Biological Feedbacks in Global Desertification

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Studies of ecosystem processes on the Jornada Experimental Range in southern New Mexico suggest that long-term grazing of semiarid grasslands leads to an increase in the spatial and temporal heterogeneity of water, nitrogen, and other soil resources. Heterogeneity of soil resources promotes invasion by desert shrubs, which leads to a further localization of soil resources under shrub canopies. In the barren area between shrubs, soil fertility is lost by erosion and gaseous emissions. This positive feedback leads to the desertification of formerly productive land in southern New Mexico and in other regions, such as the Sahel. Future desertification is likely to be exacerbated by global climate warming and to cause significant changes in global biogeochemical cycles.

CLIMATE MODELS SUGGEST THAT DURING THE NEXT CENTURY the average values of temperature and precipitation are likely to change over large areas of the globe. As a result, widespread adjustments are likely to occur in the distribution of terrestrial vegetation. Changes in global climate due to increasing concentrations of greenhouse gases may be supplemented by changes driven by the deforestation of tropical regions, particularly in the Amazon Basin. Tropical forests and arctic regions have been the focus of much attention; however, changes in other areas are expected as well. Emanuel *et al.* (*1*) predicted a 17% increase in the world area of desert land during the climate changes expected with a doubling of atmospheric CO_2 content. Any directional shift to a greater area of arid land potentially represents a permanent loss in the productive capacity of the biosphere on which all life depends (*2*). In this article, we focus on changes that can be expected at the transition between semiarid and arid lands and on the potential for an increasing area of arid land—desertification—to alter biogeochemical processes at the global level.

No explicit definition exists for the concept of desertification (*3*). Areas that have been arid during the last several centuries cannot be said to have become "desertified," even if they are now also affected by human exploitation. Historical evidence indicates that natural climatic patterns produce cycles of drought, followed by periods of relatively higher rainfall (*4*). Losses of agricultural productivity and the associated social and economic disruptions during drought cannot be said to represent desertification unless the landscape is so altered that a full recovery during relatively moist conditions is impossible. When a long-term change in ecosystem function has been observed in arid lands, direct intervention by humans, rather than climatic change, usually appears to be responsible (*5, 6*), although there are clear exceptions (*7*).

Several climate models suggest that future global warming may reduce soil moisture over large areas of semiarid grassland in North America and Asia (*8*). This climate change is likely to exacerbate the degradation of semiarid lands that will be caused by rapidly expanding human populations during the next decade (*9*). Because marginal areas are particularly sensitive to change, studies of ecosystem function at the transition between semiarid and arid ecosystems offer an effective index of human perturbation of the global system.

Conceptual Models for Desertification

We suggest that the changes in ecosystem function at the transition between arid and semiarid regions are best understood in the context of the spatial and temporal distribution of soil resources. In our hypothesis, when net, long-term desertification of productive grasslands occurs, a relatively uniform distribution of water, N, and other soil resources is replaced by an increase in their spatial and temporal heterogeneity. This heterogeneity leads to the invasion of grasslands by shrubs. In these new plant communities, soil resources are concentrated under shrubs, while wind and water remove materials from intershrub spaces and transport soil materials to new positions on the landscape (*10*). Our hypothesis is based on studies in the Jornada Experimental Range of southern New Mexico, but we believe that this model applies to desertification in other areas of the globe.

The Jornada Experimental Range comprises 78,266 ha of the Chihuahuan Desert, which extends from the south-central United States to central Mexico. In our study area, mean annual temperature is 15.6°C and mean precipitation is 21 cm $year^{-1}$, with 53% of the precipitation occurring from July to September (*11, 12*). During the last 100 years, large areas of black grama (*Bouteloua eriopoda*) grassland have been replaced by communities dominated by shrubs, especially creosote bush (*Larrea tridentata*) and mesquite [*Prosopis glandulosa* (*12, 13*)]. Similar shrub invasion in formerly productive grasslands has occurred in a large area of western Texas and eastern New Mexico that represents the transition between semiarid and arid lands in North America (*14*).

