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**EVOLUTION OF CARYOPSIS GIGANTISM AND AGRICULTURAL  
ORIGINS**

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# EVOLUTION OF CARYOPSIS GIGANTISM AND AGRICULTURAL ORIGINS

## I. Introduction

The environmental conditions associated with the origins of agriculture are attracting increasing attention (Sauer, 1952; Flannery, 1969; Zohary, 1969; Butzer, 1971; Whyte, 1977; Wright, 1977; Bintliff and van Zeist, 1982; Blumler, 1984; Moore, 1985; Byrne, 1987; Lewin, 1988; Henry, 1989; Hillman *et al.*, 1989). Archaeological evidence indicates that domestication occurred at approximately the same time in both the Old and New Worlds, and was synchronous with or followed closely upon the dramatic climatic changes of the Pleistocene/Holocene transition (Byrne, 1987). It is difficult to reconcile this pattern with population pressure models or other explanations that emphasize cultural factors (Blumler and Byrne, 1991), or with Harlan's (1975:57) "no-model model", which proposes that agriculture began in different regions for different reasons. Byrne (1987) argued that there was a shift to seasonally dry climates at the beginning of the Holocene, which would have favored the evolution, expansion in range, and increase in abundance of annual grasses and legumes, and tubers; in his view, consequent shifts in gathering strategies led to agriculture. Blumler (1984) showed that seasonally dry (Cs, Aw, and Am) climates are characterized by an abundance of annuals that achieve a wide adaptive range, including perhaps the ability to be "climax" (i.e., to dominate in the absence of disturbance). He also suggested that large seed size in annual plants was most likely to evolve in climax species of seasonally dry environments, as an adaptation to intense seedling competition, and that the evolution of large-seeded annual grasses and legumes may have been a necessary prerequisite for agricultural beginnings.

This hypothesis is explored in greater depth in this paper. I show that:

1) large grain size in annual grasses is associated with seasonal precipitation patterns, and with competitiveness or shade-tolerance in productive environments;

2) unusually large-grained annual grasses are of central importance to the agricultural origins question;

3) a case can be made that agriculture would not have arisen if large-seeded annuals had not evolved.

In addition, some evolutionary implications are discussed.

## II. Materials and Methods

I obtained mean seed (caryopsis) weight data for most large-grained members of the Gramineae (excluding cultivated plants and the Bambuseae),<sup>1</sup> here defined as those taxa that produce caryopses that weigh at least 10 mg, on average. Median grass caryopsis weight is probably about an order of magnitude less. Where possible, I collected at least 100 ripe grains from vigorously growing individuals, to minimize phenotypic effects; in other cases, seed collections (at Beltsville, Wakefield [Kew], and Sacramento) or herbarium specimens (from the University of California and the Hebrew University) were used. Caryopses were weighed on an electronic balance.

Weights also were obtained from the literature, when available, though a few obvious instances of decimal point or other errors were excluded from the analysis (e.g. Nevo *et al.*, 1982; Snow and Brody, 1984). I also ignored data

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<sup>1</sup>Bamboos often produce very large seeds, but are adaptively different from most other grasses. Their growth habit, long life span, and often extremely irregular flowering (Janzen, 1976) preclude their cultivation as cereal crops.

derived from very small samples (e.g. Bar-Yosef and Kislev, 1989), except when no other information was available for a given species. Mean values often varied widely within species, due to both phenotypic and genetic effects as well as to sampling error. Investigators have not always described accurately the plant parts weighed: in *Stipa*, for instance, "caryopsis" weight usually refers to anthoecium, with awn removed.<sup>2</sup> I attempted to determine if part or all of the husk was weighed along with the caryopsis, and adjusted the reported values accordingly; for instance, if diaspore rather than caryopsis weight was reported, I estimated the latter based on caryopsis/diaspore ratios in related taxa (e.g. Wilkes [1967] and Doebley [1984] for *Zea/Tripsacum*, and my data on *Bromus*, *Hordeum*, and other genera [Blumler, 1992b]). I also adjusted the data to allow for variations in growing conditions and sample reliability. When plants were subjected to severe post-anthesis moisture stress, I assumed that some phenotypic reduction in seed size would have occurred. For instance, when accessions from montane environments or from countries that experience a comparatively long rainy season are grown out in Israeli uniform garden experiments, seed maturation is likely to occur in extremely hot, dry weather; native accessions, on the other hand, will have ripened their seeds at an earlier date, under more favorable conditions (e.g. Brody, 1983). Bagging of immature spikes to prevent dispersal (e.g. Sharma *et al.*, 1981), also probably causes phenotypic reductions in grain weight.<sup>3</sup> Nonetheless, the rank order of mean

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<sup>2</sup>In grasses, use of "fruit" to refer to diaspore or seed plus husk is misleading: the caryopsis is a fruit. Anthoecium is the correct term for lemma, palea, and enclosed caryopsis (McClure and Soderstrom, 1972).

<sup>3</sup>Phenotypic reduction in seed weight in this particular study is also indicated by the suspiciously high protein content of close to 30 % (Sharma *et al.*, 1981:556). Wild wheats normally produce kernels with about 20-22 % protein (Avivi, 1979; Sharma *et al.*, 1981; Grama *et al.*, 1983; Nevo *et al.*, 1986b) – which gives some indication of the magnitude of grain shriveling induced by bagging, and perhaps other phenotypic stresses, in the study by Sharma *et al.* (1981).

grain weight when bagged should correlate well with rank order under unstressed conditions (cf. Fischer, 1981). Accessions of species that are able to hybridize with domesticates also can provide unreliable data, because of effects of introgression on seed size. This is especially important in *Triticum dicoccoides* (Percival, 1921; Jakubziner, 1932; Blumler, 1998), but fortunately, seed weight patterns in nature are sufficiently well-known that probable introgressed genotypes could be excluded.

Heterocarpic synaptosperms such as *Aegilops* (goatgrass) (Datta *et al.*, 1970; 1972; Marañon, 1987ab; Blumler, 1992b) are particularly problematic, because some scholars may not have weighed representative samples of every seed morph. The small kernels in the upper florets and spikelets of the goatgrasses are easily overlooked, and some reported seed weight values for *Ae. spp.* are suspiciously high; at the same time, goatgrasses often grow in unproductive environments, so it is possible that they would manufacture much larger seeds under garden conditions. Datta *et al.* (1972) reported an enormous variability in *Ae. geniculata* seed weight, depending on photoperiod and temperature; however, their experiments were carried out in pots, so it is likely that much of the variance was due to moisture stress.<sup>4</sup> Plants in the low temperature (i.e., low moisture stress) treatments produced seeds of mean weight approximately equal to those reported by others under favorable field and garden conditions (Datta *et al.*, 1970; Fritsch *et al.*, 1977; Marañon, 1987b; Blumler, unpublished). On this basis, I tentatively concluded that *Ae. spp.* in natural habitats can produce grains of equal or almost equal size to those produced under garden conditions. Seed weights of *Ae. spp.* reported by Fritsch *et al.* (1977) often seem too large, but in some cases are the only data available. Inspection of the data suggested that

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<sup>4</sup>It is well-established that seed size can be greatly reduced when plants are grown in small pots (Choudhury and Wardlaw, 1978; Blumler, 1992b).

Fritsch *et al.* (1977) often overestimated mean weight by about 10 mg, presumably due to failure to sample small seeds in upper florets; accordingly, their weights were reduced by 10 mg when they differed greatly from the data of other authors or seemed strongly out of line with taxonomic descriptions.

After making adjustments based on these considerations, I averaged the results for each taxon to produce rough estimates of mean caryopsis weight.

