

sus sequence for binding of MYB transcription factors resulted in abrogation of the gibberellin response, which is essential for promotion of flowering in *Arabidopsis* during noninductive short days.

The investigators observed normal flowering in response to long days with the mutant constructs. When *CO* was overexpressed, constitutively activating the photoperiodic pathway, reporter gene expression in the mutant construct was also constitutively activated. However, when *FT* was overexpressed, activating the photoperiodic pathway, reporter gene expression was silent, indicating that *LFY* acts downstream of *CO* but not of *FT*. Therefore, *LFY* must be in a signaling pathway that is parallel to that containing *FT* (see the figure). Similarly, when the same disrupted promoter region was used to drive expression of the *LFY* gene, the

construct was able to rescue flowering in plants deficient in *LFY* during long days but not short days. This confirms that the disruption constitutes a short-day defect. The *LFY* promoter thus defines another site where different environmental stimuli that control flowering converge and are integrated.

The integration of diverse stimuli in the control of a response is a feature of many biological systems. The two new studies provide inroads into understanding how several signaling pathways converge to control flowering in higher plants, but there is still much to learn. We do not know the mechanism by which different signaling components integrate the large number of environmental stimuli that regulate flowering. A further question is the way in which these various environmental stimuli are detected. It is still a mystery how signals

from photoreceptors and the endogenous circadian clock interact to enable plants to detect day length (9) or how cold temperatures are sensed, triggering the vernalization response (10).

References

1. A. Samach et al., *Science* **288**, 1613 (2000).
2. M. A. Blázquez and D. Weigel, *Nature* **404**, 889 (2000).
3. B. Thomas and D. Vince-Prue, *Photoperiodism in Plants* (Academic Press, London, 1997).
4. K. Napp-Zinn, *Manipulation of Flowering*, J. G. Atherton, Ed. (Butterworths, London, 1987), p. 123.
5. H. Smith, *Photomorphogenesis in Plants*, R. E. Kendrick and G. H. M. Kronenberg, Eds. (Kluwer, Dordrecht, Netherlands, ed. 2, 1994), p. 377.
6. G. G. Simpson, A. R. Gendall, C. Dean, *Annu. Rev. Cell Dev. Biol.* **15**, 519 (1999).
7. J. Putterill, F. Robson, K. Lee, R. Simon, G. Coupland, *Cell* **80**, 847 (1995).
8. M. F. Yanovsky, *Annu. Rev. Plant Physiol. Plant Mol. Biol.* **46**, 167 (1995).
9. D. E. Somers, P. F. Devlin, S. A. Kay, *Science* **282**, 1488 (1998).
10. J. Chandler, A. Wilson, C. Dean, *Plant J.* **10**, 637 (1996).

PERSPECTIVES: ARCHAEOLOGY

The Cradle of Agriculture

Simcha Lev-Yadun, Avi Gopher, Shahal Abbo

A crucial event in human history was the beginning of agriculture about 10,000 years ago in the Pre-Pottery Neolithic Near East. The accumulation of surplus food supplies enabled large settlements to be established, resulting in the emergence of Western civilization. There has been much debate about exactly when and where agriculture first began.

Enhanced online at
www.sciencemag.org/cgi/content/full/288/5471/1602

Kislev (1) proposed that cereals were domesticated after 7000 B.C., later than previously assumed (non-calibrated ¹⁴C dates). In contrast, Hillman and Colledge (2) recently suggested that rye and pulses were first domesticated during the late Epipaleolithic at Tel Abu Hureyra 1, 8900 to 8600 B.C. If confirmed, these would be the earliest domesticated crops reported.

Regarding the "where" question, it is generally believed that plant domestication first took place in the Jordan Valley and adjacent areas of the southern Levant (in present-day Israel and Jordan). However, we think that botanical, genetic, and ar-

chaeological evidence point to a small core area within the Fertile Crescent—near the upper reaches of the Tigris and Euphrates rivers in present-day southeastern Turkey/northern Syria—as the cradle of agriculture (see the figure).

