themselves, as their spikelets are not efficiently disseminated and protected from predation. Indeed, even if their ears were eventually to disintegrate in the autumn rains, the fact that their spikelets lack the self-implantation features of the wild types ensures that they will fail to bury themselves: the rough break in the rachis impedes penetration of the ground litter, the glumes lack the recurved hairs and prominent barbs, and the awns are weak and readily deciduous and so fail in their task of pointing the spikelet downwards through leaf litter (Fig. 3B). Such spikelets quickly fall prey to birds, rodents and ants, a fact that is evident from the complete absence in the Near East of feral domesticated cereals (*contra* the misleading suggestions in Jarman, 1972). This absence of feral cereals is the more significant in view of the widespread spillage of cereal grains and spikelets which regularly occurs along the waysides between field, threshing yard and granary. (For amounts lost, see ICARDA, 1980; BSTID *et al.*, 1981). Outside cultivation, therefore, the domestic mutant is doomed.

CHOICE OF DOMESTICATION CRITERION FOR THE PRESENT STUDY

Our measure of the 'degree of domestication' in our study populations was the ratio of plants with semi-tough rachises to plants with brittle rachises. The merits of using this criterion are as follows: (a) rachis fragility plays a crucial role in the process of domestication, as the tougher forms of rachis are lethal in the wild but are favoured under certain forms of cultivation; (b) the different states of rachis toughness are potentially recognizable in archaeological remains (see below); and (c) it is much easier to study in modern crop populations than characters such as seed dormancy.

However, this should not be taken to imply that use of rachis fragility is without problems as a criterion for recognizing domestication in archaeological remains, and some of these problems are discussed below. It should also be stressed that, in reality, domestication is a complex syndrome involving changes in many different features—of which rachis fragility is but one.

ARCHAEOLOGICAL EVIDENCE OF DOMESTICATION

Rachis remains

Rachis remains of cereals such as wheat, barley, rye and oats are quite commonly preserved on Iron Age and later archaeological sites. On most sites, they have resisted microbial decay only by virtue of having been charred by fire immediately prior to their deposition. When preservation is good, these rachis remains can often provide clear evidence of whether the cereal was either (1) of the wild type with a fully brittle rachis (as in wild einkorn and emmer), (2) of the domestic type with a *semi-tough* rachis (as in domestic einkorn and emmer) or (3) of the domestic type with a *fully* tough rachis (as in bread or macaroni wheats). Distinguishing states (1) and (2) can prove difficult, but, generally, disarticulation in wild cereals leaves a clean, semi-circular or reniform scar, while, in the semi-tough-rachised domestic derivatives, the scar is linear, jagged and irregular, with no clean abscission surface. Certainly, these two rachis fragility states in wheat are not as indistinguishable as implied by Kislev (in press

a), a point reinforced by the recent work of Willcox (in press). (Exceptions to this rule are discussed in Hillman & Davies, in press).

However, rachis remains of all types are remarkably rare on Old World archaeological sites dating from the earliest phases of the Aceramic Neolithic when cultivation was in its infancy. In consequence, archaeobotanists generally attempt to distinguish wild wheats and barleys from their domestic derivatives using secondary features such as grain shape. In the wheats, these grain features are often unsatisfactory, although in the barleys they can perform a useful role in distinguishing six-rowed and naked domesticates from the wild type.

Present chronology of remains of domestication

On the basis of these often problematic grain-based characteristics, the earliest appearance of seemingly fully domesticated cereals in western Eurasia is currently dated to c. 8800 BC (= c. 7800 BC in radiocarbon years) at Neolithic Aswad in south-west Syria, and fractionally later at Jericho, Gilgal and Netiv Hagdud in Palestine, the Neolithic site at Abu Hureyra in northern Syria, and slightly later again at Çayönü in south-east Turkey and Ali Kosh in Iran. In each case, the cereals identified were emmer wheat and barley, except at Neolithic Abu Hureyra and Çayönü where einkorn was also found (Bar-Yosef & Kislev, 1989; Helbaek, 1969; Hillman, 1975; Hillman, Colledge & Harris, 1989; Hopf, 1983; Kislev, in press b—as cited by Zohary (1989b); Kislev, Bar-Yosef & Gopher, 1986; van Zeist 1972; van Zeist & Bakker-Heeres, 1979). Of these sites, only Netiv Hagdud and Neolithic Abu Hureyra produced useful quantities of rachis remains.

Dating the start of cultivation (rather than domestication)

Such finds do not necessarily date the beginnings of cultivation; they merely date the completion of the ensuing process of domestication. If we are to date the beginnings of *cultivation*, we must take the earliest date for the emergence of ostensibly domesticated forms (currently c. 8800 BC—calibrated) and add to it that block of time required to achieve full domestication once the crop was under cultivation. This we have termed the period of 'pre-domestication cultivation'. However, not all forms of primitive husbandry act to the advantage of tougher-rachised forms (see below), and it is therefore possible that many of the earliest farmers would have applied practices of this 'ineffective' type for an indefinite period of 'non-domestication cultivation' before eventually adopting those techniques of 'pre-domestication cultivation' which inexorably led to domestication.

This potentially long delay would have been preceded by an additional delay (i.e. more 'non-domestication cultivation') due to the absence of semi-tough-rachised mutants in the first crop populations (see Zohary, in press b). However, this preliminary delay is likely to have been very short in most cases (see below).

To date the beginnings of even 'pre-domestication cultivation', we therefore need to know (a) precisely which combination of husbandry methods would have effected domestication in a wild-type crop (including the state of maturity at which it had to be harvested); (b) whether other forms of husbandry would have been completely ineffective in this role; (c) whether the initial husbandry

methods used by the first farmers were most likely to have been the 'ineffective' ones, and, if so, how quickly they would have swapped over to the 'effective' methods; and (d) how long the process would have taken once the effective methods were applied. All four questions are addressed below.

THE RAW MATERIALS OF DOMESTICATION

The domestic forms of einkorn, emmer and barley originated from semi-tough-rachised recessive mutants produced in (and still being produced in) populations of brittle-rachised wild forms. In these wild populations, the mutants are very rare because (a) the nett forward mutation rate (per plant generation) of such genes is likely to have been low (we have assumed a nett forward mutation rate of 10^{-6} per generation), (b) the mutant (semi-tough rachis) allele is recessive to the wild-type (brittle rachis) allele and is consequently manifested only in the homozygous state, and (c) the mutation pressure is balanced by rapid elimination of these homozygous recessive individuals which have zero adaptive value in the wild. Indeed, if we take einkorn as our example, and if we assume (as do Sharma & Waines, 1980: 215) that, of the two loci they identified controlling rachis fragility, only one was initially involved in domestication (see below), then large wild stands of this essentially inbreeding species will contain only one homozygous individual (producing semi-tough-rachised ears) for every two to four million brittle-rachised individuals.

As for the concentration of additional mutant alleles carried (unmanifested) in brittle rachised heterozygotes, this, too, will be low. Because einkorn is an inbreeder and because homozygous recessives are non-viable in the wild, half the recessive alleles are eliminated in each generation: the wild types will consequently be almost entirely homozygous with, nominally, only one or two heterozygotes per two to four million brittle-rachised types (but see 'computer model', below).

However, these estimates are no more than a convenient simplification. Not only was more than one locus eventually involved, but modifier genes could have altered patterns of dominance at these loci during the past eleven millennia (see below). Nevertheless, the estimates are adequate for the purpose of the provisional mathematical model presented in this paper, particularly as we use a very broad range of values for each variable.

THE START OF CULTIVATION

We must next consider what would have happened to these rare semi-tough-rachised mutants, when, sometime around the end of the Pleistocene, groups which had hitherto lived primarily by hunting and gathering took seed from wild stands of brittle-rachised wheat or barley and sowed them on cleared land elsewhere.

It is clear that, in view of the very low frequencies of the mutants in wild populations, it is improbable that no mutants were present in the initial stocks of seed corn gathered from wild stands (Zohary, personal communication, 1988). The vast majority (maybe all) of the first crops would therefore have lacked the mutant and been entirely of the brittle-rachised type. Any selection for domesticates therefore had to wait until the mutants were generated

spontaneously within the early crops themselves. Domestication can therefore be seen to have involved two distinct stages (as advised by Zohary, personal comunication, 1988).

(a) The first (preliminary) phase involved 'non-domestication cultivation' of purely brittle-rachised populations, and will have continued until such time as semi-tough-rachised mutants were generated. The length of this phase depended on the size of the crop population, and in most cases is likely to have been very short.

(b) The second phase began with the appearance of the first mutant phenotypes (initially at very low frequencies), and its duration will have been largely independent of crop population size. This second phase would have followed one of two pathways. (1) If husbandry methods were of a type which selectively advantaged the mutant phenotypes, then a period of 'predomestication cultivation' would have automatically culminated in full domestication of the crop. (2) If, however, the husbandry methods *disadvantaged* the mutants, then the crop would have remained in its wild state indefinitely (as a continuation of 'non-domestication cultivation') until finally replaced by domesticated seed-stocks obtained from elsewhere.

THE PRELIMINARY PHASE: DELAY IN DOMESTICATION DUE TO ABSENCE OF MUTANTS IN THE FIRST CROPS

As noted above, the time required for semi-tough-rachised mutants to be generated spontaneously within the initial wild-type crop populations will have depended on the size of the crop populations: in large populations, it would have happened almost immediately; in small populations, it would have taken longer, and any possibility of domestication would then have been delayed for some years. In both cases, however, we are dealing only with probabilities, and there will have been exceptions.