### III. Results

My estimates of mean caryopsis weight are shown in Table 1 (for the raw data upon which these estimates are based, see Blumler [1992b: Appendix AVIII]). Some species have light- and heavy-seeded lines that differ greatly, so the "mean" value is in these cases somewhat artificial; furthermore, the rank order of taxa by mean caryopsis weight cannot be determined with confidence when species differ by only one or two mg. Fortunately, this is inconsequential to the present analysis, which is concerned only with general patterns. A more serious problem is that data were unavailable for a number of species that seem to produce large seeds. Grain size of two of these species could be roughly estimated from descriptions in the literature: *Coix gigantea* reportedly has larger seeds than *C. lacryma-jobi* (Jain and Banerjee, 1974), while *Avena murphyi* appears from its description (Ladizinsky, 1971) to produce slightly smaller grains than the closely related *A. magna*. Other probable large-seeded taxa include: *Tripsacum*, which has been split into 15 species in recent years (de Wet *et al.*, 1976; Wilkes, 1989),<sup>5</sup> *Zizania* spp., *Coix* spp. (and a few possibly related grasses [see

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<sup>5</sup>Taxonomic descriptions (Hitchcock, 1950) and examination of herbarium sheets suggest that some of these produce much smaller caryopses than *T. dactyloides*. The genus is especially diverse in central Mexico, a region of seasonally dry climate that was an early agricultural center. *Tripsacum* includes both tetraploids and octoploids, with the latter having completely replaced

Koul, 1974]), and a few *Stipa* and annual *Secale* spp. Also, it is unlikely but not impossible that one or two additional *Spartina* spp. may produce caryopses that weigh 10 mg or more.<sup>6</sup> Finally, there remain a number of unweighed, possibly large-seeded, wild *Oryza* spp. (of uncertain taxonomy) worldwide, including both perennials and annuals (Chang, 1976; Morishima, 1984). With the possible exceptions of *Tripsacum* and *Coix*, these species probably would fall toward the bottom of Table 1.

Even with the addition of these problematic species, it appears that less than 1 % of the world's grasses (Clayton and Renvoize, 1986) produce caryopses that weigh at least 10 mg. Yet, although few if any grasses produce inedible grains, and the nutrient content of most wild grains is nearly identical,<sup>7</sup> a surprising number of large-seeded species were progenitors of domesticated crops. This is so despite the fact that usually only one domesticate has arisen from any given genus. Furthermore, presumed secondary domesticates such as rye, oats, and the Chilean *Bromus mango* (Sauer, 1952)<sup>8</sup> tend to be derived from species that do not produce seeds as large as those manufactured by the species that appear initially in the archaeological record (such as emmer wheat, barley, and maize).

There are a surprising number of large-seeded annual grasses (40 of the 56 species) in Table 1 – and it was annual species, for the most part, that were taken under cultivation. The possible exceptions include Asian rice, job's tears, and *Bromus mango*, which were domesticated either from annual or facultative

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the primitive tetraploids in Mexico (de Wet, 1987). Since polyploidy is often associated with seed size increase, it may be that the Mexican species manufacture relatively large grains.

<sup>6</sup>*S. anglica*, the single species included in Table 1, is a recent, high polyploid (Elton, 1958; Clayton and Renvoize, 1986). It seems to have larger seeds than other members of the genus.

<sup>7</sup>Being composed mostly of starch, with moderate amounts of protein and a small percentage of oil (Barclay and Earle, 1974).

<sup>8</sup>Secondary domesticates are those that originated as crop weeds, often replacing a primary crop when the latter was taken into new climatic regions or cultivated on poor soil (Vavilov, 1926).

annual (short-lived perennial) ancestors (Chang, 1976; Morishima, 1984; Dean, n.d.), and rye, which arose either from a wild annual species, *S. vavilovii* (for which no seed weight data are available), or from weedy annual races that are derived from the perennial *S. montanum* (Hillman, 1978; Vences *et al.*, 1987; Zohary and Hopf, 1988). In general, annual plants produce smaller seeds than perennials (Baker, 1972; Levin, 1974), probably because they have only a short period of time in which to accumulate photosynthate, and because so many annuals are adapted to disturbance (which requires the production of large numbers of seeds at the expense of size, to ensure colonization of disturbed spots [Harper *et al.*, 1970]). Thus, one would expect a list of large-seeded herbaceous taxa to be dominated by perennials; but this is not so in the Gramineae, even if *Tripsacum* and other probable large-seeded but unweighed species are added to those in Table 1. This is all the more surprising given that the world's perennial grass species considerably outnumber annuals. A few annuals in Table 1 may be recently evolved weeds (e.g. *Avena fatua*, *Lolium temulentum*, *Oryza spontanea*, and *O. stapfii*, but also the perennial *Spartina anglica*), but most are common in natural habitats and probably precede agropastoralism.<sup>9</sup>

Taxonomically, most of the species in Table 1 fall into only a few groups: Triticeae (especially the wheat group, *Triticum/Aegilops*, with 19 species),

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<sup>9</sup>Zohary (1965) asserted that the polyploid members of the wheat group (*Triticum/Aegilops* spp.) evolved and spread only as a result of agropastoralism. This is certainly not true of *T. dicoccoides*, since it was the progenitor of emmer wheat (*T. dicoccum*), probably the first Near Eastern domesticate (Harlan, 1975; van Zeist and Bakker Heeres, 1985; Zohary and Hopf, 1988). Nor is it likely to be true of *T. araraticum*, which is almost completely nonweedy and decreases in importance under grazing (Zohary, 1969; Sakamoto, 1982). While many of the polyploid goatgrasses are quite weedy, they also are often found in natural habitats. For instance, the four common polyploid *Ae.* spp. in Israel (*Ae. biuncialis*, *Ae. geniculata*, *Ae. kotschyii*, and *Ae. peregrina*) often occur in undisturbed environments that are characterized by a complete absence of diploid goatgrasses (e.g. Kaplan, 1984; Noy-Meir *et al.*, 1989; Blumler, 1992b). Although many of the polyploids have unquestionably expanded their ranges with the spread of agropastoralism, their original evolution appears to be tied to climatic changes, specifically increasing seasonality of precipitation regime, that favored increased seed size (Blumler, 1994).

*Zea/Tripsacum*, *Avena*, *Stipa*, *Coix*, *Sorghum*, *Bromus*, and the emergent aquatics *Oryza*, *Zizania*, and *Spartina*. Aside from these, there are only *Lygeum spartum*, *Rottboellia exaltata*, and *Lolium temulentum*, the latter probably a recently evolved crop mimic. Thus, phylogenetic constraint appears to play an important role in the evolution of large grain size, which seems to be a more difficult evolutionary task for most grass genera than one might expect. Despite its diversity and wide geographic range, *Bromus* is scarcely represented in Table 1, for instance, which suggests that it is more phylogenetically constrained than *Avena*. On the other hand, *Bromus* was better able to evolve large seed size than members of the Festuceae such as *Festuca* and *Poa* that characteristically produce small seeds. Perhaps inflorescence structure was conducive to the evolution of large grain weight in the Triticeae and Maydeae, while plant height and vigor were important in *Avena*, *Sorghum*, and the emergent aquatics.

