PROTEINS INVOLVED IN BOTH DNA REPLICATION AND SILENCING

Element	Replication	Silencing
HMR ARS	Binds ORC	Binds ORC
ORC	Scaffold for preinitiation complex	Recruits Sir1p
CAF	Nucleosome assembly during replication	Assembly of silent chromatin?
DNA polymerase α	Initiate nascent DNA chains	?
DNA polymerase ε	Elongation; repair	?
PCNA	Sliding clamp	?
RF-C	Clamp loader; elongation processivity	?

A variety of DNA sequences and proteins are important for transcriptional silencing. The ORC is involved in both DNA replication and silencing, and different portions of ORC proteins carry out its separate functions (*16*). The ORC recruits Sir1p, which is required for silencing to be established (*9*). In contrast, other components of the ORC involved in replication seem to be important for movement of the replication fork along the DNA; any part that they may play in silencing remains obscure. Although some ORC components are required for efficient silencing, others inhibit silencing; differential effects of these proteins are seen depending on whether silencing is examined in yeast mating-type loci or in ribosomal DNA (*12, 13, 17*). ARS, autonomously replicating sequence (the site of ORC binding); RF-C, replication factor C.

reduce the stable inheritance of silencing at telomeres and impair the maintenance of silencing at *HMR**a***, *HML*α, and other loci (*10–12*). The connection with DNA replication is that CAF-I deposits newly synthesized histones onto newly replicated DNA. Furthermore, mutations in proliferating cell nuclear antigen (PCNA) that disrupt the association of this replication protein with CAF-I also impair the inheritance of silencing (*13*). The implication is that DNA replication may well prove crucial for "persistence" of the silent state.

This returns us to the original question: What makes S phase important for transcriptional silencing? Strictly speaking, the phase of the cell cycle required for silencing to be established is somewhere between early S phase (the point where hydroxyurea blocks cell cycle progression) and mitosis (where nocodazole has its inhibitory effect) (*1*). This suggests that the S-phase requirement for silencing may in reality be a point somewhere in late S phase, in G_2, or possibly even in early mitosis.

The cell's DNA replication machinery is fully capable of replicating conventional chromatin or previously silenced chromatin. However, it may be challenged by the drastic alterations in chromatin structure that accompany the establishment of silencing, during which the chromatin changes from the relatively open unsilenced state to the closed heterochromatic state. To prevent such molecular conflicts, the silencing machinery may be activated by an intracellular signal sent when DNA replication has been completed. In fact, Sir proteins can move to new locations inside the cell in response to various forms of DNA damage (*14, 15*), indicating that they can respond to signals sent by changes in DNA state. Needless to say, there are many other possible events that could control the establishment of silencing through the generation of specific cell cycle signals or changes in nuclear structure. But what was once considered the most likely event—replication of the DNA prior to silencing—does not appear to be among them.

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PERSPECTIVES: ARCHAEOLOGY

What Drives Societal Collapse?

Harvey Weiss and Raymond S. Bradley

The archaeological and historical record is replete with evidence for prehistoric, ancient, and premodern societal collapse. These collapses occurred quite suddenly and frequently involved regional abandonment, replacement of one subsistence base by another (such as agriculture by pastoralism), or conversion to a lower energy sociopolitical organization (such as local state from interregional empire). Each of these collapse episodes has been discussed intensively within the archaeological community, commonly leading to the conclusion that combinations of social, political, and economic factors were their root causes.

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That perspective is now changing with the accumulation of high-resolution paleoclimatic data that provide an independent measure of the timing, amplitude, and duration of past climate events. These climatic events were abrupt, involved new conditions that were unfamiliar to the inhabitants of the time, and persisted for decades to centuries. They were therefore highly disruptive, leading to societal collapse—an adaptive response to otherwise insurmountable stresses (*1*).

In the Old World, the earliest well-documented example of societal collapse is that of the hunting and gathering Natufian communities in southwest Asia. About 12,000 years ago, the Natufians abandoned seasonally nomadic hunting and gathering activities that required relatively low inputs of labor to sustain low population densities and replaced these with new labor-intensive subsistence strategies of plant cultivation and animal husbandry. The consequences of this agricultural revolution, which was key to the emergence of civilization, included orders of magnitude increases in population growth and full-time craft specialization and class formation, each the result of the ability to generate and deploy agricultural surpluses.

What made the Natufians change their lifestyle so drastically? Thanks to better dating control and improved paleoclimatic interpretations, it is now clear that this transition coincided with the Younger Dryas climate episode about 12,900 to 11,600 years ago. Following the end of the last glacial period, when southwest Asia was dominated by arid steppe vegetation, a shift to increased seasonality (warm, wet winters and hot, dry summers) led to the development of an open oak-terebinth parkland of woods and wild cereals across the interior Levant and northern Mesopotamia. This was the environment exploited initially by the hunting and gathering Natufian communities. When cooler and drier conditions abruptly returned during the Younger Dryas, the harvests of wild resources dwindled, and foraging for these resources could not sustain Natufian subsistence. They were forced to transfer settlement and wild cereals to adjacent new locales where intentional cultivation was possible (*2*).

