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Changes in Earth's surface temperatures caused by anthropogenic emissions of greenhouse gases are expected to affect global and regional precipitation regimes. Interactions between changing precipitation regimes and other aspects of global change are likely to affect natural and managed terrestrial ecosystems as well as human society. Although much recent research has focused on assessing the responses of terrestrial ecosystems to rising carbon dioxide or temperature, relatively little research has focused on understanding how ecosystems respond to changes in precipitation regimes. Here we review predicted changes in global and regional precipitation regimes, outline the consequences of precipitation change for natural ecosystems and human activities, and discuss approaches to improving understanding of ecosystem responses to changing precipitation. Further, we introduce the Precipitation and Ecosystem Change Research Network (PrecipNet), a new interdisciplinary research network assembled to encourage and foster communication and collaboration across research groups with common interests in the impacts of global change on precipitation regimes, ecosystem structure and function, and the human enterprise.

Keywords: global change, community, ecosystem, precipitation, soil moisture

The responses of terrestrial ecosystems to global environmental change, and the resulting impacts on the natural resources on which humans depend, are topics of great societal concern and current scientific interest (Vitousek 1994). Anthropogenic emissions of greenhouse gases are expected to raise the mean temperatures of Earth's surface by 1.4°C to 5.8°C during this century (Houghton et al. 2001). Such warming is likely to alter patterns of global air circulation and hydrologic cycling that will change global and regional precipitation regimes (Houghton et al. 2001). Corresponding changes in air and soil temperatures, soil water and nutrient contents, and concentrations of atmospheric carbon dioxide ([CO_2]) are likely to alter the functioning of natural and managed ecosystems in terrestrial environments. Because these changes will co-occur with ongoing changes in global land use and land cover that have already affected biodiversity and natural resources, impacts on human societies are expected (Vitousek 1994).

Considerable research has been directed at understanding the effects of increased temperature and [CO_2] on the

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structural and physiological dynamics of terrestrial ecosystems (e.g., Koch and Mooney 1996, Shaver et al. 2000). Although there is a long history of investigation of linkages between precipitation and terrestrial ecosystems (Noy-Meir 1973, Leith 1975), little research has focused on how anticipated changes in precipitation might affect terrestrial ecosystems. We suggest that shifts in precipitation regimes may have an even greater impact on ecosystem dynamics than the singular or combined effects of rising [CO_2] and temperature, especially in arid and semiarid environments. For example, precipitation substantially influenced plant and ecosystem response to elevated [CO_2] in an arid ecosystem (Smith et al. 2000). Moreover, environmental degradation in drought-susceptible regions negatively affects nearly one billion people occupying about 30% of the world's land surface (FAO 1993). Thus, a research focus on these regions and on the effects of changing precipitation patterns would yield information necessary to mitigate potentially negative impacts of climate change on human well-being.

This article addresses the following basic questions concerning precipitation change research:

- How will global and regional precipitation patterns change in the near future?
- How does precipitation influence the dynamics of natural ecosystems?
- Which ecosystems and ecosystem processes are sensitive to changes in precipitation?
- How will changes in precipitation alter human–ecosystem interactions?
- What approaches are available to study the effects of precipitation change?

We will highlight the need for multidisciplinary approaches and the challenges in interpreting limited data sets within the context of global change. These factors have motivated the formation of an interdisciplinary research network, PrecipNet (Precipitation and Ecosystem Change Research Network), to promote additional precipitation studies, strengthen collaborative research, and facilitate exchange of information about the impacts of precipitation change on terrestrial ecosystems and on the natural resources that support human activities.

How will global and regional precipitation patterns change in the near future?

General circulation models (GCMs) are used to describe the complex dynamics of mass and energy exchange, momentum, and hydrologic cycling within Earth's surface–atmosphere system. The most widely accepted models predict increases in mean global precipitation of up to 7% during this century, depending on the model used and on how the exchange of greenhouse trace gases from terrestrial and oceanic sources is defined (Houghton et al. 2001). One common prediction from these models, regardless of the model used or the scenario of trace gas emissions employed, is that the amount of precipitation in the tropics and at midlatitudes and high latitudes will increase over this century, while precipitation at subtropical latitudes will decrease. Moreover, the intensity of precipitation events and the frequency of extreme events, which have already increased across the globe, are predicted to increase further (Easterling et al. 2000).

However, scenarios for many specific geographic regions remain ambiguous, with unresolved discrepancies between the outputs of different models. For example, a Canadian Centre for Climate Modelling and Analysis model (CGCM1) predicts reductions in summer and winter precipitation in the Southeast and Great Plains regions of the United States by 2095, whereas a model developed by the Hadley Centre for Climate Prediction and Research (HadCM2) predicts increased precipitation throughout most of the United States, and particularly the Southwest, over the same time period (figure 1; NAST 2000). Both models predict that tropospheric warming will increase evaporation rates and thus increase the severity of drought despite potential increases in precipitation in some regions (NAST 2000).

One of the major challenges in predicting precipitation patterns at scales that are meaningful for ecosystem function and land management is the representation of effects imposed by surface topography and other landscape features. Most recent GCMs operate with a spatial resolution of about 2.5° (latitude/longitude) square or coarser. At this scale, varied topography and other landscape features (e.g., coastline, lake, and orographic effects) can modify local precipitation patterns. Thus, the uncertainty associated with predictions for topographically complex regions such as the western United States is relatively high. Regional climate models (e.g., Giorgi et al. 1998) can bring resolution to about 45 kilometers square (Snyder et al. 2002). However, the improved resolution must be weighed against uncertainty in long-term predictions. Moreover, interactions between El Niño–Southern Oscillation (ENSO) and the Pacific Decadal Oscillation, which operate at different spatial and temporal scales, may affect regional precipitation in complex and as yet unpredictable ways (Collier and Webb 2002). Analogous to the need for enhanced spatial resolution in climate models, there is also a need for greater temporal resolution. Most models produce output on seasonal or monthly time steps, but the organisms that dominate ecosystem responses to climate change can be sensitive to precipitation patterns on shorter scales, such as the number of storms per rainy season, the relationship between precipitation timing and magnitude (e.g., fewer large storms versus more frequent small storms), or variation in the duration of the rainy or dry season.

