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ARTICLES

# WAS AGRICULTURE IMPOSSIBLE DURING THE PLEISTOCENE BUT MANDATORY DURING THE HOLOCENE? A CLIMATE CHANGE HYPOTHESIS

Peter J. Richerson, Robert Boyd, and Robert L. Bettinger


*Several independent trajectories of subsistence intensification, often leading to agriculture, began during the Holocene. No plant-rich intensifications are known from the Pleistocene, even from the late Pleistocene when human populations were otherwise quite sophisticated. Recent data from ice and ocean-core climate proxies show that last glacial climates were extremely hostile to agriculture—dry, low in atmospheric $CO_2$, and extremely variable on quite short time scales. We hypothesize that agriculture was impossible under last-glacial conditions. The quite abrupt final amelioration of the climate was followed immediately by the beginnings of plant-intensive resource-use strategies in some areas, although the turn to plants was much later elsewhere. Almost all trajectories of subsistence intensification in the Holocene are progressive, and eventually agriculture became the dominant strategy in all but marginal environments. We hypothesize that, in the Holocene, agriculture was, in the long run, compulsory. We use a mathematical analysis to argue that the rate-limiting process for intensification trajectories must generally be the rate of innovation of subsistence technology or subsistence-related social organization. At the observed rate of innovation, population growth will always be rapid enough to sustain a high level of population pressure. Several processes appear to retard rates of cultural evolution below the maxima we observe in the most favorable cases.*

*Varias trayectorias independientes de la intensificación del sustento, muchas de las cuales conducieron a la agricultura, empezaron durante el Holoceno. No conocemos ninguna intensificació que usara muchos recursos vegetales durante el Pleistoceno, incluyendo el Pleistoceno último, cuando las poblaciones humanas fueron muy sofisticadas en otros ámbitos. Datos recientes de cilindros de hielo sacados de Groenlandia, y de sedimentos oceánicos, muestran que la última glaciación fué extremadamente hostil a la agricultura, ya que fué—seca, baja en $CO_2$, y extremadamente variable en el corto plazo. Proponemos que la agricultura fué imposible en estas condiciones de la última glaciación. La súbita mejora del clima al final de la glaciación fué seguida inmediatamente por la iniciación de usos mas intensivos de los recursos vegetales en algunos lugares, aunque mucho mas tarde en otras partes. Casi todo les trajectores de intensificación en el Holoceno eran occurrieron sin retroceso. Finalmente, la agricultura se convirtió en el modo principal de sustento en todas partes, excepto por zonas muy frías o muy secas. En el Holoceno, hacemos el hipótesis que la agricultura se vuelve, a final de cuentas, obligatoria. Usamos un análisis matemático para formular el hipótesis que los procesos limitante de la taza de intensificación debe generalmente ser la taza de la inovación tecnológica en las estrategias de sustento, o la taza de inovación en las formas de organazación social en relación al sustento. Con las tazas de inovación que se observan, el crecimiento de la población siempre es suficientemente rapido como para crear alto nivel de presión poblacional. Al parecer, varios processos normalmente retardan la velocidad de la evolución cultural abajo de las tazas máximas que observamos en el modelo.*


Evolutionary thinkers have long been fascinated by the origin of agriculture. Darwin (1874) declined to speculate on agricultural origins, but twentieth-century scholars were bolder. The Soviet agronomist Nikolai Vavilov, the American geographer Carl O. Sauer, and the British archaeologist V. Gordon Childe wrote influential books and papers on the origin of agriculture in the 1920s and 1930s (see Flannery 1973 and MacNeish 1991:4–19 for the intellectual history of the origin of agriculture question). These explorations were necessarily speculative and vague, but stimulated interest in the question.


**Peter J. Richerson** ■ Department of Environmental Science and Policy, University of California–Davis, Davis, CA 95616, pjricherson@ucdavis.edu
**Robert Boyd** ■ Department of Anthropology, University of California–Los Angeles, Los Angeles, CA 90095, rboyd@anthro.ucla.edu
**Robert L. Bettinger** ■ Department of Anthropology, University of California–Davis, Davis, CA 95616, rlbettinger@ucdavis.edu


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Immediately after World War II, the American archaeologist Robert Braidwood (Braidwood et al. 1983) pioneered the systematic study of agricultural origins. From the known antiquity of village sites in the Near East and from the presence of wild ancestor species of many crops and animal domesticates in the same region, Braidwood inferred that this area was likely a locus of early domestication. He then embarked on an ambitious program of excavation in the foothills of the southern Zagros Mountains using a multidisciplinary team of archaeologists, botanists, zoologists, and earth scientists to extract the maximum useful information from the excavations. The availability of $^{14}C$ dating gave his team a powerful tool for determining the ages of the sites. Near Eastern sites older than about 15,000 B.P. excavated by Braidwood (Braidwood and Howe 1960) and others were occupied by hunter-gatherers who put much more emphasis on hunting and unspecialized gathering than on collecting and processing the seeds of especially productive plant resources (Goring-Morris and Belfer-Cohen 1998; Henry 1989). Ages are given here as calendar dates before present (B.P.), where present is taken to be 1950, estimated from $^{14}C$ dates according to Stuiver et al.'s (1998) calibration curves. The Braidwood team showed that about 11,000 years ago, hunter-gatherers were collecting wild seeds, probably the ancestors of wheat and barley, and were hunting the wild ancestors of domestic goats and sheep. At the 9000 B.P. site of Jarmo, the team excavated an early farming village. Using much the same seed-processing technology as their hunter-gather ancestors 2,000 years before, the Jarmo people were settled in permanent villages cultivating early-domesticated varieties of wheat and barley.

Numerous subsequent investigations now provide a reasonably detailed picture of the origins of agriculture in several independent centers and its subsequent diffusion to almost all of the earth suitable for cultivation. These investigations have discovered no region in which agriculture developed earlier or faster than in the Near East, though a North Chinese center of domestication of millet may prove almost as early. Other centers seem to have developed later, or more slowly, or with a different sequence of stages, or all three. The spread of agriculture from centers of origin to more remote areas is well documented for Europe and North America. Ethnography also gives us cases where hunters and gatherers persisted to recent times in areas seemingly highly suitable for agriculture, most notably much of western North America and Australia. Attempts to account for this rather complex pattern are a major focus of archaeology.

## Origin of Agriculture as a Natural Experiment in Cultural Evolution

The processes involved in such a complex phenomenon as the origin of agriculture are many and densely entangled. Many authors have given climate change a key explanatory role (e.g., Reed 1977:882–883). The coevolution of human subsistence strategies and plant and animal domesticates must also play an important role (e.g., Blumler and Byrne 1991; Rindos 1984). Hunting-and-gathering subsistence may normally be a superior strategy to incipient agriculture (Cohen and Armelagos 1984; Harris 1977), and, if so, some local factor may be necessary to provide the initial impetus to heavier use of relatively low-quality, high-processing-effort plant resources that eventually result in plant domestication. Population pressure is perhaps the most popular candidate (Cohen 1977). Quite plausibly, the complex details of local history entirely determine the evolutionary sequence leading to the origin and spread of agriculture in every region. Indeed, important advances in our understanding of the origins of agriculture have resulted from pursuit of the historical details of particular cases (Bar-Yosef 1998; Flannery 1986).

Nonetheless, we propose that much about the origin of agriculture can be understood in terms of two propositions:

*Agriculture Was Impossible During The Last Glacial.* During the last glacial, climates were variable and very dry over large areas. Atmospheric levels of $CO_2$ were low. Probably most important, last-glacial climates were characterized by high-amplitude fluctuations on time scales of a decade or less to a millennium. Because agricultural subsistence systems are vulnerable to weather extremes, and because the cultural evolution of subsistence systems making heavy, specialized, use of plant resources occurs relatively slowly, agriculture could not evolve.

*In The Long Run, Agriculture Is Compulsory In The Holocene.* In contrast to the Pleistocene, stable Holocene climates allowed the evolution of agriculture in vast areas with relatively warm, wet climates, or access to irrigation. Prehistoric populations tended to grow rapidly to the carrying capacity set by the environment and the efficiency of the prevailing subsistence system. Local communities that discover or acquire more intensive subsistence strategies will increase in number and exert competitive pressure on smaller populations with less intensive strategies. Thus, in the Holocene, such inter-group competition generated a competitive ratchet favoring the origin and diffusion of agriculture.[1]

The great variation among local historical sequences in the adoption and diffusion of agriculture in the Holocene provides data to test our hypothesis. In the Near East, agriculture evolved rapidly in the early Holocene and became a center for its diffusion to the rest of western Eurasia. At the opposite extreme, hunting-and-gathering subsistence systems persisted in most of western North America until European settlement, despite many ecological similarities to the Near East. *Thus, each local historical sequence is a natural experiment in the factors that limit the rate of cultural evolution of more intensive subsistence strategies.* For our hypothesis to be correct, the evolution of subsistence systems must be rapid compared to the time cognitively modern humans lived under glacial conditions without developing agriculture, but slow relative to the climate variation that we propose was the main impediment to subsistence intensification in the late Pleistocene. By cultural evolution we simply mean the change over time in the attitudes, skills, habits, beliefs, and emotions that humans acquire by teaching or imitation. In our view (Bettinger 1991; Boyd and Richerson 1985), culture is best studied using Darwinian methods. We classify the causes of cultural change into several "forces." In a very broad sense, we recognize three classes of forces: those due to random effects (the analogs of mutation and drift), natural selection, and decision-making (invention, individual learning, biased imitation, and the like). The decision-making forces will tend to accelerate cultural evolution relative to organic evolution, but by how much is a major issue in the explanation of agricultural origins.

