from the conformal attachment of microscopic fibers to surfaces and objects and their subsequent entanglement (*17*, *28*). The observed mechanical interlocking in our artificial, spirally assembling bristle can be used in a similar manner and may lead to an effective adhesive and particle-trapping system. Figure 5 shows microspheres that are captured through conformal wrapping and twisting of the nanobristle. The adhesion is extremely stable, and the particles remain attached even after rigorous sonication. The process is equally applicable for attaching to objects with arbitrary shapes and surfaces with various topographies.

Though lateral adhesion is known to occur in high–aspect ratio structures such as photoresists and soft lithographic stamps (*29*, *30*), arrays of carbon and ZnO nanotubes (*31*, *32*), and biomimetic setal adhesives (*33*), this process has been generally described as an unwanted outcome that leads to the uncontrolled collapse of the structures. The clustered features were usually irregular in size, and no order over the large area was observed unless templating was used (*34*). Here we have demonstrated that the process can, in fact, be finely tuned to yield organized nontrivial, helical assemblies with controlled size, pattern, hierarchy, and handedness over large areas. These mesoscale coiled structures may be useful in a number of applications: They have the ability to store elastic energy and information embodied in the adhesive patterns that can be created at will. Additionally, they may be used as an efficient adhesive or capture-and-release system, provide the foundation for hierarchically assembled structural materials, and be used to induce chiral flow patterns in the ambient flow and thus be applied for enhanced mixing and directed transport at the micron and submicron scale. These structures may serve as the seed for the spontaneous breaking of symmetry on large scales, just as

chirally spinning cilia ultimately control the left-right asymmetry in vertebrate morphogenesis (*6*).