Finally, large-grained grasses are remarkably prevalent in the Mediterranean and Near East (32 of the 48 non-aquatic species in Table 1), and also seem to be common in other seasonally dry (Cs, Aw, and Am) climates, as well as in aquatic habitats. Of the large-grained annuals, only *Zizania* spp. are not native to seasonally dry environments; within the Mediterranean region, the largest-grained annuals are found where seasonality of precipitation is particularly pronounced (*Avena magna* and *A. murphyi* in southern Spain and Morocco, and wild emmer wheats and barley in the Fertile Crescent). At least 20 large-seeded species can be found in natural habitats in the deciduous oak-park zone of the Fertile Crescent (Table 2), where Near Eastern agriculture probably began (Zohary and Hopf, 1988). The striking predominance of Mediterranean/Near Eastern species in Table 1 strongly suggests that evolution there has been to some degree nonconvergent with other mediterranean-climate regions, especially considering how important grasses often are in herbaceous

communities. Large-grained perennials are found in semi-arid (*Stipa*, *Lygeum*) to humid (*Coix*, *Tripsacum*, *Oryza*, *Spartina*) environments that often are seasonally dry. There do not seem to be any true desert species in Table 1.

## IV. Discussion

### 1. Seed Size and Environment

Ecologists have concluded that large seed size is adaptive where there is shade (Salisbury, 1942), competition (Black, 1958), or drought (Baker, 1972). The aquatic species in Table 1 probably require large food reserves to emerge above the water surface, i.e., for shade tolerance (in an environment that is not normally thought of as shaded). *Zizania palustris*, for instance, typically establishes in 15-30 cm of water and may be submerged for as long as six weeks because of rising spring flood waters (Atkins, 1986); wild *Oryza* spp. also must deal with rising flood waters (Takahashi, 1984); and *Spartina* often dominates the most deeply submerged salt marsh zone. In fact, I suspect that the spectacular success of *S. anglica* in invasion of deep-water estuarine marshes, a source of puzzlement to many (Thompson, 1991), may be due simply to its having unusually large seeds as a result of its allopolyploid origin. At the same time, some evidence indicates that in emergent aquatic grasses large grain size may confer competitive ability (Mullins and Marks, 1987; Weiner and Whigham, 1988). Williams *et al.* (1990) studied the effect of rice paddy water depth on weed infestation. Rice was less affected by deep water than two species of *Echinochloa* (that have smaller seeds [Barrett, 1983]), while *E. oryzoides* performed better than *E. crus-galli*. Barrett (1983) also showed that *E. oryzoides* emerges from deep water better than *E. crus-galli*, and noted that the former produces larger seeds. On the other hand, *E.*

*crus-galli* is often found away from paddies in initially moist spots that dry out in summer, while *E. oryzoides* is almost exclusively a paddy weed. Thus, it is unlikely that emergent aquatics (or semi-aquatics) could have evolved large seed size as an adaptation to moisture stress.

The other large-grained grasses, with the probable exceptions of *Stipa* spp. and *Lygeum spartum*, are mesic in their requirements. For instance, *Tripsacum dactyloides* is found mainly in damp habitats, especially flood plains and stream banks (Hitchcock, 1950; De Wet *et al.*, 1982); *Coix gigantea* grows in wet places, and *C. lacryma-jobi* in moist spots (Bor, 1960; Dean, n.d.) *Hystrix californica*, which grows in moist forests along the central California coast, is the largest-grained native species in the state; presumably its seedlings require abundant reserves because they typically encounter deep shade and perhaps severe competition. Doebley (1984) argued that large seed size in the teosintes is an adaptation to drought stress, but all members of the group appear to be mesic (Wilkes, 1967). Of course, agricultural crops are almost by definition mesophytes, since they are usually programmed for rapid production of a large biomass; their progenitors are almost always similar in this respect (e.g. Chapin *et al.*, 1989).

Given Baker's (1972) conclusion that drought stress is far more important than competition or shade in selection for large seed size in California, one might expect drought stress to be the primary factor favoring the evolution of seed gigantism in the similar environment of the Mediterranean region. However, most of the Mediterranean annuals in Table 1 typically grow where there is at least 350 mm of rainfall during a single, short, cool season. Some taxa do spread into desert regions, but do so primarily along wadis or in other mesic microsites (Holden, 1969; Zohary, 1969; personal communication; Blumler, unpublished). This should not be surprising, since the dry-farming limit for the domesticated derivatives of some of these species is about 240 mm (Perrin de Brichambaud

and Wallén, 1963), and wild plants probably need somewhat more rainfall than crops because they are not protected by humans from competition and grazing. Xeric ecotypes of Mediterranean annuals, such as the "wadi race" of wild barley (Harlan and Zohary, 1966), typically produce smaller seeds than mesic varieties of the same species (Blumler, 1992b). As Blumler (1992b) demonstrated, large seed size in winter annuals seems primarily related to shade and seedling competition in productive environments.

That aridity does not inherently favor large-seeded annuals is indicated also by the tendency of drought-tolerant crops to produce comparatively small seeds. For instance, the most xeric domesticated *Phaseolus*, the tepary bean (*P. acutifolius*), also has the smallest seeds – and the wild var. *tenuifolius* has smaller seeds than the more mesic var. *acutifolius* (Pratt and Nabham, 1988). Similarly, cowpea (*Vigna unguiculata*) varieties grown in comparatively dry regions of Africa manufacture smaller seeds than those of more mesic areas (Murray, 1984). In general, domesticated legumes derive from vining types (such as the Viciaeae) that have very large seeds probably to provide the necessary reserves to allow escape from shade and competition. Among the tropical cereals, the small-seeded pearl millet (*Pennisetum americanum*) is more drought tolerant than sorghum, which in turn is adapted to more xeric conditions than corn (Leonard and Martin, 1963; Harlan, 1989). Small-seeded forms of barley are preferred in the drier parts of Syria, and larger-seeded types are grown in more favorable regions (Ceccarelli *et al.*, 1987; Weltzien and Fischbeck, 1990).<sup>10</sup>

Nonetheless, seasonal drought is important in that it creates conditions that

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<sup>10</sup>Barley, which has large seeds, is often regarded as a very drought-tolerant temperate cereal; however, it is more accurate to label it drought-escaping, since it is physiologically no more tolerant of low soil moisture availability than wheat, but often yields better than the latter in seasonally-dry regions as a result of its rapid early growth and early maturity (Klages, 1942; Fischer, 1981).

allow annuals to compete effectively with perennials (Westoby, 1979/80; Blumler, 1984; 1992b; 1993). The environments that favor large-seeded annuals are xeric yet mesic: xeric enough in the dry season that perennial survival is problematic, yet mesic enough during the rainy season that vigorous, mesophytic annuals can form a lush carpet that excludes perennial seedlings, and later produce plentiful seed crops. Dry conditions during the periods of seed maturation and dormancy may also enhance the survival of large-seeded taxa by reducing the incidence of disease. Azzi (1956) stated that all crops maximize fertilization and seed set under clear, sunny skies; this is true even of rice (Turner and McCauley, 1983). Cereal production is problematic where rainfall is high, due to disease, poor soil (excessive leaching), lodging, and difficulty in land preparation (Leonard and Martin, 1963).