## Was Agriculture Impossible in the Pleistocene?

The Pleistocene geological epoch was characterized by dramatic glacial advances and retreats. Using a variety of proxy measures of past temperature, rainfall, ice volume, and the like, mostly from cores of ocean sediments, lake sediments, and ice caps, paleoclimatologists have constructed a stunning picture of climate deterioration over the last 14 million years (Bradley 1999; Cronin 1999; Lamb 1977; Partridge et al. 1995). The Earth's mean temperature dropped several degrees and the amplitude of fluctuations in rainfall and temperature increased. For reasons that are as yet ill understood, glaciers wax and wane in concert with changes in ocean circulation, carbon dioxide, methane and dust content of the atmosphere, and changes in average precipitation and the distribution of precipitation (Broecker 1995). The resulting pattern of fluctuation in climate is very complex. As the deterioration proceeded, different cyclical patterns of glacial advance and retreat involving all these variables have dominated the pattern. A 21,700-year cycle dominated the early part of the period, a 41,000-year cycle between about 3 and 1 million years ago, and a 95,800-year cycle during the last million years (deMenocal and Bloemendal 1995). Milankovich's hypothesis that these variations are driven by changes in the earth's orbit, and hence the solar radiation income in the different seasons and latitudes, fits the estimated temperature variation well, although doubts remain (Cronin 1999: 185–189).

### *Rapid Climate Variation in the Late Pleistocene*

The long-time-scale climate change associated with the major glacial advances and retreats is not directly relevant to the origins of agriculture because it occurs so slowly compared to the rate at which human populations adapt by cultural evolution. However, the ice ages also have great variance in climate at much shorter time scales. For the last 400,000 years, very high-resolution climate proxy data are available from ice cores taken from the deep ice sheets of Greenland and Antarctica. Resolution of events lasting little more than a decade is possible in Greenland ice 80,000 years old, improving to monthly resolution 3,000 years ago. During the last glacial, the ice core data show that the climate was highly variable on time scales of centuries to millennia (Clark et al. 1999; Dansgaard et al. 1993; Ditlevsen et al. 1996; GRIP 1993). Figure 1 shows data from the GRIP Greenland core. The $\delta^{18}O$ curve is a proxy for temperature; less negative values are warmer. $Ca^{2+}$ is a measure of the amount of dust in the core, which in turn reflects the prevalence of dust-producing arid

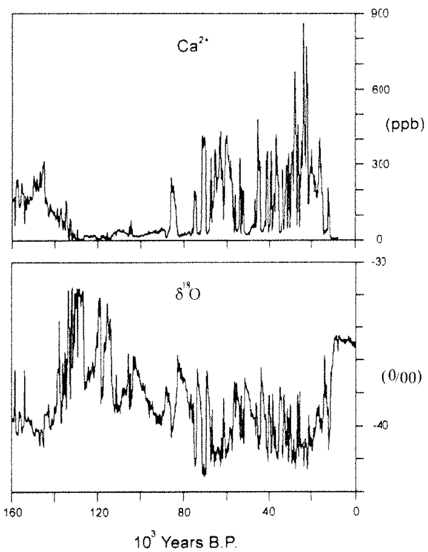


Figure 1. Profiles of a temperature index, $\delta^{18}O$, and an index of dust content, $Ca^{2+}$, from the GRIP Greenland ice core. 200-year means are plotted. The parts of the GRIP profile representing the last interglacial may have been affected by ice flow so their interpretation is uncertain (Johnsen et al. 1997). Note the high-amplitude, high-frequency variation in both the temperature and dust records during the last glacial. The Holocene is comparatively much less variable. Plotted from original data obtairable at: ftp://ftp.ngdc.noaa.gov/paleo/icecore/greenland/summit/ grip/isotopes/gripd18o.txt and ftp:// ftp.ngdc.noaa.gov/paleo/icecore/greenland/summit/grip/chem/ca.txt.

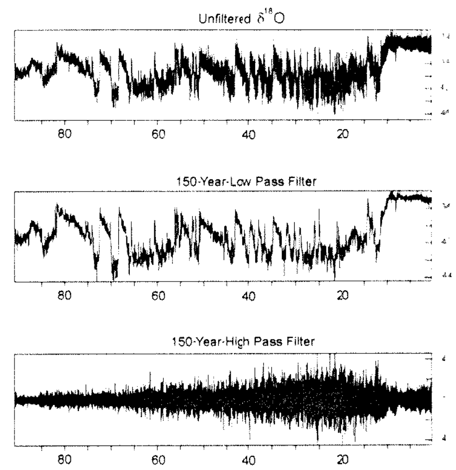


Figure 2. High-resolution analysis of the GRIP ice core $\delta^{18}O$ data by Ditlevsen et al. (1996). The low-pass filtered data shows that the Holocene is much less variable than the Pleistocene on time scales of 150 years and longer. The high-pass filtered data shows that the Pleistocene was also much more variable on time scales less that 150 years. The high- and low-pass filtering used spectral analytic techniques. These are roughly equivalent to taking a 150-year moving average of the data to construct the low-pass filtered series and subtracting the low-pass filtered series from the original data to obtain the high-pass filtered record. Since layer thinning increasingly affects deeper parts of the core by averaging variation on the smallest scales, the high-pass variance is reduced in the older parts of the core. In spite of this effect, the Pleistocene/Holocene transition is very strongly marked.

climates. The last glacial period was arid and extremely variable compared to the Holocene. Sharp millennial-scale excursions occur in estimated temperatures, atmospheric dust, and greenhouse gases. The intense variability of the last glacial carries right down to the limits of the nearly 10-year resolution of the ice core data. The highest resolution records in Greenland ice (and lower latitude records) show that millennial-scale warmings and coolings often began and ended very abruptly and were often punctuated by quite large spikes of relative warmth and cold with durations of a decade or two (e.g., Grafenstein et al. 1999). Figure 2 shows Ditlevsen et al.'s (1996) analysis of a Greenland ice core. Not only was the last glacial much more variable on time scales of a century-and-a-half or more (150-year low-pass filter) but also on much shorter time scales (150-year high-pass filter). Even though diffusion and thinning within the ice core progressively erases high-frequency variation in the core (visible as the narrowing with increasing age of the 150-year high-pass data in Figure 2), the shift from full glacial conditions about 18,000 years ago to the Holocene interglacial is accompanied by a dramatic reduction in variation on time scales shorter than 150 years. The Holocene (the last relatively warm, ice free 11,600 years) has been a period of very stable climate, at least by the standards of the last glacial.[2]

The climate fluctuations recorded in high-latitude ice cores are also recorded at latitudes where agriculture occurs today. Sediments overlain by anoxic water that inhibits sediment mixing by burrowing organisms are a source of low- and mid-latitude data with a resolution rivaling ice cores. Events recorded in North Atlantic sediment cores are closely coupled to those recorded in Greenland ice (Bond et al. 1993), but so are records distant from Greenland.



Hendy and Kennett (2000) report on water temperature proxies from sediment cores from the often-anoxic Santa Barbara Basin just offshore of central California. This data shows millennial- and sub-millennial-scale temperature fluctuations from 60–18 thousand years ago with an amplitude of about 8°C, compared to fluctuations of about 2°C in the Holocene. As in the Greenland cores, the millennial-scale events often show very abrupt onsets and terminations and are often punctuated by brief spikes of warmth and cold. Schulz et al. (1998) analyzed organic matter concentrations in sediment cores at oxygen minimum depths from the Arabian Sea deposited over the past 110 thousand years. The variation in organic matter deposited is thought to reflect the strength of upwelling, driven by changes in the strength of the Arabian Sea monsoon. AMS $^{14}C$ dating of both the Arabian Sea and Santa Barbara cores gives good time control in the upper part of the record, and the climate proxy variation is easily fit to Greenland ice millennial-scale interstadial-stadial oscillations. Allen et al. (2000) examine the pollen profiles from the laminated sediments of Lago Grande di Monticcio in southern Italy. Changes in the proportion of woody taxa in the core were dominated by large-amplitude changes near the limits of resolution of the data, about a century. The millennial-scale variations in this core also correlate with the Greenland record. Peterson et al. (2000) show that proxies for the tropical Atlantic hydrologic cycle have a strong millennial-scale signal that likewise closely matches the Green and pattern.

Reports of proxy records apparently showing the ultimate Younger Dryas millennial-scale cold episode, strongly expressed in the North Atlantic records 12,600–11,600 B.P., have been reported from all over the world, including southern German oxygen isotope variations (Grafenstein et al. 1999), organic geochemistry of the Cariaco Basin, Venezuela (Werne et al. 2000), New Zealand pollen (Newnham and Lowe 2000), and California pollen (West 2000). The Younger Dryas episode has received disproportionate attention because the time period is easily dated by $^{14}C$ and is sampled by many lake and mountain glacier cores too short to reach older millennial-scale events. As Cronin (1999:202–221) notes, the Younger Dryas is frequently detected in a diverse array of Northern Hemisphere climate proxies from all latitudes. The main controversy involves data from the Southern Hemisphere, where proxy data often do not show a cold period coinciding with the Younger Dryas, although some records show a similar Antarctic Cold Reversal just antedating the Northern Hemisphere Younger Dryas (Bennett et al. 2000).

Other records provide support for millennial-scale climate fluctuations during the last glacial that cannot be convincingly correlated with the Greenland ice record. Cronin (1999:221–236) reviews records from the deep tropical Atlantic, Western North America, Florida, China, and New Zealand. Recent notable additions to his catalog include southern Africa (Shi et al. 2000), the American Midwest (Dorale et al. 1998), the Himalayas (Richards et al. 2000), and northeastern Brazil (Behling et al. 2000). Clapperton (2000) gives evidence for millennial-scale glacial advances and retreats from most of the American cordillera—Alaska and western North America through tropical America to the southern Andes.