While current climate models seem unable to make reliable predictions about the magnitude or even the direction of precipitation change on smaller, biologically meaningful scales, they do indicate that many regions of the world will experience alterations in precipitation regimes over the next 100 years. The scientific community should consider the consequences of a range of possible climate scenarios, and land and

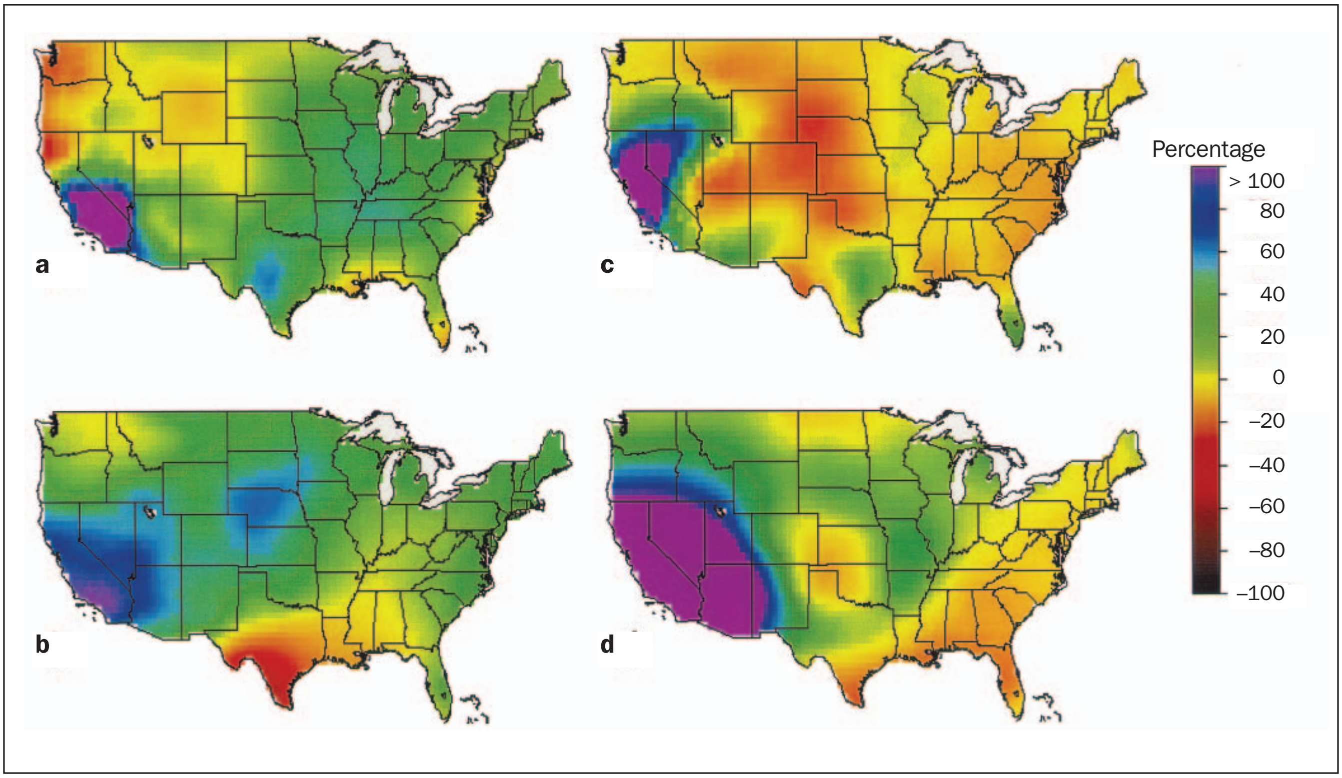

Figure 1. Predictions of seasonal precipitation regimes for the continental United States from the HadCM2 model, Hadley Centre for Climate Prediction and Research, for (a) summer (June, July, August) and (b) winter (December, January, February), and from the CGCM1 model, Canadian Centre for Climate Modelling and Analysis, for (c) summer and (d) winter. Colors indicate trend in precipitation for 2090 as percentage changes relative to the period 1960–1990 (NAST 2000). Source: US Global Change Research Program public archives (19 August 2003; **www.usgcrp.gov/usgcrp/nacc/background/scenarios/found/figs.html**).

water managers should develop strategies to mitigate the most negative impacts of likely climate scenarios on natural ecosystems and human society.

How does precipitation influence the dynamics of natural ecosystems?

Soil moisture is the direct link between precipitation and ecological systems. Therefore, understanding the effects of precipitation on soil moisture has been a central goal for hydrologists and soil physicists for many years (Noy-Meir 1973) and remains an active field of research (e.g., Eagleson 2002). The basic phenomena associated with precipitation events—interception, infiltration, and runoff—are relatively well understood; the main difficulty lies in describing rates of soil moisture change between precipitation events (McAuliffe 2003). These rates are driven chiefly by evaporation from soils, transpiration by plants, horizontal and vertical soil water transport, and hydraulic redistribution of soil water, all of which depend in complex ways on vegetation and soil characteristics and on the timing and size of precipitation inputs.