References and Notes

1. M. M. Green, R. J. M. Nolte, E. W. Meijer, *Materials-Chirality*, vol. 24 of *Topics in Stereochemistry*, S. E. Denmark, J. Siegel, Eds. (Wiley, Hoboken, NJ, 2003).
2. N. Rubin, E. Perugia, M. Goldschmidt, M. Fridkin, L. Addadi, *J. Am. Chem. Soc.* **130**, 4602 (2008).
3. H. Lichtenegger, M. Muller, O. Paris, C. Riekel, P. Fratzl, *J. Appl. Crystallogr.* **32**, 1127 (1999).
4. W. Wagermaier *et al.*, *Biointerphases* **1**, 1 (2006).
5. S. Weiner, H. D. Wagner, *Annu. Rev. Mater. Sci.* **28**, 271 (1998).
6. J. J. Essner *et al.*, *Nature* **418**, 37 (2002).
7. H. C. Kolb, M. S. Vannieuwenhze, K. B. Sharpless, *Chem. Rev.* **94**, 2483 (1994).
8. J. W. Goodby, *J. Mater. Chem.* **1**, 307 (1991).
9. E. D. Sone, E. R. Zubarev, S. I. Stupp, *Angew. Chem. Int. Ed.* **41**, 1705 (2002).
10. J. S. Moore, S. I. Stupp, *J. Am. Chem. Soc.* **114**, 3429 (1992).
11. T. E. Gier, X. H. Bu, P. Y. Feng, G. D. Stucky, *Nature* **395**, 154 (1998).
12. J. Zhu *et al.*, *Nat. Nanotechnol.* **3**, 477 (2008).
13. C. A. Orme *et al.*, *Nature* **411**, 775 (2001).
14. A. E. Cohen, L. Mahadevan, *Proc. Natl. Acad. Sci. U.S.A.* **100**, 12141 (2003).
15. J. Bico, B. Roman, L. Moulin, A. Boudaoud, *Nature* **432**, 690 (2004).
16. H. Y. Kim, L. Mahadevan, *J. Fluid Mech.* **548**, 141 (2006).
17. T. Eisner, D. J. Aneshansley, *Proc. Natl. Acad. Sci. U.S.A.* **97**, 6568 (2000).
18. O. Betz, G. Kolsch, *Arthropod Struct. Dev.* **33**, 3 (2004).
19. S. Neukirch, G. van der Heijden, *J. Elast.* **69**, 41 (2002).
20. M. M. Nicolson, *Proc. Cambridge Philos. Soc.* **45**, 288 (1949).
21. This is a simplification of the actual geometry of the pillars that are attached to a substrate at one end and free at the other. Yet, the case of free pillars that can bend, twist, and adhere is sufficient to understand the conditions when helical structures can arise. In the experimental setup, however, it is this broken symmetry induced by the attachment that leads to the observed complex braided structures of generalized helices of variable pitch and radius.
22. K. L. Johnson, *Contact Mechanics* (Cambridge Univ. Press, Cambridge, 1985).
23. For a pillar with a circular cross section, the twist of the cross section is a constant. Although adhesion can lead to twisting, because there is a lubricating layer of fluid between the pillars, we will assume that the pillars can bend without twisting as they wind around each other. The bending energy of a filament of length L is $U_b \sim B\kappa^2 L$. Therefore, for a helix of radius R and pitch p ($P = p/2\pi R$) that has curvature $\kappa = 1/R(1 + P^2)$, $U_b \sim BL/R^2(1 + P^2)^2$. For helically entwined pillars that are relatively straight (i.e., have a large pitch), the contact zone is straight and thus smaller than the pillar length (a consequence of the relative inextensibility of the pillars) and confers no energetic advantage. However, when the pitch of the tightly entwined pillars falls below a threshold, contact itself occurs over a helical patch (*19*) with a length that scales as $L(1 + 1/P^2)^{1/2}$, so that the adhesion energy $U_a \sim -JaL(1 + 1/P^2)^{1/2}$ increases as the pitch decreases further.
24. B. Pokroy, A. Epstein, M. C. M. Persson Gulda, J. Aizenberg, *Adv. Mater.*, published online 18 November 2008; 10.1002/adma.200801432.
25. A. Ahuja *et al.*, *Langmuir* **24**, 9 (2008).
26. A. Tuteja *et al.*, *Science* **318**, 1618 (2007).
27. P. J. Collings, M. Hird, *Introduction to Liquid Crystals* (Taylor and Francis, Bristol, UK, 1997).
28. K. Autumn *et al.*, *Nature* **405**, 681 (2000).
29. C. Y. Hui, A. Jagota, Y. Y. Lin, E. J. Kramer, *Langmuir* **18**, 1394 (2002).
30. Y. G. Y. Huang *et al.*, *Langmuir* **21**, 8058 (2005).
31. A. Dev, S. Chaudhuri, *Nanotechnology* **18**, 175607 (2007).
32. H. Liu, J. Zhai, L. Jiang, *Soft Matter* **2**, 811 (2006).
33. A. K. Geim *et al.*, *Nat. Mater.* **2**, 461 (2003).
34. A. Sidorenko, T. Krupenkin, A. Taylor, P. Fratzl, J. Aizenberg, *Science* **315**, 487 (2007).
35. This work was partially supported by the Materials Research Science and Engineering Center under NSF award no. DMR-0213805. We acknowledge the use of the facilities at the Harvard Center for Nanoscale Systems supported by NSF award no. ECS-0335765. B.P. is grateful to the Fulbright Visiting Scholar Program for financial support.

Historical Warnings of Future Food Insecurity with Unprecedented Seasonal Heat

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Higher growing season temperatures can have dramatic impacts on agricultural productivity, farm incomes, and food security. We used observational data and output from 23 global climate models to show a high probability (>90%) that growing season temperatures in the tropics and subtropics by the end of the 21st century will exceed the most extreme seasonal temperatures recorded from 1900 to 2006. In temperate regions, the hottest seasons on record will represent the future norm in many locations. We used historical examples to illustrate the magnitude of damage to food systems caused by extreme seasonal heat and show that these short-run events could become long-term trends without sufficient investments in adaptation.

The food crisis of 2006–2008 demonstrates the fragile nature of feeding the world's human population. Rapid growth in demand for food, animal feed, and biofuels, coupled with disruptions in agricultural supplies caused by poor weather, crop disease, and export restrictions in key countries like India and Argentina, have created chaos in international markets (*1*). Coping with the short-run challenge of food price volatility is daunting. But the longer-term challenge of avoiding a perpetual food crisis under conditions of global warming is far more serious. History shows that extreme seasonal heat can be detrimental to regional agricultural productivity and human welfare and to international agricultural markets when policy-makers intervene to secure domestic food needs.