While the complex feedback processes operating in the atmosphere-biosphere-ocean system are not completely understood (Broecker 1995:241–270), plausible physical mechanisms could have linked temperature fluctuation in the both hemispheres. For example, Broecker and Denton (1989) proposed an explanation based upon the effects of glacial meltwater on the deep circulation of the North Atlantic. Today, cold, salty water from the surface of the North Atlantic is the source of about half of the global ocean's deep water. This large outflow of deep water currently must be balanced by an equally enormous inflow of warm surface and intermediate water into the high North Atlantic. If glacial melt water lowered the salinity of the North Atlantic and interrupted the flow of deep water, the whole coupled atmosphere-ocean circulation system of the world would be perturbed. Broecker and Denton's hypothesis explains how the northern and southern Hemisphere temperature and ice fluctuations could have been in phase even though the direct effects of orbital-scale variation on the two hemispheres are out of phase.

### *Impacts of Millennial- and Sub-Millennial-Scale Variation on Agriculture*

We believe that high-frequency climate and weather variation would have made the evolution of methods for intensive exploitation of plant foods extremely difficult. Holocene weather extremes significantly affect agricultural production (Lamb 1977). For example, the impact of the Little Ice Age

(400–150 B.P.) on European agriculture was quite significant (Grove 1988). The Little Ice Age is representative of the Holocene millennial-scale variation that is very much more muted than last-glacial events of similar duration. Extreme years during the Little Ice Age caused notable famines and such extremes would have been more exaggerated and more frequent during last glacial times. The United Nations Food and Agriculture Organization's (2000) Global Information and Early Warning System on Food and Agriculture gives a useful qualitative sense for the current impacts of inter-annual weather variation on food production. Quantitative estimates of current crop losses due to weather variation are difficult to make, but reasonable estimates run 10 percent on a country-wide basis (Gommes 1999) and perhaps 10–40 percent on a state basis in Mexico, depending upon mean rainfall (Eakin 2000). Gommes believes that weather problems account for half of all crop losses.

If losses in the Holocene are this high and if high-frequency climate variation in the last glacial increased at lower latitudes roughly as much as at Greenland, a hypothetical last-glacial farming system would face crippling losses in more years than not. Devastating floods, droughts, windstorms, and other climate extremes, which we experience once a century, might have occurred once a decade. In the tropics, rainfall was highly variable (Broecker 1996). Few years would be suitable for good growth of any given plant population. Even under relatively benign Holocene conditions agriculturalists and intensive plant collectors have to make use of risk-management strategies to cope with yield variation. Winterhalder and Goland (1997) use optimal foraging analysis to argue that the shift from foraging to agriculture would have required a substantial shift from minimizing risk by sharing to minimizing risk by field dispersal. Some ethnographically known Eastern Woodland societies that mixed farming and hunting, for example the Huron, seemed not to have made this transition and to have suffered frequent catastrophic food shortages. Storage by intensive plant collectors and farmers is an excellent means of meeting seasonal shortfalls, but is a marginal means of coping with inter-annual risk, much less multi-year shortfalls (Belovsky 1987:60).[3]

If Winterhalder and Goland are correct that considerable field dispersal is required to manage Holocene yield risks, it is hard to imagine that further field division would have been successful at coping with much larger amplitude fluctuations that occurred during the last glacial. We expect that opportunism was the most important strategy for managing the risks associated with plant foods during the last glacial. Annual plants have dormant seed that spreads their risk of failure over many years, and perennials vary seed output or storage organ size substantially between years as weather dictates. In a highly variable climate, the specialization on exploitation on one or a few especially promising species would be highly unlikely, because "promise" in one year or even for a decade or two would turn to runs of years with little or no success. However, most years would likely be favorable for some species or another, so generalized plant-exploitation systems are compatible with highly variable climates. The acorn-reliant hunter-gatherers of California, for example, used several kinds of oak, gathering less favored species when more favored ones failed (Baumhoff 1963:Table 2). Reliance on acorns demanded this generalized pattern of species diversification because the annual production of individual trees is highly variable from year to year, being correlated within species but independent between species (Koenig et al. 1994). Pleistocene hunter-gatherer systems must have been even more diversified, lacking the kind of commitment to a single resource category (acorns) observed in California.

The evolution of intensive resource-use systems like agriculture is a relatively slow process, as we document below. If ecological time-scale risks could be managed some way, or if some regions lacked the high-frequency variation detected by the as yet few high-resolution climate proxy records, the evolution of sophisticated intensive strategies would still be handicapped by millennial-scale variation. Plant and animal populations responded to climatic change by dramatically shifting their ranges, but climate change was significant on the time scales shorter than those necessary for range shifts to occur. As a result, last-glacial natural communities must have always been in the process of chaotic reorganization as the climate varied more rapidly than they could reach equilibrium. The pollen record from the Mediterranean and California illustrates how much more dynamic plant communities were during the last glacial (Allen et al. 1999; Heusser 1995). Pleistocene fossil beetle faunas change even more rapidly than plants because many species, especially generalist predators, change



their ranges more rapidly than plants. Hence they are better indicators of the ecological impacts of the abrupt, large-amplitude climate changes recorded by the physical climate proxies from the last glacial (Coope 1987).

Could the evolution of intensive plant-exploitation systems have tracked intense millennial- and submillennial-scale variation? Plant food-rich diets take considerable time to develop. Plant foods are generally low in protein and often high in toxins. Some time is required to work out a balanced diet rich in plant foods, for example, by incorporating legumes to replace part of the meat in diets. Whether intensification and agriculture always lead to health declines due to nutritional inadequacy is debatable, but the potential for them to do so absent sometimes-subtle adaptations is clear (Cohen and Armelagos 1984; Katz et al. 1974). The seasonal round of activities has to be much modified, and women's customary activities have to be given more prominence relative to men's hunting. Changes in social organization either by evolution *in situ* or by borrowing tend to be slow (Bettinger and Baumhoff 1982; North and Thomas 1973). We doubt that even sophisticated last-glacial hunter-gatherers would have been able to solve the complex nutritional and scheduling problems associated with a plant-rich diet while coping with unpredictable high-amplitude change on time scales shorter than the equilibration time of plant migrations and shorter than actual Holocene trajectories of intensification. In keeping with our argument, the direct archaeological evidence suggests that people began to use intensively the technologies that underpinned agriculture only after about 15,000 B.P. (Bettinger 2000).

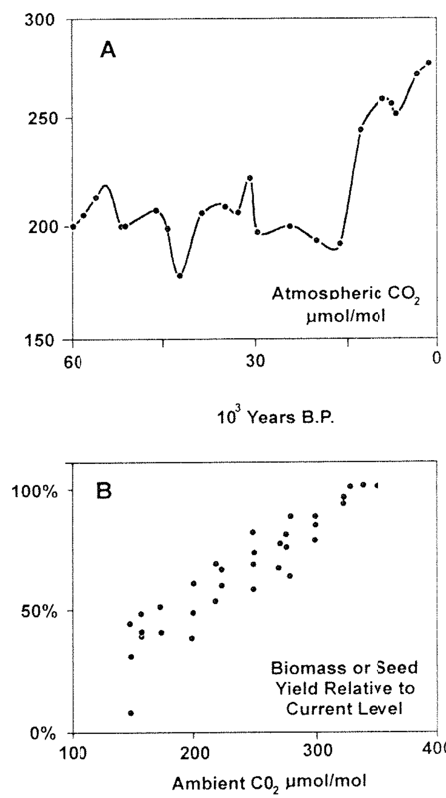


**Figure 3. Panel A shows the curve of atmospheric $CO_2$ as estimated from gas bubbles trapped in Antarctic glacial ice. Data from Barnola et al. (1987). Panel B summarizes responses of several plant species to experimental atmospheres containing various levels of $CO_2$. Based on data summarized by Sage (1995).**

### *Carbon Dioxide Limitation of Photosynthesis*

Plant productivity was also limited by lower atmospheric $CO_2$ during the last glacial. The $CO_2$ content of the atmosphere was about 190 ppm during the last glacial, compared to about 250 ppm at the beginning of the Holocene (Figure 3). Photosynthesis on earth is $CO_2$-limited over this range of variation (Cowling and Sykes 1999; Sage 1995). Beerling and Woodward (1993; see also Beerling et al. 1993) have shown that fossil leaves from the last glacial have higher stomatal density, a feature that allows higher rates of gas exchange needed to acquire $CO_2$ under more limiting conditions. This higher stomatal conductance also causes higher transpiration water losses per unit $CO_2$ fixed, exacerbating the aridity characteristic of glacial times. Beerling (1999) estimates the total organic carbon stored on land as a result of photosynthesis during the Last Glacial Maximum using a spatially disaggregated terrestrial plant production model coupled to two different global climate models to provide the environmental forcing for plant growth. The model results differ substantially, one indicating a 33 percent lower, and the other a 60 percent lower, terrestrial carbon store at the Last Glacial Maximum compared to the Holocene. Mass balance calculations based on stable isotope geochemistry also indicate a qualitatively large drop.

but uncertainties regarding terrestrial $\delta^{13}C$ lead to a similarly large range of estimates. Low mean productivity, along with greater variance in productivity, would have greatly decreased the attractiveness of plant resources during the last glacial.

Lower average rainfall and carbon dioxide during the last glacial reduced the area of the earth's surface suitable for agriculture (Beerling 1999). Diamond (1997) argues that the rate of cultural evolution is more rapid when innovations in local areas can be shared by diffusion. Thus, a reduction in the area suitable for agriculture and the isolation of suitable areas from one another will have a tendency to reduce the rate of intensification and make the evolution of agriculture less likely in any given unit of time. Since the slowest observed rates of intensification in the Holocene failed to result in agriculture until the European invasions of the last few hundred years, a sufficient slowing of the rate of evolution of subsistence could conceivably in itself explain the failure of agriculture to emerge before the Holocene. A slower rate of cultural evolution would also tend to prevent the rapid adaptation of intensive strategies during any favorable locales or periods that might have existed during the last glacial.