While the evolution of large-seeded annuals is favored by seasonal drought, the degree to which such evolution has occurred varies between regions; for instance, although California grasslands are large-seeded (Baker, 1972; Blumler, 1984; 1992b), Mediterranean/Near Eastern grasslands are far more so. Perhaps the absence of *Avena* and the genomically depauperate representation of Triticeae (Dewey, 1982) precluded the evolution of giant-seeded annual grasses in California and Chile, although *Bromus* made some evolutionary moves in that direction (Blumler, 1984).<sup>11</sup>

## 2. Seed Size, Seasonal Drought, and Agricultural Origins

Consider now the relationship between seasonal drought, large seed size, and

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<sup>11</sup>See Blumler (1992b) for additional hypotheses concerning the causes of evolutionary nonconvergence (especially as regards competitiveness in annual plants) between the Mediterranean and other regions of similar climate.

agricultural origins. All the centers of early agriculture are located in seasonally dry environments, which favor the evolution and dominance of annuals, especially large-seeded ones (Blumler, 1984; Byrne, 1987). The Fertile Crescent, which has the most extreme summer-dry climate in the world, and which dominates the list of large-seeded grasses, also is the region with the earliest soundly attested dates for domestication (van Zeist and Bakker Heeres, 1985; Zohary and Hopf, 1988). The two largest-grained Near Eastern grasses, wild emmer and wild barley, gave rise to what on present evidence were the initial Near Eastern domesticates: one or both appear at the basal agricultural levels of every early Neolithic site. Einkorn, derived from the largest-grained diploid member of the wheat group,<sup>12</sup> is also present very early (though not nearly so consistently). Secondary crops (rye and oats) derive from ancestors that appear nearer the bottom of Table 1. Annual legumes with large seeds also were early Near Eastern domesticates (e.g. Singh *et al.*, 1990).

Central Mexico also was an early agricultural center. Maize, derived from the region's only large-grained annual genus, is much earlier there than formerly realized. At first, the most primitive *Zea* at Tehuacan was incorrectly regarded as wild (Mangelsdorf *et al.*, 1964; Beadle, 1977; Iltis, 1983); in fact, it is the earliest certain domesticate in the archaeological sequence (see MacNeish, 1967; Pickersgill and Heiser, 1977). Squashes (*Cucurbita* spp.) and beans, which also produce large seeds, are also very early in the Mexican record (Whittaker, 1981; Byrne, 1987; Heiser, 1989). Sauer (1941) pointed out long ago that the Mesoamerican triumvirate of corn, beans, and squash is mesophytic, requiring high moisture availability during growth, and dry conditions during maturation.

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<sup>12</sup>*Triticum urartu* produces caryopses that appear to be slightly larger than those produced by the progenitor of einkorn (*T. boeoticum*), but these two taxa are so similar that there is considerable debate concerning whether they should be treated as separate species (D. Zohary, personal communication). It is safe to assume that hunter-gatherers would not have distinguished them.

On this basis, he suggested that the Pacific flank of the central Mexican highlands would be the area to search for agricultural beginnings. Thus far, archaeologists have paid little attention to this region, but it is now known that most teosinte populations are found there (Wilkes, 1967; Doebley, 1983), and that Mesoamerican forms of the common bean (*Phaseolus vulgaris*) probably originated there (Gepts, 1990; Blumler, 1992a).

Callen (1967) claimed that *Setaria geniculata*, a small-grained grass, was cultivated prior to maize at Ocampo, Tamaulipas. Since *S. geniculata* is a rhizomatous perennial, however, it is unlikely that it was ever cultivated. This may not be a crucial point, since species identification probably rested upon the presumption that it is the only *Setaria* at Ocampo today. Global climate models incorporating Milankovitch cycles suggest that climate was possibly more seasonally dry in the early Holocene (Byrne, 1987; COHMAP Members, 1988). Thus, annual *S. spp.*, such as are found at Tehuacan today (Callen, 1967), may have been common at Ocampo, too. Regardless, the actual evidence for cultivation and domestication of *Setaria* at Ocampo is weak. Callen's (1967:535) claim was based on the fact that "quite a number" of grains were unusually large. However, carbonization distorts seeds and usually causes size increases (Renfrew, 1973), while seeds that are boiled prior to carbonization will be larger than those that are not (King, 1987). Furthermore, it is not known if Callen compared his archaeological material to *S. spp.* other than *S. geniculata*. Finally, and most important, Callen presented no evidence that seed size increased over time in the Ocampo sequence, as one would expect if domestication were occurring.<sup>13</sup>

Peru has no grasses that manufacture large grains, apparently; domestication

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<sup>13</sup>A misleading statement in Callen's (1967) abstract is often mistakenly interpreted as indicating that he did find a seed size increase with time.

there seems to have begun with beans and perhaps chilis and cucurbits (Kaplan and Kaplan, 1988).<sup>14</sup> As in Mexico, these large-seeded crops were derived from annual or facultative annual ancestors (Smartt, 1969; Heiser, 1989; Nee, 1990). When agriculture spread to mediterranean Chile, a single cereal (the now extinct *Bromus mango*) was domesticated from a group that produces the largest-grained material available in that country.

Agriculture may have begun independently in several parts of monsoon Asia, or much of the region may have constituted a single interaction sphere (Higham, 1989). Along the Chinese coast, both domesticated rice and *Zizania caduciflora* (which probably produces large grains) are present at the earliest levels thus far excavated (Li, 1983; Zhimin, 1989). Apparently, there are no other large-grained wild grasses in China. The Indian and Southeast Asian sequences remain unclear (Higham, 1989), though there is evidence that rice was important early in both regions (Byrne, 1987); the timing of job's tears domestication is unknown. In general, then, agriculture originated in seasonally dry climates via cultivation of large-seeded annual species (grasses, legumes, and cucurbits).

Subsaharan Africa developed agriculture comparatively late, probably in part as a result of diffusion from the Near East (Clark, 1976; Blumler, 1992a). It has an appropriate, seasonally-dry climate — more so than East Africa, for instance — but only a few large-grained grasses. Many cereals, of varying seed size, were domesticated. Archaeological evidence sheds little light on the domestication sequence, but it is clear that sorghum was one of the first, if not the first cultivated grains there (Harlan, 1975; Harlan *et al.*, 1976; Clark, 1976; Vishnu-Mittre, 1977). In the subsaharan African grass flora, only rice produces larger

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<sup>14</sup>Tubers also may have been important, but the archaeological record is less forthcoming concerning their use. Wilson's (1990) claim that quinoa (*Chenopodium quinoa*), a small-seeded grain, is an ancient primary crop is not supported by the archaeological evidence (Pearsall, 1989) which suggests domestication about 1600 BC.

grains than wild sorghum; but hydrological control difficulties probably precluded rice cultivation initially. In any case, it is my contention that small-grained grasses are most likely to be taken under cultivation as secondary crops, after diffusion of agriculture into a region – as almost certainly occurred in Africa.<sup>15</sup>

A possible illustration of this point is the only apparent exception to the rule that initial independent invention of agriculture involved large-seeded annual taxa: north China. The small-seeded millets (*Setaria italica* and *Panicum miliaceum*) associated with north Chinese early Neolithic sites are derived from annual ancestors. It is possible that in the loess region natural disturbance was so pervasive that these species were abundant prior to the initiation of the farming; if so, they could have been staple foods for hunter-gatherers. However, the archaeological sequence is still poorly understood, and proof of independent agricultural origins is lacking. For instance, the important Yang-Shao site of Pan-p'o, from which millets have been reported, also supposedly yielded chinese cabbage (*Brassica chinensis*) (Li, 1983). This species is a hybrid between two mustards, and is of recent origin; furthermore, it is doubtful that any *B. spp.* are native to China, which does not have an appropriate climate for the survival of winter annuals in the absence of disturbance. Rather, mustards may have come in from the west with wheat or other Near Eastern agricultural products (possibly via India [Song *et al.*, 1990]). Since wheat is a late introduction to China (Ho, 1977), the dating of Pan-p'o and other early Neolithic sites with reported mustard finds (Chang, 1983; Zhimin, 1989), and their supposed independence

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<sup>15</sup>Wheat and barley are poorly suited to conditions in Africa, except in Ethiopia (where teff is cultivated) and the Saharan massifs (where wild pearl millet grows); thus, most African cereals are probably not secondary domesticates in the Vavilovian sense of the term. However, the pastoralists who spread into Africa with Near Eastern animals were almost certainly familiar with agriculture, so any subsequent cultivation experiments with local grasses would have been secondary in a more general sense.

from earlier agricultural experiments elsewhere, are questionable. Although it is often stated that both *S. italica* and *P. miliaceum* are characteristic of the Chinese Neolithic, the latter is only rarely and uncertainly reported;<sup>16</sup> *S. italica* is genetically surprisingly uniform in China, but is more variable in Central Asia and Europe (De Wet *et al.*, 1979). Thus, domestication of foxtail millet may well have taken place to the west.