So, just how big an area of cereals were the first farmers likely to have sown, and just how long would the resulting pre-domestication delay have been? Sadly, the degree of initial dependence on cultivated grain foods amongst the first farmers (and the areas they consequently needed to sow) remains unknown. It is, nevertheless, clear from the range of possibilities considered below that the areas sown were likely to have been sufficiently large to ensure that the mutant became available within less than 20 years in most of the early crops of wheat and barley.

Table 1 presents estimates of the areas that might have been sown to provide a modest 25% of the total calorie needs of each nuclear family of five. There is no agreed figure for the likely grain yields per unit area or for calorie yields from consumed grain, and we have, therefore, used two levels of each. The assumption that cereals provided 25% of calorie needs is not unreasonable if the shift from foraging to farming was, indeed, prompted by population pressure—as most modellers propose (cf. Binford, 1968; Cohen, 1977; Flannery, 1969; Harris, 1977; Hillman, 1987). On this basis, the areas under cultivation could have ranged from 0.3 to 3 hectares. (A hectare plot is 100×100 m, or c. 2.5 acres). If, however, cultivated grain foods provided only 1/10 of their calorie needs, then the sown areas could have ranged from 0.1 to 1.2 hectares.

TABLE 1. Size of early crop populations—as basis for estimating the time required for the emergence of domestic mutants in the first wild-type cereal crops. The Table suggests the hectarage of wild-type cereals likely to have been sown (by the first farmers) for each nuclear family of five, assuming that grain from cultivated cereals provided a modest 25% of their calorie requirements

	Grain needs of family of five per year (to provide 25% of total calorie requirements) (kg)	Areas sown to provide grain sufficient for 25% of calorie needs of nuclear family of five (ha)	
		Assuming yields of 5000 kg per ha[c]	Assuming yields of 1000 kg per ha[d]
Calculations based on 25% of 'economic grain equivalent' consumed by present-day subsistence farmers of Near East[a]	700	1.4	2.8
Calculations based on (i) 25% of minimum caloric need of modern humans; (ii) laboratory measurements of calorie content of modern wheat grain[b]	330	0.75	0.4

[a] Clark & Haswell (1967) cite consumption of mean 'economic grain equivalent' (i.e. the economic equivalent of total dependence on grain) of 650 kg/adult/year. Such a figure allows for incomplete digestion/absorption of grain foods and for consumption in excess of theoretical minimum energy needs, but it is nevertheless, well below the levels observed in recent Anatolian villages practising traditional forms of subsistence (Hillman, 1973).

[b] Calorie needs of humans are based on 'standard nutritional unit' of 10^6 kcal/adult/year. The laboratory measurements of calorie yield of whole wheat flour used here $= c.$ 330 kcal/100 g (at 12% moisture). (Both figures are taken from Legge, 1989).

[c] 500 kg ha^{-1} accords with the lowest returns from wild or primitive domestic cereals (see, e.g. Hillman, 1973; Russell, 1988; Willcox, in press; Zohary, 1969).

[d] 1000 kg ha^{-1} exceeds Zohary's (1969) top figures for wild emmer in primary habitats, but is well below some of Willcox's (in press) top figures for wild einkorn under primitive cultivation.

However, it is generally considered that there is little point in going to the considerable trouble of cultivating staple sources of carbohydrate unless they meet a major part of total calorie needs. (This contrasts with the situation for other food crops such as pulses.) The smaller areas suggested above are therefore rather improbable. Furthermore, all the above estimates assume separate cultivation by each family of five. Not only does this ignore other dependents, but the collaborative subsistance strategies of most recent hunter-gatherers suggests that the earliest attempts at cultivating staples probably involved whole bands working jointly. The collective crops of each band would clearly have occupied areas much larger than those in Table 1.

It was noted above that, given a mutation rate of 10^{-6}, one homozygous mutant plant can be expected in every two to four million of the brittle-rachised wild type. At a modest sowing rate of $c.\,200$ spikelets per m^2, therefore, such a mutation could be expected to appear (in a single growing season) in a cultivated area of no larger than 1–2 hectares. All the areas cited above (needed to provide just 25% of the calorie need of mere nuclear families) would have allowed mutants to be generated within just five years, and in inbreeders such as wheat and barley, the homozygous recessive would appear one year later. With the areas likely to have been collectively cultivated by whole bands, the mutants probably appeared in just two years.

Even if the sown areas were as small as, say, 1/10 hectare (a plot of roughly 30×30 m), the mutant form is likely to have appeared in 10–20 years. Potentially longer delays from cultivating yet smaller plots would probably have been cut short by the farmers obtaining domestic seed stocks from bands in whose crops the process of domestication started almost immediately.

For the majority of early cultivators, therefore, the constraints of crop population size and mutant availability are unlikely to have delayed the start of domestication to a degree which we can now detect archaeologically.

CONSCIOUS OR UNCONSCIOUS SELECTION?

All the available evidence would suggest that, in the early stages of cultivation, selection favouring semi-tough-rachised mutants was entirely unconscious (i.e. unintentional). Indeed, estimates of the frequency of homozygous recessives cited above suggest that farmers gathering their first seed stocks from wild stands will have been totally unaware of the existence of these tough-rachised mutant forms, and that they would have remained oblivious of them for as long as the crop stayed in its essentially wild-type state. The reasons are as follows. (a) The mutants forms were extremely rare (see above). (b) In cereals such as wild einkorn, the ears ripen very unevenly (both within and between plants) such that mutant ears will have looked no different from the thousands of ears which had not yet shattered because they were still slightly unripe. (c) Any ears which remained intact in the field after all the others had shattered would have been rapidly predated by birds because they are much more readily available if still attached to the top of a culm. The mutants could not therefore have been picked out by simply waiting until the end of the spikelet-shedding season.

There would therefore have been no real possibility of conscious selection during either 'non-domestication cultivation' or the early stages of 'pre-

domestication cultivation'. Only once the frequency of semi-tough-rachised mutants had risen to a level at which they were obvious in the crop stand (perhaps around the 1–5% level) is conscious selection likely to have been applied (see below and Fig. 8).

Similar arguments also allow us to dismiss the 'thunderstorm theory'. This theory proposes that, in wild stands of cereals or in early wild-type crops, passing thunderstorms would have shattered all the brittle ears, leaving only the rare, semi-tough-rachised ears as the source of seed for next year's crop. A fully domesticated crop would thus have been generated in just one year—with or without conscious awareness on the part of the farmers. However, the uneven ripening of einkorn ears, coupled with rapid predation of isolated tough-rachised ears, renders such a scenario highly improbable.

Our conclusion that unconscious selection was involved in at least the early stages of domestication accords with conventional wisdom on the matter. Unconscious selection in early crops was first proposed by Darwin (1859, 1868), and its nature and possible consequences were subsequently explored by Vavilov (1926), Darlington (1963, 1969), Ladizinsky (1987), Zohary (1969, 1984, 1989b, in press), Harlan et al. (1973), Harlan (1975), and Rindos (1984), and were recently reviewed by Heiser (1988).

THE HUSBANDRY SYSTEMS NECESSARY FOR DOMESTICATION

The next question must be: did this unconscious selection occur automatically at each and all the early settlements cultivating wild-type cereals? Our studies suggest not: the semi-tough-rachised homozygotes would have experienced a positive selective advantage only under specific conditions.

Assuming unconscious selection, evidence presented below suggests that semi-tough-rachised homozygotes would have been selectively advantaged in crops of wild-type wheat or barley only if (a) particular harvesting methods were used (cf. Wilke et al., 1972); and (b) the crops were harvested when partially ripe or 'near-ripe'. In some cases, there would have been two additional pre-requisites, namely (c) annual extensions or shifts in the areas under cultivation; and (d) each year's seed corn to be drawn from the harvests of the previous season's new plots.

In theory, these husbandry methods would not necessarily have been the most efficient nor the most familiar (from their hunter-gatherer backgrounds). Theoretically, therefore, the cereals of many of the earliest farmers could have continued in their wild-type, brittle-rachised state for a long time until they were eventually replaced by domesticated forms brought in as seed-corn from other farming settlements where the effective (domestication-inducing) combination of husbandry techniques had been applied (cf. Hillman 1978: 167).

Terms used to describe states of ripeness

A 'fully ripe' crop of a wild-type cereal is one in which the spikelets have all been shed, and 'harvesting' then involves picking them up from the ground. The traditional methods considered below (beating, reaping, uprooting, etc.) can thus be applied only to (a) partially- or near-ripe crops (in which disarticulation has begun but is still incomplete), or (b) to completely unripe crops (in which no

spikelets have yet started disarticulating). Because wild einkorn ripens very unevenly, the terms 'partially-' and 'near-ripe' necessarily refer to the *average* state of the crop as a whole. (Note—the 'completely unripe' category used here refers strictly to rachis ripeness, rather than ripeness of the grains, and it includes both the 'green' and 'half-green' categories used by Willcox, in press.)

Harvesting methods and the state of crop maturity at harvest

Our evidence indicates that, of the range of harvesting methods available, domestication would have occurred only if the crops were harvested while partially ripe or near ripe, by means of sickle reaping or uprooting.