In arid and semiarid ecosystems, there is a good correlation between event size and infiltration depth: Water from larger rainfall events infiltrates more deeply (Sala et al. 1981), but infiltration, storage, and use depend on the season and on patterns of organismal activity. In summer, evaporation and transpiration remove nearly all water from shallow soil layers within days of rainfall, so that in the absence of rapid drainage through macropores, water does not infiltrate deeply into the soil profile. In winter, evaporation and transpiration are limited, so water can accumulate and infiltrate deeper into the soil profile. This spatial and temporal partitioning of water has been shown to have ecological and evolutionary implications for plant water use strategies (e.g., physiology and morphology; Cohen 1970, Walter 1979, Schwinning and Ehleringer 2001). Thus, changes in the seasonality or variability of precipitation—both predictions of most GCMs (Houghton et al. 2001)—are likely to affect the distribution of soil moisture in space and time, with ramifications for the performance of species and their interactions with other organisms. Hydraulic redistribution (Burgess et al. 1998) and phenotypic plasticity may buffer the effects of changes in soil moisture regimes and thereby increase the resilience of ecosystems to changes in patterns of precipitation, but the potential for this buffering effect is not known.

Heterogeneity in environmental conditions and resource supply rates plays a central role in producing and maintaining patterns of species diversity (Tilman and Pacala 1993, Chesson 2000). Changes in the stochastic patterns of a variable environmental factor, such as precipitation, may have potentially stronger effects on ecological systems than changes in average conditions or changes in other factors that are relatively stable over time and space (e.g., [CO_2]) (Knapp et al. 2002). Therefore, it is important to focus research on spatial and temporal variation in precipitation rather than on yearly or seasonal averages.

Studying the consequences of precipitation variability is far more difficult than studying the consequences of averages or gradual changes in climate factors. Patterns and processes of precipitation regimes occur across a broad spectrum of spatial and temporal scales (figure 2). Moreover, there may be lag effects in the responses of ecosystems to changes in precipitation regimes; for example, if changes in patterns of precipitation that occur at decadal scales are expected, the effects of these changes may become apparent only after perhaps a century under the new regime, when actual climate patterns may have already shifted again. Faced with this logistical and conceptual challenge, researchers across all disciplines must pay special attention to developing experiments at appropriate spatial and temporal scales, practicing restraint in data interpretation, and developing models and analyses that prudently extrapolate long-term effects from short-term data. This will require understanding (or at least considering) the relative importance of the various biotic and abiotic factors that drive the ecosystem; the sensitivities and lag times of the component species and processes; and the recent climatic, evolutionary, and societal history of the ecosystem.

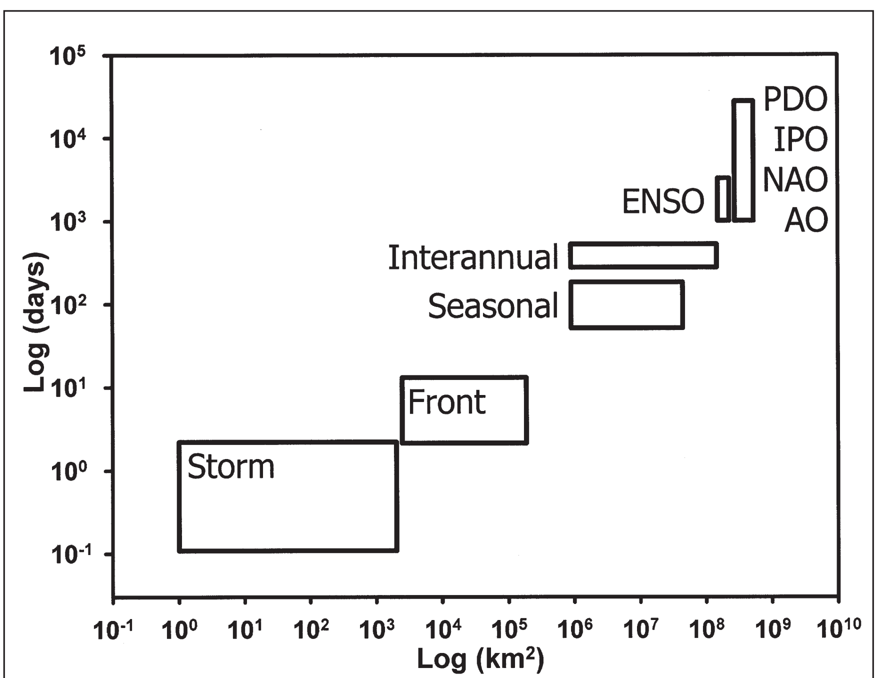

Figure 2. Variations in the spatial and temporal distribution of various factors that comprise or dictate precipitation regimes, from individual convective storms with local distributions and short duration to hemisphere and global-scale oscillations in atmospheric conditions that occur on a decadal scale. Abbreviations: AO, Arctic Oscillation; ENSO, El Niño–Southern Oscillation; IPO, Interdecadal Pacific Oscillation; NAO, North Atlantic Oscillation; PDO, Pacific Decadal Oscillation.

Which ecosystems and ecosystem processes are sensitive to changes in precipitation?

Clearly, arid and semiarid regions of the world are highly dependent on the availability of water, which more than any other factor dominates recruitment, growth and reproduction, nutrient cycling, and net ecosystem productivity (figure 3; Noy-Meir 1973, Leith 1975, Smith et al. 1997). For example, predicted increases in summer precipitation might contribute to a substantial "greening" across wide areas of the arid Southwest, primarily by increasing the density and relative production of C_4 grasses (Neilson and Drapek 1998). In addition, precipitation is often a limiting factor in more mesic terrestrial ecosystems. For example, native tallgrass prairies in the US Central Plains experience substantial interannual variations in production that are tightly coupled to annual precipitation (Sala et al. 1998). Similarly, prairie irrigated to replace evapotranspiration losses during the growing season produced on average 26% more biomass than control plots that received only ambient precipitation (Knapp et al. 2001). Knapp and Smith (2001) concluded that herbaceous-dominated systems, such as grasslands and old fields of the central United States, exhibit greater interannual variability than other systems in aboveground net primary production (ANPP) under current precipitation regimes and thus may be more responsive to future shifts in precipitation. In temperate forests, net primary production and stand water use are correlated with interannual variation in precipitation and the frequency and periodicity of drought, and differential growth and survivorship of juvenile trees may ultimately shift species composition (Hanson and Weltzin 2000). Thus, it appears that most ecosystems are sensitive to precipitation change; however, at this point the potential consequences of these sensitivities are largely unknown.

