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• PERSPECTIVE

AGRICULTURE

Location, Location, Location: The First Farmers

Jared Diamond [\[HN1\]](#)

[±](#) Author Affiliations

Human history's most important event since the last Ice Age was the first rise of agriculture in Southwest Asia's Fertile Crescent. The origin of agriculture triggered a long train of economic, political, and technological developments, which began there and spread outward. As one example, this wave of changes explains why this journal, published in a land originally inhabited by Native Americans, is nevertheless written in a language of the Indo-European language family [\[HN2\]](#), [\[HN3\]](#) that arose 10,000 years earlier and 10,000 miles distant, in or near the crescent. Why did agriculture first develop in the narrow swath of hills extending only from southeast Turkey to western Iran (see the [figure](#))? A report on page [1312](#) of this issue ([1](#)) helps answer that question by pinpointing the site of domestication for einkorn wheat, one of eight so-called "founder crops" that launched crescent agriculture around 9000 B.C. ([2](#)). [\[HN4\]](#), [\[HN5\]](#), [\[HN6\]](#)



The spread of food production from the Fertile Crescent.

The purple-shaded area is the crescent itself, where food production was established by 8000 B.C. Lines denote how far food production, on the basis mostly of Fertile Crescent crops and livestock, had spread by the indicated dates (calibrated radiocarbon B.C. dates). Based on maps 2 and 20 of [\(3\)](#), as modified in [\(4\)](#).

Botanists already knew that cultivated einkorn's ancestor was a very similar wild cereal that still grows in natural habitats in the crescent [\(3\)](#). It was unknown, however, where within the crescent wild einkorn was first taken into cultivation. Heun *et al.* ([1](#)) analyzed DNA from 68 lines of cultivated einkorn, plus 261 wild einkorn lines sampled over the crescent's whole expanse as well as outside the crescent.

Among those wild lines, the most distinct genetically proved to be a group of 11 from the Karacadağ mountains of southeast Turkey. [\[HN7\]](#), [\[HN8\]](#), [\[HN9\]](#), [\[HN10\]](#), [\[HN11\]](#) Those 11 also turned out to be the ones genetically most similar to cultivated einkorn, and so presumably the crop's immediate ancestors. This discovery is compatible with previous nonmolecular evidence. The Karacadağ mountains were already known to support stands of wild einkorn so dense and extensive that they were being harvested by hunter-gatherers even before einkorn's domestication. Nearby archaeological sites contain remains of both wild and cultivated einkorn and are among the crescent's oldest farming sites.

What are some of the broad implications of these findings? Genetically and morphologically, cultivated einkorn is quite similar to wild einkorn in general. Now that the specific wild ancestral line has been identified as being even more similar to the crop, we can better appreciate why einkorn's domestication was so easy and quick. The crescent's archaeological record shows that at most a few centuries were required for the transition from hunter-gatherer villages harvesting wild plants to farming villages planting fully domesticated crops. For einkorn (and probably for the other founder crops as well), that transition required changes in only a few genetic loci, which account for the few morphological changes distinguishing the crop from wild einkorn ([1](#)).

But those few changes were of great value to the earliest farmers. They included heavier seeds and denser seed masses (yielding a crop even more productive than its wild ancestor), plus a firm stalk making seeds more easily harvestable by preventing them from dropping to the ground. Repeated cycles of sowing, growing, and harvesting wild einkorn would have selected automatically for those mutations (3). The first cultivators could have had no conscious intent to produce a crop, and no way of anticipating how radically agriculture would change their societies.

These few, simple changes during einkorn's domestication contrast sharply with the drastic biological reorganization required for the domestication of Native Americans' leading cereal, maize, from its wild ancestor, teosinte. [HN12], [HN13] This difference alone helps explain why densely populated agricultural societies arose so much earlier and developed so much more rapidly in the crescent than in the New World.

