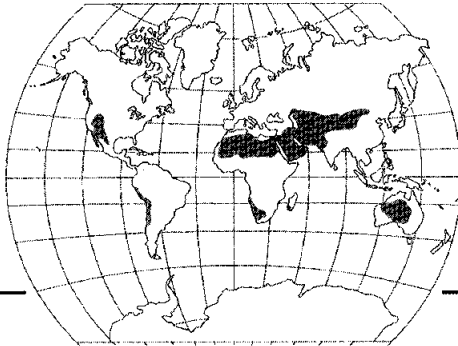# 15

Productivity of Deserts

James R. Ehleringer

I. Nature and Extent of Deserts

Moving along a geographic gradient of decreasing precipitation from either shrub–woodlands (e.g., Mediterranean climate) or grasslands (see Chapters 14 and 12, this volume), one encounters desert ecosystems, which typically receive less than 250 mm annual precipitation (Fig. 15-1). Arid lands are extensive, occupying nearly 30% of the land surface globally (Noble and Gitay, 1996), and their extent is thought to be increasing annually through desertification into areas previously occupied by arid grasslands (Schlesinger *et al.,* 1990; Kassas, 1995; Bullock and Le Houérou, 1996). Desert ecosystems are typically characterized by extremes, having the lowest standing biomasses, lowest primary productivities, and lowest precipitation inputs. Precipitation is, of course, the principal driver regulating primary productivity rates. Even though rainfall patterns are usually seasonal, these rains come as intermittent pulses, causing desert ecosystems to shift between inactive and active states, depending on soil moisture availability (Noy-Meir, 1985). Only in the higher elevation, cold desert ecosystems of North America, central Asia, and the Middle East do low wintertime temperatures prevent growth and also reduce evaporation, allowing for somewhat longer growth periods in the spring (Caldwell *et al.,* 1977; Goodall and Perry, 1979; Caldwell, 1985).

One feature that distinguishes productivity patterns in desert ecosystems
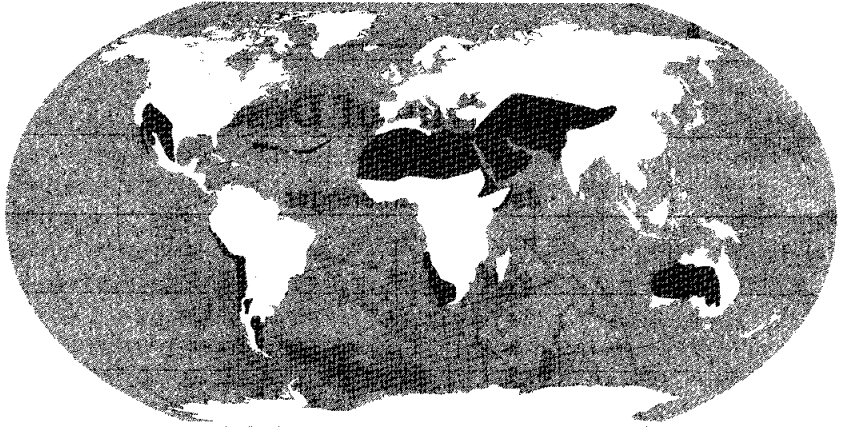
Figure 15-1   Distribution of arid land ecosystems on a global basis. Deserts are typically defined as those nonpolar regions that receive less than 250 mm of precipitation annually. The map is based on information in Logan (1968), McGinnies *et al.* (1977), and Walter and Breckle (1984).

from all others is the increased interannual variability in precipitation. At low precipitation means, both long-term annual and seasonal precipitation (in a biseasonal environment) amounts follow a gamma distribution—not a normal distribution. The consequence is that most years are drier than the arithmetic mean. Additionally, as the mean precipitation amount decreases, the interannual variability increases (Fig. 15-2). The consequence of this is that the drier desert regions are often characterized by several years of below-average precipitation amounts, punctuated by a relatively high precipitation year. Ehleringer (1994) observed that the relative frequency distribution of storm sizes did not differ among North American desert sites receiving different total precipitation amounts. Instead, what differed was simply the number of storm events at a site: annual precipitation was proportional to the total number of storm events in a given year.

## II. Standing Biomass and Aboveground Net Primary Productivity Rates

Total standing biomass in desert ecosystems is highly variable, depending on factors such as the seasonal distribution of the precipitation, grazing and human impacts, importance of woody versus herbaceous components, and soil fertility (Noble and Gitay, 1996). A reasonable standing biomass range of 2000–5000 kg ha^{-1} is not uncommon for shrub-dominated desert ecosys-
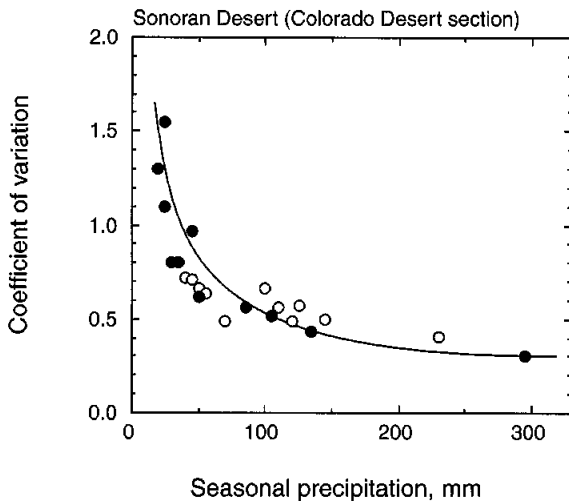
Figure 15-2   A plot of the relationships between long-term mean seasonal precipitation in the Sonoran Desert and the coefficient of variation in that precipitation.

tems (National Academy of Sciences, 1975; Whittaker and Niering, 1975; Goodall and Perry, 1979; Gibbens *et al.*, 1996; Rundel and Gibson, 1996; Schulze *et al.*, 1996). Most of this aboveground mass is associated with woody shrubs, which tend to increase in importance in response to grazing (Schlesinger *et al.*, 1990; Grover and Musick, 1990; Le Houérou, 1990; Pickup, 1996). Overall, the aboveground annual net primary productivity values in desert ecosystems tend to be less than 1500 kg ha^{-1} yr^{-1} (National Academy of Sciences, 1975; Whittaker and Niering, 1975; Goodall and Perry, 1979; Szarek, 1979; Hadley and Szarek, 1981; Rundel and Gibson, 1996), which is low compared to most other ecosystems except possibly grasslands. Much of the interannual variability in primary productivity may be associated with herbaceous components (both annuals and grasses), making it challenging to calculate a general value of net primary productivity for desert ecosystems unless the grazing pressures are well understood. It is possible, however, that remote-sensing approaches may be a valuable approach here; Prince and Goward (1995) and Prince *et al.* (1998) have shown large Normalized Difference Vegetation Index (NDVI) changes in surface spectral characterisitics in response to interannual variations in precipitation.