The wild progenitors of all seven Neolithic founder crops (einkorn wheat, emmer wheat, barley, lentil, pea, bitter vetch, and chickpea) as well as flax are found together only in this core area of the Fertile Crescent (see the figure). Wild chickpea grows only in this restricted core area, and its limited distribution is an important clue to the origins of farming in the Near East (3). It is unlikely that such a rare species would have been domesticated as a founder crop 10,000 years ago had farming originated outside of this restricted core area. Furthermore, the putative site of einkorn wheat domestication lies within the limited distribution of wild chickpea (see the figure) (4). The archaeological record also provides evidence to support the view that the wealthy, farming-based Neolithic societies of the core area were the earliest settlements of this type in the Fertile Crescent.

Near-Eastern Neolithic agriculture was based on three cereals (einkorn wheat, emmer wheat, and barley), four pulses (lentil, pea, chickpea, and bitter vetch), and a fiber crop (flax). Wild chickpea has been found in only 10 locations within a small area in southeastern Turkey/northern Syria (3). The distribution of the wild progenitors of the other crops extends across the

Fertile Crescent and beyond (5) (see the figure). The genetic founder stocks that gave rise to domesticated einkorn wheat (4), pea (5), and lentil (6) have been traced to a small region in or near the limited range of wild chickpea. The notion of a single core area of plant domestication is further supported by the limited genetic variability of modern crops compared with their wild progenitors (3) and by genetic evidence suggesting that these crops were domesticated only once (with the possible exception of barley) (7). Given the revolutionary nature of the transition from foraging to farming, it seems unlikely that agriculture was invented independently in several locations within the Fertile Crescent in a short period. Had such a transition taken place at different locations, it should have been possible to trace the original founder stocks to different areas. But this has not been the case.

Remains of wild forms of einkorn and emmer wheat, barley, chickpea, lentil, bitter vetch, flax, and possibly pea have been found in pre-Neolithic sites of the Fertile Crescent core area (1, 5) including Tell Abu Hureyra 1 (the site described by Hillman and Colledge) and Tell Mureybet I and II (9000 to 8000 B.C.). They have also been discovered in Neolithic sites at Jerf el-Ahmar, Mureybet III, Djade, and Cayönü (8000 to 7500 B.C.). Wild forms have been unearthed at sites near the core area, such as pre-Neolithic Hallan Çemi Tepesi and Neolithic Qermez Dere and M'lefaat (8) (see the figure). Domesticated forms of einkorn wheat, emmer wheat, and barley appeared in core-area Neolithic sites at Tell Abu Hureyra 2A and Cafer Hüyük about 7500 B.C., and soon thereafter at Cayönü and Nevalı Çori (1, 9).

S. Lev-Yadun is in the Department of Agronomy and Natural Resources, Agricultural Research Organization, Volcani Center, 50250 Bet Dagan, Israel. E-mail: vcfield@agri.gov.il. A. Gopher is at the Sonia and Marco Nadler Institute of Archaeology, Tel Aviv University, 69978 Tel Aviv, Israel. E-mail: agopher@post.tau.ac.il. S. Abbo is in the Department of Field Crops, Faculty of Agricultural, Food and Environmental Quality Sciences, Hebrew University of Jerusalem, 76100 Rehovot, Israel. E-mail: abbo@agri.huji.ac.il

In regions beyond the core area, there is no evidence for domesticated forms of cereals and pulses earlier than 7300 to 7000 B.C. Excavation of the Pre-Pottery Neolithic B site in Jericho (present-day Palestinian Authority) yielded plant seeds but these have not been dated directly as yet. We think domesticated cereals from Jericho probably date to the seventh millennium B.C. in contrast to an earlier date proposed by Jones *et al.* (10). The remnants of domesticated emmer wheat found at the Tell Aswad IA site in the Damascus Basin (7800 to 7600 B.C.) may be the temporal and geographical exception (9). Indeed, glossed flint sickle blades from Tell Aswad IA suggest that emmer wheat could have been harvested from the wild at this site as long ago as 7800 B.C. Plant remains from

prehistoric sites that extend beyond the natural range of the plants' wild progenitors are good indicators of domestication. Such evidence exists for: einkorn wheat at the Pre-Pottery Neolithic B Jericho site and at Tell Aswad II (6900 B.C.) (11), lentils at Yiftah'el in Israel (6800 B.C.) (12), and chickpea in Jericho (6500 B.C.) (5).

