in antibody levels [exceeding the ~20-day half-life of human IgG (19)] are consistent with the generation of long-lived plasma cells that turn over with a half-life of ~40 days.

Taken together, the above results indicate that memory B cells have two response modes. In the antigen-dependent mode, they undergo a massive expansion and differentiation toward short-lived plasma cells. This response is transient, because of the negative feedback exerted by the high level of antibody present (20). However, some plasma cells generated in this way become long-lived if rescued in available niches such as bone marrow (21). These cells sustain serum antibody levels, but can do so only for a few months, because of their limited life-span. In contrast, in the polyclonal mode, all memory B cells respond to environmental stimuli by undergoing continuous proliferation and differentiation. In this way, a constant level of plasma cells and serum antibodies could theoretically be maintained throughout a human life-span. Because this mechanism is non-specific, it would act indiscriminately to maintain the broad spectrum of antibody specificities generated during the antigen-driven immune response.

The sensitivity to polyclonal stimuli represents a key feature of human memory B cells and adds a novel property to the concept of “memory stem cells” (22, 23). The differential response to polyclonal stimuli may reflect distinct roles of switch and IgM memory B cell subsets. Thus, although the exquisite sensitivity of switch memory B cells to bystander help may be instrumental in maintaining systemic IgG antibody levels, the capacity of IgM memory B cells to respond to CpG in the absence of cytokines could be instrumental in maintaining levels of natural antibodies to bacterial antigens (24–26). This may also underpin the propensity to develop mucosa-associated lymphatic tissue (MALT) lymphomas under chronic infection by Helicobacter pylori (27). It is possible that polyclonal stimuli in addition to CpG or T cell help activate memory B cells in vivo within the microenvironment of secondary lymphoid organs or of the bone marrow, where memory B cells and proliferating plasma cell precursors are present (28, 29).

Our results discriminate between a “short-term serological memory,” which is antigen-dependent and lasts for a few months, and a “long-term serological memory” that results from an antigen-independent polyclonal activation and differentiation of memory B cells. The possibility of selectively targeting one component or the other may open new ways for effective vaccination.

References and Notes
14. See supporting data on Science Online.
15. N. L. Bernasconi, E. Traggiai, unpublished data.
18. These observations may explain why a correlation between serum antibodies and antigen-binding memory B cells was not detected in a previous study where recently boosted individuals were analyzed (30).
31. We thank J. C. Howard, K. Karjalainen, G. Natoli, and F. Sallusto for critical reading of the manuscript. A.L. is supported by the Helmut Horten Foundation and by the Swiss National Science Foundation (grant 31-63885).

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Rainfall Variability, Carbon Cycling, and Plant Species Diversity in a Mesic Grassland

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Ecosystem responses to increased variability in rainfall, a prediction of general circulation models, were assessed in native grassland by reducing storm frequency and increasing rainfall quantity per storm during a 4-year experiment. More extreme rainfall patterns, without concurrent changes in total rainfall quantity, increased temporal variability in soil moisture and plant species diversity. However, carbon cycling processes such as soil CO2 flux, CO2 uptake by the dominant grasses, and aboveground net primary productivity (ANPP) were reduced, and ANPP was more responsive to soil moisture variability than to mean soil water content. Our results show that projected increases in rainfall variability can rapidly alter key carbon cycling processes and plant community composition, independent of changes in total precipitation.

Anthropogenic climate change is projected to include increasingly variable precipitation regimes, as well as atmospheric warming (1). General circulation models forecast a higher frequency of extreme rainfall events from intense convective storms, a lower frequency of rainfall days, and longer intervening dry periods (1–5). Evidence is mounting that an increase in precipitation extremes has begun to occur worldwide (3–8). Most aspects of terrestrial ecosystem structure and function are vulnerable to these hydrologic changes, perhaps independent of changes in annual precipitation quantity (1, 9, 10), and important interactions with elevated temperatures and atmospheric carbon dioxide can be expected (11). Thus, models and policy analyses of the consequences of climate change should not rely on scenarios that focus primarily on climatic means (12, 13). Yet, our ability to forecast ecosystem responses to climate change is constrained by a lack of
field studies and proxy data sets capable of projecting the long-term consequences of increased climatic variability.