There are five main harvesting methods with which the earliest cereal cultivators are likely to have been familiar from their earlier experience as foragers. These methods will have included *beating* ripe spikelets into baskets—applied to partially- or near-ripe stands in either a single pass or in multiple passes (though never, of course, to completely unripe stands); *reaping* with sickles or other cutting implements—whether on near-ripe crops or on unripe ones; *uprooting*—likewise on near-ripe or unripe ears; *plucking* or *hand-stripping*; and harvesting by *burning*. The viability of each of these methods is attested by ethnographic studies of recent wild grass-seed foragers—whether hunter-gatherers or farmers supplementing their harvests of domestic grains, by archaeological evidence, by our own field experiments, by the field observations of agricultural botanists such as Harlan (1989, in press) and Zohary (in press), and by experiments at archaeo-agricultural research establishments such as Butser Ancient Farm (see Reynolds, 1981, in press), and the Jalés-based Institut de Préhistoire Orientale (see Willcox, in press & Anderson-Gerfaud, in press).

(i) Harvesting by beating the ripe spikelets into baskets

Beating the ears such that all ripe spikelets are knocked into a basket can be very quick and efficient, and it involves the least stooping. Applied to partially- or near-ripe wild wheats or barley, beating automatically harvests the spikelets from ripe brittle-rachised ears, but leaves behind any tough-rachised ears together with large numbers of unripe ears of the brittle type. (The latter—or a proportion of them—can be harvested a few days later in subsequent rounds of beating.) Tough-rachised ears left behind after the harvest are stripped by birds, and even if their spikelets were to fall to the ground, their almost complete failure to penetrate ground litter and self-implant ensures their predation by rodents, birds and ants. In consequence, they do not contribute to the ensuing generations of crops, even when the same patch is cultivated next season.

Some spikelets from brittle-rachised ears invariably fall to the ground during harvest, and if the farmer relies on these to seed next year's crop, this will inevitably be of the wild type. Likewise, new plots sown from the harvested seed will be entirely of the wild type. Harvesting by beating thus selects strongly in favour of the wild type and against tough-rachised forms—regardless of what other husbandry practices accompany it.

Harvesting by beating was the method we found the least effort and also produced the greatest yields per unit time whenever we harvested wild-type einkorn in dry weather. Correspondingly, after trying many different methods on a wide range of grasses in four continents, Harlan (in press) notes:

"of the traditional gathering techniques, the beater and basket method produced the cleanest and most uniform material. . . . Having used both sickle and beater, I had to wonder why the sickle was ever preferred to the beater". It comes as no surprise, therefore, to find that beating was the method favoured by the majority of those recent hunter-gatherers who were heavily dependent on wild grass seed (see literature review in Hillman & Davies, in press).

(ii) Sickle-reaping applied to partially ripe crops (see Fig. 4)

This method can select strongly in favour of tough-rachised forms. However, in some cases this selection will occur only if the grain is sown on new plots of land each year using 'seed-corn' from last year's new plots.

When a sickle is applied to the culms of wild wheats and barley, some spikelets from the top (ripest) parts of the most mature ears promptly disarticulate and fall to the ground. No equivalent loss is experienced by the semi-tough-rachised ears, and their percentage representation in the harvested spikelets is therefore greater than it was in the parent field. Crops sown from the harvested grain will reflect this increased proportion of tough-rachised forms, and this increase will continue, year on year, for as long as crops are always sown on new land from harvests taken from the previous year's new plot(s). Eventually, the crop will be composed entirely of tough-rachised forms, and at this point, domestication (in respect of the fixation of semi-tough rachis) is complete.

By contrast, those plots cultivated in previous years will maintain crops of exclusively wild types because they are self-sown by spikelets shed from brittle-rachised ears during the previous season's harvest. Clearly, then, seed-corn taken from this old land and sown on virgin plots would reverse the process of domestication. (The effect of sowing additional harvested grain (containing mutants) on these old plots is considered below.)

(iii) Sickle-reaping applied to unripe crops

(1) Applied to *completely* unripe (green) stands, this method would have had no selective effect either way: potentially brittle rachises fail to disarticulate while still unripe (unless dried), so both types get harvested in the same proportions in which they are represented in the field. Fields sown from the harvested spikelets will thence produce the same proportions of either type as in the previous year.

(2) However, if the crop is even fractionally ripe, there will be some loss of spikelets from the tops of some brittle-rachised ears, and the semi-tough-rachised phenotype will thus be selectively favoured. In view of the uneven ripening of einkorn, this effect will be avoided only in *very* unripe crops, and this is rare, because such crops produce shrivelled, unfilled (and therefore underweight) grain. In practice, therefore, 'unripe' generally means 'partially ripe', and sickle reaping applied to such crops will still selectively advantage domesticates, albeit at lower intensities (see below).

Harvesting wild cereals and other grasses in a partially (or fully) unripe state offers the clear advantage of pre-empting most of the loss of spikelets from brittle-rachised ears which otherwise occurs during harvesting. This is especially so in species which ripen more evenly, such as wild emmer (*T. dicoccoides*), in which Unger-Hamilton (1989) found that potential loss of spikelets was almost completely pre-empted by reaping it while it was still 'green' (cf. also Anderson-Gerfaud, in press; Willcox, in press).

Figure 4. Harvesting trial plots of wild-type einkorn with a flint-bladed sickle (in this case, of the Natufian type) at the Cleppa Park facilities of the Department of Plant Science, University College, Cardiff in 1979. (Photo: Isobel Ellis.)

However, we know of only two cases of sickle-reaping of unripe wild grasses amongst recent hunter-gatherers: the first is the Kawaiisu harvest of *Oryzopsis* in southern California (Zigman 1941: 142, as cited by Bohrer 1972: 147); the second is Allen's (1974: 314) citation of an Aboriginal people of SW Queensland (Australia) using flint knives to cut a wild millet—presumably in the partially unripe state in both cases, in order to avoid losses from shattering. In reviewing the Australian evidence for grass-seed harvesting, Harris (1984: 65) also notes that Allen's example is the only case of blade harvesting known to him.

Figure 5. Children harvesting barley by uprooting; near Gölü Dağ in central Turkey, 1974. Until very recently, barley was generally harvested by uprooting, whether with bare-hands or with the help of an uprooting hook (Turkish: *kılıç*) (cf. Hillman, 1984, 1985). (Photo: G.C.H.)

(iv) Harvesting partially ripe wild-type crops by uprooting (see Fig. 5)

This method shakes the ears in a manner similar to sickle-reaping, and the resulting loss of spikelets from the ripe tops of near-ripe brittle-rachised ears selects for tough-rachised mutants exactly as described in (ii) above. Once again, however, this selective effect can be guaranteed in all cases only if the seed corn is always (a) taken from grain from last year's new crops, and (b) sown on new land each year.

(v) Uprooting completely unripe crops

Applied to *completely* unripe crops, this harvesting method, like the sickle-reaping (of completely unripe crops), has no selective effect either way (see (iii) above) but, again, offers the advantage of sweeter grain and pre-empting grain loss during harvest. However, if the crop is even *fractionally* ripe, some positive selection for the semi-tough-rachised phenotype will occur, as above. Harvesting unripe grasses by uprooting has been recorded for a number of different Aboriginal peoples of Australia; e.g. Mitchell in 1835 (as cited by Allen, 1974: 313–4) observed it being applied on a massive scale in the Darling River valley.

(vi) Harvesting by hand-plucking or stripping

'Hand-stripping' was apparently used by a number of hunter-gatherer groups for harvesting the seed of paniculate grasses (see e.g. O'Connell, Latz & Barnett, 1983). We have found that loose-handed stripping of the ripe, disarticulating spikelets (leaving behind the lower part of the ear) works like an inefficient form of beating—with similar selective effects (see (i) above). However, it is very slow

compared with beating, and seems unlikely to have been used on any scale for wild cereals in prehistory. (For a different view, see Anderson-Gerfaud, 1988.)

(vii) Harvesting ripe or unripe crops with the aid of fire

The crop can simply be fired and the singed spikelets (or ears) thereafter gathered from the ground. However, there is no selective effect in either direction as the grain is killed by the parching, and the seed for subsequent crop generations has to be harvested from separate plots by one of the other methods.

(viii) Summary of harvesting methods

Of the range of harvesting methods that would have been available to the first farmers, the only ones which would have induced domestication were sickle reaping and uprooting applied when the crops were partially- or near-ripe. Although these methods were relatively unpopular amongst recent hunter-gatherers exploiting wild-grass seed, there would have been good reasons for their use amongst some of the first farmers (see below, pp. 69–72).

WAS SHIFTING CULTIVATION NECESSARY FOR DOMESTICATION?

Existing evidence is equivocal but suggests that, while annual shifts to virgin land using seed corn from last year's new plots may sometimes have been supplementary pre-requisites for domestication, in most cases domestication could probably have occurred without them.

Only a small proportion of the harvested spikelets are needed as seed corn for sowing next year's crop. As a result, only a small proportion of the harvested domestic-type mutant spikelets finally get sown. In crops regularly re-sown on old plots, the correspondingly reduced number of domestic mutants (present in the seed corn) could possibly get 'swamped' by the self-sown wild-type spikelets shed spontaneously during the preceding harvest. On any re-used plots where this 'swamping' occurs, domestication clearly cannot proceed. Domestication at such settlements will then occur only if the farmer annually extends cultivation onto virgin land using seed corn harvested from last year's new plots, as such a strategy automatically avoids the self-sown wild-type spikelets from the old plots ever contributing to subsequent crop generations.