In desert ecosystems, net primary productivity is typically linearly related to precipitation input (Walter, 1939; Noy-Meir, 1985; Le Houérou, 1984; Sala *et al.*, 1988). This would include productivity of all vegetation components—woody, herbaceous, and annual. Soil nitrogen secondarily limits primary productivity. Linear productivity–precipitation relationships have
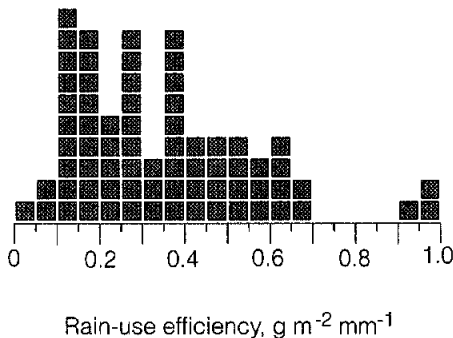
Figure 15-3 Rain use efficiency values for 72 different arid land sites. Data are from Le Houérou *et al.* (1988).

been described in more than 100 separate biomass-based studies throughout arid regions around the globe (Le Houérou, 1984; Le Houérou *et al.*, 1988). Similar tends are also found using satellite-based observations (Tucker *et al.*, 1991; Peters *et al.*, 1993; Prince and Goward, 1995; Prince *et al.*, 1998). Most of the data sets have been produced by measuring the variations in net primary productivity at a particular site from year to year. Le Houérou (1984) proposed the term "rain use efficiency" to describe the slope of the relationship between net primary production and precipitation. He has shown that this linear relationship not only typifies desert regions, but can also be extended into semiarid grassland ecosystems.

Globally, rain use efficiency values range between 0 and 1 g m^{-2} mm^{-1} (Fig. 15-3) (Le Houérou, 1984; Le Houérou *et al.*, 1988). There is a tendency for higher precipitation input sites to have higher rain use efficiencies, but not always. There is an even more evident tendency for disturbed ecosystems to have lower rain use efficiencies (Le Houérou *et al.*, 1988; Varnamkhasti *et al.*, 1995). These include overgrazed sites, regions of soil surface disruption, and areas with wood-harvesting activities. One factor contributing to a decreased rain use efficiency on disturbed sites is likely to be the loss of soil nitrogen, which impacts leaf nitrogen and constrains maximum photosynthetic rates when soil water is available. A second possibility is that in regions with bimodal precipitation patterns, some woody vegetation components may not be equally responsive to winter versus summer moisture inputs, leading to potentially lower rain use efficiencies. These relationships will be discussed further in a later section.

It is perhaps surprising that rain use efficiency values do not show clear differences in C$_3$- versus C$_4$-dominated ecosystems (Le Houérou, 1984). Consider, for example, the four major desert regions of western North America (Chihuahuan, Great Basin, Mohave, and Sonoran). These ecosys-

tems differ in C_3/C_4 abundances; rain use efficiency values can be calculated for nongrazed sites based on previously published observations (Whittaker and Niering, 1975; Szarek, 1979; Turner and Randall, 1989). Calculated values range between 0.40 and 0.65 g m^{-2} mm^{-1}, with the Chihuahuan (C_3/C_4, 0.65 g m^{-2} mm^{-1}), Great Basin (C_3/C_4, 0.58 g m^{-2} mm^{-1}), and Mohave (C_3, 0.64 g m^{-2} mm^{-1}) being indistinguishable from each other. One possible explanation for the lack of a relationship between rain use efficiency and photosynthetic pathway is that the more efficient C_4 plants tend to be more summer active, whereas C_3 plants tend to be more spring active (Ehleringer and Monson, 1993). The higher evaporative demand associated with warmer temperatures in the summer would require a greater photosynthetic efficiency in order to attain a rain use efficiency value similar to that of a spring-growing vegetation.

Although both annual and perennial vegetation components contribute to the linear rain use efficiency relationship, it is not evident from regression coefficients that these two vegetation components respond differently to precipitation (Beatley, 1974). Figure 15-3 shows the year-to-year net primary productivity as related to precipitation for Mohave Desert vegetation
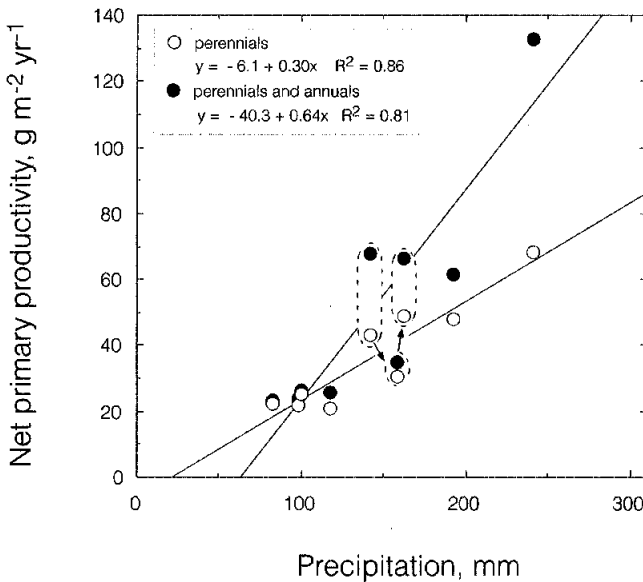
Figure 15-4 The relationship between net primary productivity and precipitation for perennials and all vegetation at the Mohave Desert site, Rock Valley, Nevada. The slope of the regression is known as the rain use efficiency. Arrows and areas enclosed by dashed lines indicate productivity patterns for three successive years. Based on data in Turner and Randall (1989).

in Rock Valley, Nevada. The x intercept values indicate that net primary productivity begins at a lower precipitation threshold for perennials than is required to initiate production in annuals. Primary productivity in both annuals and perennials in linearly related to precipitation, yet productivity of annuals is negligible below 100 mm precipitation.