On present evidence we cannot determine whether aridity, low $CO_2$ levels, millennial-scale climate variability, or sub-millennial-scale weather variation was the main culprit in preventing the evolution of agriculture. Low $CO_2$ and climate variation would handicap the evolution of dependence on plant foods everywhere and were surely more significant than behavioral or technological obstacles. Hominids evolved as plant-using omnivores (Milton 2000), and the basic technology for plant exploitation existed at least ten thousand years before the Holocene (Bar-Yosef 1998). At least in favorable localities, appreciable use seems to have been made of plant foods, including large-seeded grasses, well back into the Pleistocene (Kislev et al. 1992). Significantly, we believe, the use of such technology over spans of last-glacial time that were sufficient for successive waves of intensification of subsistence in the Holocene led to only minor subsistence intensification, compared to the Mesolithic, Neolithic, and their ever-more-intensive successors.

*Subsistence Responses to Amelioration*

As the climate ameliorated, hunter-gatherers in several parts of the world began to exploit locally abundant plant resources more efficiently, but only, current evidence suggests, during the Bølling-Allerød period of near-interglacial warmth and stability. The Natufian sequence in the Levant is the best-studied and so far earliest example (e.g., Bar-Yosef and Valla 1991). One last siege of glacial climate, the Younger Dryas from 12,900 B.P. until ≈11,600 B.P., reversed these trends during the Late Natufian (e.g., Goring-Morris and Belfer-Cohen 1998). The Younger Dryas climate was appreciably more variable than the preceding Allerød-Bølling and the succeeding Holocene (Grafenstein et al. 1999; Mayewski et al. 1993). The ten abrupt, short, warm-cold cycles that punctuate the Younger Dryas ice record were perhaps felt as dramatic climate shifts all around the world. After 11,600 B.P., the Holocene period of relatively warm, wet, stable, $CO_2$-rich environments began. Subsistence intensification and eventually agriculture followed. Thus, while not perfectly instantaneous, the shift from glacial to Holocene climates was a very large change, and took place much more rapidly than cultural evolution could track.

Might we not expect agriculture to have emerged in the last interglacial 130,000 years ago or even during one of the even older interglacials? No archaeological evidence has come to light suggesting the presence of technologies that might be expected to accompany forays into intensive plant collecting or agriculture at this time. Anatomically modern humans may have appeared in Africa as early as 130,000 years ago (Klein 1999: Ch.7), but they were not behaviorally modern. Humans of the last interglacial were uniformly archaic in behavior. Very likely, then, the humans of the last interglacial were neither cognitively nor culturally capable of evolving agricultural subsistence. However, climate might also explain the lack of marked subsistence intensification during previous interglacials. Ice cores from the thick Antarctic ice cap at Vostok show that each of the last four interglacials over the last 420,000 years was characterized by a short, sharp peak of warmth, rather than the 11,600-year-long stable plateau of the Holocene (Petit et al. 1999). Further, the GRIP ice core suggests the last interglacial (130,000–80,000 B.P.) was more variable than the Holocene, although its lack of agreement with a nearby replicate core for this time period makes this interpretation tenuous (Johnsen et al. 1997). On the other hand, the atmospheric concentration of $CO_2$ was higher in the three previous interglacials than during the Holocene, and was stable at high levels for about 20,000 years following the warm peak during the last interglacial. The highly continental Vostok site unfortunately does not record the same high-frequency variation in the climate as most other proxy climate records, even those in the southern hemisphere (Steig et al. 1998). Some northern hemisphere marine and terrestrial records suggest that the last interglacial was highly variable while other data suggest a Holocene-length period of stable climates ca. 127,000–117,000 B.P. (Frogley et al. 1999). Better data on the high-frequency part of the Pleistocene beyond the reach of the Greenland ice cores is needed to test hypotheses about events antedating the latest Pleistocene. Long marine cores from areas of rapid sediment accumulation are beginning to reveal the millennial-scale record from previous glacial-interglacial cycles (McManus et al. 1999). At least the last five glacials have millennial-scale variations much like the last glacial. The degree of fluctuations during previous interglacials is still not clear, but at least some proxy data suggest that the Holocene has been less variable than earlier interglacials (Poli et al. 2000).

## During The Holocene, Was Agriculture Compulsory In The Long Run?

Once a more productive subsistence system is possible, it will, over the long run, replace the less-productive subsistence system that preceded it. The reason is simple: all else being equal, any group that can use a tract of land more efficiently will be able to evict residents that use it less efficiently (Boserup 1981; Sahlins and Service 1960:75–87). More productive uses support higher population densities, or more wealth per capita, or both. An agricultural frontier will tend to expand at the expense of hunter-gatherers as rising population densities on the farming side of the frontier motivate pioneers to invest in acquiring land from less-efficient users. Farmers may offer hunter-gatherers an attractive purchase price, a compelling idea about how to become richer through farming, or a dismal choice of flight, submission, or military defense at long odds against a more numerous foe. Early farmers (and other intensifiers more generally) are also liable to target opportunistically high-ranked game and plant resources essential to their less-intensive neighbors, exerting scramble competitive pressure on them even in the absence of aggressive measures. Thus, subsistence improvement generates a *competitive ratchet* as successively more land-efficient subsistence systems lead to population growth and labor intensification. Locally, hunter-gatherers may win some battles (e.g., in the Great Basin, Madsen 1994), but in the long run the more intensive strategies will win wherever environments are suitable for their deployment.

The archaeology supports this argument (Bettinger 2000). Societies in all regions of the world undergo a very similar pattern of subsistence efficiency increase and population increase in the Holocene, albeit at very different rates. Holocene hunter-gatherers developed local equilibria that, while sometimes lasting for thousands of years, were almost always replaced by more intensive equilibria.

## Alternative Hypotheses Are Weak

Aside from other forms of the climate-change hypotheses described above, archaeologists have proposed three prominent hypotheses—climate stress, population growth, and cultural evolution—to explain the *timing* of agricultural origins. They were formulated before the nature of the Pleistocene-Holocene transition was understood, but are still the hypotheses most widely entertained by archaeologists (MacNeish 1991). None of the three provides a close fit with the empirical evidence or to theory.

*Climate Stress Was First Too Common, Then Too Rare*

Childe (1951) proposed that terminal Pleistocene desiccation stressed forager populations and led to agriculture. Wright (1977) argued that Holocene climate amelioration brought pre-adapted plants into the Fertile Crescent areas where agriculture first evolved. Bar-Yosef (1998) and Moore and Hillman (1992) argue that Late Natufian sedentary hunter-gatherers probably undertook the first experiments in cultivation under the pressure of the Younger Dryas climate deterioration. Natufian peoples lived in settled villages and exploited the wild ancestors of wheat and barley beginning in the Alleröd-Bølling warm period (14,500–12,900 B.P.) (Henry 1989), and then reverted to mobile hunting-and-gathering during the sharp, short Younger Dryas climate deterioration (12,600–11,600 B.P.), the last of the high-amplitude fluctuations that were characteristic of the last glacial (Bar-Yosef and Meadow 1995; Goring-Morris and Belfer-Cohen 1997). Post-Natufian cultures began to domesticate the same species as warm and stable conditions returned after the Younger Dryas, around 11,600 B.P. Unfortunately, a flat spot in the $^{14}C$/calendar-year calibration curve makes precise dating difficult for the most critical several hundred years centered on 11,600 B.P. (Fiedel 1999). As a component of an explanation of a local sequence of change, such hypotheses may well be correct. Yet, they beg the question of why the 15 or so similar deteriorations and ameliorations of the last glacial did not anywhere lead to agriculture or why most of the later origins of agriculture occurred in the absence of Younger Dryas-scale deteriorations. Note also that, in principle, populations can adjust downward to lower carrying capacities through famine mortality even more quickly than they can grow up to higher ones. Such hypotheses cannot, we believe, explain the longer time- and larger spatial-scale problem of the absence of agriculture in the Pleistocene and its multiple origins and rapid spreads in the Holocene.

The details of subsistence responses to the Younger Dryas in the areas of early origins of agriculture will eventually produce a sharp test of the variability hypothesis. We suggest that the late Natufian de-intensification in response to the Younger Dryas was a retreat from the trend leading to agriculture and was unlikely to have produced the first steps toward domestication. More likely, the late Natufian preserved remnants of earlier, more intensive Natufian technology and social organization that served to start the Levantine transition to agriculture at an unusually advanced stage after the Younger Dryas ended. Events in the Younger Dryas time period also provide an opportunity to investigate the effects of $CO_2$ concentration partly independently of climate variability. The rise in $CO_2$ concentration in the atmosphere began two to three millennia before temperatures began to rise and continued to increase steadily through the Younger Dryas (Sowers and Bender 1995). The Younger Dryas period de-intensification of the Natufian suggests an independent effect of millennial and/or sub-millennial variability.

*Population Growth Has the Wrong Time Scale*

Cohen's (1977) influential book argued that slowly accumulating global-scale population pressure was responsible for the eventual origins of agriculture beginning at the 11,600 B.P. time horizon. He imagines, quite plausibly, that subsistence innovation is driven by increases in population density, but, implausibly we believe, that a long, slow buildup of population gradually drove people to intensify subsistence systems to relieve shortages caused by population growth, eventually triggering a move to domesticates. Looked at one way, population pressure is just the population growth part of the competitive ratchet. However, this argument fails to explain why pre-agricultural hunter-gatherer intensification and the transition to agriculture began in numerous locations after 11,600 years ago (Hayden 1995). Assuming that humans were essentially modern by the Upper Paleolithic, they would have had 30,000 years to build up a population necessary to generate pressures for intensification. Given any reasonable estimate of the human intrinsic rate of natural increase under hunting-and-gathering conditions (somewhat less than 1% $yr^{-1}$ to 3% $yr^{-1}$), populations substantially below carrying capacity will double in a century or less, as we will see in the models that follow.