Black grama grassland is shallow rooted, with seasonal patterns of photosynthesis closely coupled to the availability of soil moisture (*15, 16*). Infiltration of incident rainfall is enhanced under black grama because a complete canopy cover lowers the effective energy of raindrops (*17*). A large percentage of the incident rainfall enters

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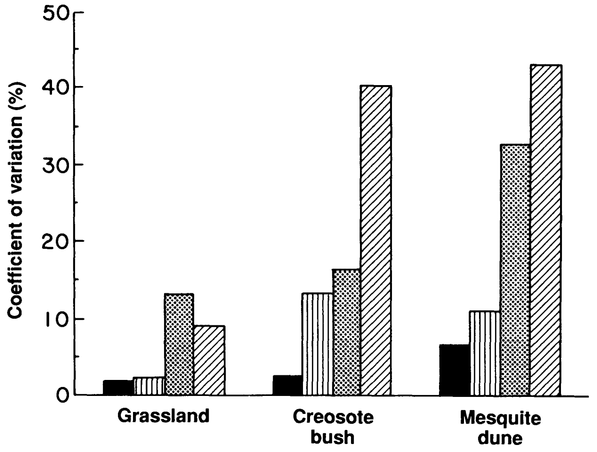

Fig. 1. Coefficient of variation associated with mean values for soil properties measured in 200 samples taken in each of three habitats on the Jornada Experimental Range (*105*). Bars are represented as follows: solid, *p*H; parallel lines, saturation percentage; dotted, soil moisture; and diagonal lines, total N.

the soil, and horizontal transport of water and nutrients in runoff is infrequent (*18*). Although soil moisture varies seasonally with rainfall, high infiltration is thought to result in a relatively uniform horizontal availability of soil water (Fig. 1) (*19*). Uptake and transpiration losses of soil moisture by black grama are closely coupled to input (*15, 20*), so that the soil rarely receives moisture at great depth, and most biotic processes are confined to the upper soil layers (*21*). Mineralization and uptake of N occur primarily in the top 30 cm of the soil profile (*22, 23*).

Large herds of domestic livestock disrupt this tight connection of soil and plant processes and lead to a decline in the cover of black grama and other species in semiarid grasslands. Heavy grazing during the short summer wet season contributes to the loss of grass cover during moderate drought and to lowered competitive potential of grasses (*24*). Trampling compacts the soil and reduces infiltration rates (*25*). Greater runoff results in erosion and increased transport of water, N, and other plant nutrients between geomorphic units in the basin. The net effect of these changes is to reduce the availability of soil moisture and nutrients in the landscape and to increase the heterogeneity of their horizontal distribution.

The redistribution of water by overland flow results in heterogeneity in the spatial distribution of soil moisture. We suggest that the cover of shrubs increases as a direct result of nonuniform distributions of water in space and time. Shrubs can exploit the additional soil moisture that infiltrates under intermittent streambeds and in local areas where water accumulates during runoff. Shrub cover and net primary production are often greatest in these areas (*26*). In large areas of the Mojave Desert in which overland flow has been diverted for 45 years, Schlesinger and Jones (*27*) showed that shrub biomass and density were significantly lower and the cover of perennial grasses was greater than in adjacent areas that received runoff.

Shrub dominance leads to a further heterogeneity of soil properties because effective infiltration of rainfall is confined to the area under shrub canopies (*28*), whereas barren intershrub spaces generate overland flow, soil erosion by wind and water, and nutrient loss (*29*). Runoff removes an average of 20% of the incident precipitation that falls in creosote bush desert (*30*). The cycling of plant nutrients, largely controlled by biotic processes in any ecosystem, is progressively confined to the zone beneath shrubs; this process leads to the development of well-known "islands of fertility" that characterize desert shrublands (*31, 32*). Initially these islands may not represent local accumulations of nutrients as much as remnants of the original homogeneous and fertile soil of the grassland ecosystem. In time, the islands of fertility become favored sites for shrub regeneration (*33*) and yield self-augmented levels of local fertility. One measure of the degree of development of local patches of fertility is the coefficient of variation in soil N. In the study area on the Jornada Experimental Range, the coefficient measured in 200 samples taken at 1-m intervals along a transect was about four times as great in areas dominated by creosote bush and mesquite as in relict areas of black grama grassland (Fig. 1).