Although the relationship between precipitation and primary productivity is usually linear in desert ecosystems, detailed analyses of year-to-year productivity data often suggest nutrient limitations as a secondary factor. For example, when three successive years of above-average precipitation fell at the Rock Valley site (Fig. 15-4), overall net primary productivity fell in the middle year. This is shown by the circled data in Fig. 15-4, with the arrows showing total net primary productivity from year 1 to year 2 to year 3. Notice that in year 2, the net primary productivity of perennials decreased (well below the regression line) and the productivity of annuals was very low. At the end of any growing season, approximately one-third of the nitrogen may not be recovered and will persist in standing dead plant parts. The likely explanation of the observed pattern in year two is that a significant fraction of the nitrogen within the ecosystem was still in standing dead, leftover from year 1, limiting the capacity of vegetation to photosynthesize even though adequate moisture might have been available. This nutrient limitation was likely removed by year 3, allowing the vegetation productivity to respond as it had in the first year.

III. Seasonality Components of Net Primary Production

Given limited soil moisture availability in deserts and its direct effect on productivity rates, it is essential to understand how different plants will respond to year-to-year changes in the seasonality of precipitation, especially because it is becoming more clear that a macroscale phenomenon, such as El Niño, can influence the duration and amounts of both summer and winter precipitation inputs. How well do desert plants utilize winter-derived and summer, monsoonal moisture inputs?

Cold desert ecosystems of North America and Asia occur at higher elevations. They receive moisture inputs from frontal storms and have a wintertime recharge of deeper soil layers (Gee *et al.,* 1994; Smith *et al.,* 1997), a feature that does not occur in lower elevation, warm desert ecosystems, where plants can be active throughout the winter–spring period. One interesting feature is that many woody species in the cold desert or cold-to-warm desert transition zone in North America tend to use moisture in the upper soil layers only during the spring, but not in the summer (Ehleringer *et al.,* 1991; Donovan and Ehleringer, 1994; Evans and Ehleringer, 1994). This is most evident in evaluating plant responses to summer moisture input, whereby
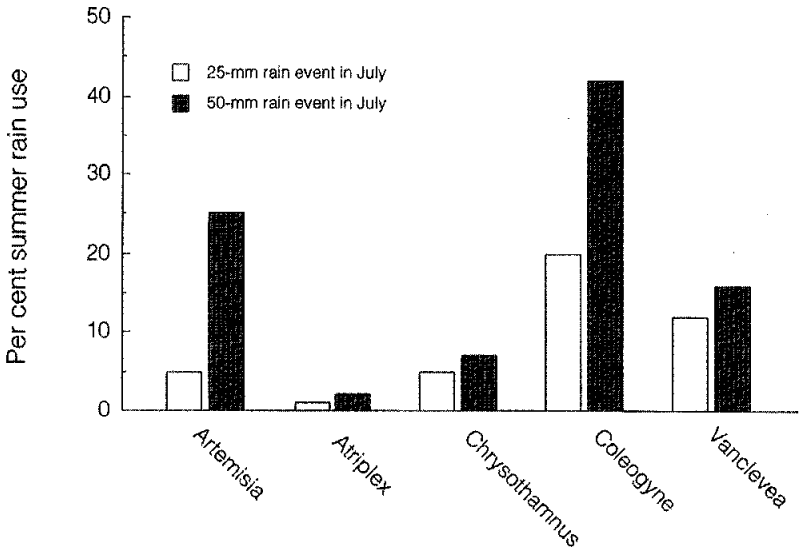
Figure 15-5   A calculation of the percentage use of moisture derived from upper soil layers (summer-derived rain) by five common woody perennials in the Colorado Plateau desert shrub community (Utah). Data are derived from Lin *et al.* (1996) and are based on measured hydrogen isotope ratios of xylem water and a two-member mixing model of deep and shallow soil isotope ratio values of soil water.

monsoon precipitation events often saturate only the upper soil layers. Yet the limited use of monsoonal moisture in the upper soil layers by desert plants is not limited to cold desert species, but can also occur in warm desert woody perennials (Reynolds and Cunningham, 1981; Ehleringer and Cook, 1991).

It is essential to reiterate that soil moisture availability in the upper soil layers is a pulse phenomenon. Because temperatures are warmer in the summer than in the spring, the duration of this pulse will be shorter in the summer than in the spring. Lin *et al.* (1996) have shown that woody perennials in Colorado Plateau deserts have a limited capacity to respond to 25- or 50-mm precipitation events in the summer (Fig. 15-5), although it is known that these plants respond to precipitation events in the spring (Ehleringer *et al.*, 1991). For those woody perennials responding to summer moisture inputs (such as *Coleogyne*), less than 40% of the moisture extracted from the soil and transpired by the shrub is derived from these upper soil layers. Instead it appears that plants are relying to a large degree on moisture stored in deeper soils layers (Thorburn and Ehleringer, 1995; Lin *et al.*, 1996). However, there are life form-dependent differences in the use of moisture in these upper soil layers during the summer. Annuals derive virtually all of their water from
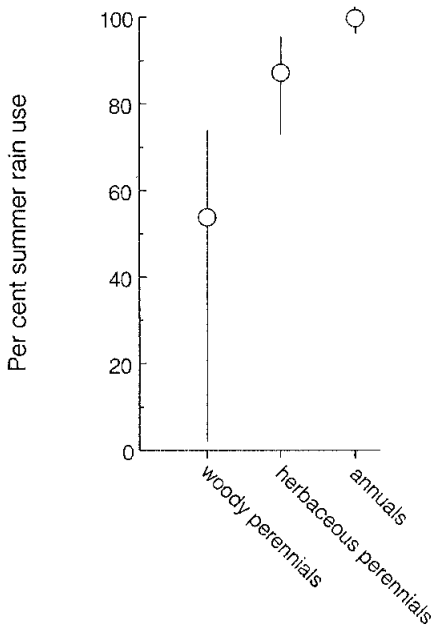
Figure 15-6 The calculated percentage use of moisture derived from summer (August) precipitation events by three life forms on the Colorado Plateau desert shrub community (Utah). Data are means and total ranges for all species within a category. Data are derived from Ehleringer *et al.* (1991).