*A Basic Model of Population Pressure.* Since the population explanation for agriculture and other adaptive changes[4] connected with increased subsistence efficiency remains very popular among archaeologists, we take the time here to examine its weakness formally. The logistic equation is one simple, widely used model of the population growth. The rate of change of population density, $N$, is given by:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \qquad (1)$$

where $r$ is the "intrinsic rate of natural increase"—the rate of growth of population density when there is no scarcity—and $K$ is the "carrying capacity," the equilibrium population density when population growth is halted by density-dependent checks. In the logistic equation, the level of population pressure is given by the ratio $N/K$. When this ratio is equal to zero the population grows at its maximum rate; there is no population pressure. When the ratio is one, density dependence prevents any population growth at all. It is easy to solve this equation and calculate the length of time necessary to achieve any level of population pressure, $\pi = N/K$.

$$T(\pi) = -\frac{1}{r}\ln\left(\left(\frac{\pi}{1-\pi}\right)\left(\frac{1-\pi_0}{\pi_0}\right)\right) \qquad (2)$$

where $\pi_0$ is the initial level of population pressure. Let us very conservatively assume that the initial



population density is only 1 percent of what could be sustained with the use of simple agriculture, and that the maximum rate of increase of human populations unconstrained by resource limitation is 1 percent per year. Under these assumptions, the population will reach 99 percent of the maximum population pressure (i.e., $\pi = .99$) in only about 920 years. Serendipitous inventions (e.g., the bow and arrow) that increase carrying capacity do not fundamentally alter this result. For example, only the rare single invention is likely to so much as double carrying capacity. If such an invention spreads within a population that is near its previous carrying capacity, it will still face half the maximum population pressure and thus significant incentive for further innovation. At an $r$ of 1 percent such an innovating population will again reach 99 percent of the maximum population pressure in 459 years.

One might think that this result is an artifact of the very simple model of population growth. However, it is easy to add much realism to the model without any change of the basic result. In Appendix A we show that a more realistic version of the logistic equation actually leads to even more rapid growth of population pressure.

*Allowing for Dispersal.* Once, after listening to one of us propound this argument, a skeptical archaeologist replied, "But you've got to fill up all of Asia first." This understandable intuitive response betrays a deep misunderstanding of the time scales of exponential growth. Suppose that the initial population of anatomically modern humans was only about $10^4$ and that the carrying capacity for hunter-gatherers is very optimistically 1 person per square kilometer. Given that the land area of the Old World is roughly $10^8$ $km^2$, $\pi_0 = 10^4/10^8 = 10^{-4}$. Then using equation 2 and again assuming $r = .01$, Eurasia will be filled to 99 percent of carrying capacity in about 1,400 years. The difference between increasing population pressure by a factor of 100 and by a factor of 10,000 is only about 500 years!

Moreover, this calculation seriously *over*-estimates the amount of time that will pass before any segment of an expanding Eurasian population will experience population pressure because populations will approach carrying capacity locally long before the entire continent is filled with people. R. A. Fisher (1937) analyzed the following partial differential equation that captures the interaction between population growth and dispersal in space:

$$\frac{\partial N(x)}{\partial t} = \underbrace{rN(x)\left(1 - \frac{N(x)}{K}\right)}_{\text{population growth}} + \underbrace{d^2\frac{\partial^2 N(x)}{\partial x^2}}_{\text{dispersal}} \qquad (3)$$

Here $N(x)$ is the population density at a point $x$ in a one-dimensional environment. Equation (3) says that the rate of change of population density in a particular place is equal to the population growth there plus the net effect of random, density-independent dispersal into and out of the region. The parameter $d$ measures the rate of dispersal and is equal to the standard deviation of the distribution of individual dispersal distances. In an environment that is large compared to $d$, a small population rapidly grows to near carrying capacity at its initial location, and then, as shown in Figure 4 (redrawn from Ammerman and Cavalli-Sforza 1984), begins to spread in a wave-like fashion across the environment at a constant rate. Thus at any given point in space, populations move from the absence of population pressure to high population pressure as the wave passes over that point. Figure 4 shows the pattern of spread for $r = .01$ and $d = 30$. With these quite conservative values, it takes less than 200 years for the wave front to pass from low population pressure to high population pressure. More realistic models that allow for density-dependent migration also yield a constant, wave-like advance of population (Murray 1989), and although the rates vary, we believe that the same qualitative conclusion will hold.

*The Dynamics of Innovation.* So far we have assumed that the carrying capacity of the environment is fixed (save where it is increased by fortuitous inventions). However, we know that people respond to scarcity caused by population pressure by intensifying production, for example, by shifting from less labor-intensive to more labor-intensive foraging, or by innovations that increase the efficiency of subsistence (Boserup 1981). Since innovation increases carrying capacity, intuition suggests that it might therefore delay the onset of population pressure. However, as the model in Appendix B shows, this intuition, too, is faulty.

Figure 5 shows the results of the model in Appendix B. A small population initially grows rapidly. As population pressure builds, population growth rate slows to a steady state in which population pressure is constant, and just enough innovation occurs to compensate for population growth. For plausible parameter values the second phase of population

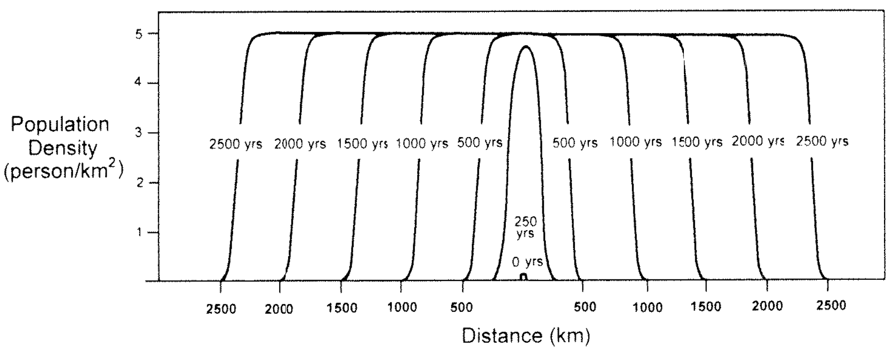


**Figure 4. A numerical simulation of Fisher's equation showing that after an initial period, population spreads at a constant rate so that at any point in space population pressure increases to its maximum in less than 500 years for reasonable parameter values. (Redrawn from Ammerman and Cavalli-Sforza, 1984).**

growth steady state is reached in less than a thousand years. Interestingly, increasing the intrinsic rate of innovation or the innovation threshold reduces the waiting time until population pressure is important. Innovation allows greater population increases over the long run, but it does not change the time scales on which population pressure occurs. The most important factor on time scales of a millennium or greater (if not a century or greater given realistic starting populations) is the rate of intensification by innovation, not population growth.

This picture of the interaction of demography and innovation leads to predictions quite different from those of scholars like Cohen (1977). For example, we do not expect to see any systematic evidence of increased population pressure immediately prior to major innovations, an expectation consistent with the record (Hayden 1995). If people are motivated to innovate whenever population pressure rises above an innovation threshold, and if, in the absence of successful innovation, populations adjust relatively quickly to changes in $K$ by growth or contraction.

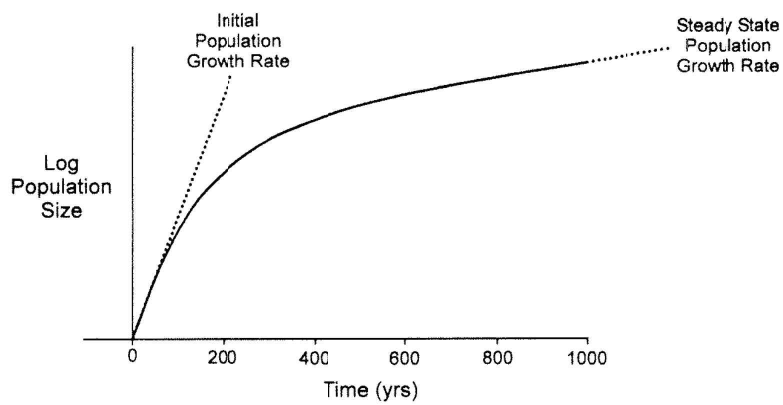


**Figure 5. This plots the logarithm of population size as a function of time for the model described in Appendix B. Initially, when there is little population pressure, population grows at a high rate. As the population grows, per capita income decreases, and people intensify. Eventually the population growth rate approaches a constant value at which the growth of intensification balances growth in population. For reasonable parameters ($a = 0.005$, $r = 0.02$, $\gamma_m = 1$, $y_s = 0.1$, $y_i = 0.2$, initial population size 1 percent of initial carrying capacity), it takes less than 500 years to shift from the initial low population pressure mode of growth to the final high population pressure mode of growth.**



than evidence of extraordinary stress—for example, skeletal evidence of malnutrition—is likely only when rapid environmental deterioration exceeds a population's capacity to respond via a combination of downward population adjustment and innovation.[5] Thus, for parameter values that seem anywhere near reasonable to us, population growth on millennial time scales will be limited by rates of improvement in subsistence efficiency, not by the potential of populations to grow, just as Malthus argued. Populations can behave in non-Malthusian ways only under extreme assumptions about population dynamics and rates of intensification, such as the modern world in which the rate of innovation, but also the rate of population growth, is very high.