Millet agriculture also could be derived from the east. The early rice-growing site of Homutu (south of the Yangtze) is on a drowned seacoast, and clearly postdates the initial agricultural phase (Chang, 1983); that is, the origins of south Chinese agriculture are older than presently dated. Furthermore, the earliest millet culture of the north shows some cultural similarities to the south and the coast, and may be derivative (Ho, 1977; Chang, 1983). It may be that rice farmers spread as far as the Wei River Valley, where the crop would have been marginal, and were then forced to domesticate some other food resource. If so, the domestication of foxtail millet would be another example of secondary domestication of a relatively small-seeded taxon. Zhimin (1988) reported that domesticated rice has been found in the earliest Neolithic in the north, although the exact sequence or quality of the evidence was not discussed.

In any case, it is by no means certain that the millet finds in north China actually represent domesticated grains. That the Chinese should believe so fervently in the independent origins of millet agriculture is not surprising, since it developed near the seat of the first Chinese empire at Xian, the traditional hearth of the Han people. The region south of the Yangtze, on the other hand, apparently was not settled by the Han until much later.

The midwestern United States may also constitute an exception. This is the

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<sup>16</sup>See the discussion in Ho (1977).

only putative example of a center of agricultural origins that lacks significant seasonal drought, and hence it is also a region in which large-seeded annuals are unimportant. Opinions concerning the independence of agricultural origins there from events in Mexico swing rapidly back and forth with each new archaeobotanical find (Ford, 1985; Nee, 1990; Smith, 1990; Wilson, 1990). A *Cucurbita* sp. was present from a very early date, but there is considerable controversy concerning whether this was *C. texana* or the domesticated *C. pepo*, diffused from Mexico. Watson (1989) claimed that although possibly domesticated, this squash was used only as a container and not as a food plant; this is implausible, however, because its large, nutritious seeds would have been very attractive (Heiser, 1985; 1989). Smith (1990) and others believe that in the midwestern United States domestication began during the second millennium B.C., when several smaller-seeded native annuals appear to increase in seed size, and that this development was entirely independent. However, maize had already diffused as far south as Ecuador and Peru by that time (Zevallos *et al.*, 1977; Kaplan and Kaplan, 1988). It is unlikely that it would not also have reached the Midwest, unless unable to adapt to temperate climatic conditions. Furthermore, one of the “native” domesticates was closely related to and not necessarily distinct from an important Mexican crop, *Chenopodium berlandieri* subsp. *nuttalliae* (Wilson, 1990). The latter would probably have been better adapted to temperate latitudes than corn, as would have Mexican *Cucurbita pepo* (see Nee, 1990). Mesoamerican agriculturalists probably had already attempted to move up the Mississippi valley; agricultural beginnings there were probably the result of diffusion of the idea of cultivation, if not of actual crop plants. Thus, the rule that seasonal drought is a precondition for agricultural origins (Byrne, 1987) appears to be valid.

I believe it is no coincidence that agriculture started at an early date in the

Mediterranean region, while it only spread to California with the arrival of the Spanish.<sup>17</sup> Those seasonally dry regions that never developed agriculture, such as California and much of Australia, have almost no large-seeded grasses. The single exception to this rule is southern Iberia/Morocco, which supports two rare, locally distributed wild oat species with very large caryopses. Perhaps this region was impacted by Near Eastern developments at such an early date that there was no time for indigenous agriculture to arise. Alternatively, it may be that the two large-seeded wild oats were not distinguished from the much more ubiquitous *A. sterilis*, which is of marginal seed size for a primary cereal crop.<sup>18</sup>

Wildrice ranges south as far as the Gulf of Mexico (Dore and McNeill, 1980), but seems to be most abundant in northern regions where snowmelt causes large annual fluctuations in lake levels – which reduces competition from perennials in a manner analogous to the effect of seasonal drought (see Schultz, 1978). Although such an important staple that wars were fought over access to the best stands (Schultz, 1978), wildrice was not domesticated until recently, perhaps because of the absence of seasonal drought in its distribution area. Alternatively, it may be that hunter-gatherers would have found it impossible to exert the necessary hydrological control. Certainly, wildrice's modern domestication was accomplished only with difficulty, despite intentional plant breeding (Fernald *et al.*, 1958; Schulz, 1978). On the other hand, there are claims that the related *Zizania caduciflora* was domesticated at a very early date in China (Li, 1983). Today this plant is grown exclusively as a stem vegetable, but it may have been

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<sup>17</sup>Indians along the Colorado River and in adjacent southern California practiced agriculture (Bean and Lawton, 1973; Shipek, 1989), but this, too, was clearly a recent phenomenon, the result of diffusion from the Southwest.

<sup>18</sup>That the two tetraploid *Avena* spp. were only recently discovered and classified, and then only as a result of intensive gathering of wild cereal genetic material (Murphy *et al.*, 1968; Ladizinsky, 1971), suggests that hunter-gatherers would not have distinguished them from *A. sterilis*.

used as a grain in the past, prior to the rise to overwhelming dominance of rice. The fungus infection that causes it to become a succulent vegetable also prevents it from producing seeds (Thrower and Chan, 1980), so it would not be as high-yielding as rice if cultivated as a cereal.

### 3. Why Large-Seeded Annuals?

It is often assumed that large seeds are preferred by hunter-gatherers (e.g. Hawkes, 1969), and to some extent this is probably true; however, small-seeded taxa are also often used as staples (Bohrer, 1975; Harlan, 1975; Harris, 1984; Harris and Hillman, 1989). Typically, large seeds are enclosed in heavy, difficult to remove husks (Fenner, 1983), presumably to minimize their attractiveness to birds, rodents, and other granivores. It is difficult to imagine how job's tears, for instance, could have been processed for food efficiently prior to the evolution of the soft-shelled domesticate. Wild barley has thin but tightly adherent pales that are difficult to remove.<sup>19</sup> Harlan (1967) reported that wild einkorn spikelets have 46 % nutritive tissue (grains), while the smaller-seeded *Aegilops speltoides* produces spikes with only about 10 % grain content. This huge disparity is almost certainly due to sampling error, however.<sup>20</sup> It certainly is not a general rule that large-seeded species have a relatively high investment in nutritive as opposed to inedible (husk) tissue; in fact, the opposite is usually the case (Fenner, 1983). For the most part, hunter-gatherers probably select their staples according to stand density and ease of processing, not seed size. Small seeds that fall free

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<sup>19</sup>Perhaps parching would do the trick. Barley is the grain of choice in the production of beer (the pales are beneficial for this purpose), possibly in part because of the difficulties encountered in processing it for food.

<sup>20</sup>Since it is an outcrosser, isolated individuals of *Ae. speltoides* might have very poor seed set.

of the husk, such as those of *Sporobolus* (dropseed), are often collected avidly. Thus, it is unlikely that large-grained plants were domesticated first because gatherers preferred such species. Furthermore, if such preference tends to lead to agriculture, then one would expect that gatherers around the globe would have developed agriculture independently, by taking the largest-grained taxon (which might manufacture quite small seeds) in a given region under cultivation. Instead, agriculture originated only, or primarily, in areas that had unusually large-seeded annual grasses and legumes.