However, this 'swamping' effect assumes that large numbers of the spontaneously-shed wild-type spikelets survive ant and rodent predation between harvest and autumn sowing. If, conversely, the proportion of harvested spikelets sown on old plots by the farmer (say 12%) is greater than the proportion of spontaneously shed spikelets which survive predation between harvest time and sowing (say 10%), then domestication could still occur—assuming the method used to select the seed corn from the harvested grain either maintains or increases the relative abundance of mutants in the seed corn, compared with their abundance in the bulk of harvested grain.

The determining factors are therefore as follows: (a) the % survival of the wild-type spikelets (from fully brittle ears) which fall to the ground during harvesting by sickle or uprooting; (b) the % of the harvested grain set aside as seed corn for sowing next year's crop: this will correspond to the yield ratio anticipated by the farmer ('yield ratio' = grain yield per unit of grain sown); and (c) the method used for selecting the grain for sowing.

Factor (a). Zohary (personal communication, 1988) notes that "from the time of harvesting to the time of the next planting, those seeds that evaded the reaper and got spread [spontaneously] in the field ... are exposed to strong predation by ants, rodents, etc. I estimate that, under Near Eastern conditions, at least 50–80% of these wild-type seeds will be eliminated". However, this is for wild stands. On tilled ground Zohary (personal communication, 1989) suggests that the shed spikelets are less protected from predation, and as many as 90% of them might be lost.

Factor (b). Yield ratios observed (e.g. by Hillman, 1973) in traditional, rain-fed wheat and barley cultivation in eastern Turkey fall in the range 1 : 6.5–1 : 9. In such cases, therefore, the farmers set aside c. 11–17% (c. 1/6 to 1/9) of their harvested grain for resowing. However, in the first two years of his experimental cultivation of wild einkorn, Willcox (in press) obtained yield ratios ranging from 1 : 2 to 1 : 33. Differences of this order clearly argue against using any one value in the present calculations. Nevertheless, it is clear that most of Hillman's values and half of Willcox's values would allow farmers to use a smaller proportion of the harvested grain as seed corn than the 20–50% survival of spontaneously shed wild-type spikelets estimated by Zohary for wild stands. However, if we use Zohary's "off the cuff" estimate of just 10% survival of spikelets shed from wild-type plants growing on cultivated ground, then there is substantial overlap between the two sets of figures. On the basis of this spread of values, therefore, re-use of old plots which are already partially self-sown with spontaneously shed wild-type spikelets could have either permitted domestication or prevented it.

Factor (c). It is impossible to know whether the first farmers' methods of selecting seed corn from harvested spikelets would have increased or decreased the proportion of mutants, and no estimates are offered here.

From the above, it is clear that, at one end of the spectrum of possibilities, re-use of old plots could have precluded all possibility of domestication. Under such conditions, domestication would have occurred only if harvesting with sickles or by uprooting was combined with annual shifts to virgin land using seed corn from last year's new plots. At the other end of the spectrum of possibilities, domestication could have occurred even if the farmers consistently re-used old plots. Zohary has now convinced us that the latter scenario is more probable. However, as noted by Zohary (personal communication, 1988), in this latter case, domestication will have proceeded more slowly than under a system of annual shifts to virgin land.

HOW RAPIDLY WILL DOMESTICATION HAVE OCCURRED (ONCE THE MUTANT PHENOTYPE WAS PRESENT IN THE CROP)?

To produce a mathematical model of domestication rate (i.e. the rate of increase in semi-tough-rachised mutants in wild-type crops under primitive cultivation), we needed measurements of (a) mutation rates at the relevant loci, (b) rates of inbreeding/outbreeding in wild einkorn wheat, and (c) the selection coefficients which arise from those husbandry methods capable of inducing domestication at all.

Reliable estimates exist for the first two factors (see below), but not for selection coefficient. In initiating this study in the early 1970s, therefore, our primary objective was to measure the selection pressures which can result from

combinations of primitive husbandry of the sort likely to have been applied by the first farmers, as outlined above.

Preliminary measurements of selection coefficient

Selection pressure can be affected by several factors. We nevertheless limited our field measurements to selective pressures generated by the different methods of *harvesting*, because, (a) harvesting method is the primary factor determining selective pressure in all systems, (b) it can produce a wide range of different selection values, and (c) these values are easily measured by field experiment. In contrast, annual shifts in cultivation (where these are necessary for domestication) generally either permit domestication or prevent it altogether, and even though different rates of re-sowing old plots could theoretically produce a range of different values for selection coefficient, we were not in a position to measure them.

After exploratory harvesting in earlier years (during which we were able to eliminate the most unworkable methods), a preliminary set of simple harvesting trials were undertaken in 1974 in relatively dense stands of near-ripe wild einkorn growing in primary habitats in both the Munzur Mountains (near Çemişgezek) in East Turkey and on Karadağ (near Karaman) in Central Turkey. Four areas of wild stands in either area were simply divided into a series of 1 m squares, and the different harvesting techniques were applied to a scatter of these squares. In each square, counts were made of the numbers of spikelets harvested and the numbers lost on the ground. In this way, a measure was obtained of the relative fitness of the brittle-rachised phenotype under each harvesting regime. (In this case, therefore, fitness provides a measure of the probability that the seed would contribute to the next generation as a result of being incorporated into the harvest from which next year's 'seed corn' is to be taken.) To obtain a rough measure of the fitness of the *semi-tough-rachised* phenotype, it was necessary to compromise and use a cultivated glume wheat. (Semi-tough-rachised phenotypes are too rare in wild stands to be measureable.)

One of the harvesting treatments (treatment 1) involved beating applied repeatedly to the same plots. The first of these 'passes' was timed to coincide with disarticulation of the tops of the earliest ears, and the last with the point when only the bottom third of the spikelets survived·on last ears to ripen. In order to avoid trampling, this treatment was applied to isolated metre squares. In reality, however, early farmers would not have enjoyed this luxury, and trampling would have produced losses which are not reflected in the present result for this 'repeated passes' treatment.

In these preliminary trials, no attempt was made to measure fitness in totally unripe plants in which disarticulation had yet to begin. Exploratory harvestings had suggested that the failure of completely unripe brittle-rachised ears to disarticulate pre-empted any possibility of positive selection for the tough-rachised phenotype. Thus, no form of harvesting applied to *totally* unripe crops could lead to domestication, and there seemed little point in including such treatments in the hastily assembled preliminary trials.

The results of the preliminary measurements of relative fitness appear in Table 2. The most notable features of the results were as follows. (a) The brittle-rachised phenotype showed intermediate levels of fitness under each of the

TABLE 2. Preliminary measurements of the relative fitness of two rachis-fragility phenotypes present in populations of wild-type einkorn wheat under the four principal harvesting methods available to early cultivators. In this case, the 'fitness' of either phenotype represents the probability of its being harvested and thereby contributing to ensuing generations via 'seed corn' taken from harvested spikelets

Harvesting treatments		% of available spikelets harvested within either phenotype		Relative fitness of either phenotype		Total no. of wild-type spikelets counted in col. iii
		Wild type	Tough-eared type	Wild-type	Tough-eared type	
1. Beating—repeated passes	a	84%	c. 5% (1–10%)	0.84	c. 0.05	1280
2. Beating—single pass	a	30				990
Beating—single pass	b	48	c. 5% (1–10%)	0.44	c. 0.05	1100
Beating—single pass	c	45				1340
Beating—single pass	mean	44%				Total 2330
3. Reaping with sickles	a	35				1050
Reaping with sickles	b	43	100%	0.40	1	1520
Reaping with sickles	c	43				860
	mean	40%				3430
4. Uprooting	a	41				2300
Uprooting	b	37	100%	0.43	1	1240
Uprooting	c	51				1310
	mean	43%				4850

harvesting treatments 2, 3 & 4, and (remarkably) the values were almost the same for each (40%, 43% and 44% respectively). The exception was a very high fitness of 80% obtained when harvesting by beating was applied in a series of 'passes' (but see preceding two paragraphs). (b) In contrast, ripe, semi-tough-rachised plants (the domestic type) showed a high fitness (tending to 100%) when harvested with sickles or by uprooting, but a correspondingly low fitness when harvested by beating. (Selection coefficient against each type under the various harvesting treatments can be calculated as 1-fitness.)

A fitness of around 40% for brittle-rachised plants in three of the treatments accords with the recent estimate from Harlan (in press) for recovery rates when harvesting wild grasses: he observed "I estimate that no [harvesting] method will recover more than half of the potential production". Nevertheless, substantially different values could be expected with different degrees of average ripeness. The extreme fitness values for the semi-tough-rachised (domestic) plants were as expected, and more rigorous measurement would probably have produced the same 'all-or-nothing' result.

However, it was never intended that the results of these preliminary trials should be used statistically: the trials were badly designed from the statistical viewpoint, and a metal (rather than flint-bladed) sickle had been used. The trials were therefore repeated on a much larger scale using sown populations under controlled conditions with properly randomized treatments (using a split-plot design) and with more ample replication. Brittle-rachised wild einkorn (collected in the Munzur Mts.—coll. no. GCH 3177) was sown with a controlled admixture of the domestic type at a rate of c. 200 spikelets per m² in a field at the Cleppa Park facilities of the University of Wales College of Cardiff. This time, we used flint-bladed sickles of three types: the Fayum type, a Natufian type and a British Neolithic single-piece sickle. We found the Fayum type by far the most efficient. The first year's trial was ruined by a spring drought followed by an extremely wet summer. The crop grew (eventually), but the wet conditions at harvest-time prevented the ears from disarticulating in the 'beating' treatment. Despite this, many of the reaped ears disarticulated as soon as the sheaves were placed in a heated room.