Changes in global and regional precipitation regimes are expected to have important ramifications for the distribution, structure, composition, and diversity of plant, animal, and microbe populations and communities and their attendant ecosystems (Easterling et al. 2000, Houghton et al. 2001, Weltzin and McPherson 2003). Long-term monitoring studies suggest that recent climatic and atmospheric trends, which are anomalous relative to past climate variation, are

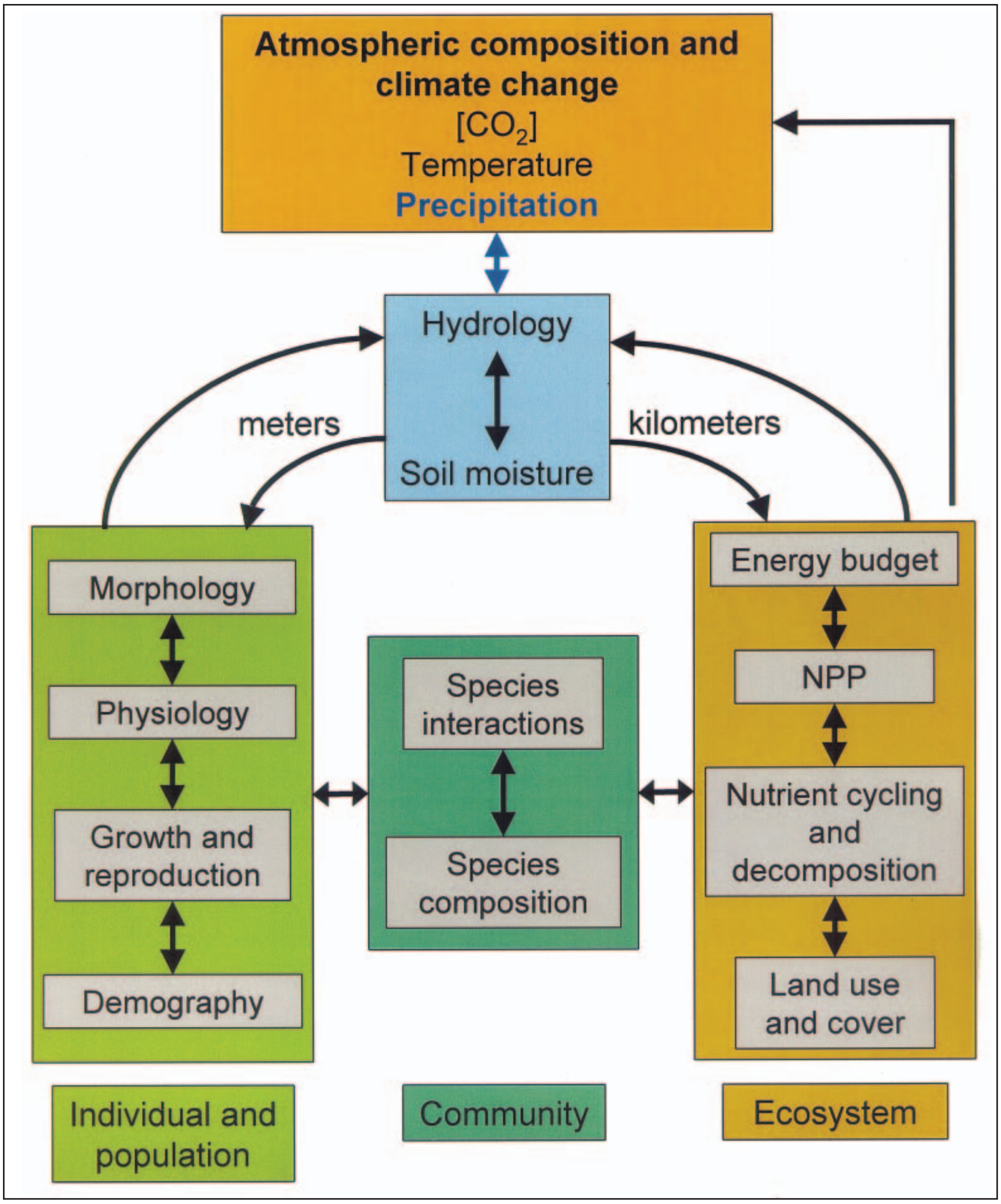

Figure 3. Conceptual model of interactions between global-scale climate processes; land use and cover; soil moisture; and ecosystem-, community-, population-, and individual-level processes. Soil moisture is also controlled by local- to landscape-scale characteristics of soil and hydrologic characteristics (e.g., texture, slope, vegetation cover, antecedent moisture conditions). Climate change and soil moisture affect each level of the hierarchy across a range of spatial and temporal scales (solid lines). Responses of individuals and populations indirectly control soil moisture and community-, ecosystem-, and global-scale processes. Factors within each level of the hierarchy are capable of interacting. Abbreviations: [CO_2], concentration of carbon dioxide; NPP, net primary production.

already affecting species physiology, distribution, and phenology (Hughes 2000). Moreover, the secondary effects of changes in species composition on ecosystem processes are likely to be as important as the direct effects of climate change. Changes in species composition could affect primary and secondary production, rates of decomposition and biogeochemical cycling, frequency and intensity of wildfire, availability of water resources, and fluxes of energy and materials between the biosphere and the atmosphere (see figure 3; Pastor and Post 1988, Hungate et al. 1996, Grime et al. 2000, Bachelet et al. 2001). In time, changes in community and ecosystem structure are likely to cause feedback effects: A change in soil organic matter content and concordant changes in water-holding capacity, for example, might engender further changes in plant composition, litter chemistry, and rates of decomposition. Changes in precipitation may also increase the susceptibility of ecosystems to invasion by nonnative plant species (Weltzin et al. 2003) and affect the spatial and temporal dynamics of consumers at other trophic levels (Ernest et al. 2000, Staddon et al. 2003).