We calculated the difference between projected and historical seasonally averaged temperatures (*2*) throughout the world by using output from the 23 global climate models contributing to the Intergovernmental Panel on Climate Change's (IPCC) 2007 scientific synthesis (*3*). Our results show that it is highly likely (greater than 90%

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chance) that growing season temperatures by the end of the 21st century will exceed even the most extreme seasonal temperatures recorded from 1900 to 2006 for most of the tropics and sub-tropics. Presently there are more than 3 billion people living in the tropics and subtropics, many of whom live on under $2 per day and depend primarily on agriculture for their livelihoods (4). With growing season temperatures rising beyond historical bounds, the inevitable question arises: Will people in these regions have sufficient access to food to meet population- and income-

driven growth in demand in the future, and thus to achieve food security?

The IPCC concluded that elevated green-house gas concentrations are likely to lead to a general drying of the subtropics by the end of this century, creating widespread stress on agriculture (3, 5). Although much attention is focused on threats of increased droughts in subtropical agri-culture, the potential impacts of seasonal average temperature changes in both the tropics and sub-tropics, which are expected to be large relative to the historical range of variation, are often over-

looked (6). Experimental and crop-based models for major grains in these regions show direct yield losses in the range of 2.5 to 16% for every 1°C increase in seasonal temperature (7, 8) [sup-porting online material (SOM)]. Large additional losses are expected from sea level rise and de-creased soil moisture caused by higher average temperatures (3, 5, 9). Despite the general per-ception that agriculture in temperate latitudes will benefit from increased seasonal heat and supply food to deficit areas, even mid-latitude crops will likely suffer at very high temperatures in the ab-sence of adaptation (10). Global climate change thus presents widespread risks of food insecurity.

It is conceivable that the warmest summers during the past century will represent the norm by the end of this century (Fig. 1A). But what if the average future seasonal temperature were to exceed the hottest seasons on record (Fig. 1B)? Entering a whole new realm of high seasonally averaged temperatures, not just multiday heat waves, will surely challenge the global popula-tion's ability to produce adequate food in the fu-ture or even to cope physically with chronic heat stress, unless major adaptations are made.

To put Fig. 1A in perspective, recall the re-cord hot summer in Western Europe in 2003

Fig. 1. Hypothetical distributions of summer season temperatures from 1900–2000 and 2080–2100. x axis indi-cates seasonal temper-ature; y axis, probability of occurrence (number of years in the century). (**A**) The highest growing-