To quantify the impact of increased intra-annual rainfall variability on an intact ecosystem, we altered the temporal distribution and size of rainfall events, without changing total precipitation amounts, for four growing seasons in a native grassland. Here we examine responses in C cycling and plant community composition, which are key ecosystem attributes with the potential to impart feedback on climate change (9). Grasslands are ideal for such experiments because they are extensive biomes with large C storage capacity, are often highly productive and species-rich, and are among the most responsive of terrestrial ecosystems to interannual variability in precipitation (14–16).

In a native grassland ecosystem in northeast Kansas, United States, where C₄ perennial grasses dominate in biomass and cover (14), we manipulated rainfall variability and reduced rainfall quantity in 12 rainfall manipulation plots (RaMPs) from 1998 to 2001 (17, 18). For this analysis, we focus only on responses to the increased rainfall variability treatment. Rainfall patterns were altered relative to control (ambient) treatments by extending the intervals between natural rain events by 50%, collecting and storing all rain falling during these intervals, and then applying the accumulated quantities as single large events. As a result, control plots received 25 to 30 rain events based on actual rainfall patterns during each growing season (mean per event = 14 mm), whereas plots exposed to altered rainfall patterns received fewer but larger events (6 to 8 per growing season; mean per event = 42 mm), with longer dry periods between storms and more total dry days (Fig. 1). The large size and low frequency of rainfall events in the altered precipitation treatment are well within the range of documented rainfall regimes of the past 100 years in this region (18). Thus, rainfall variability was increased without imposing unrealistic drought periods or extraordinary storm intensities. These manipulations allowed us to assess responses of this grassland to the predicted rainfall regime of more intense storms and an increased number of dry days during the growing season (3, 4), without the confounding effects of altered total precipitation inputs (Fig. 1).

Temporal patterns of soil water content were strongly influenced by increased rainfall variability (Fig. 1). Over the 4-year study, average soil water content in the upper 30 cm, where >70% of root biomass occurs in this and most grasslands (19, 20), was reduced by 11.6% [F(1,8) = 31.00, P = 0.0005] in altered versus ambient rainfall plots (Fig. 1). Reduced mean soil water content was caused by more frequent and prolonged periods of low soil moisture due to extended intervals between rainfall inputs. We used an unbiased distance function, the mean absolute difference in soil water content between consecutive measurements (21), to quantify temporal dynamics in soil moisture. This estimate of soil moisture variability increased by 27% [F(1,8) = 21.4, P = 0.002] across all years in plots exposed to altered rainfall patterns, with increases as much as twofold in some years (Fig. 1B, inset). Thus, stability in soil moisture supply decreased as precipitation variability increased.

Increased variability in rainfall and soil water content significantly affected three key C cycling processes in this grassland (17). Midsummer net photosynthesis (leaf-level CO₂ uptake) by the dominant grass, Andropogon gerardii, was reduced ~20% in plants subjected to increased rainfall variability, consistent with increased leaf-level water stress at midseason (14% lower midday leaf water potential) (Fig. 2A). This is a critical period in the growing season when this dominant species (79.4 ± 3.2% canopy cover) achieves maximum vegetative growth, initiates flowering, and produces seed (14). Over the 4-year experiment, exposure to fewer but larger rainfall events reduced aboveground net primary production (ANPP) by ~10% as compared to ambient rainfall patterns (Fig. 2A), with the greatest reduction in ANPP (107.9 g/m²) occurring during the driest year of the study, when annual precipitation was 22% below the long-term average (835 mm). The majority (86%) of this decline in ANPP was due to reduced productivity of the C₄ grasses. Thus, reduced CO₂ uptake by the dominant grass, A. gerardii, provides a
mechanistic link among alterations in resource availability, increased plant stress, and subsequent ecosystem-level responses.

The strong and direct effect of increased rainfall variability on C inputs to this ecosystem was further illustrated by comparing the relationships between ANPP and mean soil water content, and ANPP and variability in soil moisture (Fig. 2). Despite growing-season precipitation amounts that varied twofold over the 4-year study, ANPP was not related to mean soil water content (Fig. 2B). However, ANPP was strongly and negatively related to the temporal variability in soil water content (Fig. 2C), which is evidence that ecosystem C inputs from ANPP can be directly affected by altered rainfall variability, independent of precipitation quantity.