Such changes alter not only the local distribution of soil resources but also the extent and location of other ecosystem processes in the landscape. Erosion of soil from intershrub areas results in a greater horizontal transport of nutrients in runoff, which may then result in greater rates of denitrification and ammonia volatilization in the heavy soils that accumulate in basin depressions, known as playas. The overall amount of N loss from the basin may rise as runoff transports N between landscape positions. The N that enters the ecosystem in areas of mesquite, which engages in symbiotic fixation of atmospheric N, may now be transported to sites where it can be lost through the production of reduced gases.

Although desertification is often assumed to result in a reduced level of plant growth, net primary productivity is similar in the native grasslands and the invasive shrub communities in southern New Mexico (*26*). However, changes in the quality of net primary production with shrub invasion lower the economic potential of the landscape, especially as rangeland. Thus, total net primary production may not always be the best measure of the desertification process. As an alternative, changes in soil properties may be a general measure of the changes in ecosystem function that underlie various forms of desertification.

Feedback Processes

Our studies in southern New Mexico provide a model that can be used to link processes in dryland ecosystems to the global level (Fig. 2). Aspects of the model reflect the concept of Charney (*34*) of a biogeographical feedback leading to increasing global desertification, but important details have been modified by more recent work. Because the removal of soil moisture by the transpiration of semiarid grassland is greater than in shrubland or bare ground (*20, 35*), there is greater cooling of the soil in grasslands by the loss of latent heat. As grassland is replaced by shrubland and a greater percentage of the soil is bare, soil surface and air temperatures increase, even though the albedo of exposed desert soil is greater (*36, 37*). Higher surface temperatures promote thermal circulation of the atmosphere, but there is lower relative humidity and precipitation. Hot, dry soils retard the accumulation of organic N in the soil, and thus further promote the spread of shrubland in which plant growth is less closely tied to N turnover in the surface soils. As these abiotic factors predominate over biotic factors, the balance tips further in favor of the development of arid ecosystems. This transition may result from direct human exploitation, as in southern New Mexico, or from indirect causes, such as global climate change (*8*). Once begun, the increasing heterogeneity of soil resources in arid lands is likely to develop a positive feedback that will reinforce the new functional properties of the ecosystem.

A large increase in the area of arid lands may affect processes at the global level. For example, desertification of the Sahelian region of West Africa may increase the regional albedo by as much as 4% (*38, 39*). Such changes in radiation balance are likely to affect regional climate and potentially lead to further decreases in regional rainfall (*40*). Other effects include the long-range transport of materials and a greater contribution of arid lands to global biogeochemical function.

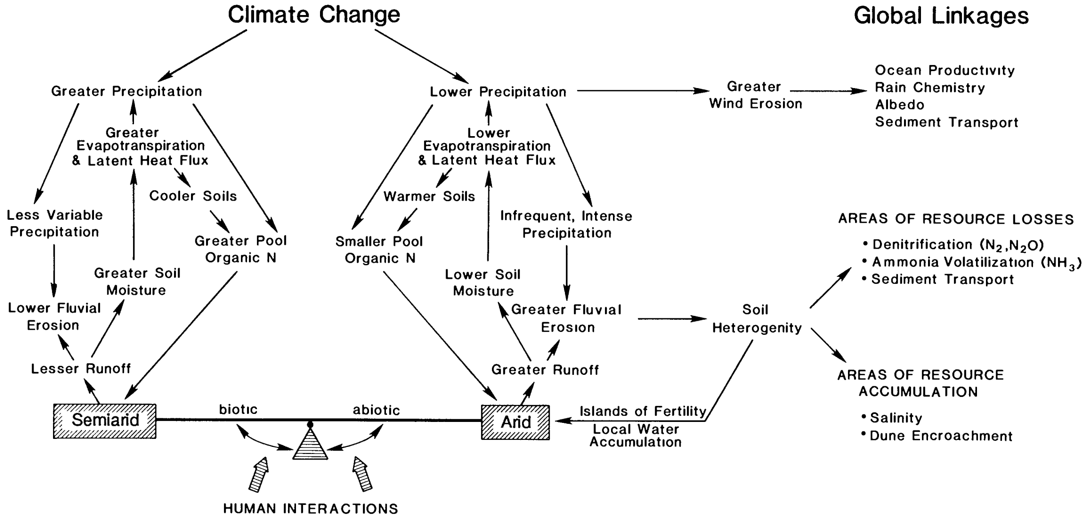

Fig. 2. A model linking changes in ecosystem properties during desertification to changes in global biogeochemistry.