season temperature of the 20th century represents the median seasonal temperature by the end of the 21st century. (**B**) Future temperatures are out-of-bounds hot: that is, it is certain that the growing season temperature at the end of the 21st century will exceed the hottest growing season ever observed.
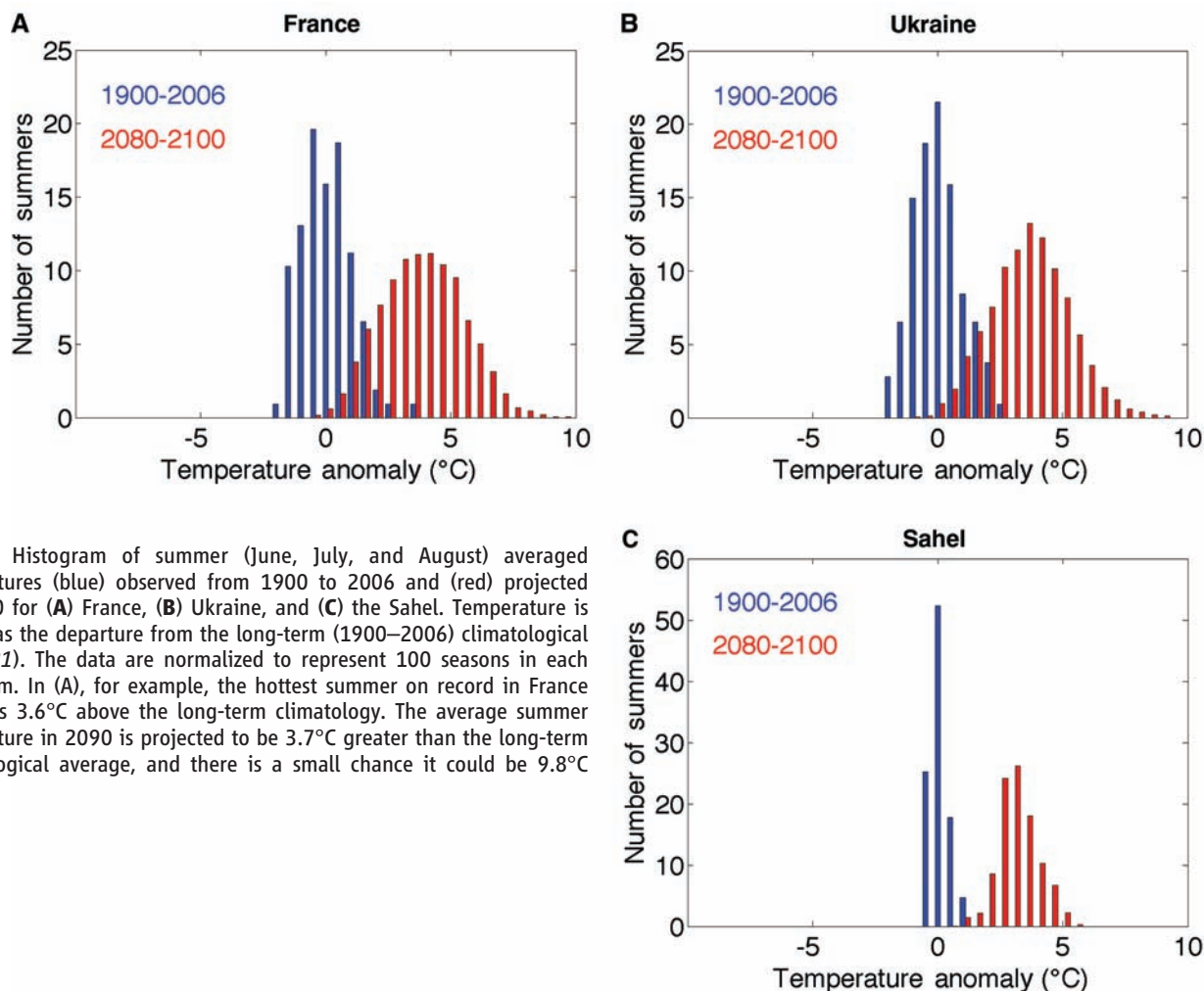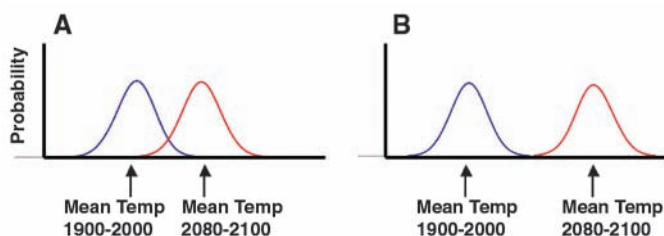

Fig. 2. Histogram of summer (June, July, and August) averaged temperatures (blue) observed from 1900 to 2006 and (red) projected for 2090 for (**A**) France, (**B**) Ukraine, and (**C**) the Sahel. Temperature is plotted as the departure from the long-term (1900–2006) climatological mean (21). The data are normalized to represent 100 seasons in each histogram. In (**A**), for example, the hottest summer on record in France (2003) is 3.6°C above the long-term climatology. The average summer temperature in 2090 is projected to be 3.7°C greater than the long-term climatological average, and there is a small chance it could be 9.8°C higher.

when an estimated 52,000 people died between June and August from heat stress, making it one of the deadliest climate-related disasters in Western history (*11*). The most intense seasonal temperature and the majority of fatalities were centered in France and northern Italy, where over 30,000 people perished from heat-related causes (*11*, *12*). In France, the mean summer temperature (June to August) was 3.6°C (3.5 standard deviations) above the long-term mean. Unfortunately, by the end of the century, summer heat like that of 2003 is likely to be the norm for the country (Fig. 2A).