In the following year, an identical crop was sown under glass. However, we sowed too late and, although the *domestic* type came into ear, the wild type merely formed grassy tussocks lacking ears. Ears would presumably have developed in the second year of growth had we left the tussocks to grow on. In the absence of further opportunities to re-run the trials, it was decided to use the preliminary data from the earlier trials in Turkey—albeit merely as a means of obtaining provisional estimates.

THE COMPUTER SIMULATION OF DOMESTICATION RATE

The purpose of recording fitness as outlined above was to provide measurements for a computer model that would simulate the increase in frequency of the semi-tough-rachised (domestic) phenotype in otherwise brittle-rachised (wild type) crops under primitive systems of husbandry. However, such a simulation also required measurements (or estimates) or two other determining factors: firstly, the frequency of selfing or outcrossing; secondly, the frequency of the semi-tough-rachised allele in the crop population at generation 0, i.e. at the

start of cultivation (see pp. 48–51 above). The working assumptions of the computer simulation were as follows.

(a) *Husbandry methods.* The simulation necessarily assumes that the husbandry methods used were those capable of selecting for semi-tough-rachised phenotypes in a brittle-rachised einkorn crop, namely harvesting when partially ripe by sickle-reaping or uprooting (combined, if necessary, with sowing on virgin plots every year with seed-corn taken from the previous year's new plot(s)). Using the fitness values generated by other methods (for example harvesting by beating) merely produces a situation of zero change, with the crop remaining brittle rachised indefinitely. We took no account of the lower selective intensities which could result from resowing old plots (in cases where this would not altogether prevent domestication) as no reliable measurements were available.

(b) *Fitness levels.* In running the simulation, we used the levels of fitness observed with sickle reaping and uprooting in the preliminary Turkish field trials described above, namely 40–45% for the wild type and 100% for the domestic type. However, in view of the preliminary nature of the measurements of fitness in the wild-type, and its potential susceptibility to variations in (i) the aptitude of the harvester and (ii) the mean state of ripeness of the crop, we also added a broad spread of much more conservative values for fitness of the wild type ranging from 45–95%. Values in this range clearly produce slower rates of domestication, and correspond to the effect of harvesting the crop when much less ripe. (Selection coefficients against the wild type are 1-fitness).

(c) *Inbreeding frequency in einkorn.* For the purpose of this simulation, we have tested the effects of breeding behaviour ranging from complete outcrossing to complete inbreeding (selfing). However, Daniel Zohary (personal communication, 1980) informed us that the rate of outcrossing in wild wheats is probably below 1%. Thus, for *Triticum dicoccoides* he notes that "... there is very little cross-pollination under natural conditions. ... This is clear from (i) their floral biology (anther dehiscence occurs within the florets prior to lodicule inflation and anther emergence), (ii) the almost complete lack of intermediates when different forms are grown together, and (iii) more recently, from electrophoretically discernable protein markers revealing the predominance of homozygosity in the individuals examined". He concludes (personal communication, 1988) "all in all, I think that it is safe to consider *Triticum dicoccoides*, *T. boeoticum* and *Hordeum spontaneum* as predominantly self-pollinated plants. In all three, the amount of cross pollination could vary between 0.5% and 5%". Willcox (in press) cites what seems to be an aberrant exception to this pattern observed by Boyeldieu (10–15% outcrossing under hot conditions in N. Africa), however, the broad range of values used in our computer model (0%–90% outcrossing) clearly allows for such eventualities, and for the unlikely possibility that there has been a major shift in breeding behaviour of these cereals during the past eleven millennia.

(d) *Allele frequency and mutation rate.* It was noted above (see 'raw materials for domestication') that, in wild populations growing in primary habitats, the semi-tough-rachis recessive alleles act effectively as lethals when in homozygous state, since the grains never leave the plant and cannot contribute to the next generation. They therefore occur only in heterozygotes. In an inbreeder such as

einkorn, such heterozygotes will be rare and will occur at a nominal frequency only a little above the mutation rate. The same applies to the first crops. In gathering seed-corn from wild stands to sow the initial crops of, say, wild-type wheats, semi-tough-rachised phenotypes will generally have been left behind if the spikelets were gathered by beating, so this low frequency of semi-tough-rachised alleles probably continued into the first crops. Indeed, for the simulation, we have chosen to err on the side of caution and use a mutation rate of the brittle-rachised allele to the semi-tough-rachis allele of 10^{-6} per locus per generation. But even at this mutation rate, and given the total area of, say, einkorn crops sown by early Near Eastern farmers (see above, pp. 49–51), the semi-tough-rachised mutant will doubtless have been present in the fields of at least *some* of them from the outset, and soon emerged in most of the others.

Results

The results of the computer simulations are presented in Figs 6 & 7 and in Table 3. Figure 6 shows patterns of increase in the semi-tough-rachised (domestic) phenotype under a range of selective intensities but with inbreeding at a constant 100%. With the selection coefficient of 0.6 against the wild type (fitness = 0.4) measured in our preliminary field trials, domestication occurs within 20 generations (i.e. within 20 years—if the crop is sown annually). Even with a selection coefficient as low as 0.1 against the brittle-rachised phenotype
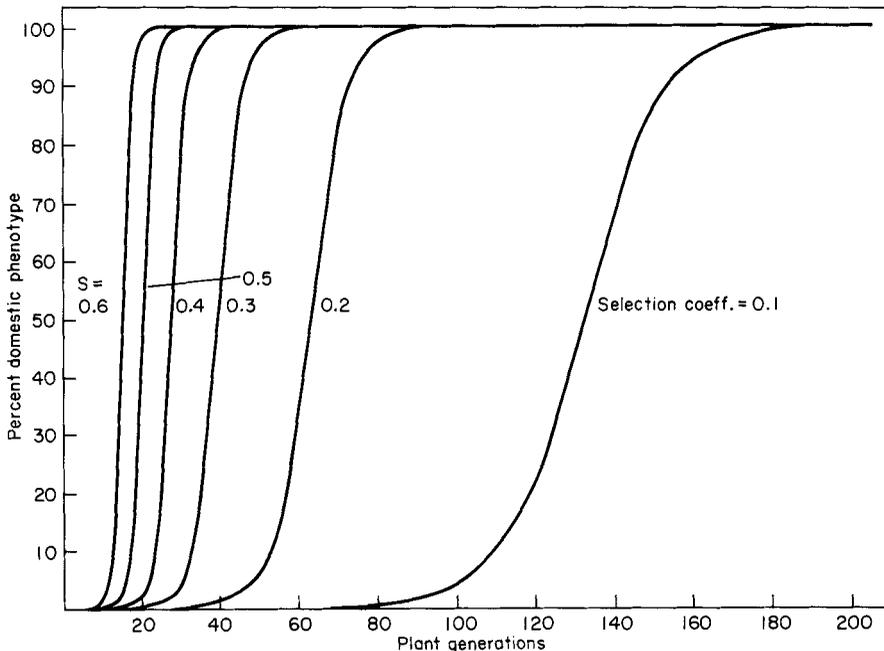

Figure 6. Relative abundance of semi-tough-rachised domestic phenotypes in populations of brittle-rachised wild-type einkorn under a range of selective intensities, but with a constant 100% inbreeding and with the initial frequency of the semi-tough-rachis allele taken as a conservative 10^{-6}. The first (left hand) curve is the one closest to the selection coefficients measured in our field trials (see Table 1). (With annual sowing, 1 plant generation = 1 year.)
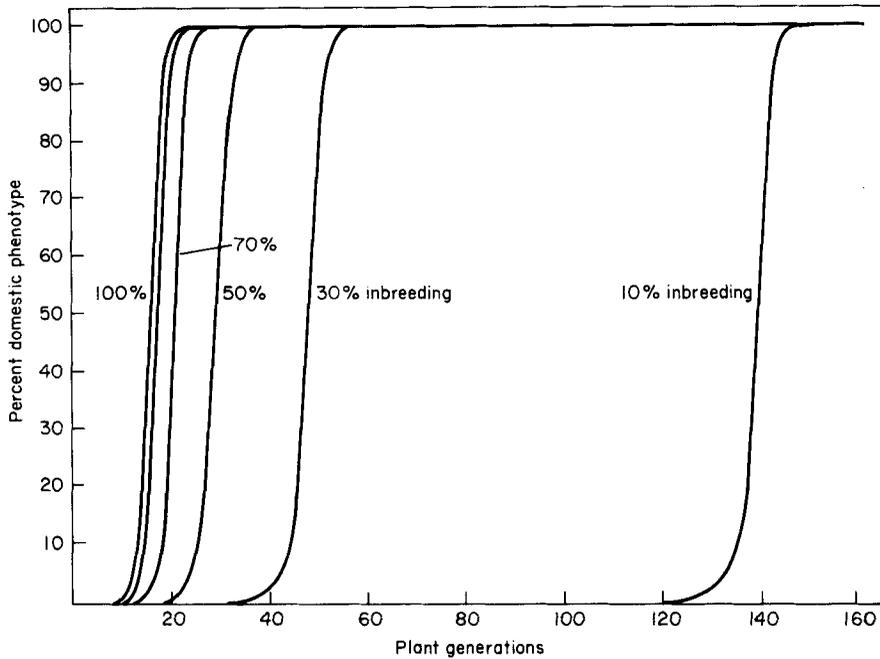
Figure 7. Relative abundance of semi-tough-rachised (domestic) phenotypes in cultivated populations of brittle-rachised wild-type einkorn with a range of levels of inbreeding but under constant selective intensity of 0.6 (which was the value measured in preliminary field trials). The inbreeding rate in wild wheat suggested by Zohary (personal communication, 1980) was "probably greater than 99%"; i.e. close to the first curve. (With annual sowing, 1 plant generation = 1 year.)