Biogeochemistry in Deserts

Understanding the function of desert ecosystems in the context of limited moisture as the single controlling factor has diverted attention from an equally important role of N in determining plant productivity (*41, 42*). In addition, arid soils frequently show accumulations of calcium carbonate (caliche) that buffer soil *p*H in the range of 7 to 8, and complex P in unavailable forms (*23, 43*). In response to deficiencies of N and P, *Larrea tridentata* in southern New Mexico shows some of the highest levels of nutrient use efficiency that have been found in woody plants (*44*). Losses of soil N that are associated with the transition from grassland to desert may result in an environment that favors N-fixing shrubs, such as mesquite, which augment local levels of fertility (*32*).

The limited nutrient supply in desert soils is not the result of slow nutrient cycling. Decomposition in deserts is surprisingly fast (*45*) and is driven by an abundant soil microfauna that contributes to nutrient turnover (*46*). Relatively rapid turnover in desert soils leads to low levels of nutrient accumulation (*47*) and to potential losses of available nutrients from the ecosystem (*48*). For desert soils of the southwestern United States, Peterjohn (*49*) has developed a mass balance model for N during the Holocene period (Table 1). In his model, more than 77% of the N deposited during the last 10,000 years has been removed from desert ecosystems, and most of that must have been lost to the atmosphere because river transport to the ocean and deep seepage to ground water are minimal (*50*). Ammonia volatilization, denitrification, and wind erosion contribute to losses of N from deserts, and all of these processes are likely to increase when grasslands are converted to desert shrubland.

Table 1. A N budget for desert ecosystems of the southwestern United States during the last 10,000 years. All data are in kilograms of N per square meter (*49*).

Process	Flux
Atmospheric input	2.99
Accumulation	
Vegetation	0.036
Soil	0.604
Total	0.640
Output	
Runoff	0
Deep seepage	0.028
Total	0.028
Inferred loss to the atmosphere	2.32

In soils of high *p*H, ammonium is converted to NH_3, which is lost to the atmosphere by the reaction

$$NH_4^+ + OH^- \rightarrow NH_3 \uparrow + H_2O$$

This reaction is favored in alkaline soils, and the loss of NH_3 is maximized in dry permeable soils with low cation exchange capacity (*51*). Dawson (*52*) used a model of soil N transformations to estimate that the flux of NH_3 from nonagricultural lands of the world was 47×10^{12} g year^{-1}, including 21.8×10^{12} g year^{-1} from the latitudinal belts between 20° and 40°, which contain most of the world's arid lands.

The loss of ammonia to the atmosphere is especially significant because ammonia is the only substance capable of generating alkalinity in rainfall (*53*). Ammonia has a short lifetime in the atmosphere, and undoubtedly some of the flux from arid regions is deposited locally. However, because of the low rainfall in desert regions, a significant amount of NH_3 is likely to undergo long-range transport. This NH_3 can potentially neutralize acid rain in areas that are downwind of deserts. As early as 1958, Junge (*54*) noted high concentrations of NH_4 in the rainfall of the southwestern United States, and during our study in southern New Mexico, NH_4 concentrations were greater in rainfall collected in the summer, when NH_3 volatilization should be greatest (Fig. 3), than at other times. The volatilization of NH_3 should increase as grassland soils erode and $CaCO_3$ is then exposed at the surface (Table 2).

Several studies suggest that denitrification is also an important process in the removal of N from desert soils (*55*). Westerman and Tucker (*56*) found that about 70% of the N from added NH_4 and 95% of the N from added NO_3 were lost to the atmosphere after 1 year under field conditions. Peterjohn (*49*) reported that denitrifying bacteria are optimally adjusted to the temperature and *p*H of desert soils, and levels of organic C and nitrate are often nonlimiting to in situ enzyme activity. Bursts of denitrification presumably occur during the moist conditions that prevail after rainstorms (*57*). In semiarid grasslands, competition with grasses for available nitrate and rapid plant uptake of soil moisture probably limit denitrification. When shrublands replace grasslands and greater overland flow transports NO_3 to basin depressions, greater levels of denitrification are expected. The fine-textured soils found in these areas promote anaerobic conditions for denitrification for long periods after rainfall (*58*). Bowden (*59*) suggests that one-third of the gaseous loss of N from terrestrial ecosystems to the atmosphere (283×10^{12} g of N per year) occurs in desert regions. To the extent that the product of denitrification is N_2O, deserts make a contribution to the atmospheric burden of a gas that is involved in ozone destruction and greenhouse warming (*60*).