these surface soil layers, whereas herbaceous perennials derive nearly 85% of their moisture from the shallow depths (Fig. 15-6). On average, only 54% of the water transpired by woody perennials at this site is derived from upper soil layers. Thus, in evaluating the rain use efficiency of a site, an essential factor may be the life form diversity and the capacity to use a specific moisture source. Grazing activities tend to reduce the abundance of annuals and herbaceous vegetation components, which may result in surface-layer moisture being evaporated rather than transpired from a site. It is likely that this relationship explains the observations of reduced rain use efficiencies on impacted arid land sites.

Although the woody shrub *Coleogyne ramosissima* will extract and utilize summer-derived soil moisture, that moisture is not as effective as winter moisture in promoting growth. Ehleringer (unpublished) evaluated the interactions of both competition and water limitations in constraining growth of this dominant shrub. Both the elimination of immediate neighbors and supplemental winter precipitation increased net primary productivity (Fig. 15-7). However, neither supplemental summer precipitation (50 mm) nor
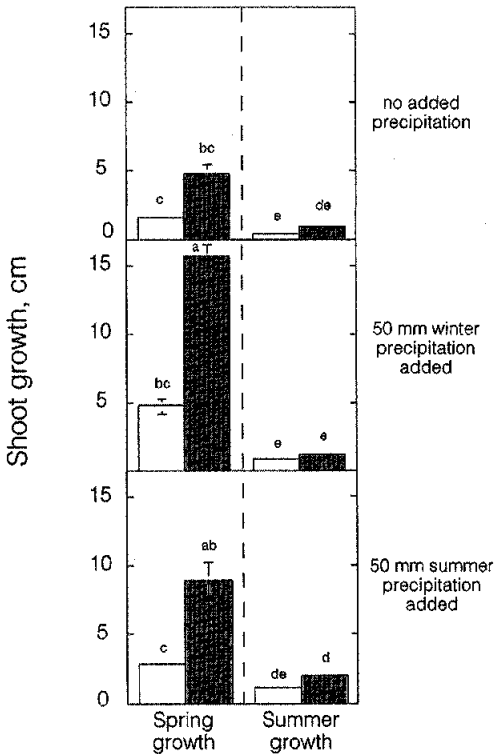
Figure 15-7 The relationships between growth of *Coleogyne ramosissima* and time of the year for treatments receiving supplemental precipitation and/or having their immediate neighbors removed (shaded regions) or neighbors present (unshaded regions). Data are from Ehleringer and Phillips (unpublished).

neighbor removal promoted net primary productivity during the summer period. Thus, it would appear rain use efficiencies in ecosystems dominated by spring-active woody shrub components would decrease under conditions of elevated monsoonal precipitation, particularly if grazing were present to restrict the growth of herbaceous vegetation components.

IV. Human Impacts on Primary Productivity in Desert Regions

The relationships between net primary productivity and human impacts may be generalizable using a simple model illustrating rain use efficiency (Fig. 15-8). Although net primary productivity increases linearly with cu-
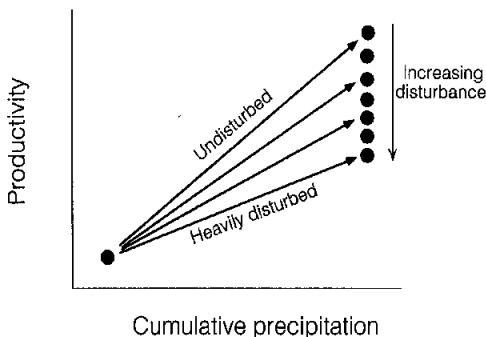
Figure 15-8   A simple model of the relationship between cumulative precipitation and net primary production in desert ecosystems under different levels of soil disturbance.
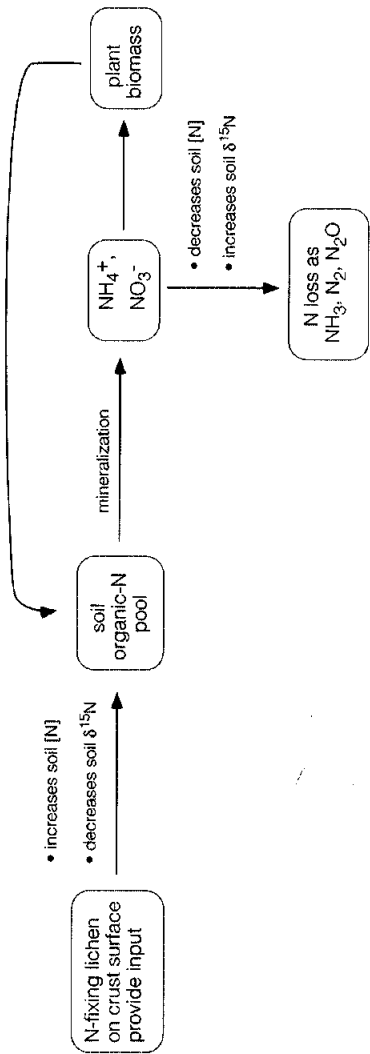
mulative precipitation inputs through the growing season, human impacts tend to be associated with reductions in the slope of this relationship (i.e., rain use efficiency). The decrease in rain use efficiency is based on two primary factors. First is the reduction in the standing biomass of herbaceous vegetation components through grazing pressures. The second factor is associated with degradation of the land. The causes here may be variable, but it appears that at least in the Colorado Plateau (if not other deserts as well) that breaking up of the biological crust (also known as the cryptobiotic crust) by trampling is perhaps more subtle, but just as important. Arid land ecosystems throughout the world are dominated by a biological crust (Belnap, 1995, 1996), which consists of a diverse mixture of bacteria, fungi, algae, mosses, and lichens. For many desert ecosystems, the biological crust is the primary source of nitrogen input (Evans and Ehleringer, 1993; Evans and Johansen, 1998). Disruption of the crust surface by hooves of cattle, sheep, or goats (or visitors to national recreation areas) results in death of the nitrogen-fixing lichens and algae as they are buried by loosened soil particles (Belnap, 1995, 1996). In the Colorado Plateau desert, where the surface biological crust has been best studied, it is the keystone component influencing both input and loss of nitrogen from the ecosystem. Thus, the biological crust appears to play a central role in affecting primary productivity through its influence on nitrogen availability to higher plants.