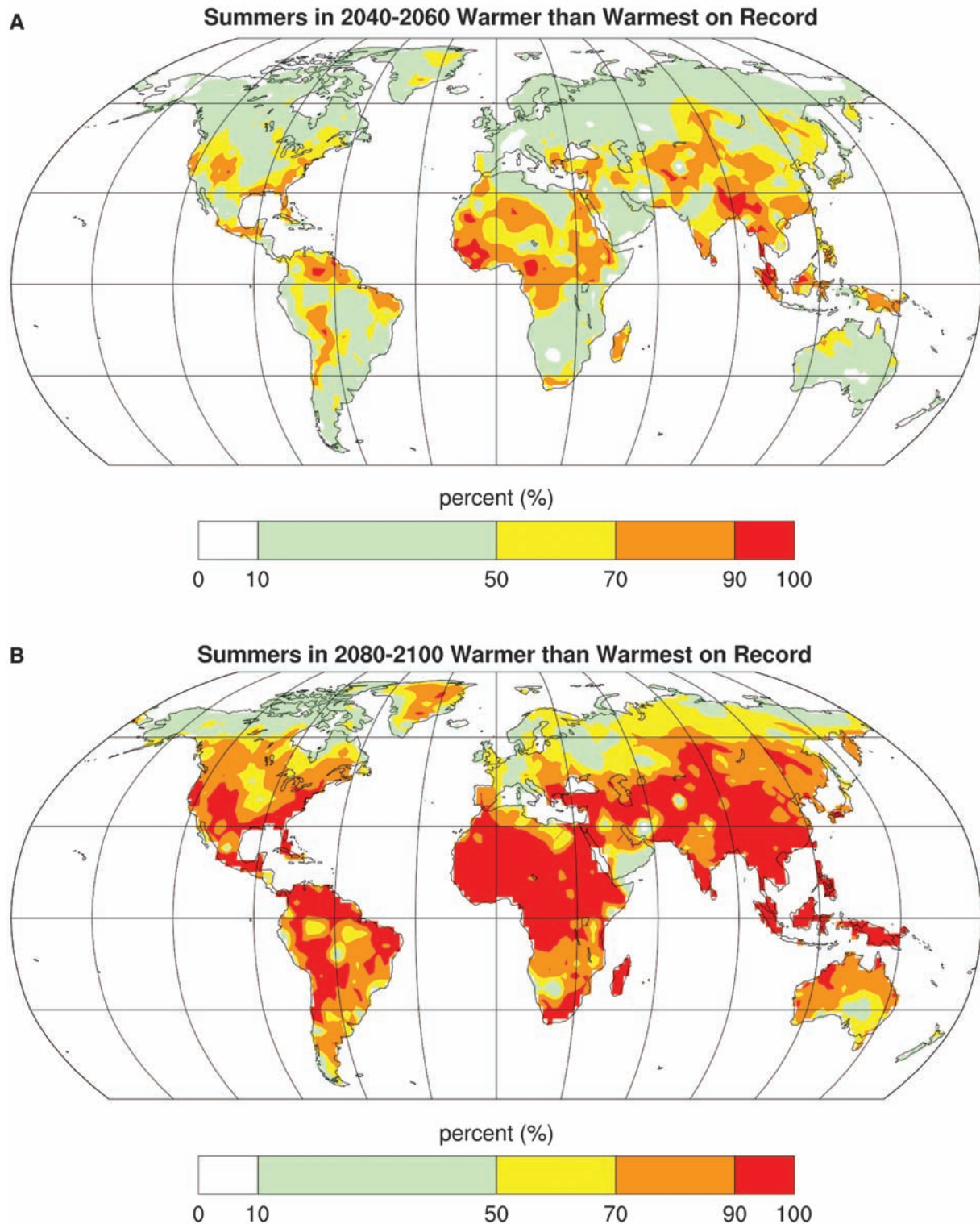Severe heat in the summer of 2003 affected food production as well as human lives in Eu-

Fig. 3. Likelihood (in percent) that future summer average temperatures will exceed the highest summer temperature observed on record (**A**) for 2050 and (**B**) for 2090. For example, for places shown in red there is greater than a 90% chance that the summer-averaged temperature will exceed the highest temperature on record (1900–2006) (*22*).

rope. Record high daytime and nighttime temperatures over most of the summer growing season reduced leaf and grain-filling development of key crops such as maize, fruit trees, and vineyards; accelerated crop ripening and maturity by 10 to 20 days; caused livestock to be stressed; and resulted in reduced soil moisture and increased water consumption in agriculture (5, 13) (SOM). Italy experienced a record drop in maize yields of 36% from a year earlier, whereas in France maize and fodder production fell by 30%, fruit harvests declined by 25%, and wheat harvests (which had nearly reached maturity by the time the heat set in) declined by 21% (5). These production shortfalls hurt the region's farmers economically, although global food trade, subsidies, and insurance compensation helped to avert serious price hikes or reductions in regional or global food security.