Can we attach any significance to the new finding that, within the crescent, einkorn was domesticated specifically in southeast Turkey rather than at some other site? Here we find another clue to the early rapid rise of crescent agriculture. In different parts of the crescent lived wild species ancestral to some of the world's earliest and most useful species of crops and livestock. With the discovery by Heun *et al.* (1), we can pinpoint the origins of three of the crescent's eight founder crops (chickpea,[HN14] bitter vetch, and now einkorn) to eastern Turkey. Grapes and olives were domesticated nearby to the south; sheep, pigs, goats, and cattle close by in possibly the central, north central, eastern, and western crescent, respectively; and barley,[HN15] emmer wheat,[HN16] peas, lentils, and flax in still-to-be-identified parts of the crescent. Only slightly to the northeast of the crescent, on the shores of the Caspian Sea, grows the wild grass *Aegilops squarrosa*. When it hybridized with cultivated emmer wheat spreading east from the crescent, the result was bread wheat, the most valuable single crop in the modern world. Thus, the crescent's diversity of useful wild plant and animal species, living in close proximity to each other, enabled the crescent's first farmers quickly to assemble a balanced package of domesticates meeting all of humanity's basic needs: carbohydrates, protein, oil, milk, animal transport and traction, and vegetable and animal fiber for rope and clothing (3, 4).

That valuable package spread rapidly through and beyond the crescent (see the figure), not only outcompeting hunter-gatherer economies in productivity, but also preempting alternative sequences of plant and animal domestication that might otherwise have arisen elsewhere in western Eurasia. The spread was accelerated by the west-east axis of the whole Eurasian continent as well as of the crescent itself, permitting crops, livestock, and people to expand at the same latitude without having to adapt to new day lengths, climates, and diseases. Cultivated einkorn's rapid diffusion from the Karacadağ mountains preempted possible independent domestications of einkorn elsewhere in its wild range. The rapid diffusion of both einkorn and emmer in turn preempted widespread cultivation of other related domesticable wild grasses, such as Timopheev's wheat. In contrast, the New World's north-south axis required domesticates to adapt to changes of latitude as they spread. The resulting slow spread of crops within Native America permitted numerous independent domestications of the same crop or of related crops (for example, squashes and cottons) in different areas. Within less than 2000 years of the beginnings of domestication in the crescent, its results had been carried east and west to launch the origins of food production over a huge swath of Eurasia (see the figure), from Pakistan to the Balkans (3). Food production's expansion over the Americas, Africa, and the Indian subcontinent was much slower because of the north-south axes of those landmasses (4).

In short, einkorn domestication in the Karacadağ mountains exemplifies the enormous head start that western Eurasian societies gained from Fertile Crescent biogeography. For history's broad patterns, as for real estate investment, location is almost everything. Plant and animal domestication was prerequisite to the growth of large, dense, sedentary human populations, in which the food-producing activities of part of the population yielded storable food surpluses to feed non-food-producing parts of the population. Hence, food production triggered the emergence of kings, bureaucrats, scribes, professional soldiers, and metal-workers and other full-time craftspeople (4). Literacy, metallurgy, stratified societies, advanced weapons, and empires rested on food production. In addition, smallpox and the other crowd epidemic diseases of Eurasia could evolve only in those dense, sedentary human populations living in close contact with domesticated animals, whose own pathogens evolved into those specialized pathogens afflicting us (4). Thus, a long straight line runs through world history, from those first domesticates at the Karacadağ mountains and elsewhere in the Fertile Crescent, to the "guns, germs, and steel" by which European colonists in modern times destroyed so many native societies of other continents.

HyperNotes Related Resources on the World Wide Web

GENERAL HYPERNOTES

[GrainGenes](#) is a compilation of molecular and phenotypic information on wheat, barley, oats, rye, and sugarcane. The project is supported by the USDA/NAL Plant Genome Research Program. Kinds of information offered by *GrainGenes* include: genetic and cytogenetic maps; genomic probes and nucleotide sequences; genes, alleles, and gene products and associated phenotypes; pathologies and pathogens; a taxonomy of the *Triticeae* and *Avena*; and relevant bibliographic citations.

[Plants, Genes and Global Food Production](#) provides information to accompany a course offered by the Cornell University Department of Plant Breeding. [The Index of Course Readings](#) provides links to the full text of selected readings on food crops and their domestication. Readings for Lecture 2, Evolution and Domestication of Food Crops, present discussions of plants, genes, and the emergence of agriculture.

[The South-West Asia Synthesis Report](#) is one of a series of country and sub-regional reports on plant and genetic resources developed by the Food and Agriculture Organization of the United Nations. This report provides information on plant species of agricultural importance in the region and their wild relatives, the history of agriculture in the region, plant genetic resources conservation activities, and socioeconomic conditions of the nations and territories in southwest Asia. [The Country Report for the Republic of Turkey](#) provides additional

information on einkorn wheat and its wild relatives in western Asia. [Indigenous Plant Genetic Resources](#), a chapter of the [Country Report for Ethiopia](#), suggests that Ethiopia may be the center of origin of the chickpea and the lentil.