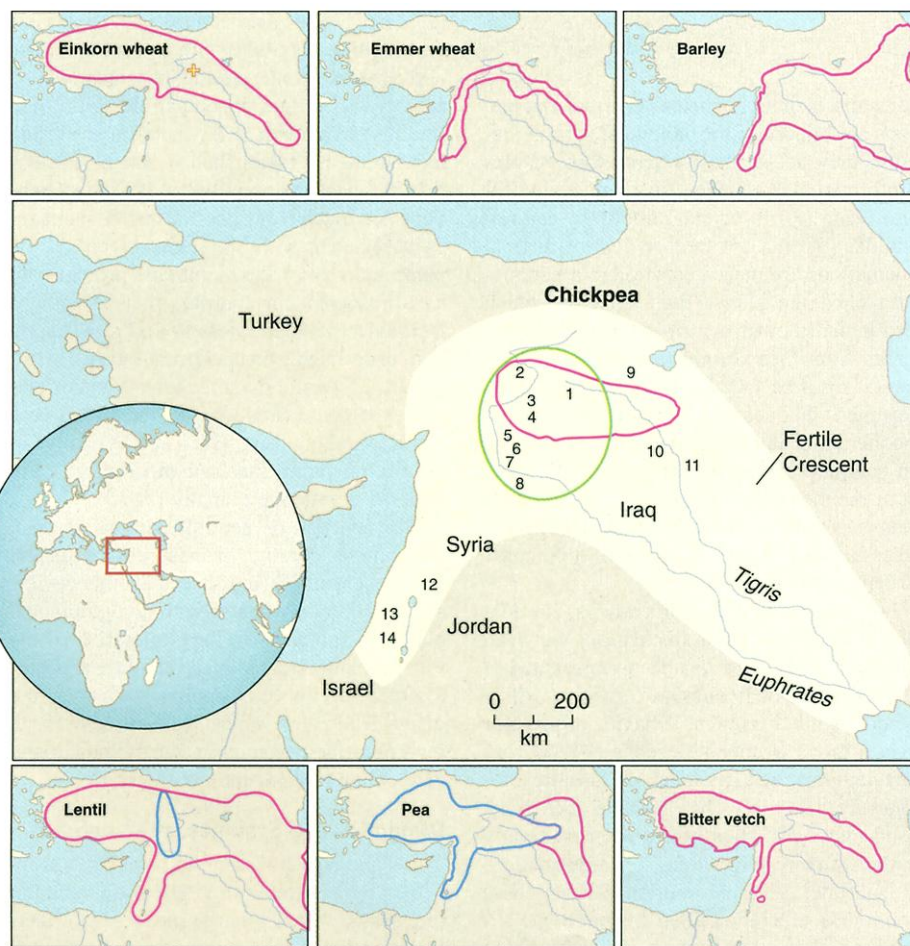
The spread of domesticated plants throughout the Levant accords well with the migration of other Neolithic innovations. Knowledge of flint and stone tools—the Helwan arrowhead (13), new methods for producing long, straight blades for sickles (13), and the “stepped” stone quern for grinding cereal crops—diffused from the Middle Euphrates to the central and southern Levant as early as 8000 B.C. The core area between the upper Tigris and Eu-

phrates rivers seemed to be a center for innovation, with an archaeological record that indicates a wealthy society with plenty of food. Impressive architecture, images, and objects of prestige appear in abundance in core area sites such as Cayönü, Nevali Çori, and Göbekli Tepe (14). Early Neolithic sites in this region appear to be larger than those in other parts of the Fertile Crescent (15), possibly because successful farming was first practiced here.