Evans and Ehleringer (1994) and Evans and Belnap (1999) provided evidence that soil disturbance was one of the primary factors now decreasing soil nitrogen in desert ecosystems and possibly contributing to desertification (Fig. 15-9). Their model has been evaluated through comparisons of both plant and soil nitrogen on adjacent disturbed and undisturbed sites. Both studies examined the long-term impacts of crust disturbance on

30 years of recovery following cryptobiotic soil crust disturbance in Canyonlands National Park

	Undisturbed	Disturbed	Difference
soil $\delta^{15}N$ (‰)	3.6 ± 0.4	5.1 ± 0.3	1.5 ‰
plant $\delta^{15}N$ (‰)	1.1 ± 0.7	2.6 ± 0.3	1.5 ‰
soil N (mg/g)	0.41 ± 0.01	0.27 ± 0.03	33 %
plant N (mg/g)	- -	- -	

Soil crusts with moderate grazing at Coral Pink Sand Dunes State Park

	Undisturbed	Disturbed	Difference
soil $\delta^{15}N$ (‰)	1.1	2.9	1.8‰
plant $\delta^{15}N$ (‰)	1.1	2.7	1.6‰
soil N (mg/g)	0.44	0.26	69 %
plant N (mg/g)	2.9	2.4	21 %

N-fixing lichen on crust surface provide input
- increases soil [N]
- decreases soil $\delta^{15}N$

→ soil organic-N pool

mineralization → NH_4^+, NO_3^-

→ plant biomass
- decreases soil [N]
- increases soil $\delta^{15}N$

→ N loss as NH_3, N_2, N_2O

Figure 15-9 Relationships between soil and plant nitrogen isotope ratios and soil and plant nitrogen contents for disturbed and nondisturbed sites within arid land ecosystems on the Colorado Plateau, Utah. Data from Coral Pink Sand Dunes State Park are derived from Evans and Ehleringer (1994); data from Canyonlands National Park are derived from Evans and Belnap (1999).
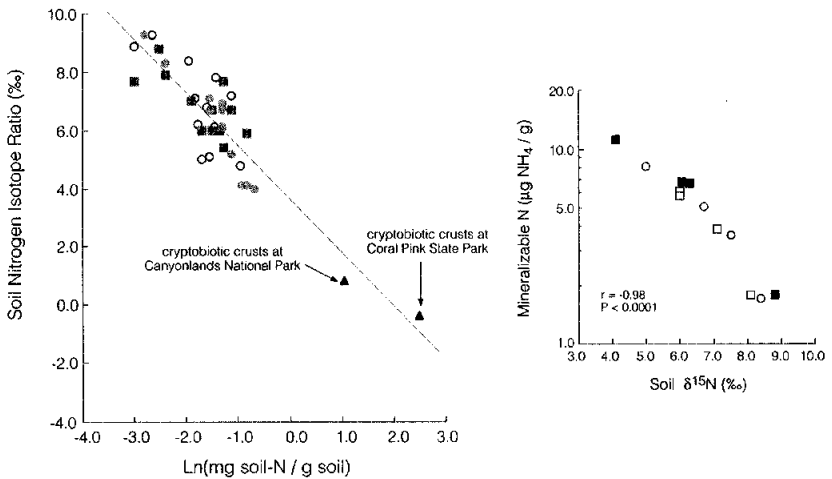
Figure 15-10   The relationships between nitrogen isotope ratio ($\delta^{15}N$) of soil and soil nitrogen content (left) and mineralizable soil nitrogen and nitrogen isotope ratio (right) for soils in arid land ecosystems on the Colorado Plateau. Data are derived from Evans and Ehleringer (1993, 1994).

ecosystem nitrogen relationships by comparing two contrasting ecosystems. At Canyonlands National Park, one site was left undisturbed by cattle (Virginia Park) and the adjacent site (Chessler Park) received light grazing for a decade. Grazing in Chessler Park stopped more than 30 yr ago. Yet recent nitrogen isotope ratio ($\delta^{15}N$) and nitrogen content data indicate that the crusts have not recovered and that the ecosystem continues to lose nitrogen. Chessler Park has only 66% of the soil nitrogen compared to that in the undisturbed Virginia Park. At the Coral Pink Sand Dunes State Park, very light grazing continues on an irregular basis. Note that the disturbed soils are similar to those found in Chessler Park, even though one site is still occasionally disturbed (keeping it from recovering), whereas the other has had 30 yr of recovery time. Both data sets show that soil disturbance and disruption of the biological crusts resulted in substantial decrease in both soil and plant nitrogen. Because plant photosynthesis is directly proportional to leaf nitrogen content (Field and Mooney, 1986; Evans, 1989), disruption of the biological crusts results in very long-term decreases in ecosystem primary productivity. These decreases should be quantifiable in terms of lower rain use efficiencies. At some point, soil nutrition will be impacted sufficiently by disturbance activities such that C_4 species may be expected to out-compete the native C_3 species. This is because photosynthesis is intrinsically more nitrogen-use efficient in C_4 plants, which may translate into a competitive advantage.

The impacts of soil surface disturbance on ecosystem nitrogen cycling and its impact on primary productivity appear to be related to the soil and vegetation $\delta^{15}N$ values. Nitrogen isotope ratios of soils follow a Rayleigh distillation curve (Fig. 15-10), whereby the $\delta^{15}N$ value of the soil N changes in a manner highly correlated with the abundance of nitrogen in the soil. That is, when biological crusts are disturbed, there is a shift in the nitrogen input–loss balance, resulting in a continual loss of nitrogen from the ecosystem. That nitrogen is lost by both dentrification and ammonification processes (Schlesinger, 1997). Because ^{14}N is preferentially lost, the remaining nitrogen is enriched. Nitrogen isotope ratios of nitrogen incorporated into plants reflect the soil enrichment processes (Fig. 15-9).