Of course, in a time as variable as the Pleistocene, populations may well have spent considerable time both far above and far below instantaneous carrying capacity. If agricultural technologies were quick and easy to develop, the population-pressure argument would lead us to expect Pleistocene populations to shift in and out of agriculture and other intensive strategies as they find themselves in subsistence crises due to environmental deterioration or in periods of plenty due to amelioration. Most likely, minor intensifications and de-intensifications were standard operating procedure in the Pleistocene. However, the time needed to progress much toward plant-rich strategies was greater than the fluctuating climate allowed, especially given $CO_2$- and aridity-limited plant production.

### *Cultural Evolution Has the Wrong Time Scale*

The timing of the origin of agriculture might possibly be explained entirely by the rate of intensification by innovation. For example, Braidwood (1960) argued that it took some time for humans to acquire enough familiarity with plant resources to use them as a primary source of calories, and that this "settling in" process limited the rate at which agriculture evolved. This proposal may explain the post-Pleistocene timing of the development of agriculture. However, if we interpret his argument to be that the settling in process began with the evolution of behaviorally modern humans, the time scale is wrong again. There is no evidence that people were making significant progress at all toward agriculture for 30,000 years, and Braidwood's excavations at Jarmo show that some 4,000 years was enough to go from un-intensive hunting-and-gathering subsistence system to settled village agriculture in a fast case. Ten thousand years in the Holocene was ultimately sufficient for the development of plant-intensive gathering technologies or agriculture everywhere except in the coldest, plant-poor environments.

## The Pattern Of Intensification Across Cases Implicates Climate Change

We have argued that Malthusian processes lead to population pressure much more quickly than assumed by such writers as Cohen (1977) and that the rate of cultural "settling in" and intensification is faster than Braidwood (1960) imagined, but not fast enough to intensify more than a small distance toward agriculture in the highly variable environments of the Pleistocene. Thus, our hypothesis that the abrupt transition from glacial to Holocene climates caused the origin of agriculture requires that Holocene rates of intensification be neither too slow nor too fast.

### *Agriculture Was Independently Evolved About 10 Times*

The sample of origins is large enough to support some generalizations about the processes involved. Table 1 gives a rough time line for the origin of agriculture in seven fairly well-understood centers of domestication, two more controversial centers, three areas that acquired agriculture by diffusion and two areas that were without agriculture until European conquest.[6] The list of independent centers is complete as far as current evidence goes, and while new centers are not unexpected, it is unlikely that the present list will double. Numerous areas acquired agriculture by diffusion (societies acquire most of their technological innovations by diffusion, not independent invention), so the three areas in Table 1 are but a small sample. The number of non-arctic areas without agriculture at European contact is small and the two listed, western North America and Australia, are the largest and best known.

Two lines of evidence indicate that the seven centers of domestication are independent. First, the domesticates taken up in each center are distinctive and no evidence of domesticates from other centers turns up early in any of the sequences. For example, in the eastern North American center a sunflower, a goosefoot, marsh elder, an indigenous squash, and other local plants were taken into cultivation around

Table 1. Dates Before Present in Calendar Years of Achievement of Plant Intensive Hunting and Gathering and Agriculture in Different Regions, mainly after Smith (1995).

| Region | Intensive Foraging | Agriculture |
|---|---|---|
| *Centers of Domestication* | | |
| Near East: Bar-Yosef and Meadow 1995 | 15,000 | 11,500 |
| North China: An 1991; Elston et al. 1997 | 11,600 | > 9,000 |
| South China: An 1991 | 12,000? | 8,000 |
| Sub-Saharan Africa: Klein 1993 | 9,000 | 4,500 |
| Southcentral Andes: Smith 1995 | 7,000 | 5,250 |
| Central Mexico: Smith 1995 | 7,000 | 5,750 |
| Eastern United States: Smith 1995 | 6,000 | 5,250 |
| *Controversial Centers* | | |
| Highland New Guinea: Golson 1977 | ? | 9,000? |
| Amazonia: Pearsall 1995 | 13,000? | 9,000? |
| *Acquisition by Diffusion* | | |
| Northwestern Europe | 12,500 | 7,000 |
| Southwestern U.S.: Cordell 1984; Doelle 1999 | 6000 | 3,500 |
| Japan: Aikens and Akazawa 1996; Crawford 1992 | 10,500 | 3,000 |
| *Never Acquired Agriculture* | | |
| California: Bettinger 2000 | 4,000 | n/a |
| Australia: Hiscock 1994; Smith 1987 | 3,500 | n/a |

6000 B.P. Mesoamerican maize subsequently appeared here around 2000 B.P., but remained a minor domesticate until around 1100 B.P., when it suddenly crowded out several traditional cultivars (Smith 1989). Second, archaeology suggests that none of the centers had agricultural neighbors at the time that their initial domestications were undertaken. The two problematic centers, New Guinea and Lowland South America, present difficult archaeological problems (Smith 1995). Sites are hard to find and organic remains are rarely preserved. The New Guinea evidence consists of apparently human-constructed ditches that might have been used in controlling water for taro cultivation. The absence of documented living sites associated with these features makes their interpretation quite difficult. The lowland South American evidence consists of starch grains embedded in pottery fragments and phytoliths, microscopic silicious structural constituents of plant cell walls. The large size of some early starch grains and phytoliths convinces some archaeologists that root crops were brought under cultivation in the Amazon Basin at very early dates.

The timing of initiation of agriculture varies quite widely. The Near Eastern Neolithic is the earliest so far attested. In northern, and possibly southern, China, however, agriculture probably followed within a thousand years of the beginning of the Holocene, even though the best-documented, clearly agricultural complexes are still considerably later (An 1991; Crawford 1992; Lu 1999). Agriculture may prove to be as early in northern China as in the Near East, since the earliest dated sites, which extend back to 8500 B.P., represent advanced agricultural systems that must have taken some time to develop. Excavations in northern China north of the earliest dated agricultural sites document a technological change around 11,600 B.P., signaling a shift toward intensive plant and animal procurement that may have set this process in motion (Elston et al. 1997).

The exact sequence of events also varies quite widely. For example, in the Near East, sedentism preceded agriculture, at least in the Levantine Natufian sequence, but in Mesoamerica crops seem to have been added to a hunting-and-gathering system that was dispersed and long remained rather mobile (MacNeish 1991:27–29). For example, squash seems to have been cultivated around by 10,000 B.P. in Mesoamerica, some 4,000 years before corn and bean domestication began to lead to the origin of a fully agricultural subsistence system (Smith 1997). Some mainly hunting-and-gathering societies seem to have incorporated small amounts of domesticated plant foods into their subsistence system without this



leading to full-scale agriculture for a very long time. Perhaps American domesticates were long used to provide specialized resources or to increase food security marginally (Richard Redding, personal communication) and initially raised human carrying capacities relatively little, thus operating the competitive ratchet quite slowly. According to MacNeish, the path forward through the whole intensification sequence varied considerably from case to case.

### *A Late Intensification of Plant Gathering Precedes Agriculture*

In all known cases, the independent centers of domestication show a late sequence of intensification beginning with a shift from a hunter-gatherer subsistence system based upon low-cost resources using minimal technological aids to a system based upon the procurement and processing of high-cost resources, including small game and especially plant seeds or other labor-intensive plant resources, using an increasing range of chipped and ground stone tools (Hayden 1995). The reasons for this shift are the subject of much work among archaeologists (Bettinger 2000). The shifts at least accelerate and become widespread only in the latest Pleistocene or Holocene. However, a distinct tendency toward intensification is often suggested for the Upper Paleolithic more generally. Stiner et al. and commentators (2000) note that Upper Paleolithic peoples often made considerable use of small mammals and birds in contrast to earlier populations. These species have much lower body fat than large animals, and excessive consumption causes ammonia buildup in the body due to limitations on the rate of urea synthesis ("rabbit starvation," Cordain et al. 2000). Consequently, any significant reliance on low-fat small animals implies corresponding compensation with plant calories, and at least a few Upper Paleolithic sites, such as the Ohalo II settlement on the Sea of Galilee (Kislev et al. 1992), show considerable use of plant materials in Pleistocene diets. Large-seeded annual species like wild barley were no doubt attractive resources in the Pleistocene when present in abundance, and would have been used opportunistically during the last glacial. If our hypothesis is correct, in the last glacial no one attractive species like wild barley would have been consistently abundant (or perhaps productive enough) for a long enough span of time in the same location to have been successfully targeted by an evolving strategy of intensification, even if their less intensive exploitation was common. The broad spectrum of *species*, including small game and plants, reflected in these cases is not *per se* evidence of intensification (specialized use of more costly but more productive resources using more labor and dedicated technology), as is sometimes argued (Flannery 1971). In most hunter-gatherer systems, marginal diet cost and diet richness (number of species used) are essentially independent (Bettinger 1994:46–47), and prey size is far less important in determining prey cost than either mode or context of capture (Bettinger 1993:51–52; Bettinger and Baumhoff 1983:832; Madsen and Schmitt 1998). For all these reasons, quantitative features of subsistence *technology* are a better index of Pleistocene resource intensification than species used. We believe that the dramatic increase in the quantity and range of small chipped stone and groundstone tools only after 15,000 B.P. signals the beginning of the pattern of intensification that led to agriculture.

Early intensification of plant resource use would have tended to generate the same competitive ratchet as the later forms of intensification. Hunter-gatherers who subsidize hunting with plant-derived calories can maintain higher population densities, and thus will tend to deplete big game to levels that cannot sustain hunting specialists (Winterhalder and Lu 1997). Upper Paleolithic people appear to be fully modern in their behavioral capacities (Klein 1999). Important changes in subsistence technology did occur during the Upper Paleolithic, for example the development of the atlatl. Nevertheless, modern abilities and the operation of the competitive ratchet drove Upper Paleolithic populations only a relatively small distance down the path to the kind of heavy reliance on plant resources that in turn set the stage for domestication.