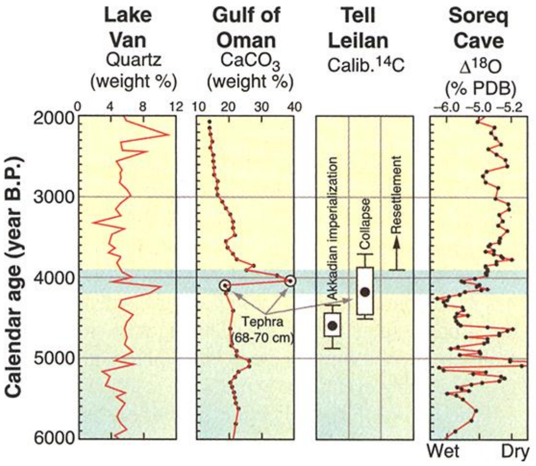
The population and socioeconomic complexity of these early agricultural settlements increased until about 6400 B.C., when a second postglacial climatic shock altered their developmental trajectory. Paleoclimatic evidence documents abrupt climatic change at this time (*3*), the last major climatic event related to the melting continental ice sheets that flooded the North Atlantic (*4*). In the Middle East, a ~200-year drought forced the abandonment of agricultural settlements in the Levant and northern Mesopotamia (*5*, *6*). The subsequent return to moister conditions in Mesopotamia promoted settlement of the Tigris-Euphrates alluvial plain and delta, where breachable river levees and seasonal basins may have encouraged early southern Mesopotamian irrigation agriculture (*7*).

By 3500 B.C., urban Late Uruk society flourished in southern Mesopotamia, sustained by a system of high-yield cereal irrigation agriculture with efficient canal transport. Late Uruk "colony" settlements were founded across the dry-farming portions of the Near East (*8*). But these colonies and the expansion of Late Uruk society collapsed suddenly at about 3200–3000 B.C. Archaeologists have puzzled over this collapse for the past 30 years. Now there are hints in the paleoclimatic record that it may also be related to a short (less than 200 year) but severe drought (*9–11*).

Following the return to wetter conditions, politically centralized and class-based urban societies emerged and expanded across the riverine and dry-farming landscapes of the Mediterranean, Egypt, and West Asia. The Akkadian empire of Mesopotamia, the pyramid-constructing Old Kingdom civilization of Egypt, the Harappan C3 civilization of the Indus valley, and the Early Bronze III civilizations of Palestine, Greece, and Crete all reached their economic peak at about 2300 B.C. This period was abruptly terminated before 2200 B.C. by catastrophic drought and cooling that generated regional abandonment, collapse, and habitat-tracking. Paleoclimatic data from numerous sites document changes in the Mediterranean westerlies and monsoon rainfall during this event (see the figure), with precipitation reductions of up to 30% that diminished agricultural production from the Aegean to the Indus (*9–11*).

These examples from the Old World illustrate that prehistoric and early historic societies—from villages to states or empires—were highly vulnerable to climatic disturbances. Many lines of evidence now point to climate forcing as the primary agent in repeated social collapse.

High-resolution archaeological records from the New World also point to abrupt climatic change as the proximal cause of repeated social collapse. In northern coastal Peru, the Moche civilization suffered a ~30-year drought in the late 6th century A.D., accompanied by severe flooding. The capital city was destroyed, fields and irrigation systems were swept away, and widespread famines ensued. The capital city was subsequently moved northward, and new adaptive agricultural and architectural technologies were implemented (*12*). Four hundred years later, the agricultural base of the Tiwanaku civilization of the central



Climatic effects. High-resolution lake, marine, and speleothem cores and tephrochronostratigraphy document abrupt aridification and linkage with Akkadian empire collapse at Tell Leilan, Syria (*9–11*).

Andes collapsed as a result of a prolonged drought documented in ice and in lake sediment cores (*13*). In Mesoamerica, lake sediment cores show that the Classic Maya collapse of the 9th century A.D. coincided with the most severe and prolonged drought of that millennium (*14*). In North America, Anasazi agriculture could not sustain three decades of exceptional drought and reduced temperatures in the 13th century A.D., resulting in forced regional abandonment (*15*).

Climate during the past 11,000 years was long believed to have been uneventful, but paleoclimatic records increasingly demonstrate climatic instability. Multidecadal- to multicentury-length droughts started abruptly, were unprecedented in the experience of the existing societies, and were highly disruptive to their agricultural foundations because social and technological innovations were not available to counter the rapidity, amplitude, and duration of changing climatic conditions.

These past climatic changes were unrelated to human activities. In contrast, future climatic change will involve both natural and anthropogenic forces and will be increasingly dominated by the latter; current estimates show that we can expect them to be large and rapid (*16*). Global temperature will rise and atmospheric circulation will change, leading to a redistribution of rainfall that is difficult to predict. It is likely, however, that the rainfall patterns that societies have come to expect will change, and the magnitude of expected temperature changes (*17*) gives a sense of the prospective disruption. These changes will affect a world population expected to increase from about 6 billion people today to about 9 to 10 billion by 2050. In spite of technological changes, most of the world's people will continue to be subsistence or small-scale market agriculturalists, who are similarly vulnerable to climatic fluctuations as the late prehistoric/early historic societies. Furthermore, in an increasingly crowded world, habitat-tracking as an adaptive response will not be an option.

We do, however, have distinct advantages over societies in the past because we can anticipate the future. Although far from perfect and perhaps subject to unexpected nonlinearities, general circulation models provide a road map for how the climate system is likely to evolve in the future. We also know where population growth will be greatest. We must use this information to design strategies that minimize the impact of climate change on societies that are at greatest risk. This will require substantial international cooperation, without which the 21st century will likely witness unprecedented social disruptions.

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