V. Anticipated Impacts of Global Change on Deserts

Human impacts through grazing activities and land degradation, such as disruption of the biological crusts, are likely to be the dominant factors influencing net primary productivity rates in deserts for some time to come. These stressor impacts may only tend to decrease net primary productivity in desert ecosystems. Nitrogen isotope ratio measurements in plants may be one way of quantifying these long-term ecosystem impacts. Yet, leaf-level ecophysiological responses to elevated carbon dioxide may mitigate these stressors to some degree.

Mooney *et al.* (1991) predicted that water use efficiency would increase under elevated carbon dioxide conditions and that this would increase primary productivity in arid ecosystems. Carbon dioxide acts directly at the stomatal level, reducing stomatal conductance, which results in an increased photosynthesis:transpiration ratio (Knapp *et al.*, 1996). One additional direct, long-term consequence of the reduced stomatal activity will be an extension of the growing season, because under elevated carbon dioxide levels soil moisture is transpired through the vegetation at a slower rate (Ham *et al.*, 1995; Field *et al.*, 1997). In grassland microcosms, Field *et al.* (1997) observed that a doubling of carbon dioxide levels over present-day values reduced evapotranspiration rates by nearly 50%, allowing plant growth substantially longer into the summer drought period.

Although equivalent long-term data on water-use efficiencies are not yet available for desert ecosystems, the same extension of the growing season into the drought period is expected to occur (Fig. 15-11). Modeling studies have calculated the expected impact of an enhanced water use efficiency on seasonal activity and on the increase in leaf area that can be supported by a plant given a reduced transpiration at the single leaf level (Skiles and Hanson, 1994; Neilson, 1995; VEMAP, 1995). Neilson (1995) predicted that as a consequence of elevated carbon dioxide, the leaf area of desert plants in southwestern North America should increase by 25–50% or more (Fig. 15-
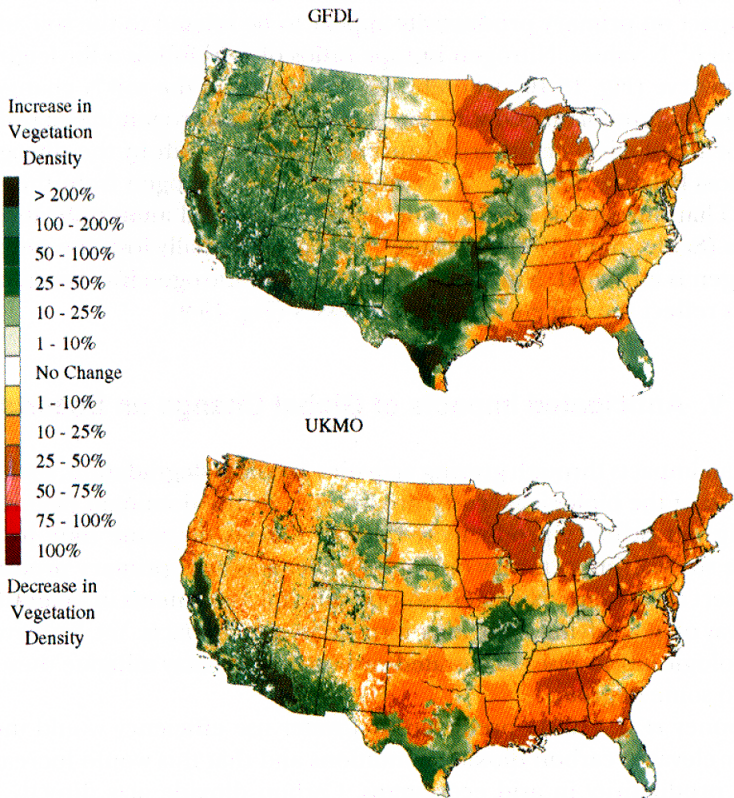
Figure 15-11   Model simulations of the predicted long-term change in vegetation density within the United States in response to a doubling of atmospheric carbon dioxide above present-day values. The Geophysical Fluid Dynamics Laboratory (GFDL) and the United Kingdom Meteorological Office (UKMO) developed two general circulation models. Data are derived from models described in Neilson (1995) and VEMAP (1995). This particular figure first appeared on the back cover of "Our Changing Planet, The FY 1998 U.S. Global Change Research Program," and was a supplement to the President's Fiscal Year 1998 Budget.

11). He refers to this phenomenon as the "greening of the desert," with the expected impact predicted to extend over all arid and semiarid ecosystems in North America. Although global modeling of this phenomenon has not yet be done, it is likely that enhanced water use efficiencies are likely to extend the growing season in most arid ecosystems.

Is there currently strong evidence for broad, climate-induced changes in desert ecosystems? Le Houérou (1996) recently reviewed the available data

and concluded that the answer is "no." Although there have been some detectable changes in precipitation of desert regions over the past century, these changes have been region specific and have not shown a consistent, predictable pattern. Desert regions in central Chile and the Sahel have become drier during the past century (Le Houérou, 1996). Yet, in contrast, the deserts of North America may have become wetter during this same period (Nichols *et al.,* 1996). However, there is strong evidence for changes associated with anthropogenic activities, such as those associated with grazing, surface disturbance, and wood harvesting (Le Houérou, 1996). These changes decrease the ability of desert ecosystems to respond to pulse precipitation events. When gas-exchange activities resume following moisture inputs into these impacted regions, it appears that primary productivity usually reflects a reduced rain use efficiency. Yet in satellite-level studies of rain use efficiency in the Sahel, Prince *et al.* (1998) have not been able to detect reduced rain use efficiencies or increased desertification on many of these impacted lands. Future efforts should be directed at resolving this discrepancy, because it lies at the heart of our ability to understand change in primary productivity of desert ecosystems at the global scale.