Large seeds are relatively easy to cultivate. For example, wheat and barley are introduced crops in Ethiopia, where they are not considered to be as good food as teff (*Eragrostis tef*), which makes the best injera (Simoons, 1960). The grains of teff average only about 0.4 mg (Simoons, 1960), and a great deal of care is needed in field preparation prior to planting to ensure a good stand; in addition, teff is a poor competitor against weeds, but is difficult to hand weed because it is broadcast sown (Mersie and Parker, 1983). It probably cannot be sown in rows, however, because burial would be a problem: small seed size precludes successful emergence from all but the shallowest depths.

Also, wild annuals that produce large seeds often are very abundant, and hence, excellent food resources (e.g. Harlan and Zohary, 1966; Zohary, 1969). The tendency of these species to dominate large stretches of the landscape is probably associated with competitive ability conferred in part by their large seeds. At the same time, vegetation dominated by annual plants is relatively easy to clear with primitive tools; Sauer's (1952) point that a dense perennial grass sod would have been uncultivable during early agricultural stages is well-taken, although he erred in assuming that Near Eastern grasslands were

perennial-dominated, hence that agriculture must have diffused into the region.<sup>21</sup>

Although large seed size is clearly associated with agricultural beginnings, not all large-grained grasses within any given region were domesticated. In particular, only one member of the sibling species pairs *Triticum dicoccoides*/*T. araraticum*, *T. boeoticum*/*T. urartu*, and *Zea mays*/*Z. luxurians* was domesticated (Blumler, 1992a).<sup>22</sup> Within *Z. mays*, an endemic variety of *ssp. parviglumis* seems to be the sole progenitor (Doebley, 1990). These species pairs display only slight morphological differentiation, and almost certainly would have been classified as single taxa by hunter-gatherers. However, their distributions are almost, or entirely, allopatric (Doebley, 1983; Chapman, 1985; Miller, 1987) – that is, large regions are almost exclusively populated by the member of each species pair that was not domesticated. That only one member of each species pair was domesticated is strong evidence against Harlan's (1975; 1986) extreme independent inventionist views, but tends to support Zohary's (1989; Zohary and Hopf, 1988) diffusionist perspective (Blumler, 1992a).

## V. Conclusions

These results and discussion suggest that several widely-held beliefs concerning evolution under domestication are invalid. For instance, a dramatic increase in seed size is universally said to be a consequence of domestication (Schwanitz, 1966; Smartt, 1969; Evans and Dunstone, 1970; Harlan *et al.*, 1973; Evans, 1975; Lush and Wien, 1980; Cook and Evans, 1983; Donald and Hamblin,

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<sup>21</sup>Of course, Sauer based his belief that the region is naturally dominated by perennials upon the unanimous (but mistaken) assertions of the greatest authorities on Mediterranean/Near Eastern vegetation (Blumler, 1984; 1992b).

<sup>22</sup>*Triticum araraticum* eventually gave rise to the half-weed *T. timopheevii*, which is cultivated to a limited extent in Soviet Georgia (Zohary, 1989).

1983; Murray, 1984; Rindos, 1984). While this certainly has occurred in some cases (such as maize and the larger varieties of faba beans), the progenitors of our earliest crops already had unusually large seeds; further increases in mean weight may have been partly phenotypic, due to improvement in growing conditions during seed ripening (see Helbaek, 1959; Blumler, 1992b). Cook and Evans (1983) claimed that seed size increased during domestication in rice, but their empirical data show the opposite trend in the African species. In the wheat group, increase in grain weight is sometimes traced by comparing wild diploid *Aegilops* spp. or *Triticum boeoticum* to modern polyploid cultivars (e.g. Evans and Dunstone, 1970; Dunstone and Evans, 1974; Donald and Hamblin, 1983); however, there is no evidence that wild einkorn was taken under cultivation before wild emmer (in fact, the opposite seems to be the case [Harlan, 1975; van Zeist and Bakker-Heeres, 1985; Blumler and Byrne, 1991]). Some forms of the latter produce grains that are approximately the same size as those of bread wheat.<sup>23</sup> Thus, much of the increase in seed size in the wheat group occurred prior to cultivation. A trend of increasing grain weight with increase in ploidy level can also be traced in *Aegilops* (Fritsch *et al.*, 1977), and in fact is even more pronounced than in *Triticum*.<sup>24</sup>

Grain size increases that did occur under domestication, such as from wild to cultivated einkorn and within the tetraploid wheat group, were associated with changes in grain shape (Dunstone and Evans, 1974). Wild Near Eastern cereal caryopses tend to be narrow and elongate, because they are fitted into diaspores that must attempt to drill themselves into the ground; with domestication, pales and glumes no longer need to be so tightly enveloping, and grains become fatter

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<sup>23</sup>Some forms of wild emmer produce still larger seeds, but these almost certainly are the result of introgression from durum (Blumler, 1998).

<sup>24</sup>Increase in size of plant parts is one of the most common effects of polyploidy.

(Blumler, 1998). This is particularly true in the 'naked' or free-threshing species, such as *Triticum durum* and *T. aestivum*. On the other hand, increase in grain number per spikelet becomes possible with the loosening of the glumes; this probably explains the relatively small mean seed weight of bread wheat, since its basal grain does not seem to be significantly smaller than that of durum (see Dunstone and Evans, 1974). In short, there is no reason to believe that increases in mean grain weight in cultivated wheats were necessarily adaptive, except in increasing harvest index.

Crop geneticists sometimes assume, without evidence, that small-seeded genotypes of crop progenitors are truly wild, or primitive, while large-seeded varieties are advanced, often the products of introgression or the result of selection for crop mimicry; paleobotanists may make similar assumptions concerning the archaeological record. The evidence presented here suggests, however, that seed size evolution did not always follow a simple, linear pattern. Kaplan and Kaplan (1988) noted that domesticated common beans are much larger than their progenitors from the beginning of the archaeological sequence, both in Mexico and South America, yet they do not continue to increase in seed size afterwards. They suggested that reduction in bruchid parasitism rates during the transition to agriculture caused a rapid increase in seed size. While this is possible, an alternative possibility is that wild seeds were even larger in the early Holocene than today, because of the increased seasonality of precipitation/evaporation regime due to Milankovitch cycles (cf. Byrne, 1987).

Harlan (1975) suggested that the lower protein content (on a percentage basis) of domesticated grains is partly due to selection for increased yield. In this regard, transfer of assimilate from diaspore husk to grain could account for the increase in carbohydrate content with grain size increase under domestication, since husks have lower protein content than their seeds. Harlan (1975; Harlan *et*

*al.*, 1973) also asserted that domesticated species need larger seeds because competition is severe in cultivated fields, and claimed mistakenly that the increase in carbohydrate and decrease in protein percentage would increase vigor (cf. Ries and Everson, 1973; Chapin *et al.*, 1989; Blumler, 1992b). Seedling density in cultivated fields is lower than in annual grasslands, however; hence, initial competitive interactions are less severe under cultivation. Thus, an adaptive explanation for seed size increase may be invalid, at least with respect to the primary domesticates discussed here. On the other hand, increase in seed size of less competitive taxa such as legumes and many secondary domesticates may possibly be related to selection for competitiveness against weeds, or perhaps for successful emergence after burial during sowing (shade-tolerance).