By comparison, extremely high summer-averaged temperature in the former Soviet Union (USSR) in 1972 contributed to disruptions in world cereal markets and food security that remain a legacy in the minds of food policy analysts to this day. What sticks in most people's minds is the towering price spike between 1972 and 1974 that occurred within a long-term trend decline in grain prices during a 50-year period after World War II. Nominal prices for wheat— the crop most affected by the USSR weather shock—rose from $60 to $208 per metric ton in international markets between the first quarters of 1972 and 1974, and real prices more than tripled (14). Although extreme summer averaged temperature in the USSR was among several factors contributing to the international price spike, this climate event was largely responsible for setting the dynamics in motion (15).

The prolonged hot period in the summer of 1972 in southeast Ukraine and southwest Russia— major breadbaskets in the former USSR—ranks in the top 10% of temperature anomalies over the observational period 1900–2006. Summer temperatures in this region ranged from 2° to 4°C above the long-term mean. The vast majority of news reports at the time focused on drought as opposed to extreme heat, although fully one-third of summers in this area over the past 100 years were drier than in 1972 (only 0.5 standard deviations below the long-term mean). A peak of high temperatures exceeding 30°C set in during July and August during key crop development stages for wheat and coarse grains, causing a 13% decline in grain production from a year earlier for the USSR as a whole (16) (SOM). Such high summer temperatures in the region will likely be the norm in 2050 and well below the median of projected summer temperature by the end of the century (Fig. 2B).

The USSR had long been known for its variable climate and crop yields. What changed in 1972 was the Soviets' unexpected intervention in international markets to compensate for anticipated crop shortfalls—a marked shift from their earlier policy of internal adjustments through the culling of livestock herds (16). The USSR entered the world grain market at a time when import demand was rising rapidly in Asia because of expanding populations, low-yield growth, and (in the same year) weak monsoon rains (15). Governments in several developing countries, particularly in Asia, feared political instability with rising grain prices and implemented food self-sufficiency (minimum trade) policies that remained in effect for decades.

A major lesson from this case and the recent food crisis is that regional disruptions can easily become global in character. Countries often respond to production and price volatility by restricting trade or pursuing large grain purchases in international markets—both of which can have destabilizing effects on world prices and global food security. In the future, heat stress on crops and livestock will occur in an environment of steadily rising demand for food and animal feed worldwide, making markets more vulnerable to sharp price swings. High and variable prices are most damaging to poor households that spend the majority of their incomes on staple foods.

Another region at risk from higher temperatures is the Sahel, where crop and livestock production play an essential role in the region's economy, employing roughly 60% of the active population and contributing 40% to gross national product (17). The Sahel suffered a prolonged drought from the late 1960s to the early 1990s that caused crop and livestock productivity to plummet, and which contributed to countless hunger-related deaths and unprecedented rates of migration from north to south, from rural to urban areas, and from landlocked to coastal countries (18). Although the Sahel's climate disaster was largely one of extended drought, the specter of high and rising temperature lurks in the background. Year-to-year temperature variability in the Sahel has been low during the past century (particularly in comparison with temperate countries like France and Ukraine), but the growing season temperature has been very high, with long-term daily averaged summer temperature ranging from 25°C in the south to 35°C in the north. Moreover, temperatures have trended upward since 1980. Despite rains returning to some locations of the Sahel during the past 15 years, the growing season for staple crops has been reduced, maize yields have remained far below varietal potential, and millet and sorghum yields continue to stagnate (18). Hundreds of thousands of children and infants in the region still die each year from hunger-related causes, and malnutrition contributes to long-term mental and physical disabilities. Over recent decades most of the region's poorest households have lost their livestock or other assets; they remain net consumers of food and struggle to purchase staples even when they are available in the market. These households farm at an extreme disadvantage irrespective of climate change, with limited access to improved crop varieties, seed supplies, fertilizers, credit, and irrigation and transportation infrastructure (19).

Most worrisome for the Sahel is that average growing season temperatures by the end of this century, and even earlier for some parts of the region, are expected to exceed the hottest seasons recorded during the past century (Fig. 2C). Such heat will compound food insecurity caused by variable rainfall in the region, and it will increase the incidence of agricultural droughts (as opposed to meteorological droughts) defined by elevated evapotranspiration, low soil moisture, and high rates of water runoff from hard pan soils when it rains. Even today, temperatures in the Sahel can be so high that the rain evaporates before it hits the ground (18). New bounds of heat stress will make the region's population far more vulnerable to poverty and hunger-related deaths and will likely drive many people out of agriculture altogether, thus expanding migrant and refugee populations.