Braidwood's reasoning that pioneering agriculturalists would have gained their intimate familiarity with proto-domesticates first as gatherers is logical and supported by the archaeology. Once the climate ameliorated, the rate of intensification accelerated immediately in the case of the Near East. In other regions changes right at the Pleistocene-Holocene transition were modest to invisible (Straus et al. 1996). The full working out of agrarian subsistence systems took thousands of years. Indeed modern breeding programs illustrate that we are still working out the possibilities inherent in agricultural subsistence systems.

The cases where Holocene intensification of plant gathering did not lead directly to agriculture are as interesting as the cases where it did. The Jomon of Japan represents one extreme (Imamura 1996). Widespread use of simple pottery, a marker of well-developed agricultural subsistence in western Asia, was very early in the Jomon, contemporary with the latest Pleistocene Natufian in the Near East. By 11,000 yrs B.P., the Jomon people lived in settled villages, depended substantially upon plant foods, and used massive amounts of pottery. However, the Jomon domesticated no plants until rather late in the sequence. Seeds of weedy grasses are found throughout, but only in later phases (after about 3000 B.P.) do the first unambiguous domesticates occur, and these make up only a small portion of the seeds in archaeological contexts (Crawford 1997). Sophisticated agriculture came to Japan with imported rice from the mainland only about 2,500 B.P. Interestingly, acorns were a major item of Jomon subsistence. The people of California were another group of sedentary hunter-gatherers that depended heavily on acorns. However, in California the transition to high plant dependence began much later than in the Jomon (Wohlgemuth 1996). Millingstones for grinding small seeds became important after 4500 B.P., although seeds were of relatively minor importance overall. After 2800 B.P. acorns processed with mortars and pestles became an important subsistence component and small seeds faded in comparative importance. In the latest period, after 1200 B.P., quantities of small seeds were increasingly added back into the subsistence mix alongside acorns in a plant-dominated diet. Other peoples with a late onset of intensification include the Australians. The totality of cases tells us that any stage of the intensification sequence can be stretched or compressed by several thousand years but reversals are rare (Harris 1996; Price and Gebauer 1995). Farming did give way to hunting-and-gathering in the southern and eastern Great Basin of North America after a brief extension of farming into the region around 1000 B.P. (Lindsay 1986). A similar reversal occurred in southern Sweden between 2400 and 1800 B.P. (Zvelebil 1996). Horticultural Polynesian populations returned substantially to foraging for a few centuries while population densities built up on reaching the previously uninhabited archipelagos of Hawaii and New Zealand (Kirch 1984). Had intensification on plant resources been possible during the last glacial, even the slowest Holocene rates of intensification were rapid enough to produce highly visible archaeological evidence on the ten-millennium time scale, one-third or less time than Upper Paleolithic peoples lived under glacial climates.

*More Intensive Technologies Tend to Spread*

One successful and durable agricultural origin in the last glacial on any sizeable land mass would have been sufficient to produce a highly visible archaeological record, to judge from events in the Holocene. Once well-established agricultural systems existed in the Holocene, they expanded at the expense of hunting-and-gathering neighbors at appreciable rates (Bellwood 1996). Ammerman and Cavalli-Sforza (1984) summarize the movement of agriculture from the Near East to Europe, North Africa and Asia. The spread into Europe is best documented. Agriculture reached the Atlantic seaboard about 6000 B.P. or about 4,000 years after its origins in the Near East. The regularity of the spread, and the degree to which it was largely a cultural diffusion process as opposed to a population dispersion as well, are matters of debate. Cavalli-Sforza et al. (1994:296–299) argue that demic expansion by western Asians was an important process with the front of genes moving at about half the rate of agriculture. They imagine that pioneering agricultural populations moved into territories occupied by hunter-gatherers, and intermarried with the preexisting population. The then-mixed population in turn sent agricultural pioneers still deeper into Europe. They also suppose that the rate of spread was fairly steady, though clearly frontiers between hunter-gatherers and agriculturalists stabilized in some places (Denmark, Spain) for relatively prolonged periods. Zvelebil (1996) emphasizes the complexity and durability of frontiers between farmers and hunter-gatherers and the likelihood that in many places the diffusion of both genes and ideas about cultivation was a prolonged process of exchange across a comparatively stable ethnic and economic frontier. Further archaeological and paleogenetic investigations will no doubt gradually resolve these debates. Clearly, the spread process is at least somewhat heterogeneous.

Other examples of the diffusion of agriculture are relatively well documented. For example, maize domestication is dated to about 6200 B.P. in Central Mexico, spreading to the southwestern U.S. (New Mexico) by about 4000 B.P. (Matson 1999; Smith 1995). In this case, the frontier of maize agriculture stabilized for a long time, only reaching the eastern U.S. at the comparatively late date noted above. Maize failed entirely to diffuse westward into the Mediterranean parts of California even though peoples growing it in the more arid parts of its range in the Southwest used irrigation techniques that have eventually worked in California with modest modifications to cope with dry-season irrigation. As with the origin process, the rate of spread of agriculture exhibits an interesting degree of variation.



Table 2. Processes that may Retard the Rate of Cultural Evolution and Create Local Optima that Halt Evolution for Prolonged Periods.

| Process | Authors (examples) |
|---|---|
| *Geography*: Eurasia, having the largest land mass, has more local populations to exchange innovations by diffusion, hence the fastest Holocene rate of subsistence intensification. | Diamond 1997 |
| *Minor climate change*: The late medieval onset of the Little Ice Age caused the extinction of the Greenland Norse colony. Agriculture at marginal altitudes in places like the Andes seems to respond to Holocene climatic fluctuation. | Kent 1987; Kleivan 1984 |
| *Preadapted plants*: The Mediterranean Old World is unusually well endowed with large-seeded grasses susceptible to domestication pressures. American domesticates, especially maize, may outcross too much to respond quickly to selection. | Blumler 1992; Blumler and Byrne 1991; Diamond 1997; Hillman and Davies 1990 |
| *Diseases*: Density dependent epidemic diseases may evolve that slow or stop the population growth, pending the evolution of resistance, that would otherwise drive the competitive ratchet. Local diseases that attack foreigners may protect otherwise-vulnerable systems. | Cavalli-Sforza et al. 1994; Crosby 1986; Gifford-Gonzalez 2000; McNeill 1976 |
| *New technological complexes evolve slowly*: Nutritional adequacy in plant-rich diets requires discovering cooking techniques, acquiring balancing domesticates, developing the potential of animal domesticates, and the like. | Katz et al. 1974 |
| *New social institutions evolve slowly*: Social institutions are generally deeply involved in subsistence but are also liable to be regulated by norms that make adaptive evolution away from current local optima difficult. | Bettinger 1999; Bettinger and Baumhoff 1982; North and Thomas 1973; Richerson and Boyd 1999 |
| *Ideology may play a role*: The evolution of fads, fashions, and belief systems may act to drive cultural evolution in non-utilitarian directions that sometimes carry them to new adaptive slopes. | Weber 1930 |

## Changes in the Cultural Evolutionary System?

A possible alternative to our hypothesis would be that a substantial modernization of the cultural system occurred coincidently at the end of the Pleistocene and that this resulted in a general acceleration of rates of cultural evolution, including subsistence intensification. The modernization of culture capacities leading up to the Upper Paleolithic transition was presumably such an event, as were later inventions like literacy (Donald 1991; Klein 1999:Ch. 7). We are not aware of any proposals for major changes in the intrinsic rate of cultural evolution coincident with the Pleistocene-Holocene boundary. Students of the evolution of subsistence intensification and social complexity in the Holocene have suggested a series of plausible processes that will probably turn out to be at least part of the explanation for why the trend to intensification has taken such diverse forms in different regions (Table 2). This list of diversifying and rate-limiting processes does not include any that should have operated more stringently on Upper Paleolithic, as opposed to Mesolithic and Neolithic societies, climate effects aside. Holocene rates of intensification do have the right time scale to be drastically affected by millennial- and submillennial-scale variation that is rapid with respect to observed rates of cultural evolution in the Holocene.

If climate variation did not limit intensification during the last glacial to vanishingly slow rates compared to the Holocene, the failure of intensive systems to evolve during the tens of millennia anatomically and cultural modern humans lived as sophisticated hunter-gatherers before the Holocene is a considerable mystery.

## Conclusion

The large, rapid change in environment at the Pleistocene-Holocene transition set off the trend of subsistence intensification of which modern industrial innovations are just the latest examples. If our hypothesis is correct, the reduction in climate variability, increase in $CO_2$ content of the atmosphere, and increases in rainfall rather abruptly changed the earth from a regime where agriculture was impossible everywhere to one where it was possible in many places. Since groups that use efficient, plant-rich subsistence systems will normally out-compete groups that make less efficient use of land, the Holocene has been characterized by a persistent, but regionally highly variable, tendency toward subsistence intensification. The diversity of trajectories taken by the various regional human sub-populations since ≈ 11,600 B.P. are natural experiments that will help us elucidate the factors that control the tempo of cultural evolution and that generate historical contingency against the steady, convergent adaptive pressure toward ever more intense production systems. A long list of processes (Table 2) interacted to regulate the nearly unidirectional trajectory of subsistence intensification, population growth, and institutional change that the world's societies have followed in the Holocene. Notably, even the slowest evolving regions generated quite appreciable and archaeologically visible intensification, demanding some explanation for why similar trajectories are absent in the Pleistocene.

Those who are familiar with the Pleistocene often remark that the Holocene is just the "present interglacial." The return of climate variation on the scale that characterized the last glacial is quite likely if current ideas about the Milankovich driving forces of the Pleistocene are correct. Sustaining agriculture under conditions of much higher amplitude, high-frequency environmental variation than farmers currently cope with would be a considerable technical challenge. At the very best, lower $CO_2$ concentrations and lower average precipitation suggest that world average agricultural output would fall considerably.