It is possible that changing conditions in the core area during the cool, dry climatic episode of the Younger Dryas (about 9000 to 8000 B.C.) triggered the end of a nomadic life-style and the beginning of farming settlements. Competition within these communities for social status may have intensified plant domestication and crop production and encouraged the accumulation of surplus food (16). Alternatively, it has been proposed (17) that growth in the core area promoted emigration of sectors of the population to marginal zones at the area's periphery. These newly populated zones would have been close to the chickpea core area so that the emigrating communities still remembered the chickpea founder species. Further research on the distribution and domestication of barley, emmer wheat, and bitter vetch (for which there are no data on founder stocks as yet) will be needed to clarify when and where agriculture and the dawn of modern civilization began.

References

1. M. E. Kislev, in *Prehistoire de l'Agriculture: Nouvelles Approches Expérimentales et Ethnographiques*, P. C. Anderson, Ed. (Monographie du CRA no. 6, Paris, 1992), p. 87.
2. G. Hillman and S. Colledge, *The Transition from Foraging to Farming in Southwest Asia*, International Workshop, Groningen, Netherlands, September 1998.
3. G. Ladizinsky, *Plant Evolution Under Domestication*, (Kluwer, Dordrecht, Netherlands, 1998), pp. 123 and 175.
4. M. Heun *et al.*, *Science* **278**, 1312 (1997).
5. D. Zohary and M. Hopf, *Domestication of Plants in the Old World* (Clarendon, Oxford, ed. 2, 1993).
6. G. Ladizinsky, *Genet. Res. Crop Evol.* **46**, 115 (1999).
7. D. Zohary, in *The Origins and Spread of Agriculture and Pastoralism in Eurasia*, D. R. Harris, Ed. (UCL, London, 1996), p. 142.
8. M. Nesbitt, *The transition from Foraging to Farming in Southwest Asia*, International Workshop, Groningen, Netherlands, September 1998.
9. M. Nesbitt and D. Samuel, *Science* **279**, 1433 (1998).
10. M. K. Jones, R. G. Allaby, T. A. Brown, *Science* **279**, 302 (1998).
11. W. van Zeist and J. A. H. Bakker-Heeres, *Palaeohistoria* **24**, 165 (1985).
12. Y. Garfinkel, M. E. Kislev, D. Zohary, *Israel J. Bot.* **37**, 49 (1988).
13. A. Gopher, *Arrowheads of the Neolithic Levant. A Seriation Analysis* (Eisenbrauns, Winona Lake, IN, 1994).
14. M. Özdoğan, *J. Eur. Archaeol.* **5.2**, 1 (1997).
15. O. Bar-Yosef and R. Meadow, in *Last Hunters, First Farmers*, T. D. Price and A. B. Gebauer, Eds. (Advanced Seminar Series School of American Research, Santa Fe, CA, 1995), p. 39.
16. B. Hyden, *J. Anthropol. Archaeol.* **9.1**, 31 (1990).
17. L. R. Binford, in *New Perspectives in Archaeology*, S. R. Binford, and L. R. Binford, Eds. (Aldine, Chicago, IL, 1968), p. 313.



East of Eden. The geographical distribution of the seven Neolithic founder crops in the Fertile Crescent (yellow) of the Near East. Large map shows the distribution of wild chickpea (red line) in a core area (green line) within the upper reaches of the Tigris and Euphrates rivers (present-day southeastern Turkey/northern Syria). Neolithic sites are numbered as follows: (1) Cayönü, (2) Cafer Hüyük, (3) Nevali Çori, (4) Göbekli Tepe, (5) Djade, (6) Jerf el-Ahmar, (7) Tell Mureybet, (8) Tell Abu Hureyra, (9) Hallan Çemi Tepesi, (10) Qermez Dere, (11) Milefaat, (12) Tell Aswad, (13) Yiftahiel, and (14) Jericho. Inset maps show the distribution of founder cereal crops—einkorn wheat (cross indicates the putative site of its domestication), emmer wheat, and barley—and founder legumes (lentil, pea, bitter vetch). Blue lines delineate the range of genetic founder stocks for lentil and pea, and red lines the range of emmer wheat, barley, and bitter vetch (no data are available on their genetic founder stocks). Red lines also indicate the distribution of einkorn wheat, lentil, and pea beyond that of their genetic founder stocks. [Botanical data compiled from (4–7)].