VI. Conclusions

Primary productivity rates within a desert ecosystem tend to be less than 1500 kg ha^{-1} yr^{-1}, with the productivity rate within a specific location being linear with precipitation inputs. However, the year-to-year primary productivity of a desert ecosystem is challenging to predict, because of high interannual variation in precipitation amounts compounded with human impact (usually grazing related) in many regions. Remote-sensing approaches may be a valuable tool for quantifying productivity in some arid land ecosystems, where vegetation cover is sufficient. Not all perennial plants utilize moisture from the same soil layers, leading to interseasonal differences in the responsiveness of vegetation to biseasonal precipitation inputs. Biological crusts may be a key nitrogen source in many arid regions and disruption of these crusts by grazing is suggested to be a contributing factor to decreased productivity in disturbed arid land ecosystems.

References

Beatley, J. C. (1974). Phenological events and their environmental triggers in Mohave Desert ecosystems. *Ecology* **55,** 856–863.

Belnap, J. (1995). Surface disturbances: their role in accelerating desertification. *Environ. Monitor. Assess.* **37,** 39–57.

Belnap, J. (1996). Soil surface disturbances in cold deserts: Effects on nitrogenase activity in cyanobacterial-lichen soil crusts. *Biol. Fertil. Soils* **23**, 362–367.

Bullock, P., and Le Houérou, H. (1996). Land degradation and desertification. *In* "Climate Change 1995" (R. T. Watson, M. C. Zinyowera, and R. H. Moss, eds.), pp. 171–189. Cambridge Univ. Press, Cambridge.

Caldwell, M. (1985) .Cold desert. *In* "Physiological Ecology of North American Plant Communities" (H. A. Mooney and B. F. Chabot, eds.), pp. 189–212. Chapman and Hall, London.

Caldwell, M. M., White, R. S., Moore, R. T., and Camp, L. B. (1977). Carbon balance, productivity, and water use of cold-winter desert shrub communities dominated by C_3 and C_4 species. *Oecologia* **29**, 275–300.

Donovan, L. A., and Ehleringer, J. R. (1994). Water stress and use of summer precipitation in a Great Basin shrub community. *Funct. Ecol.* **8**, 289–297.

Ehleringer, J. R. (1994). Variation in gas exchange characteristics among desert plants. *In* "Ecophysiology of Photosynthesis" (E.-D. Schulze and M. M. Caldwell, eds.), pp. 361–392. Ecological Studies Series. Springer-Verlag, New York.

Ehleringer, J. R., and Cook, C. S. (1991). Carbon isotope discrimination and xylem D/H ratios in desert plants. "Stable Isotopes in Plant Nutrition, Soil Fertility, and Environmental Studies," pp. 489–497. IAEA, Vienna.

Ehleringer, J. R., and Monson, R. K. (1993). Evolutionary and ecological aspects of photosynthetic pathway variation. *Annu. Rev. Ecol. Syst.* **24**, 411–439.

Ehleringer, J. R., Phillips, S. L., Schuster, W. F. S., and Sandquist, D. R. (1991). Differential utilization of summer rains by desert plants: implications for competition and climate change. *Oecologia* **88**, 430–434.

Evans, J. R. (1989). Photosynthesis and nitrogen relationships in leaves of C_3 plants. *Oecologia* **78**, 9–19.

Evans, R. D., and Belnap, J. (1999). Long-term consequences of disturbance on nitrogen dynamics in an arid grassland ecosystem. *Ecology* **80**, 150–160.

Evans, R. D., and Ehleringer, J. R. (1993). A break in the nitrogen cycles in aridlands: evidence from $\delta^{15}N$ of soils. *Oecologia* **94**, 314–317.

Evans, R. D., and Ehleringer, J. R. (1994). Water and nitrogen dynamics in an arid woodland. *Oecologia* **99**, 233–242.

Evans, R. D., and Johansen, J. R. (1999). Microbiotic crusts and ecosystem processes. *Crit. Rev. Plant Sci.* **18**, 183–225.

Field, C. B., and Mooney, H. A. (1986). The photosynthesis–nitrogen relationship in wild plants. *In* "On the Economy of Plant Form and Function" (T. J. Givnish, ed.). Cambridge Univ. Press, Cambridge.

Field, C. B., Lund, C. P., Chiariello, N. R., and Mortimer, B. E. (1997). CO_2 effects on the water budget of grassland microcosm communities. *Global Change Biol.* **3**, 197–206.

Gee, G. W., Wierenga, P. J., Andraski, B. J., Young, M. H., Fayer, M. J., and Rockhold, M. L. (1994). Variations in water balance and recharge potential at three western desert sites. *Soil Sci. Soc. Am. J.* **58**, 63–72.

Gibbens, R. P., Hicks, R. A., and Dugas, W. A. (1996). Structure and function of C_3 and C_4 Chihuahuan Desert plant communities. Standing crop and leaf area index. *J. Arid Environ.* **34**, 47–62.

Goodall, D. W., and Perry, R. A., eds. (1979). "Arid-land Ecosystems," Vol. 1. Cambridge Univ. Press, Cambridge.

Grover, H. D., and Musick, H. B. (1990). Shrubland encroachment in southern New Mexico, U.S.A.: An analysis of desertification processes in the American Southwest. *Clim. Change* **17**, 305–330.

Hadley, N. F., and Szarek, S. R. (1981). Productivity of desert ecosystems. *BioScience* **31**, 747–753.

Ham, J. M., Owensby, C. E., Coyne, P. I., and Bremer, D. J. (1995). Fluxes of CO_2 and water va-

por from a prairie ecosystem exposed to ambient and elevate atmospheric CO_2. *Agric. For. Meteorol.* **77**, 73–93.

Kassas, M. (1995). Desertification: A general review. *J. Arid Environ.* **30**, 115–128.

Knapp, A. K., Hamerlynk, E. P., Ham, J. M., and Owensby, C. E. (1996). Responses in stomatal conductance to elevated CO_2 in 12 grassland species that differ in growth form. *Vegetatio* **125**, 31–41.

Le Houérou, H. N. (1984). Rain use efficiency: A unifying concept in arid-land ecology. *J. Arid Environ.* **7**, 213–247.

Le Houérou, H. N. (1990). Global change: Vegetation, ecosystems, and land use in the southern Mediterranean Basin by the mid twenty-first century. *Israel. J. Bot.* **39**, 481–508.