(fitness = 0.1), domestication is still complete within 200 generations (two centuries). These lower selection coefficients probably resemble those that would be generated by harvesting the crop when it is less ripe, and are perhaps more realistic.

In Fig. 7, selective intensity is set at the measured value of 0.6, but the values used for inbreeding frequency range from 100% to an improbable 10%. At the estimated inbreeding frequency of 99%, fixation occurs within 20 years; and with a mere 70% inbreeding, it occurs within 30 years. Even with 10% inbreeding (equivalent to a strong *out*breeder), fixation still occurs within two centuries. Total outbreeding (i.e. 0% inbreeding) was also tested in the simulation, but showed the domestic phenotype remaining at an extremely low frequency at even the 8000 year limit of the simulation programme. This might explain the belated appearance in the archaeological record of the domestic form of outbreeders such as rye.

Table 3 shows the number of generations required for the domestic phenotype to achieve a level of 99% in the crop population with the full range of values used for both selection coefficient and inbreeding frequency. It could be argued that the figures of practical relevance to studying the domestication rates feasible in wild-type einkorn wheat are those in the bottom right-hand corner, as these figures are based on (a) the value for selection coefficient that was recorded in our field trials (namely S = 0.6) and (b) Zohary's estimate of probable inbreeding frequency (namely > 99%). However, it is equally (or more) realistic

TABLE 3. The number of generations required for the semi-tough-rachised phenotype to reach a frequency of 99% at various levels of selection against the wild-type phenotype and with various levels of inbreeding. The initial frequency of the semi-tough-rachis allele was taken as a conservative 10^{-6}, and the allele was assumed to occur only in heterozygotes in generation 0. In cases marked '*', no semi-tough-rachis homozygotes were produced, even after 8000 generations.

% Inbreeding	Selection coefficient against fragile rachis phenotype						
	0.05	0.1	0.2	0.3	0.4	0.5	0.6
0	*	*	*	*	*	*	*
10	4090	1940	860	510	330	220	150
20	2130	1010	450	270	170	120	77
30	1440	680	310	180	120	78	53
40	1070	510	230	140	87	60	42
50	840	380	180	100	71	49	34
60	690	330	150	89	59	42	30
70	580	280	130	76	51	37	27
80	490	240	110	67	45	33	24
90	420	210	95	59	41	30	23
100	360	180	84	53	37	28	21

to use the domestication rates generated by the lower selection coefficients (0.3 down to 0.1), as these correspond to harvesting the crop when it is much less ripe, and Willcox (personal communication; 1990) has found the bulk harvesting of crops of wild-type einkorn is much more efficient when they are in this state. For further discussion of harvesting methods, see below, pp. 69–71.

The results of the simulation therefore suggest that domestication (in respect of the fixation of semi-tough-rachis in a brittle-rachised crop population) could be achieved within 20–30 years—so long as the crop is harvested when near-ripe by means of sickle reaping or uprooting, and so long as some of the harvested seed is sown on virgin land every year and taken from the previous year's new plots. And even if we use lower values for selection coefficient corresponding to harvesting crops when vastly less ripe, then the process is still complete within two centuries.

This result broadly concurs with the rapid rates of domestication proposed by Zohary (1969, 1984, in press) and Ladizinsky (1987). However, we would argue that somewhat longer periods may be more probable. Even so, the fact that wild wheats and barley could have been domesticated within two centuries make domestication an event of such transience that it stands little chance of being recognizable as a clinal process in samples of plant remains recovered from archaeological sites. The same is probably also true for the other Near Eastern domesticates.

Limitations of the computer model

At a general level, it should be stressed that the computer model is deterministic and takes little account of random processes. Its aim is merely to give a general idea of the time-scale of the domestication process, and to this end,

we applied a number of simplifications in selecting values for some of the variables. The most obvious simplifications were as follows.

(i) The simulation assumes that the semi-tough-rachised state in einkorn (the species used in our field measurements of selection coefficient and in the computer simulation) is determined by a single allele. However, the work of Sharma & Waines (1980: 215) demonstrates that two loci are involved in the control of the tough rachis character in subsp. *monococcum*. The 15 : 1 segregation ratio they found in the F_2 progeny of crosses between subsp. *boeoticum* and subsp. *monococcum* also indicates that the two genes were assorting independently, i.e. they were not linked. The likelihood of fixation of both alleles in a homozygous form in early generations is much less than for a single locus. However, once present, and given a high degree of selfing, the genotype would show a similar rapid increase in frequency to the single gene homozygote. However, the effects of outbreeding in slowing the rate of increase of the homozygote would be markedly more pronounced than for the single-gene model.

On the other hand, Sharma & Waines (1980: 215) suggest that

> "simultaneous mutations at two loci seem highly improbable. A plant homozygous for the recessive gene at one of the two loci may have arisen first and might have had some degree of rachis toughness. This might have led early man to select such plants in the course of harvesting. Mutation at the second locus might have been another independent event that occurred later in this already domesticated line, or this second mutation might have occurred in another *boeoticum* line. These two *boeoticum* lines, one homozygous for one locus and the other homozygous for the second locus, by hybridization and segregation might have given rise to present day *monococcum* homozygous for both loci".

Neither possibility conflicts with the basic model presented here, which is concerned merely with indicating the approximate time-scale necessary for the primary fixation of increased rachis toughness under unconscious selection. Certainly, with Sharma & Waines' results indicating that, even in plants homozygous recessive at only one of the loci, the rachis was tough enough for the ears to remain intact when "left standing in the field for about one month in the dry hot weather", homozygosity at even one locus would have been enough to have achieved domestication as understood in our model. The same would probably have been true if yet more loci had been involved. Miller (personal communication, 1988) has suggested that semi-tough rachis in modern einkorns might be controlled by even more loci, but, here again, fixation of mutants homozygous for just one of these loci would probably have achieved domestication.

(ii) The model secondly takes no account of the possible effects of introgression of wild-type alleles from nearby wild stands via occasional outcrosses. Extensive areas of entirely wild-type populations are almost certain to have existed in the vicinity of the incipient domesticates, if only on the older cultivated land where the early wheat and barley crops were probably wholly or partially self-sown with spikelets shed spontaneously from brittle-rachised ears. Introgression from these stands could clearly slow down domestication rate. However, given the high degree of selfing in wheats and barley (see above), such introgression is likely to have been relatively modest during the short period involved in the

process of domestication (contrast the effect of longer-term introgression discussed in the Appendix to Hillman & Davies, in press).

(iii) We made no attempt to measure the effect of harvesting crop populations at different stages of average ripeness, as this would clearly have involved much larger trials than those considered here. In any case, the full range of selective intensities likely to be generated by other levels of average ripeness are included within the very broad range of values for selection coefficient that were used in the simulation. In fact, in view of the clear advantages of harvesting wild-type crops when they are significantly under-ripe (see below, and Willcox, in press), it is possible that the lower selection coefficients are the more realistic ones, and that domestication required anything between 30 and 200 years (see the right-hand curves in Fig. 6).

(iv) We have also disregarded the possibility (however remote) that, when sowing virgin land, the farmers might have incorporated in their 'seed corn' some wild-type spikelets gathered from the old plots where brittle-rachised ears had disarticulated during harvesting. This would clearly have retarded domestication rate. (For further details, see Hillman and Davies, in press).

(v) We have also taken no account of the possible effects of *modifier genes* influencing the expression of the genes determining rachis toughness. If major shifts have occurred during the past eleven millennia in the expression or degress of recessiveness of the semi-tough-rachis allele, then the present model would need modification. For example, from recent work on cereal breeding at CIMMYT, Wilkes (personal communication, 1986) suggests that modifier genes might have delayed full fixation of the semi-tough-rachised phenotype, and that the 30 or so years for achieving domestication in respect of major genes (such as those determining rachis fragility) represents only one end of the range of time periods probably needed for the full fixation of modifier genes and for the consequent achievement of stability of rachis fragility state. This lack of stability in the final stages of fixation of semi-tough rachis (or, at least, the first episode of that process) could, he suggests, produce fluctuations at the top end of the sigmoid curve as notionally indicated in Fig. 8.

Fluctuations of this sort could conceivably account for the remarkable mixtures of 'primitive' and 'advanced' forms which continued to occur in essentially domesticated crops for a millennium or more—right into the late Aceramic Neolithic—at sites such as Can Hasan III in Turkey, although other explanations of these mixtures are possible. (See Hillman & Davies, in press, for the alternative explanations and for other archaeological examples).