Grassland soils are among the most important globally for long-term C storage (16). Soil CO$_2$ flux, an index of belowground plant and microbial heterotrophic activity, was reduced significantly (16%) when rainfall variability was increased (Fig. 2A). The magnitude of this effect was two times as great as the responses to increased air and soil temperatures (2.0° to 2.6°C) measured previously in a similar grassland (22). Although reduced soil CO$_2$ flux may decrease overall ecosystem C loss in the short term, it is also indicative of lower belowground productivity (23, 24). When coupled with reduced productivity aboveground, the results suggest that increased rainfall variability will decrease C inputs overall and potentially reduce long-term soil C sequestration.

Increased variability in precipitation enhanced plant community diversity (Shannon's index, H') (Fig. 3, inset) and was accompanied by increased turnover of rare and uncommon species (33 compared to 24 cumulative colonization and extinction events in altered and ambient plots, respectively). Increased diversity could be a direct response of the plant community to increased soil moisture dynamics (Fig. 3A) (25), but H' was also negatively related to ANPP in this experiment (Fig. 3B). Thus, the plant community could be responding indirectly to reduced ANPP, a commonly observed pattern in natural ecosystems (26). The increases in diversity, measured at both broad and fine scales, were due to increased richness and evenness (table S1), suggesting that long-term shifts in community composition will occur as more extreme precipitation regimes chronically alter both the mean and temporal variability of soil moisture.

Linking short-term responses to ecosystem properties that develop over longer time scales can extend the inference of this experiment. In this mesic grassland, drier and more variable temporal patterns of soil moisture occur in upland relative to lowland sites (27, 28). Increased variability in soil moisture in uplands is due to the combined effects of soil textural differences, higher evaporative demand, and more rapid soil water drainage relative to lowlands (14) rather than to differences in precipitation patterns. Nonetheless, these sites may provide insight for projecting, at least qualitatively, potential long-term effects of increased precipitation variability in this grassland. Results from a variety of Konza Prairie Long-Term Ecolog-
Small Nuclear Ribonucleoprotein Remodeling During Catalytic Activation of the Spliceosome

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Major structural changes occur in the spliceosome during its activation just before catalyzing the splicing of pre–messenger RNAs (pre-mRNAs). Whereas changes in small nuclear RNA (snRNA) conformation are well documented, little is known about remodeling of small nuclear ribonucleoprotein (snRNP) structures during spliceosome activation. Here, human 45S activated spliceosomes and a previously unknown 35S US snRNP were isolated by immunofluorescence selection and were characterized by mass spectrometry. Comparison of their protein components with those of other snRNPs and spliceosomal complexes revealed a major change in protein composition during spliceosome activation. Our data also suggest that the US snRNP is dramatically remodelled at this stage, with the Prp19 complex and other factors tightly associating, possibly in exchange for other US proteins, and suggest that after catalysis the remodelled US is eventually released from the postsplicing complex as a 35S snRNP particle.

Pre-mRNA splicing, the removal of introns from mRNA precursors, is a prerequisite for the expression of most eukaryotic genes. Catalysis of the two transesterification steps of the pre-mRNA splicing reaction takes place in the spliceosome, an elaborate molecular machine capable of catalyzing splicing (hereafter termed the activated spliceosome) entails a major structural change that results in the dissociation of the U1 and U4 snRNPs. Conversion of the mature spliceosome into a machine capable of catalyzing splicing (hereafter termed the activated spliceosome) entails a major structural change that results in the dissociation of the U1 and U4 snRNPs. Subsequently, the activated spliceosome catalyzes the first transesterification step of splicing and complex C is formed. After the second step of splicing, the mRNA is released and the postsplicing complex, containing the excised intron and the U2, U5 and, U6 snRNPs, disassembles and the snRNPs are then recycled for new rounds of splicing.

The spliceosome is, thus, a highly dynamic molecular machine whose composition is not

References and Notes
16. Materials and methods are available as supporting material on Science Online.
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Supporting Online Material
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