Although perhaps of secondary importance in arid and semiarid ecosystems, other factors of global change are expected to modify the effects of precipitation change (see figure 3). Increases in temperature will affect rates of evaporation, with ramifications for ecosystem water budgets, and may indirectly affect processes of soil respiration, net nitrogen mineralization, and plant productivity (Shaver et al. 2000). Moreover, soil moisture regimes may be affected if warming causes the primary composition of winter precipitation to shift from snow to rain or if snow melts earlier in the spring. These effects on snow may be most important in ecosystems with relatively dry summers. Increases in [CO_2] may alter rates of plant transpiration or water use efficiency or accentuate or attenuate the effects of increased temperature or water stress on rates of assimilation and production (Owensby et al. 1999, Shaw et al. 2002). Conversely, changes in precipitation may control plant and ecosystem responses to changes in [CO_2] and temperature (Smith et al. 2000).

How will changes in precipitation alter human–ecosystem interactions?

Changes in precipitation regimes are likely to alter the types and quantities of goods and services that ecosystems provide to humans. Models that incorporate predicted changes in climate and [CO_2] suggest that enhanced accumulation of biomass in natural ecosystems during wet periods will lead to greater fuel accumulation, with potential ramifications for wildland fire regimes (Smith et al. 1997, 2000). Increases in the variability of precipitation—but not necessarily in the total amount of precipitation—may reduce grassland productivity (Knapp et al. 2002) and livestock carrying capacity, exacerbate overgrazing, increase rangeland susceptibility to invasions by weed species, and lower agricultural income by increasing input costs and reducing productivity. Changes in precipitation timing and magnitude may also affect human health. Heavy rainfall associated with the ENSO events of the 1990s increased seed and rodent populations, which favored the virus that causes hantavirus pulmonary syndrome in humans (Yates et al. 2002). Studies that combine epidemiological and climate-change modeling point to northward expansion of the North American range of mosquito-borne diseases, including malaria, dengue, and West Nile virus (Rogers and Randolph 2000).

What approaches are available to study the effects of precipitation change?

Given the diversity of terrestrial ecosystems and the breadth of potential response variables of interest, accurate forecasts of the most likely response of ecosystems to changes in precipitation regimes will require considerable research. Past studies of precipitation effects fall into four broad categories: (1) long-term observations of population and community change in conjunction with records of precipitation history, (2) short-term experimental manipulations of soil moisture, (3) hydroecologic modeling, and (4) cross-site comparisons. In combination, these approaches provide the insight necessary to form a more complete framework for research and management.

Long-term observations. A number of long-term observations of community change, particularly in arid environments (e.g., Goldberg and Turner 1986), and reconstructions of prehistoric precipitation and vegetation changes (McAuliffe and van Devender 1998) have been critical to formulating the basic ideas concerning the role of precipitation variability and change in terrestrial communities and ecosystems. However, because observational approaches rely on inferences drawn from correlational analyses, conclusions from these studies are necessarily uncertain. One difficulty lies in distinguishing the effects of precipitation from the effects of other factors that vary independently during the observation interval (e.g., changes in temperature or in the activity of organisms at other trophic levels). In addition, extrapolating results from these studies to predict potential consequences of future climate scenarios is problematic because of the uncertainties associated with selecting conditions that adequately represent future climates.

Short-term experimental manipulations of soil moisture. Experimental alteration of soil moisture is a logical way to determine how precipitation change affects communities and ecosystems on relatively short time scales. Several techniques can be used to manipulate soil moisture, including plot-scale irrigation and the establishment of rainout shelters to withhold rainfall over periods of time (figure 4). However, these techniques face logistical and conceptual challenges (Weltzin and McPherson 2003). Logistical constraints on the experimental manipulation of precipitation include difficulties in simulating the characteristics of actual precipitation (e.g., drop size, intensity, nutrient content, rainfall versus snowfall, rates of infiltration and runoff); overwhelming effects of the environment external to relatively small experimental units; transport of irrigation water to often-remote field sites; and undesired experimental artifacts (e.g., increased herbivory, alteration of microclimate). Conceptual limitations include difficulties in determining the timing and magnitude of water applications or withholdings vis-à-vis natural variation in rainfall patterns; in the choice of adequate response variables and observational periods; and in scaling across space and time. Although such constraints can be overcome by careful design of experiments, funding often remains a limiting factor.

To facilitate comparison across ecosystems and regions, rainfall manipulation experiments should employ a common methodology and measure a common set of response variables over a fixed period of time. That said, it is clear that different ecological systems will require different manipulative techniques: Simulation of rainfall in grassland, for example, is certainly easier than in forest or woodland. Moreover, the particular precipitation regime chosen will vary depending on the research question, which may focus on

*Figure 4. Techniques for experimental manipulation of precipitation. Top: A precipitation shelter in mesquite (*Prosopis*) grassland south of Tucson, Arizona. Twelve experimental plots (1.5 meters [m] by 1.8 m) under each of a total of six such shelters (spread across two soil types) are hand-watered 42 times each year to mimic shifts in seasonal precipitation regimes. Photograph: Nathan English. Bottom: One of 12 precipitation shelters in tallgrass prairie at the Konza Prairie Research Natural Area in northeastern Kansas. Experimental plots (7.6 m by 7.6 m) under each shelter are watered to simulate shifts in seasonal timing of precipitation and changes in the frequency of rainfall events within the growing season. Photograph: Philip A. Fay.*

the role of means versus extremes of amount, summer versus winter precipitation, or high frequency versus high intensity of rainfall events.