Current anthropogenic global warming via greenhouse gases might at least temporarily prevent any return to glacial conditions. However, we understand the feedbacks regulating the climate system too poorly to have any confidence in such an effect. Current increases in $CO_2$ threaten to elevate world temperatures to levels that in past interglacials apparently triggered a large feedback effect producing a relatively rapid decline toward glacial conditions (Petit et al. 1999). The Arctic Ocean ice pack is currently thinning very rapidly (Kerr 1999). A dark, open Arctic Ocean would dramatically increase the summer heat income at high northern latitudes and have large, difficult-to-guess impacts on the Earth's climate system. No one can yet estimate the risks we are taking of a rapid return to colder, drier, more variable environment with less $CO_2$, nor evaluate exactly the threat such conditions imply for the continuation of agricultural production. Nevertheless, the intrinsic instability of the Pleistocene climate system, and the degree to which agriculture is likely dependent upon the Holocene stable period, should give one pause (Broecker 1997).

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## Appendix A: More Realistic Population Dynamics

The logistic equation assumes that an increment to population density has the same effect on population pressure at low densities as at high densities. We know that this assumption is not correct in all cases. For example, hunters pursuing herd animals may generate much population pressure at low human population densities because killing only a small fraction of the herd makes the many survivors difficult to hunt. On the other hand, subsistence farmers spreading into a uniform fertile plain may feel little population pressure until all farmland is occupied. If returns to additional labor on shrinking farms then drop steeply, most population pressure will be felt at densities near $K$. To allow for such effects, ecologists often utilize a generalized logistic equation

$$\frac{dN}{dt} = rN\left(1-\left(\frac{N}{K}\right)^{\theta}\right) \qquad (A1)$$

Population pressure is now given by the term $(N/K)^{\theta}$. If $\theta > 1$, population pressure does not increase until densities approach carrying capacity, as is usually the case for species like humans that have flexible behavior and considerable mobility, and thus can mitigate the effects of increasing population density over some range of densities. It seems intuitive that this would increase the length of time necessary to reach a given level of population pressure. However, this intuition is wrong. The generalized logistic can be used to derive a differential equation for $\pi = (N/K)^{\theta}$

$$\begin{aligned}\frac{d\pi}{dt} &= \frac{\theta}{N}\left(\frac{N}{K}\right)^{\theta}\frac{dN}{dt} \\ &= r\theta\left(\frac{N}{K}\right)^{\theta}\left(1-\left(\frac{N}{K}\right)^{\theta}\right) \qquad (A2) \\ &= \theta\pi(1-\pi)\end{aligned}$$

Thus, the differential equation for population pressure is always the ordinary logistic equation in which $K = 1$ and $r$ is multiplied by $\theta$. This means that when $\theta > 1$, it takes *less* time to reach a given amount of population pressure than would be the case if $\theta = 1$. Reduced population pressure at low densities leads to more rapid initial population growth. Population growth is close to exponential longer and this more than compensates for the fact that higher densities have to be reached to achieve the same level of population pressure.

## Appendix B: The Dynamics of Innovation

Consider a population of size $N$ in which the per capita income of the population is given by:

$$y = \frac{y_m I}{I+N} \qquad (B1)$$

where $y_m$ is the maximum per capita income, and $I$ is a variable that represents the productivity of subsistence technology. Thus per capita income declines as population size increases, but for a given population size, greater productivity raises per capita income. As in the previous models, we assume that as population pressure, now measured as falling per capita income, increases, population growth decreases. In particular, assume:

$$\frac{dN}{dt} = \rho N(y - y_s) \qquad (B2)$$

where $y_s$ is the per capita income necessary for subsistence. If per capita incomes are above this value, population increases; if per capita income falls below $y_s$, population shrinks. If $I$ is fixed, this equation is another generalization of the logistic equation. In an initially empty environment, population initially grows at a rate $\rho(y_m - y_s)$, but then slows and reaches an equilibrium population size

$$\frac{I(y_m - y_s)}{y_s}. \qquad (B3)$$

To allow for intensification we assume that people innovate whenever their per capita income falls below a threshold value $y_i$. Thus

$$\frac{dI}{dt} = aI(y_i - y) \qquad (B4)$$

When per capita income is less than the threshold value $y_i$ people innovate, increasing the carrying capacity and therefore decreasing population pressure. When per capita income is greater than the threshold, they "de-innnovate." This may seem odd at first, but such abandonment of more efficient technology has been observed occasionally. The maximum rate at which innovation can occur is governed by the parameter $a$.

If a small pioneer population enters an empty habitat, it experiences two distinct phases of expansion (Figure 5). Initially, per capita income is near the maximum, and population grows at the maximum rate. As population density increases, per capita income drops below $y_i$ and the population begins to innovate, eventually reaching a steady state value

$$\hat{y} = \frac{\rho y_s + a y_i}{\rho + a} \qquad (B5)$$

The steady state per capita income is above the minimum for subsistence but below the threshold at which people experience population pressure and begin to innovate. At this steady state population growth continues at a constant rate,

$$\hat{\rho} = \frac{a(y_i - y_s)}{\rho + a}, \qquad (B6)$$

that is proportional to the rate of growth of subsistence efficiency.

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## Notes

1. We define "efficiency" as the productivity per unit area of land exploited for subsistence. Efficiency of subsistence is favored by strategies that move subsistence down the food chain, especially to high-productivity plant resources. "Intensification" we define as the use of human labor to add productive lower-ranked resources to the diet or the use of technological innovations to increase the rank of more productive resources. Typically both strategies are employed simultaneously. Since increases in efficiency are achieved by either labor or technical intensification and since increases in efficiency usually also lead to population growth, we use the term "intensification" loosely for the interlinked processes of labor and technical intensification and population growth. We define "agriculture" as dependence upon domesticated crops and animals for subsistence. We mark the origin of agriculture as the first horizon in which plant remains having anatomical markers of domestication are found, or are likely on other grounds to be found in the future. Fully agricultural subsistence systems in the sense of a dominance of domesticated species in the diet typically postdate the origin of agriculture by a millennium or more.

2. It has also been argued that Pleistocene climates were less seasonally variable than during the Holocene, but this idea has scant empirical support (Miracle and O'Brien 1998). Elias (1999) has used fossil beetle faunas to estimate July and January temperatures in Holocene and Pleistocene deposits. These data suggest that the Pleistocene was more seasonal than the Holocene. However, beetle estimates of January temperatures are not very reliable because beetles in temperate and arctic climates overwinter in a dormant state so that their distributions are rather insensitive to winter as opposed to summer temperatures. Plant distributions are similarly affected. No current method of estimating winter temperatures in the Pleistocene is reliable.

3. Agronomists and climatologists have recently become interested in the impacts of climate change and climate variability in the context of $CO_2$-induced global warming (Bazzaz and Sombroek 1996; Downing et al. 1999; Kane and Yohe 2000; Reilly and Schimmelpfennig 2000; Rosenzweig and Hillel 1998; Schneider et al. 2000). Global climate models suggest that global warming may increase short time scale climate variation as well as creating a steep trend. To some degree, these conditions mimic the millennial and submillennial scale variations in the Pleistocene, and, as crop and-weather models and empirical data improve, more definitive assessments of impact of last glacial conditions on plant-based subsistence strategies will become possible.

4. By "adaptive" we mean behaviors that, by comparison with available alternatives, have the largest population mean fitness.

5. Some human populations might have curtailed birth rates in order to preserve higher incomes at any given level of intensification. In a sense, such populations have just redefined $K$ to be a lower value that permits higher incomes by employing what Malthus called the "preventative checks" on population growth. The rest of the above analysis then applies with $K$ measured in suitably emic terms. Cultural differences in the value of intensification threshold or $K$ (Coale 1986) will make evidence of stress more likely in populations where the effective carrying capacity is closer to the ultimate subsistence carrying capacity than in populations that reduce growth rates by preventative checks that keep population well below absolute subsistence limits. The perceived costs of population control, given that the main mechanism in nonmodern societies was infanticide and sexual abstinence, may mean that most populations intensified labor inputs at any given level of technology efficiency to near subsistence limits (Hayden 1981). In either event, population pressure will tend to stay constant to the extent that rates of population growth and intensification are successful in adjusting subsistence to current conditions. Normally population growth and decline are quite rapid processes relative to rates of innovation and will keep average population size quite close to $K$. Short-term departures from $K$ caused by short-term environmental shocks and windfalls should be the commonest reasons to see especially stressed or unstressed populations. If the rate of innovation is more rapid than exponential population growth for any significant time period, then per capita incomes can rise under a regime of very rapid population growth, as in the last few centuries. This regime, if it had occurred in the past, should be quite visible in the historical and archaeological record because it so rapidly leads to large populations and large-scale creation of durable artifacts. Alternatively, population growth may have been limited in past populations by the analog of the modern demographic transition. Thus, hunter-gatherers might have resisted the adoption of plant-based intensification because they viewed the life style associated with plant collecting or planting as a decrement to their incomes. However, resisting intensifications that increase human densities makes such groups vulnerable to competitive displacement by the intensifiers unless the greater wealth of the population limiters allows them to successfully defend their resource-rich territories. On the evidence of the fairly rapid rate of spread of intensified strategies once invented, such defense is seldom successful (e.g., Ammerman and Cavalli-Sforza 1984; Bettinger and Baumhoff 1982).

6. The dates in Table 1 reflect considerable recent revision stemming from accelerator mass spectrometry $^{14}C$ dating, which permits the use of very small carbon samples and can be applied directly to carbonized seeds and other plant parts showing morphological changes associated with domestication. Isolated seeds tend to work their way deep into archaeological deposits, and dates based on associated large carbon samples (usually charcoal) often gave anomalously early dates.

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