Losses of desert soil to wind erosion are globally significant (*61*). The upper limit for global estimates of the long-range transport of desert dust is approximately 1×10^{16} g year^{-1} (*62*). If we assume that the N content of surface soils is about 0.064% (*49*), the total N loss from deserts as a result of wind erosion is 6.4×10^{12} g year^{-1}, or approximately 0.14 g m^{-2} year^{-1} from the world area of desert lands (4.6×10^9 ha) (*63*). About 40 to 70% of the atmospheric nitrate over the North Pacific Ocean is derived from continental aerosols (*64*), presumably from the deserts of China. Aerosols from the deserts of North America are likely to carry nitrate eastward and contribute to the dry deposition of N in forest vegetation (*65*).

Dust transport also affects the global cycles of S, P, and other elements. Wind erosion of desert soils that are rich in gypsum contributes to the content of SO_4^{2-} in rainfall (*66*), whereas erosion of soils rich in calcium carbonate contributes to the neutralization of acid components from anthropogenic activities (*67*) by reactions such as

$$CaCO_3 + H_2SO_4 \rightarrow Ca^{2+} + SO_4^{2-} + H_2O + CO_2 \uparrow$$

Young *et al.* (*68*) link this neutralization process to the strong correlation between Ca^{2+} and SO_4^{2-} concentrations in rainfall of the western United States, compared to the strong correlation between H^+ and SO_4^{2-} concentrations in the East (*69*). In North America, atmospheric deposition of Ca decreases from west to east (*70*), although a large dryfall of Ca is recorded as far east as Tennessee (*65*).

Wind erosion of desert soils confers an atmospheric component to the global cycle of P (*71*). A net P flux of 1×10^{12} g year^{-1} is transferred from continents to the oceans, and about half of this flux occurs as a result of the transport of dust from the Sahara to the North Atlantic. The net flux is only about 10% of the input of P to the oceans by river flow, but it is delivered to the central ocean basins where the P for net primary production is more limited than in continental shelf areas (*72*). More significantly, desert dust contains an appreciable content of Fe that may stimulate phytoplankton productivity in the oligotrophic waters of the central ocean. Martin and Gordon (*73*) reported that about 95% of the available Fe in the North Pacific Ocean is deposited from the atmosphere, where it is derived from the transport of desert dust from central China (*74*).

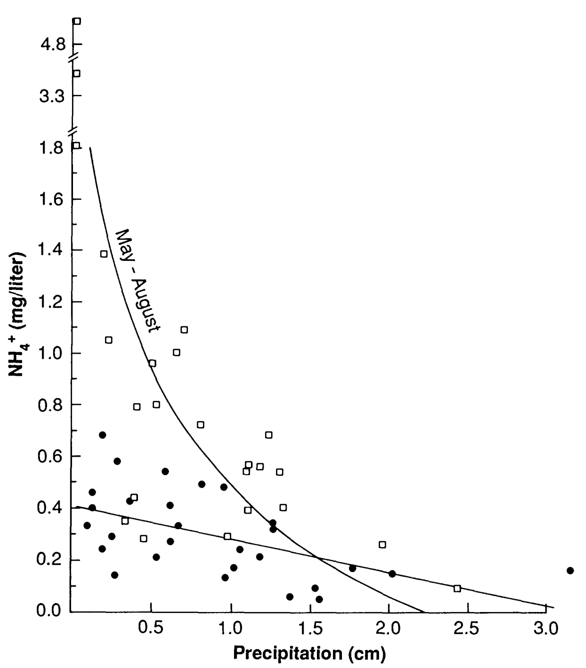

Fig. 3. Variation in the concentration of NH_4^+ in rainfall collected on the Jornada Experimental Range as a function of the volume of the precipitation event during 1987 through 1989 (*106*). Least-squares regression was used to fit a logarithmic relation to summertime (May through August) samples (□), in which concentration $= -1.44 \pm 0.215 \log_{10}(x) + 0.497$, $P < 0.0001$; and samples from other seasons (●), in which concentration $= -0.129 \pm 0.038\,x + 0.414$, $P < 0.0025$ (error limits are ± SE); x is the measured precipitation in centimeters.