Through its Web site, the [National Agricultural Library](#) provides a list of Internet resources for agriculture.

[The World Wide Web Virtual Library: Agriculture](#) is an extensive list of Internet resources for agriculture. This page is maintained by the National Science Foundation Center for Integrated Pest Management, located at North Carolina State University.

NUMBERED HYPERNOTES

1. [Jared Diamond's Web page](#) describes his research interests and lists representative publications. [Why Did Human History Unfold Differently on Different Continents for the Last 13,000 Years?](#) is a faculty research lecture by Jared Diamond on a topic related to this Perspective.
2. [The Indo-European Language Tree](#) by Dan Short is available through the [Old English Pages](#) maintained at Georgetown University.
3. [Exploration of Language](#) is a brief tutorial on linguistics and language families, including the Indo-European language family.
4. Einkorn, emmer, and other varieties of wheat are described in [Alternative Wheat Cereals as Food Grains: Einkorn, Emmer, Spelt, Kamut, and Triticale](#) by G. F. Stallknecht, K. M. Gilbertson, and J. E. Ranney. This page is one of several pages in [NewCROP](#), the Web site of the Center for New Crops and Plant Products at Purdue University.
5. [Lost Crops of Africa: Volume I: Grains](#) (Washington, DC, National Academy Press, 1996) presents a discussion of einkorn and emmer wheat.
6. [PLB143: Evolution of Crop Plants](#) is an outline of a course offered at the University of California, Davis. Detailed lecture outlines provide lists of readings in addition to facts about the domestication of plants with illustrations and tables. Lecture 08: [What is a crop? The domestication syndrome](#) outlines the changes that occurred in einkorn and emmer wheat in the process of domestication.
7. A remote sensing image of the [Karacadağ](#) region of Turkey is available from the [German Remote Sensing Data Center](#) (Deutsches Fernerkundungsdatenzentrum).
8. [Geographical Regions of Turkey](#), available through the [Republic of Turkey Web site](#), describes Karacadağ as one of the main peaks in the Central Anatolian region of Turkey.
9. Maps of Turkey and the Middle East are available from the [Perry-Castaneda Library Map Collection](#) at the University of Texas.
10. [The Classics and Mediterranean Archaeology Server](#) is a list of resources on the World Wide Web for the archaeology of the Mediterranean region.
11. Tourist maps of Turkey are available from [FOCUS Multimedia](#).
12. [Green Genes](#) by Gerald R. Fink describes teosinte and the domestication of maize. Green Genes is a chapter of Access Excellence, a national educational program on the World Wide Web that provides high school biology teachers access to sources of new scientific information about biotechnology.
13. [Poaceae](#) includes a description and photograph of teosinte (*Zea diploperennis*).
14. The NewCROP Fact Sheet for [chickpea](#) presents information on the origin of chickpea.
15. [Hordeum vulgare](#) describes common barley and includes an illustration from the [National Small Grains Collection](#).
16. [Triticum dicoccon](#) provides a brief description and an illustration of emmer wheat from the [National Small Grains Collection](#).
17. [Radiocarbon WEB-info](#) describes radiocarbon dating and calibration of radiocarbon dates. A list of other Web sites related to radiocarbon dating is included.
18. [Guns, Germs and Steel](#) by Jared Diamond is available from [W. W. Norton & Company](#).
19. [Department of Physiology, UCLA School of Medicine](#).

References and Notes

1. M. Heun, *Science* **278**, 1312 (1997). [Abstract/FREE Full Text](#)
2. All dates that I cite are so-called calibrated radiocarbon dates [HN17] which are corrected for temporal fluctuations in atmospheric carbon isotope ratios and thus correspond to approximate calendar years. The dates in (1) are younger because they instead are uncalibrated dates.
3. D. Zohary, M. Hopf, *Domestication of Plants in the Old World, ed. 2* (Oxford Univ. Press, Oxford, 1993).
4. J. Diamond, *Guns, Germs, and Steel: The Fates of Human Societies* (Norton, New York, 1997) [HN18].

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J Exp Bot 1 January 2007: 131-145.

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A single domestication for potato based on multilocus amplified fragment length polymorphism genotyping

Proc. Natl. Acad. Sci. USA 11 October 2005: 14694-14699.

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Anatomy of a Revolution

Genetics 1 June 1998: 473-477.

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