Modeling. Models used to investigate the role of precipitation and water in ecosystems are numerous, ranging from highly mechanistic models that explore the consequences of complex hydrologic–ecologic process interactions to rule-based models that seek to predict large-scale patterns. While mechanistic models employ exact mathematical relationships derived from simplified physical models, rule-based models employ "if–then" rules that summarize and synthesize system behaviors that may have complex root causes. For example, where a mechanistic model of plant water uptake during a growing season could involve equations describing the rates of water movement from the soil through the plant, as well as rates of leaf gas exchange and the transformation of carbon gain into biomass, a rule-based model could simply state, "If precipitation is below a threshold value, then some fraction of it is taken up by plants, ELSE water uptake is at a specified maximum." In reality all complex models have quantitative–mechanistic representations and rules and differ only in the degree to which rules, rather than physical processes, dominate the model results.

Mechanistic process models that link hydrology and vegetation can expose fundamental relationships between patterns of precipitation, characteristics of soil, and properties of vegetation. For example, recent advances in understanding hydrologic transport in the soil–plant–atmosphere continuum have improved predictions of transpiration regulation by plants and of limits to drought tolerance (Sperry et al. 2002). In contrast, global-scale and rule-based models can examine regional to continental relationships between precipitation and vegetation patterns or ecosystem processes (e.g., VEMAP 1995).

Rule-based models have a variety of ecohydrologic assumptions related to parameterization of precipitation inputs and modeling of soil water budgets (table 1). In general, equilibrium models (e.g., MAPSS [Mapped Atmosphere–Plant–Soil System], BIOME2, and DOLY [Dynamic Global Phytogeography Model]; table 1) adjust leaf area index or related variables to maximize annual ecosystem water uptake or use, provided that other resources (e.g., light or nutrients) are not limiting. For water-limited regions, this assumption often leads to the conclusion that almost all the water that enters the soil is removed by evapotranspiration in the course of a year. Since the location of soil moisture storage and the ratio of transpiration to evaporation depend strongly on temperature, the seasonal distribution of precipitation plays a major role in selecting vegetation characteristics, such as rooting depths and dought tolerance. However, because equilibrium models are static, they are unable to generate predictions for changes in precipitation variability.

A new generation of models called dynamic global vegetation models, or DGVMs (e.g., IBIS [Integrated Biosphere Simulator] and HYBRID; table 1), integrate the objectives of vegetation and ecosystem modeling. Because rates of growth and senescence can be calculated explicitly for all plant types, these models can be executed dynamically, and vegetation patterns emerge directly from the representation of resource competition or recruitment and mortality events. These models are also capable of simulating transient ecohydrologic conditions, such as those caused by fire or by interannual variation in precipitation (e.g., El Niño or La Niña events). Differences in the ecohydrologic assumptions of DGVMs may have a greater impact on model solutions than they do in equilibrium models, because DGVMs lack a common objective function. Tests and intermodel comparisons of these highly complex DGVMs should illustrate model sensitivities and improve their convergence (Cramer et al. 2001).

One of the greatest uncertainties in global models is the representation of root structure and function (Feddes et al. 2001), which in current models is oversimplified, with little consideration of known hydraulic transport laws. For example, hydraulic redistribution by plant roots (Burgess et al. 1998) is not considered in any global model, though it may be important for drought resilience, nutrient uptake, or competitive interactions. Furthermore, physiological integration of plant water uptake from layered soil is handled poorly across models. Another limitation of current global models is the representation of the root zone depth, which varies between models but usually does not vary between biomes within a model (but see Kleidon and Heimann 1998). Root zone depth assignments can have large-scale effects on global change predictions (Hallgren and Pitman 2000).

Cross-site comparisons. Manipulative experiments will always be limited by the length of time over which a treatment can be applied, the spatial scale over which moisture can be added or withheld, and the response variables measured. Thus, there is a need for alternative approaches that can be used to extrapolate the results of isolated experiments. These include cross-site comparisons or focused gradient studies, in which the same research question and methodology are applied along environmental gradients related to precipitation (e.g., amount, seasonality, or variations).

Most cross-site comparisons are observational, but these space-for-time substitutions can contribute substantially to scientific understanding of relationships between biotic and abiotic variables (Leith 1975, Webb et al. 1978, Le Houerou et al. 1988). For example, Knapp and Smith (2001) used data from 11 sites in the US Long Term Ecological Research Network to demonstrate that at continental scales, ANPP was strongly correlated with mean annual precipitation (MAP; figure 5). However, their research indicated that interannual variability in ANPP was not related to variability in precipitation; instead, maximum variability in ANPP occurred in biomes where high potential growth rates of

Table 1. Representation of precipitation and precipitation effects in selected global biogeography and biogeochemistry models.