Effects of conscious selection imposed midway through the domestication process

It was noted above that, once the frequency of semi-tough-rachised phenotypes had increased to a level at which they became noticeable in the wild-type crop populations (perhaps around the 1% level), then the farmers might have consciously accelerated the process by taking the semi-tough-rachised ears, sowing the spikelets in a separate plot, and multiplying up the seed-stock to a level at which they had enough to re-sow all of their cereal fields. From that point onwards, the crop would have been fully domesticated, barring fluctuations due to changes in modifier genes. If sown thinly, one spikelet
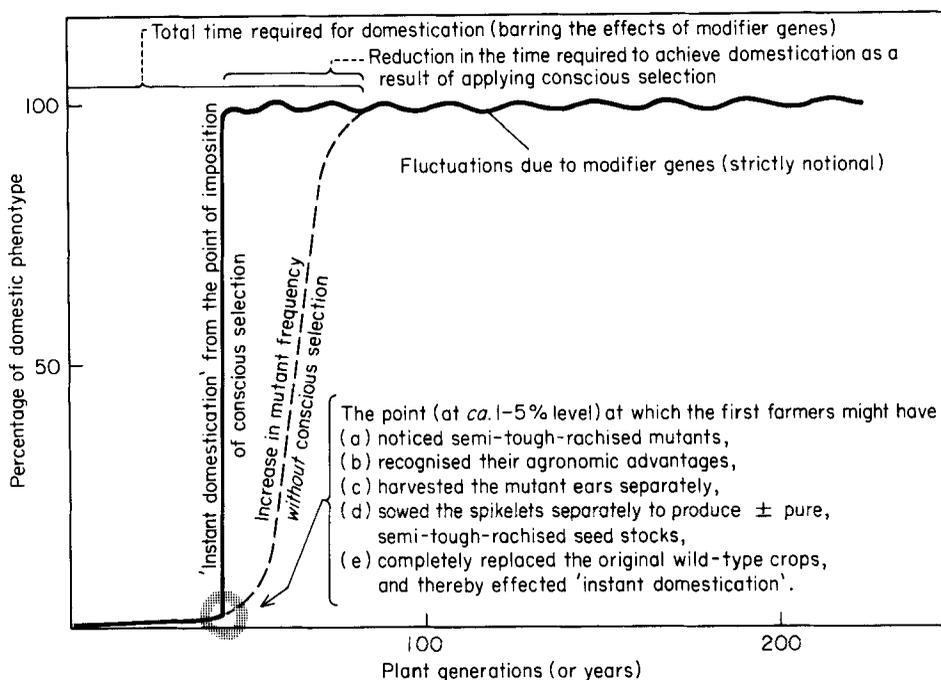
Figure 8. Notional representation of the effect of introducing conscious selection favouring semi-tough-rachised (domestic) plants once their frequency reached about 1–5%. (Compare with Figs 6 & 7.)

generally produces plants with at least 40 spikelets (and generally more), so the period of multiplying-up could have been as short as three or four years.

From the point at which they sowed the more-or-less pure, semi-tough-rachised 'seed-corn', the graph would rise near vertically (Fig 8). However, it can be seen from Figs 6 & 7 that, with even the fastest rate of domestication, the time required to reach the 1% level is at least ten generations (i.e. ten years). Intervention in the manner proposed above would therefore have reduced minimum domestication time by only half at the most.

Testing the model in long-term field trials

With the computer simulation indicating such a rapid rate of domestication, it was clear that we could test the model over a 20–30 year period by cultivating wild-type einkorn (or emmer, or barley) under the combination of husbandry systems proposed in the model. However, experience of wild einkorn cultivation at Cardiff indicated that the Welsh climate was too wet for such an experiment, and Patricia Anderson-Gerfaud and Jaques Cauvin of the Institut de Préhistoire Orientale kindly proposed including it in their *Cultures Préhistoriques Expérimentales* programme at Jalès, Ardèche, in the south of France. The trial is now in the expert hands of George Willcox and Patricia Anderson-Gerfaud as part of a broad experimental study of early agronomy, and some of their preliminary results are reported in Anderson-Gerfaud (1988) and, in greater detail, in Anderson-Gerfaud (in press), Anderson-Gerfaud & Willcox (in press), and in

Willcox (in press). If the increase in frequency of the domestic phenotype follows the pattern indicated in our simulation, then this could start to become apparent in about 15 years' time.

However, such a test can demonstrate merely that it was *feasible* for unconscious domestication of einkorn (and probably emmer and barley, too) to have occurred in this way. It does not prove that it actually happened that way 11 millennia ago.

WHY SHOULD EARLY FARMERS HAVE USED THE REQUIRED FORMS OF HUSBANDRY?

The combination of husbandry methods required to achieve domestication may appear impractical. In each case, however, there are sound agronomic reasons why they should have been used by the earliest farmers.

Why harvest partially ripe cereals with sickles or by uprooting?

(i) Harvesting grain from wild grasses/cereals by beating gives the greatest yield *per unit harvesting time*, and for the majority of hunter-gatherers with extensive resources, beating would therefore have offered the most energy efficient method of procurement. However, for cultivators expending energy on land-clearance and tillage, the pressure to maximize yields *per unit area* is likely to have favoured the harvesting or relatively unripe crops by uprooting or with sickles.

It was noted above that, in our field experiments, beating proved to be the most convenient method of harvesting wild cereals, and that it was the method favoured by most hunter-gatherers when harvesting wild grass seed. However, harvesting by beating is more efficient than other methods only in terms of the amount harvestable *per unit time*. In terms of the amount harvestable per unit *area*, beating near-ripe einkorn (with a single pass) is no better than uprooting and sickling (see Table 1, above), and, in practice, could result in much lower returns than other harvesting methods. There are three reasons for this. (1) Optimal areal returns from beating require multiple passes, and this involves trampling the crop before the final 'passes'. By contrast, hunter-gatherers with very extensive wild stands could probably have afforded to omit the second and third passes. (2) The only way of reducing the number of harvesting 'passes' is to delay harvest until the crop is starting to shatter. In practice, however, Willcox (in press) has found that mistiming the harvest by a couple of days can all too easily lead to massive losses through pre-harvest spikelet-shed. Again, when harvesting extensive wild stands as hunter-gatherers, these losses from the shedding of spikelets might have been relatively inconsequential, but on cultivated plots, extra losses mean tilling extra land to get the same nett return, and this is energy-expensive. (3) If the farmers attempt to limit spikelet shed by harvesting the crop half-green (prior to any spikelet-shed), then harvesting by beating cannot be applied, as beating works only if the ears are disarticulating. Uprooting or sickling then offer the only solution.

Thus, despite our observation that harvesting by beating gives the greatest yield *per unit harvesting time*, for cultivators, the pressure to maximize yield *per unit area* is likely to have favoured the harvesting of relatively unripe crops by uprooting or with sickles.

This difference clearly reflects the substantially altered patterns of energy

input and resource distribution that occur with the shift to cultivation. Hunter-gatherers exploit diffuse resources, and pre-processing energy expenditure is limited mainly to travel, harvest and transport costs. By contrast, cultivators generate their own highly concentrated resources, with heavy pre-harvest energy expenditure on land-clearance, tillage, sowing, weeding and crop protection. With resources limited to small areas in which there has been such heavy energy investment, it is clear that methods used by earlier generations for foraging diffuse resources may have had to be altered to maximize energy returns *per unit area of tilled land* (instead of maximizing energy returns per unit of energy spent in harvesting and travel). On this basis, harvesting by beating may have had to be replaced by sickle-reaping or uprooting. An extension of 'optimal foraging theory' can thus offer a partial explanation for shifts in technology which, in turn, could account for crop domestication.

There are three further factors which may have encouraged the first farmers to harvest with sickles or by uprooting.

(ii) The farmers may have wanted a valuable secondary product: namely straw, which could be harvested only by sickling or uprooting. Straw might have been valued for three reasons. Firstly, it is invaluable for lighting domestic fires, and it still serves in this role in areas where paper is rare. Secondly, straw may well have been needed for tempering mud brick or adobe. If sedentism in SW Asia preceded the adoption of large-scale cultivation as present evidence suggests (see Harris, 1977; Hillman, 1987; Hillman, Colledge & Harris, 1989), then the concomitant storage of grain harvests would have required the construction of storage facilities even before cereal cultivation began. Certainly, complex storage structures of heavily straw-tempered mud bricks are present in even the earliest agricultural level ('D') at Ganj Dareh Tepe in the southern Zagros, and they apparently predate the construction of equivalent (though larger) adobe structures for human habitation (Smith, 1970—for the mud-brick structures; van Zeist *et al.*, 1984—for the earliest evidence of domesticates at the same site). Either way, straw-tempered adobe structures are common throughout much of SW Asia from the Pre-Pottery Neolithic B period onwards.

Straw may also have been harvested to fire the harvest. 'Sheaf-burning' provides an effective way of eliminating much of the chaff and parching the spikelets ready for dehusking and grinding (see Hillman, 1984: 141–3). Indeed, we use this method ourselves whenever processing wild cereal grain for consumption, as it saves most of the threshing and winnowing. However, it kills the grain and would not have been used to clean the harvest from those plots providing 'seed corn' for next year's crop. Nevertheless, if uprooting or sickle-reaping (as a prelude to firing) was applied to the rest of the harvest, then the farmers may have found it convenient to harvest the 'seed-corn' plots by the same method, even though the harvested sheaves from these plots could not thereafter have been cleaned by burning. It might also be argued that the first farmers required straw as fodder for domestic animals, especially for cattle. Certainly, straw is used extensively in this role in the Near East today. However, present archaeological evidence suggests that there were no domestic cattle at this stage in the relevant parts of the Near East, and maybe few domestic sheep or goats (see, e.g. Legge & Rowley Conwy in Moore, Hillman & Legge, in press). As for the Bohrer (1972) hypothesis that pre-agrarian or early cultivator groups fed cultivated fodder to penned wild animals, all the available evidence suggests that this is highly improbable.