Also, it is sometimes said that cultivation has caused the evolution of annual domesticates from perennial ancestors (Ames, 1939; Morishima, 1984; Rindos, 1984). This view has been dying out, as a result of the excellent genetic research of the last few decades, which has established that the progenitors of many domesticates were annuals. Cotton, flax, and a few other species are descended from perennial or biennial taxa, but most of the progenitors of our earliest crops were already annuals – though they may have only recently evolved the annual habit, in response to increasing seasonality of precipitation (Byrne, 1987).

Finally, many scholars have argued that people domesticated weedy plants – plants that had already adapted to human disturbance, and were in some degree of symbiotic association with people, prior to the initiation of cultivation (Engelbrecht, 1916; Anderson, 1952; Hawkes, 1969; Evans, 1975; Harlan, 1975; 1979; Rindos, 1984). While this is certainly true of many secondary domesticates, the progenitors of our first crop plants are surprisingly well-adapted to undisturbed conditions, and in some cases do not seem to be weedy at all (Blumler and Byrne, 1991). This is true, for instance, of wild emmer and the

progenitors of lentils, chickpeas, and faba beans (Zohary, 1969; Zohary and Hopf, 1973; 1988; Sakamoto, 1982; Blumler, unpublished), while Harlan's (1975; 1979; Harlan and Zohary, 1966; Harlan *et al.*, 1973) oft-repeated claim of a weed "race" of wild barley is without empirical support (Blumler and Byrne, 1991).<sup>25</sup> Given its restriction to aquatic habitats, *Oryza* also probably was not weedy prior to cultivation.

Hawkes (1969) recognized that agriculture arose in seasonally dry regions, and realized also that perennials are disfavored in such environments; he further anticipated the present treatment in recognizing that the evolution of large seed size in annual plants predisposed those plants to be taken under cultivation. However, he mistakenly believed that the progenitors of our earliest domesticates are found only on poor soils (in fact, the opposite is usually the case [Zohary, 1969; Blumler, unpublished]), and are weedy. As a corollary, perhaps, he assumed that large seed size was needed to reduce the effects of desiccation during the hot dry season; but in fact, desiccation of seeds appears to be only a minor problem during a single season, and small seeds are probably at least as tolerant as large ones.<sup>26</sup> Furthermore, adaptation to disturbance generally requires the production of many small seeds, to ensure that gaps will be colonized (Harper *et al.*, 1970). The large seed size of the progenitors of our earliest crops seems to fit them for the role of competitive dominant in seasonally

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<sup>25</sup>Harlan (1975) admitted that the "weedy" forms of wild barley cannot be distinguished from nonweedy types, and he never provided any evidence that plant density in cultivated fields or other disturbed sites is greater than it would be if disturbance were excluded. That a species is able to persist, at a reduced density, after disturbance is not sufficient grounds for labeling it a weed (Blumler and Byrne, 1991).

<sup>26</sup>The large seeds of many tropical rain forest trees become inviable upon drying (as do acorns); however, these differ physiologically from seeds that "expect" to remain dormant through a dry season.

dry climates, not for ruderal weediness.<sup>27</sup>

Aside from trends towards increased harvest index, and the loss of dispersal mechanisms and dormancy, it is surprising how little evolution has occurred in our domesticated species. For instance, a number of physiological studies have failed to show consistent differences between wild and domesticated species, and for the most part those differences that have been observed do not seem terribly significant – though much is often made of them (Evans and Dunstone, 1970; Khan and Tsunoda, 1970ab; Dunstone *et al.*, 1973; Dunstone and Evans, 1974; Evans, 1976; Lush and Wien, 1980; Cook and Evans, 1983; Bloom, 1985; Chapin *et al.*, 1989).

I have attempted to show here that there may be a one-to-one, or almost one-to-one, correspondence between the evolution of large-seeded annual grasses and legumes in seasonally dry environments, and the initiation of the process leading to agriculture. This is perhaps an extreme position, but it is nonetheless clear that there is a remarkable association between seed size, the annual habit, and successful evolutionary transformation into primary domesticate.<sup>28</sup>

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<sup>27</sup>Some crop weeds produce very large seeds, which are adaptive because they are harvested and sown along with the crop. With the spread of modern mechanical seed-cleaning techniques, these species are rapidly disappearing (Salisbury, 1961; Holzner and Numata, 1982), and are being replaced by more typical ruderals with smaller seeds (Blumler, unpublished).

<sup>28</sup>Whyte (1977) made the somewhat similar argument that agriculture developed after annual plants evolved in response to increasing aridity at the end of the Pleistocene. However, drought *per se* does not favor the annual habit (Blumler, 1984); nor does it favor large seed size in annuals. Seasonal drought does (Westoby, 1979/80; Blumler, 1984; 1992b).

Alternatively, one could argue that seasonal drought is the key characteristic that forces the adoption of agriculture, perhaps because pronounced seasonality of climate might accentuate the need for food storage. In that case, however, one would expect that agriculture would have begun at an early date in other seasonally dry environments, such as California and central Chile, that did not have a great deal of large-seeded material available. Similarly, one could hypothesize that the rise of annual-dominated herbaceous associations, such as are so ubiquitous in the Fertile Crescent, was of crucial importance – if only because such vegetation could be manipulated relatively easily in the absence of the plow. The wild Near Eastern cereal grasses characteristically form dense stands in the absence of disturbance, and thus would have been an excellent resource. The north Chinese millets also may have been locally abundant, despite their small seed size, because of the erodability of the loess plateau. However, the Peruvian sequence does not seem to fit this hypothesis, which also would predict domestication in parts of Australia, where *Sorghum* spp. and other annuals are often abundant (Andrew and Mott, 1983). Thus, environment (the development of seasonally dry climates) and evolution (of large-seeded annual competitive dominants) both may have been crucial to the origins of agriculture, while population pressure and cultural/technological development may have been secondary.

Table 1. The world's heaviest-seeded wild grasses (excluding the bamboos).<sup>a</sup>