Le Houérou, H. N. (1996). Climate change, drought and desertification. *J. Arid Environ.* **34**, 133–185.

Le Houérou, H. N., Bingham, R. L., and Skerbek, W. (1988). Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. *J. Arid Environ.* **15**, 1–18.

Lin, G., Phillips, S. L., and Ehleringer, J. R. (1996). Monsoonal precipitation responses of shrubs in a cold desert community on the Colorado Plateau. *Oecologia* **106**, 8–17.

Logan, R. F. (1968). Causes, climates and distributions of deserts. *In* "Desert Biology" (G. W. Brown, ed.), Vol. 1, pp. 21–50.

McGinnies, W. G., Goldman, B. J., and Paylore, P. (1977). "Deserts of the World." University of Arizona Press, Tucson.

Mooney, H. A., Drake, B. G., Luxmoore, R. J., Oechel, W. C., and Pitelka, L. F. (1991). Predicting ecosystem response to elevated CO_2 concentration. *BioScience* **41**, 96–104.

National Academy of Sciences. (1975). "Productivity of World's Ecosystems." National Academy of Sciences, Washington, D.C.

Neilson, R. P. (1995). A model for predicting continental-scale vegetation distribution and water balance. *Ecol. Appl.* **5**, 362–385.

Nichols, M. H., Lane, L. J., and Gibbons, R. (1996). Time series analysis of data for raingauge networks in the Southwest. *In* "Proceedings: Shrubland Ecosystem dynamics in a Changing Environment," pp. 43–47. USDA, Ogden.

Noble, I. R., and Gitay, H. (1996). Deserts in a changing climate: Impacts. *In* "Climate Change 1995. Impacts, Adaptations and Mitigation of Climate Change: Scientific-Technical Analyses" (R. T. Watson, M. C. Zinyowera, R. H. Moss, and D. J. Dokken, eds.), pp. 159–169. Cambridge Univ. Press, New York.

Noy-Meir, I. (1985). Desert ecosystem structure and function. *In* "Ecosystems of the World" (M. Evenari, I. Noy-Meir, and D. W. Goodall, eds.), pp. 92–103. Elsevier, Amsterdam.

Peters, A. J., Reed, B. C., Eve, M. D., and Havstad, K. M. (1993). Satellite assessment of drought impact on native communities of southeastern New Mexico, U.S.A. *J. Arid Environ.* **24**, 305–319.

Pickup, G. (1996). Estimating the effects of land degradation and rainfall variation on productivity in rangelands: An approach using remote sensing and models of grazing and herbage dynamics. *J. Appl. Ecol.* **33**, 819–832.

Prince, S. D., and Goward, S. N. (1995). Global primary production: a remote sensing approach. *J. Biogeogr.* **22**, 815–835.

Prince, S. D., De Colstoun, E. B., and Kravitz, L. L. (1998). Evidence from rain-use efficiencies does not indicate extensive Sahelian desertification. *Global Change Biol.* **4**, 359–374.

Reynolds, J. F., and Cunningham, G. L. (1981). Validation of a primary production model of the desert shrub *Larrea tridentata* using soil-moisture augmentation experiments. *Oecologia* **51**, 357–363.

Rundel, P. W., and Gibson, A. C. (1996). "Ecological Communities and Processes in a Mojave Desert Ecosystem: Rock Valley, Nevada." Cambridge Univ. Press, New York.

Sala, O. E., Parton, W. J., Joyce, L. A., and Lauenroth, W. K. (1988). Primary production of the central grassland region of the United States. *Ecology* **69,** 40–45.

Schlesinger, W. H. (1997). "Biogeochemistry—An Analysis of Global Change." Academic Press, San Diego.

Schlesinger, W. H., Reynolds, J. F., Cunningham, G. F., Huenneke, L. F., Jarrell, W. F., Virginia, R. A., and Whitford, W. G. (1990). Biological concepts in global desertification. *Science* **247,** 1043–1048.

Schulze, E.-D., Mooney, H. A., Sala, O. E., Jobbagy, E., Buchmann, N., Bauer, G., Canadell, J., Jackson, R. B., Loreti, J., Osterheld, M., and Ehleringer, J. R. (1996). Rooting depth, water availability, and vegetation cover along an aridity gradient in Patagonia. *Oecologia* **108,** 503–511.

Skiles, J. W., and Hanson, J. D. (1994). Responses of arid and semiarid watersheds to increasing carbon dioxide and climate change as shown by simulation studies. *Clim. Change* **26,** 377–397.

Smith, S. D., Monson, R. K., and Anderson, J. E. (1997). "Physiological Ecology of North American Desert Plants." Springer-Verlag, Heidelberg.

Szarek, S. R. (1979). Primary production in four North American deserts: indices of efficiency. *J. Arid Environ.* **2,** 187–209.

Thorburn, P. J., and Ehleringer, J. R. (1995). Root water uptake of field-growing plants indicated by measurements of natural-abundance deuterium. *Plant Soil* **177,** 225–233.

Tucker, C. J., Dregne, H. E., and Newcomb, W. W. (1991). Expansion and contraction of the Sahara desert. *Science* **253,** 299–301.

Turner, F. B., and Randall, D. C. (1989). Net production by shrubs and winter annuals in southern Nevada. *J. Arid Environ.* **17,** 23–36.

Varnamkhasti, A. S., Milchunas, D. G., Lauenroth, W. K., and Goetz, H. (1995). Production and rain use efficiency in short-grass steppe: Grazing history, defoliation and water resource. *J. Veg. Sci.* **6,** 787–796.

VEMAP (1995). Vegetation/ecosystem modeling and analysis project: Comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO_2 doubling. *Global Biogeochem. Cycles* **9,** 407–437.

Walter, H. (1939). Grasland, Savanne und Busch der ariden Teile Afrikas in ihrer îkologischen Bedingtheit. *Wissen Bot.* **87,** 750–860.

Walter, H., and Breckle, S. W. (1984). "Ecological Systems of the Geobiosphere." Vol. 2. Springer-Verlag, Heidelberg.

Whittaker, R. H., and Niering, W. A. (1975). Vegetation of the Santa Catalina Mountains, Arizona. V. Biomass, production, and diversity along the elevation gradient. *Ecology* **56,** 771–790.