These historical examples illustrate the profound damage that can be caused (or in the near future may be caused) by high seasonal heat, but they also represent short-run impacts. We chose France (2003) and Ukraine (1972) as examples specifically because temperature deviations were large in comparison to precipitation deviations relative to the observational record. In the Sahel case, drought and heat stress are tightly coupled, with heat stress becoming increasingly important during the past decade. The threats to food security and human lives caused by unusually high seasonal temperature in France, Ukraine, and the Sahel in the 20th century were ameliorated when the extreme temperatures subsided, when markets balanced acute regional food deficits with food surpluses from other locations, and when farmers autonomously adapted their practices or migrated. The future, however, could be entirely different. If growing season temperatures by the end of the 21st century remain chronically high and greatly exceed the hottest temperature on record throughout the much of the world, not just for these three examples, then global food security will be severely jeopardized unless large adaptation investments are made.

Climate model projections from the IPCC 2007 assessment suggest that this outcome is indeed very likely (Fig. 3). Figure 3A shows that, as early as 2050, the median projected summer temperature is expected to be higher than any year on record in most tropical areas. By the end of the century, it is very likely (greater than 90% chance) that a large proportion of tropical and subtropical Asia and Africa will experience unprecedented seasonal average temperature, as will parts of South, Central, and North America and the Middle East (Fig. 3B). High seasonal temperatures beyond what has been experienced during the past century will thus become widespread.

Three important conclusions can be drawn from these projections. First, tropical countries experience less year-to-year temperature extremes than do temperate countries and therefore will be the first to experience unprecedented heat

stress because of global climate change. By the end of the century, however, the seasonal growing temperature is likely to exceed the hottest season on record in temperate countries (e.g., equivalent to what France experienced in 2003), and the future for agriculture in these regions will become equally daunting.

Second, the projected seasonal average temperature represents the median, not the tail, of the climate distribution and should therefore be considered the norm for the future. Indeed, the probability exceeds 90% that by the end of the century, the summer average temperature will exceed the hottest summer on record throughout the tropics and subtropics (Fig. 3B). Because these regions are home to about half the world's population, the human consequences of global climate change could be enormous.

Lastly, with growing season temperatures in excess of the hottest years on record for many countries, the stress on crops and livestock will become global in character. It will be extremely difficult to balance food deficits in one part of the world with food surpluses in another, unless major adaptation investments are made soon to develop crop varieties that are tolerant to heat and heat-induced water stress and irrigation systems suitable for diverse agroecosystems. The genetics, genomics, breeding, management, and engineering capacity for such adaptation can be developed globally but will be costly and will require political prioritization (5, 8, 9, 20). National and international agricultural investments have been waning in recent decades and remain insufficient to meet near-term food needs in the world's poorest countries, to say nothing of

longer-term needs in the face of climate change (1). History provides some guide to the magnitude and effects of high seasonal averaged temperature projected for the future. Ignoring climate projections at this stage will only result in the worst form of triage.