Model	Precipitation input	Number of soil layers	Hydrological processes modeled	Precipitation or soil moisture effects on biotic components	Reference
MAPSS: Equilibrium biogeography model	Monthly mean as snow or rain	3	Interception, infiltration, runoff, snowmelt, downward percolation between layers, base flow	LAI_i ~ monthly water added to layers 1 and 2 (via equilibrium assumption)	Neilson 1995
BIOME2: Equilibrium biogeography model	Monthly mean as rain	2	Runoff, downward percolation between layers, bare soil evaporation	Daily T_i ~ soil moisture in root zone for plant type i; monthly A_i ~ monthly f_i x T_i / monthly water added; $\sum f_i$ ~ monthly water added to layers 1 and 2 (via equilibrium assumption)	Haxeltine et al. 1996
DOLY: Equilibrium NPP model	Monthly mean as rain	1	Interception, unspecified outflow of prt in excess of ET	G_s ~ soil moisture content; LAI ~ monthly prt (via equilibrium assumption)	Woodward et al. 1995
CENTURY: Dynamic biogeochemistry model	Monthly mean as snow or rain	Variable	Interception, surface evaporation, saturated downward flow between layers, deep drainage	Pool decomposition rates ~ pool soil moisture; mineral N leaching ~ saturated flow between layers; production ~ monthly (prt + residual soil moisture at 0 to 60 cm)/PET; senescence ~ soil moisture at 0 to 60 cm; root/shoot ~ annual prt; monthly T ~ soil moisture content by layer	Parton et al. 1993
IBIS: Dynamic biosphere model	Hourly	6	Interception, runoff, surface evaporation, bidirectional water transport between layers, deep drainage	Hourly A_i ~ soil moisture in root zone for plant type i; hourly T_i ~ A_i	Foley et al. 1996
HYBRID: Dynamic biosphere model	Daily mean as snow or rain	1	Interception, snowmelt, unspecified outflow of soil moisture above 1.5 x field capacity	G_s ~ soil water potential; pool decomposition rates ~ percentage of water-filled pore space	Friend et al. 1997

~, is a function of; A, assimilation rate; DOLY, Dynamic Global Phytogeography Model; ET, evapotranspiration; f, ground-cover fraction; G_s, stomatal conductance for water vapor; i, plant type; IBIS; Integrated Biosphere Simulator; LAI, leaf area index; MAPSS, Mapped Atmosphere–Plant–Soil System; N, nitrogen; NPP, net primary production; PET, potential evapotranspiration; prt, precipitation; T, transpiration rate.

Note: Interactions that do not directly involve precipitation or soil moisture are omitted.

herbaceous vegetation were combined with moderate variability in precipitation. A recent analysis of the same data sets used by Knapp and Smith (2001) indicated that interannual variability in ANPP was strongly influenced by MAP at the most arid sites but only weakly related to MAP at more mesic sites, particularly those within forest biomes.

Cross-site comparisons of manipulative experiments have the potential to contribute even more information about ecosystem sensitivities, critical thresholds, and local- to broad-scale mechanisms that control the response of a variety of ecosystems to changes in precipitation regimes. Currently, opportunities for cross-site comparisons of experimental manipulations are limited because of the variety of methods employed for the application or removal of precipitation, and because response variables and assessment techniques differ from site to site (Weltzin and McPherson 2003). As scientists conducting CO_2 enrichment experiments determined more than a decade ago, cross-site comparisons would be facilitated if researchers agreed on common protocols for precipitation manipulation and sampling that are applicable to all sites and compatible with a variety of research questions. This reasoning motivated the formation of PrecipNet, described below.

PrecipNet: An interdisciplinary research network focused on changing precipitation regimes

Ecologists and hydrologists from various terrestrial ecosystem study sites, along with climate modelers and social scientists, have formed PrecipNet, an international and interdisciplinary network for precipitation and ecosystem change research *(http://zzyx.ucsc.edu/ES/PrecipNet.htm).* The purpose of this network is to promote communication, intellectual exchange, and integration of methods and results among research groups interested in how potential future precipitation regimes may affect physical and biological processes across ecological, geographic, and disciplinary boundaries (box 1). Most of the current PrecipNet participants and their study sites are located in arid or semiarid regions, where water availability imposes the strongest control over community and ecosystem dynamics and processes. However, as awareness of the network has grown, a number of national and international sites from more mesic regions have been added. To date, research at most sites focuses on mechanisms likely to govern the response of the structure and function of communities and ecosystems to changes in precipitation regimes. Study sites include academic research stations, private biological research stations, and other sites at national and international institutions dedicated to research, conservation, or management.

Research needs and directions

Predictions of future precipitation regimes depend on output from GCMs, which are constantly being improved. Most GCMs are parameterized at the global scale, with grid cells that can encompass entire biogeographic regions, although increasing numbers are executed at regional scales (e.g., Giorgi et al. 1998, Snyder et al. 2002). Prediction of the effects of precipitation change on vegetation will require output from local or regional models at monthly or even daily temporal resolutions. Such scenarios could form the basis for new field experiments in ecosystems (e.g., grasslands) predicted to be highly sensitive to precipitation change (Knapp and Smith 2001).

The relationship between climate models and experiments should be reciprocal: Model predictions can serve as most-likely scenarios of climate change that delimit field experiments, while the results from field experiments can facilitate model parameterization, particularly if they incorporate gradients of driving variables. In addition, climate models should be linked with DGVMs to model feedbacks between terrestrial vegetation and climate. Constructive interactions between modelers and empiricists will strengthen linkages between models and experiments, to the benefit of ecology, management, planning, and policymaking. Critical observations of