Table 2. Ammonia volatilization in the Chihuahuan Desert of southern New Mexico during a drying sequence after application of simulated rainfall. All data are in micrograms of N per square meter per day (*106*).

Time (hours)	Grassland	Creosote bush	Playa
Pretreatment	15	15	43
24	45	95	50
48	35	30	34
168	21	24	20

Dust from arid regions makes a significant contribution to the burden of tropospheric aerosols (*53*). Although the effects of tropospheric aerosols are uncertain in detail, most types are thought to lead to climatic cooling (*75*), and thus they may offset the effects of increasing concentrations of greenhouse gases. In layers deposited during the last glacial episode, ice cores from Antarctica contain a large concentration of aerosols, which may have enhanced global cooling (*76*). These aerosols were derived from soils, and their abundance indicates that the global area of deserts and the wind erosion of desert soils may have been larger during the last ice age (*77*).

The climatic effects of tropospheric aerosols are determined by the optical properties of the particle and the albedo of the underlying surface (*36, 75*). Over desert regions, soil dust may act to trap infrared reradiation from the earth's surface, and this trapping may lead to warming (*78*). An increasing flux of dust from deserts may lead to local warming in desert regions, while it cools other regions. Thus, an increase in the flux of soil dust from arid areas has the potential to exert widespread influence on global climate, but it is not clear exactly what those effects may be. In the future, satellite remote sensing may prove useful in tracking dust transport over large areas (*79*).

Contributions of arid lands to the atmospheric content of CH_4 and other hydrocarbons are poorly understood. Zimmerman *et al.* (*80*) suggested that there was a large CH_4 flux from termites, which are abundant in desert regions where they are important in the turnover of soil organic matter (*46*). The ant fauna of arid lands may contribute significant quantities of formic acid to the atmosphere (*81*), and desert shrubs emit a wide variety of volatile organic compounds (*82*). These emissions are subject to atmospheric reactions that produce ozone and other oxidizing substances (*83*). Studies suggest that arid and semiarid soils also release NO (*84*), which is closely involved in the production of tropospheric ozone.

Episodic Events

An increase in the desertification of marginal lands accentuates the importance of episodic events, such as torrential rainstorms and windstorms, in the control of ecosystem processes (Fig. 4). MacMahon and Wagner (*85*) have shown that the coefficient of variation associated with mean annual precipitation is greater in areas of low mean annual rainfall. An increased frequency of extreme rain events imposed on a landscape devoid of the protective cover of grassland leads to greater transport of soil materials during floods. As a result of catastrophic runoff events, lands at the margin of arid and semiarid regions typically show the highest annual rates of mechanical weathering (*86*) and high concentrations of suspended solids in rivers (*87*).

The transport of desert dust begins when wind velocity exceeds a critical threshold (*88*). Gupta *et al.* (*89*) showed that soil deflation from the Rajasthan Desert of India increases exponentially with increasing wind velocity. Deposition of dust in the cities of Kuwait is also exponentially related to the total wind flow (*90*). During synoptic weather patterns that are particularly conducive to the transport of dust, the total losses are often spectacular. Liu *et al.* (*91*) reported a dustfall of 1 g m^{-2} $hour^{-1}$ in Beijing, China, as a result of a single dust storm on 18 April 1980 in desert regions to the west. The frequency of dust storms is inversely related to mean annual rainfall (*92*), and there is evidence that dust storms have become more frequent as a result of human activities in semiarid lands (*93*). The frequency of episodic transport by wind and water from arid lands is also likely to increase in response to anticipated changes in global climate (*8*).

The increasing importance of episodic events also affects processes in the ecosystem. An environment where the recharge of soil moisture becomes less predictable and the surface layers are often dry selects for various species of shrubs that can exploit the recharge of deep soil layers that occurs in infrequent, torrential rainstorms (*94*). At first glance, the timing of plant growth in these areas will appear less coupled to rainfall (*16, 95*), but continued photosynthesis by shrubs during extended periods of drought is dependent on episodic rainfall that recharges the lower soil profile. In semiarid grasslands, growth is closely coupled to rainfall (*15*), but annual rainfall is greater and more predictable. Moreover, vegetation in semiarid grasslands can exploit soil moisture that is derived from small rain events (*96*). Rain use efficiency, defined as aboveground net primary productivity divided by annual rainfall, decreases strongly from semiarid grasslands to true deserts (*97*). Temporal heterogeneity in the availability of soil moisture reinforces the invasion of grasslands by shrubs.