References and Notes

1. R. Naylor, W. Falcon, *Boston Rev.* **33**, 13 (2008).
2. We approximated the main growing season to be summer in the extratropics. Hence north of the equator we used the three-month average temperature June through August (and for south of the equator we used December through February), periods that broadly capture growing season conditions for many crops.
3. IPCC, *Fourth Assessment Report: Synthesis*, published online 17 November 2007, www.ipcc.ch/ipccreports/ar4-syr.htm.
4. World Bank, *World Development Report 2008: Agriculture for Development* (World Bank, Washington, DC, 2007).
5. W. Easterling *et al.*, in *Climate Change 2007: Impacts, Adaptation, and Vulnerability*, M. Parry *et al.*, Eds. (Cambridge Univ. Press, New York, 2007), p. 976.
6. D. Lobell, M. Burke, *Environ. Res. Lett.* **3**, 034007 (2008).
7. S. Peng *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **101**, 9971 (2004).
8. D. B. Lobell *et al.*, *Science* **319**, 607 (2008).
9. B. Barnabas *et al.*, *Plant Cell Environ.* **31**, 11 (2008).
10. W. Schlenker, M. J. Roberts, *Rev. Agric. Econ.* **28**, 391 (2006).
11. J. Larsen, *Earth Policy Institute*, published online 28 July 2006 (www.earth-policy.org/Updates/2006/Update56.htm).
12. P. Pirard *et al.*, *Eurosurveillance* **10**, 554 (2005).
13. A. De Bono *et al.*, "Environmental alert bulletin: Impacts of summer 2003 heat wave in Europe" (United Nations Environmental Programme, Nairobi, Kenya, 2004).
14. International Financial Statistics Database, "United States Gulf ports wheat prices," published online July 2008, www.imfstatistics.org.
15. D. Hathaway *et al.*, *Brookings Pap. Econ. Act.* **1**, 63 (1974).
16. N. Dronin, E. Bellinger, *Climate Dependence and Food Problems in Russia 1900-1990* (Central European Univ. Press, New York, 2005).
17. World Bank, *Africa Development Indicators 2007* (World Bank, Washington, DC, 2007).
18. S. Kandji, L. Verchot, J. Mackensen, *Climate Change and Variability in the Sahel Region: Impacts and Adaptation Strategies in the Agricultural Sector* (United Nations Environmental Programme and World Agroforestry Center, Nairobi, Kenya, 2006).
19. T. Jayne, in *The Transformation of Agri-Food Systems: Globalization, Supply Chains, and Smallholder Farmers*, E. B. McCullough *et al.*, Eds. (Earthscan, London, 2008).
20. S. Takeda, M. Matsuoka, *Nat. Rev. Genet.* **9**, 444 (2008).
21. To calculate the projected climate for 2090, we first added the observed temperature departures (in blue) to the change in the summer temperature, taken to be the mean summer temperature for 2080–2100 minus that for 1980–2000, simulated by each of the 23 climate models from the IPCC AR4 forced by the "middle of the road" emission scenario, A1B. We then combined the 23 × 107 projections to create the probability distribution function for summer temperature in 2090 (see SOM).
22. The probability distribution of future summer temperature is calculated as described in (21). Here, summer is defined north of the equator as the average temperature from June through August and south of the equator as December through February. In the immediate vicinity of the equator, values in Fig. 3 are qualitatively insensitive to the choice of months that define the season.
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Foraminiferal Isotope Evidence of Reduced Nitrogen Fixation in the Ice Age Atlantic Ocean

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Fixed nitrogen (N) is a limiting nutrient for algae in the low-latitude ocean, and its oceanic inventory may have been higher during ice ages, thus helping to lower atmospheric CO_2 during those intervals. In organic matter within planktonic foraminifera shells in Caribbean Sea sediments, we found that the $^{15}N/^{14}N$ ratio from the last ice age is higher than that from the current interglacial, indicating a higher nitrate $^{15}N/^{14}N$ ratio in the Caribbean thermocline. This change and other species-specific differences are best explained by less N fixation in the Atlantic during the last ice age. The fixation decrease was most likely a response to a known ice age reduction in ocean N loss, and it would have worked to balance the ocean N budget and to curb ice age–interglacial change in the N inventory.

The sources of fixed N to the ocean are terrestrial runoff, atmospheric deposition, and, most important, marine N fixation. The main sinks are sedimentary denitrification, mostly in continental shelf sediments, and water column denitrification in the eastern tropical Pacific and the Arabian Sea. Sediment records

from modern denitrification zones show clear N isotopic evidence of reduced water column denitrification during the Last Glacial Maximum (LGM) relative to the current interglacial (Holocene) (1, 2). The history of other processes, especially N fixation, has proven more difficult to reconstruct. Decreased denitrification and/or

increased N fixation would have raised the N inventory of the ocean during the LGM, thereby strengthening the ocean's biological pump and contributing to the observed reduction in atmospheric CO_2 during the ice age (1–5).

N fixation produces oceanic fixed N with $\delta^{15}N$ values between –2 and 0 per mil (‰), close to that of atmospheric N_2 (6, 7). Sedimentary denitrification removes nitrate (NO_3^-) from the ocean with minimal isotope discrimination (8). In contrast, water column denitrification leaves residual nitrate enriched in ^{15}N that raises the $\delta^{15}N$ of mean ocean nitrate above that of newly

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