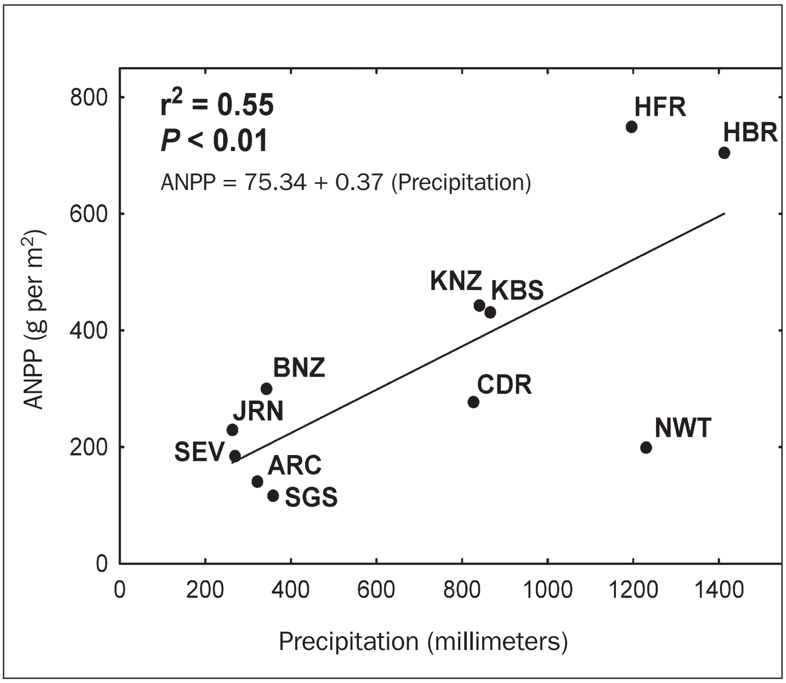

Figure 5. Relationship between annual aboveground net primary production (ANPP) and mean annual precipitation for 11 US Long Term Ecological Research sites representing five biomes: (1) arctic and alpine (ARC, Arctic Tundra; NWT, Niwot Ridge), (2) desert (JRN, Jornada; SEV, Sevilleta), (3) grassland (CDR, Cedar Creek; KNZ, Konza Prairie; SGS, Shortgrass Steppe), (4) old-field (KBS, Kellogg Biological Station), and (5) forest (BNZ, Bonanza Creek; HBR, Hubbard Brook; HFR, Harvard Forest). Reprinted with permission from Knapp and Smith (2001). © 2001 American Association for the Advancement of Science.

Box 1. PrecipNet objectives

The Precipitation and Ecosystem Change Research Network (PrecipNet) was formed to address several elements missing in the study of precipitation and ecosystem change and the assessment of resultant impacts on humans.

- **Research coordination, communication, and integration.** PrecipNet will establish a database for exhibiting and organizing precipitation manipulation experiments performed in various ecosystems on several spatial and temporal scales, using a variety of tools. This will form the basis for developing standard approaches for future experiments designed to improve opportunities for meaningful cross-experimental comparisons. It will also help identify knowledge gaps and suggest opportunities for research. PrecipNet will interact with other research networks, such as BASIN (Biosphere–Atmosphere Stable Isotope Network), C.DELSI (Center for the Dynamics and Evolution of the Land–Sea Interface), SAHRA (Sustainability of Semi-Arid Hydrology and Riparian Areas), and CIRES (Cooperative Institute for Research in Environmental Sciences) Western Water Assessment.

- **Regional comparisons of precipitation change and its effects.** The database will provide opportunities to analyze intra- and interregional patterns and processes, such as relationships between current precipitation regimes and ecosystem structure and function, and potential impacts of changes in precipitation regimes on different ecological systems.

- **Fostering multidisciplinary activities.** PrecipNet will sponsor activities that foster communication between biologists, hydrologists, climate modelers, and social scientists. These activities will include workshops to assess the impacts, vulnerability, and mitigation of precipitation change effects and to encourage the formation of multidisciplinary research groups.

- **Promoting skill development and technology transfer.** PrecipNet will coordinate the exchange of graduate students and postdoctoral researchers between research groups to promote communication, facilitate cross-site comparisons and proposal development, and increase skills for working in multidisciplinary groups.

- **Participants.** PrecipNet will also sponsor interactions between scientists, stakeholders, and the public. These interactions will serve both to disseminate knowledge generated by PrecipNet members and to help members develop and refine useful research questions.

alterations in species composition after environmental perturbations (e.g., Allen and Breshears 1998) will complement improved models of vegetation dynamics and enhance confidence in predictions about the fate of communities and ecosystems over decadal temporal periods. Moreover, additional research should focus on the representation of belowground processes, such as root structure and function, phenotypic plasticity, hydraulic redistribution, and water uptake vis-à-vis root zone depth, which may vary within and between biomes.

Although the research cited in this review provides a broad cross-section of ecological research and study systems, many important terrestrial systems remain relatively unstudied. Research is notably sparse in deciduous forests, coniferous woodlands and forests, shrublands, and tropical wet and seasonal forests. The paucity of data from these and other systems limits our ability to generalize about the response of species, growth forms, life forms, community-level properties (e.g., productivity, diversity), or ecosystem attributes (e.g., nutrient cycling, energy flows) to changing precipitation regimes.

Even in systems that are being studied, background information on the broader ecological, climatological, and sociological circumstances of the study area is usually limited. Moreover, it is unclear whether the particular site choices for experiments are highly representative of the most common background conditions of a region (e.g., characteristics of soil, frequency of disturbance, and patterns of land use). To overcome such limitations and uncertainties, experiments should focus on interactions between various precipitation regimes and other important factors. Where feasible, new precipitation experiments should include elevated [CO_2], increased temperature, or both, to reflect the multiple interacting environmental changes that will coincide with global change (e.g., Shaw et al. 2002). To this end, understanding "the responses of ecosystems to multiple stresses" is one of four current research imperatives selected by the US Global Change Research Program for the coming decade (CGCR 1999).

Most of the research described above focuses on the response of only one trophic level—primary producers—to changes in precipitation regimes. However, changes in precipitation will also affect consumers (Ernest et al. 2000) and decomposers (Staddon et al. 2003), which will have feedback effects on vegetation though changes in rates of pollination, seed dispersal, granivory, herbivory, nutrient cycling, and substrate alteration. Clearly, more studies are needed to address potential responses of other trophic levels and especially how interactions between trophic levels constrain ecosystem responses. Finally, the transfer of technology and ecological understanding to policymakers at the landscape, regional, and national levels will be critical. Effective communication will require a synthesis of information relevant to the variety of different spatial and temporal scales considered by ecologists, land managers, stakeholders, and policymakers.

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