The episodic availability of soil resources, especially moisture, leads to a "pulse-reserve" response of desert ecosystems (*98*). Primary production and soil nutrient turnover are greatest during periods of moisture availability, whereas ecosystem function during periods of drought depends on accumulated reserves. We suggest that during desertification, there is an increasing dependence of the biota on episodic, rich resources rather than more reliable, but low-level resources to which biotic activity can be closely coupled (*99*).

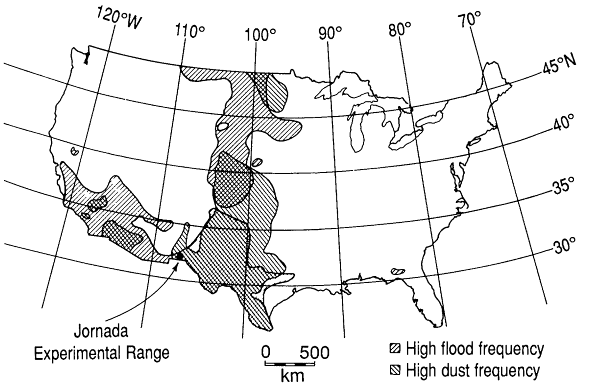

Fig. 4. Areas of the United States with a flash flood index in excess of 0.5 for a 20-year period and an annual frequency of dust hours, when visibility is <11 km, in excess of 0.4% (*107*).

Conclusions

On the basis of the Jornada desertification study, we suggest that any process that leads to an increasing heterogeneity of soil resources in space and time is likely to lead to the degradation of semiarid regions, especially grasslands, and to the increasing spread of arid regions dominated by shrublands. Grazing increases soil heterogeneity in semiarid lands, and the conversion of these areas to shrub-desert is aided when cattle disperse the seeds of desert species such as mesquite (*14*). Similarly, greater soil heterogeneity caused by off-road vehicles leads to the degradation of desert areas by increasing the channelization of runoff and the rate of soil erosion (*100*). Conversion of semiarid grasslands to row-crop agriculture adds to local heterogeneity and is likely to lead to permanent desertification of these areas during future periods of drought.

Our view of the importance of soil properties is consistent with the observations of Breman and de Wit (*42*) that nomadic livestock systems are well adjusted to the ecosystems of the southern Sahel. The impact of nomadic herders and the harvest of plant resources are spread evenly and at low levels across the landscape (*101*). When people and livestock are concentrated into small areas in which their impact leads to an increased heterogeneity of soil resources, permanent degradation of the productive capacity of the land occurs (*6*). Satellite images show that the distribution of arid land with low productivity has expanded in southern New Mexico and the Sahel (*102*). Particularly in the Sahel, human population is increasing rapidly (*9*); however, desertification of these areas is also probable if global climate change is occuring (*8*).

Currently, arid lands cover about 12% of the earth's land surface (*63*). Semiarid grasslands and woodlands occupy an even larger area, so the total extent of dryland ecosystems is about one-third of the earth's land surface (*103*). Although these lands contribute little to the net primary productivity of the biosphere (*104*), they affect a number of global conditions through abiotic processes. Arid lands are likely to play a greater role in global biogeochemical function in the future. The area of arid land is expected to increase, along with episodic, long-range transport of soil resources. These changes may affect regions that are far removed from arid lands and possibly conditions of the entire planet.

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106. The volatilization of NH_3 from covered, in situ soil cores (10 cm in diameter) was collected by absorption in 10 ml of 2% H_2SO_4 for a 24-hour period, followed by analysis for NH_4 with a Technicon Autoanalyzer. Rainfall was simulated by additions of water to bring the soil core to field capacity in a depth of 0 to 15 cm. For each storm between October 1987 and May 1989, rainfall was collected on the Jornada Experimental Range with an Aerochem Metrics Collector and analyzed for NH_4 with Technicon Autoanalyzer methods.
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