(iii) If the first farmers suffered a few decades of wet summers, they would have been forced to harvest by uprooting or sickling, even if they had hitherto harvested by beating. Our Cardiff field trials revealed that, in wet summers, brittle-rachised einkorn fails to disarticulate, and beating becomes ineffective (see above, p. 61). But while domestication could not have occurred for as long as the crop failed to disarticulate, a decade or two of wet summers could have established a tradition of harvesting by uprooting or sickling. However, it remains very uncertain whether the necessary decade or two of wet summers ever occurred in SW Asia at any point during the terminal Pleistocene.

It is worth noting that, despite his general dissatisfaction with sickle-reaping for harvesting wild grasses, it was the method used by Harlan (1967) in his experimental harvesting of near-ripe wild einkorn on Karacadağ in SE Turkey.

Why extend cereal cultivation annually onto virgin land?

There are two systems of primitive cultivation which would automatically have involved annual shifts in cultivation, and which might, therefore, account for domestication having occurred in those cases where shifting cultivation was perhaps a pre-requisite.

(i) The first system involves shifting cultivation—with regular shifts from old land onto virgin land. In view of the fact that all the old plots would have been conveniently self-sown with the wild-type crop, deserting these old plots would presumably have been entertained only in the face of serious deterioration of crop yields. Two causes of yield reduction might have been firstly, depletion of phosphates in the calcic soils typical of this region (Bunting, personal communication, 1987); secondly, build-up of weed contaminants (see below).

(ii) Annual extensions in the area under cultivation, could secondly have occurred without corresponding abandonment of old land. The most obvious reason for adopting such a strategy would have been pressure from expanding populations. Population pressure features in most models for the beginnings of cultivation in SW Asia (cf. Bar-Yosef & Kislev, 1989; Binford, 1968; Cohen, 1977; Flannery, 1969; Harris, 1977; Hassan, 1981; Hillman, 1987; Moore, 1985, 1989; Smith & Young, 1983) and present evidence suggests that the population increases accelerated still further after the adoption of agriculture. It is inevitable, therefore, that cultivation had to be regularly or episodically extended onto virgin land. The later development of intensification practices such as irrigation would have merely reduced the frequency of these extensions. In the very early phases of cultivation, therefore, *annual* extensions are not entirely improbable.

Why take 'seed-corn' exclusively from the previous year's new plots?

Such a strategy may again have been adopted to minimize weed infestation. In SW Asian steppe, field studies have shown that the concentration of most weed species (including toxic-seeded species such as *Adonis*) builds up rapidly in the first few years of cultivation, and then reaches a plateau (Hillman, Colledge & Harris, 1989: 253). Weed seed frequencies in harvested grain would therefore have been lowest in harvests from the new plots, and taking all 'seed corn' from these plots would have greatly helped control weeds.

In summary, therefore, there would have been good grounds for the first wheat and barley farmers applying all of those methods most likely to have resulted in the domestication of wild type crops—even in the perhaps improbable event that this necessitated annual shifts to virgin land using seed corn taken exclusively from last year's new plots. Such methods were probably applied by many of the early farmers of the area, though doubtless there were many who applied other methods and whose crops were never domesticated. Among the latter groups, this state of 'non-domestication cultivation' presumably persisted until they obtained seeds-stocks of the newly domesticated forms from other early farmers.

THE ARCHAEOLOGICAL RECORD

In view of the rapidity of domestication indicated in our simulation (20–200 years), the process of domestication (i.e. the period of 'pre-domestication cultivation') will be archaeologically invisible in most cases. Furthermore, cases of 'non-domestication cultivation' involving cultivation of entirely wild-type crops are generally distinguishable from the foraging of wild stands only by analysing (a) associated 'indicator assemblages' of weed remains (cf. Hillman, Colledge & Harris, 1989) or (b) use wear on associated flint blades (Unger-Hamilton, 1985, 1989). These problems are discussed in detail elsewhere (Hillman & Davies, in press).

A FURTHER STAGE OF DOMESTICATION: THE APPEARANCE OF SECONDARY CROPS WITH FULLY-TOUGH RACHISES

All the foregoing has considered domestication in terms of the fixation of semi-tough-rachised phenotypes in crop populations of the brittle-rachised (wild) type—primarily using einkorn wheat as our example. This process was justifiably termed 'domestication', as the resulting plants were incapable of surviving in the wild, and were (and still are) dependent on human intervention for their reproduction.

However, domestication in the wheats can go one step further. Tetraploid and hexaploid wheats which carry mutant forms ('Q') of the speltoid 'q' alleles produce (a) a *fully*-tough rachis that fails to disarticulate, even when thoroughly threshed and (b) thin, deciduous glumes which fail to retain the grain during threshing (Miller, 1986; Muramatsu, 1986). Such plants are termed 'free-threshing' or 'naked-grained' and include both bread wheat (*T. aestivum*) and macaroni wheat (*T. turgidum* var. *durum*)—both now grown worldwide. These free-threshing wheats emerged from already domesticated crops (such as emmer or spelt) and are therefore termed 'secondary crops'. Rye and oats are also thought to be secondary crops which, in this case, evolved from weeds infesting crops such as domestic emmer and einkorn, and, here, selection was probably unconscious (see Vavilov, 1917; Hillman, 1978; Sencer & Hawkes, 1980). In the free-threshing wheats, however, detailed models of their possible mode of emergence have yet to be formulated, and conscious selection may well have played a central role. Either way, present evidence suggests that the free-threshing wheats, rye and oats all emerged initially as 'domesticated weeds' of primary (founder) crops—complete with tough rachises (or, in oats, with tough rachillas), before becoming established as crops in their own right.

(Note—barley is different from the wheats in that, like rye, there is generally no clear intermediate semi-tough-rachised state, merely fully-brittle-rachised wild types and fully-tough-rachised domesticates.)

CONCLUSIONS

(a) Domestication of the wheats and barley appears to have occurred under cultivation, and *not* in response to selective pressures arising in wild habitats from the exploitation of wild cereal populations by hunter-gatherers. On the other hand, some form of edaphic pre-adaptation to naturally disturbed (or, less probably, ruderal) habitats remains a possibility.

(b) Correspondingly, the first cultivated wheat and barley crops were inevitably of the wild, brittle-rachised type.

(c) Although the quantities of grain used to sow these first crops would have been too small to have included domestic-type mutants, the crops would probably have been sufficiently large for the mutant to have been generated within the first two to five years, in most cases.

(d) Selection favouring the semi-tough-rachised type was necessarily unconscious during the early stages of domestication.

(e) Unconscious domestication of wild-type einkorn crops required a combination of the following husbandry methods:

(i) the crops on these plots had to be harvested by uprooting or sickle-reaping; and

(ii) the crops had to be near-ripe or partially ripe, but not so unripe that none of the ears had yet started shattering.

In certain circumstances, unconscious selection of the domestic mutants might have required two additional conditions:

(iii) annual extensions of cultivation to new plots of virgin land;

(iv) the 'seed-corn' for these new plots to be taken from last year's virgin plots.

(f) There are agronomically sound reasons why at least some of the earliest farmers should have used these particular combinations of husbandry methods.

(g) Selective pressure generated by these techniques and favouring the domestic semi-tough-rachised mutants (relative to the wild brittle-rachised type) would have been intense. Preliminary field trials gave measured values of c. 60% against the wild type, relative to the domestic type.

(h) Given selective pressures of this order, and with the high levels of inbreeding typical of modern wild einkorn, computer simulation indicates that the initially rare semi-tough-rachised (domestic) phenotypes could theoretically have achieved fixation (i.e. domestication in the classical sense) within 20–30 crop generations (i.e. within 20–30 years).

(i) It is probable that selective pressures were, in reality, far less intense—due to the crop being harvested when much less ripe. However, the computer simulation indicates that, at the correspondingly lower selective pressures, domestication could still have been achieved well within two centuries. The same is true if there had been more outbreeding.

(j) In those crops where domestication was able to proceed *without* shifting cultivation, selective pressures would have been reduced still further—due to the dilution effect of wild-type plants originating from self-sown spikelets on the re-used plots. However, this is unlikely to have added more than a century to the domestication period.

(k) Such a transient sequence of events is unlikely to be preserved on most Mesolithic or Neolithic sites as a recognizable progression, and the long-cherished hope of unearthing a sequence of charred wheat or barley remains which would manifest 'on-the-spot domestication' is unlikely ever to be realized. Thus, while it is not impossible that remains of a transitional crop will occasionally be recovered as chance finds, on most sites where domestication actually occurred, it is much more probable that we will merely find remains of wild cereals in one level and fully domestic cereals in the levels above—with no way of knowing whether the domesticates were imported from elsewhere or generated locally.

(l) Any genuine cases of 'on-the-spot domestication' might be impossible to distinguish from mixtures of wild- and domestic-type rachis remains generated by introgression or taphnomic processes.

(m) In occupation deposits containing remains of wild-type cereals, it is nevertheless possible to distinguish between cases of 'non-domestication cultivation' and gathering from wild stands, albeit *not* from the cereal remains themselves, but rather by using evidence from (i) associated remains of species other than cereals which are ecologically diagnostic; and/or (ii) use-wear analysis of associated remains of sickle blades. Chemical markers from the cereal remains themselves may also eventually prove diagnostic at this level.

Full details relating to these last two conclusions are given in the final sections of Hillman & Davies, in press.

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