Species	Common Name	Life Form	Grain Weight <sup>b</sup>	Native Distribution <sup>c</sup>	Derived Crop	Source <sup>d</sup>
<i>Coix gigantea</i>	Job's tears	P?	> 40	SE Asia		20
<i>Coix lacryma-jobi</i>	Job's tears	A/P	40	SE Asia	Job's tears	8, 13
<i>Avena magna</i>	Wild oats	A	35	S. Spain		27, 38
<i>Hordeum spontaneum</i>	Wild barley	A	35	Near East	Barley	1, 8
"wadi race"			20	Palestine		1, 8
<i>Zea luxurians</i>	Teosinte	A	35	Guatemala		12, 39
<i>Zea mays</i>	Teosinte	A	35	Mexico, Guat.	Maize	12, 13, 37, 39
<i>Zea perennis</i>	Teosinte	P	35	C. Mexico		12
<i>Zizania aquatica</i>	Wildrice	A	35	E. U.S.		37
<i>Zizania palustris</i>	Wildrice	A	35	Canada, E. U.S.		8
<i>Avena murphyi</i>	Wild oats	A	30	Morocco		
<i>Lygeum spartum</i>	Esparto	P	30	Mediterranean	8	
<i>Tripsacum dactyloides</i>	Gamagrass	P	30	New World		12, 37
<i>Triticum dicoccoides</i>	Wild emmer	A	25	Fertile Crescent	Most wheats	4, 8, 9, 14, 15, 17, 21, 23, 28, 34
<i>Zea diploperennis</i>	Teosinte	P	25	C. Mexico		8, 12
<i>Triticum araraticum</i>	Wild emmer	A	22	Near East	<i>T. timopheevi</i>	8, 15, 21, 34
<i>Aegilops triaristata</i>	Goatgrass	A	20	MedNE		8, 15, 24
<i>Oryza barthii</i>	Rice	A	20	West Africa	African rice	10
<i>Stipa spartea</i>	Porcupine grass	P	20	Great Plains		36
<i>Aegilops peregrina</i>	Goatgrass	A	19	E. Med./Nr. E.		8, 15
<i>Triticum urartu</i>	Wild einkorn	A	17	Fertile Crescent		8, 15
<i>Oryza stapfii</i>	Rice	A	16	West Africa		10
<i>Aegilops columnaris</i>	Goatgrass	A	15	Asia Minor		15
<i>Aegilops crassa</i>	Goatgrass	A	15	Near East		7, 15
<i>Avena fatua</i>	Wild oats	A	15	N. Med, C. Asia	Oats	8, 18, 19, 29, 35
<i>Avena sterilis</i>	Wild oats	A	15	MedNE	Oats	8, 27, 30
<i>Stipa pennata</i>		P	15	MedNE/Balkans		31
<i>Stipa lagascae</i>		P	15	MedNE		6, 8, 31
<i>Triticum boeoticum</i>	Wild einkorn	A	15	Near East	Einkorn wheat	6, 8, 9, 14, 15
<i>Aegilops comosa</i>	Goatgrass	A	14	Aegean		8, 9, 15
<i>Oryza spontanea</i>	Rice	A	14	Southeast Asia	10	
<i>Aegilops geniculata</i>	Goatgrass	A	13	MedNE		8, 11, 15, 25
<i>Aegilops juvenalis</i>	Goatgrass	A	13	Near East		15
<i>Avena longiglumis</i>	Wild oats	A	13	S. Mediterranean		7
<i>Bromus diandrus</i>	Ripgut brome	A	13	MedNE		5, 8, 16
<i>Sorghum intrans</i>		A	13	North Australia		2
<i>Sorghum stipoides</i>		A	13	North Australia		8
<i>Aegilops cylindrica</i>	Jointed goatgrass	A	12	Near East		6, 15
<i>Oryza nivara</i>	Rice	A	12	SE Asia	Rice	10
<i>Aegilops biuncialis</i>	Goatgrass	A	11	MedNE		8, 15
<i>Aegilops kotschyii</i>	Goatgrass	A	11	Near East		8, 15
<i>Aegilops triuncialis</i>	Barb goatgrass	A	11	MedNE		6, 8, 15, 25
<i>Bromus stamineus</i>	Chilean brome	A/P	11	C. Chile	<i>B. mango?</i>	8
<i>Rottboellia exaltata</i>		A	11	Southeast Asia	32, 33	
<i>Secale montanum</i>	Rye	P	11	MedNE	Rye	6, 8

<i>Spartina anglica</i>	Cordgrass	P	11	England		26
<i>Bromus willdenowii</i>	Rescue grass	A/P	10.5	Arg., Chile	<i>B. mango?</i>	5, 6, 8, 13

**Table 1** (cont'd). The world's heaviest-seeded wild grasses (excluding the bamboos).<sup>a</sup>

Species	Common Name	Life Form	Grain Weight <sup>b</sup>	Native Distribution <sup>c</sup>	Derived Crop	Source <sup>d</sup>
<i>Hystrix californica</i>	Cal. bottlebrush	P	10.5	C. California		8
<i>Aegilops squarrosa</i>	Goatgrass	A	10	Near East	Bread wheat	14, 15
<i>Aegilops umbellulata</i>	Goatgrass	A	10	Near East		9, 15
<i>Aegilops uniaristata</i>	Goatgrass	A	10	N. E. Med.		9, 15
<i>Aegilops ventricosa</i>	Goatgrass	A	10	Mediterranean		15
<i>Lolium temulentum</i>	Darnel	A	10	MedNE		7, 8, 22
<i>Oryza rufipogon</i>	Rice	P	10	Southeast Asia		10
<i>Sorghum bicolor</i>	Sorghum	A	10	N. + E. Africa	Sorghum	22
<i>Sorghum sudanense</i>	Sudangrass	A	10	Africa		3
<i>Stipa gigantea</i>		P	10	Mediterranean		8

<sup>a</sup>The following taxa, for which data were not available, may also produce large caryopses: *Coix* spp., *Oryza* spp., *Tripsacum* spp., perennial *Zizania* spp., and a few *Stipa*, *Spartina*, and annual *Secale* spp.

<sup>b</sup>Estimated approximate mean kernel (caryopsis) weight, in milligrams, when growing under favorable conditions.

<sup>c</sup>Distributional/ecological data from: Hitchcock, 1950; Munz and Keck, 1959; Bor, 1960; 1968; Zohary, 1965; 1969; personal communication; Harlan and Zohary, 1966; Harlan *et al.*, 1976; Murphy *et al.*, 1968; Ladizinsky, 1971; Baum *et al.*, 1972; Chang, 1976; Thurston and Phillipson, 1976; Dore and McNeill, 1980; Vecchio *et al.*, 1982; Andrew and Mott, 1983; Doebley, 1983; Morishima, 1984; Chapman, 1985; Clayton and Renvoise, 1986; Miller, 1987; Dean, n.d.; and Blumler, unpublished.

<sup>d</sup>1) Ahokas, 1982; 2) Andrew and Mott, 1983; 3) Association of Seed Analysts, 1981; 4) Avivi, 1979; 5) Baker, unpublished; 6) Barclay and Earle, 1974; 7) Bar-Yosef and Kislev, 1989; 8) Blumler, 1992b; 9) Brody, 1983; 10) Cook and Evans, 1983; 11) Datta *et al.*, 1970; 12) Doebley, 1984; 13) Earle and Jones, 1962; 14) Evans and Dunstone, 1970; 15) Fritsch *et al.*, 1977; 16) Gordon *et al.*, 1989; 17) Grama *et al.*, 1983; 18) Grime *et al.*, 1981; 19) Gulmon, 1979; 20) Jain and Banerjee, 1974; 21) Jakubziner, 1932; 22) Jones and Earle, 1966; 23) Kushnir and Halloran, 1984; 24) Marañón, 1987a; 25) Marañón, 1987b; 26) Mullins and Marks, 1987; 27) Murphy *et al.*, 1968; 28) Percival, 1921; 29) Peters, 1985; 30) Rezai, 1977; 31) Ruiz del Castillo *et al.*, 1970; 32) Schwerzel, 1970a; 33) Schwerzel, 1970b; 34) Sharma *et al.*, 1981; 35) Stevens, 1932; 36) Stevens, 1957; 37) The Yearbook of Agriculture, 1948; 38) Thomas *et al.*, 1980; 39) Wilkes, 1967. Data averaged and adjusted to produce estimated mean grain weight (fourth column), based on conditions under which seeds were collected, sample size, part weighed (naked caryopsis or with part or all of enclosing pales), sources of variability (heterocarpic, other phenotypic, and genetic), and degree of freedom from introgression from cultivated relatives. For raw data, see Blumler (1992b).

Table 2. Heavy-seeded wild grasses that can be found in natural habitats in the Fertile Crescent deciduous oak-park zone.

*Aegilops biuncialis*  
*Ae. columnaris*  
*Ae. crassa*  
*Ae. cylindrica*  
*Ae. geniculata*  
*Ae. kotschyii*  
*Ae. peregrina*  
*Ae. triaristata*  
*Ae. triuncialis*  
*Ae. umbellulata*

*Avena longiglumis*  
*A. sterilis*  
*Bromus diandrus*  
*Hordeum spontaneum*  
*Secale montanum*  
*Stipa lagascae*  
*Triticum araraticum*  
*T. boeoticum*  
*T. dicoccoides*  
*T. urartu*

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