

10 Dryland Ecosystems

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10.1 Introduction

Drylands occupy approximately 40% of the Earth's land surface and have low inputs of mean annual precipitation (P) relative to mean annual potential evapotranspirational (ET) losses (Millennium Ecosystem Assessment 2005). The United Nations Educational, Scientific and Cultural Organization (UNESCO 1979) proposed the following classification scheme for drylands: hyper-arid zone ($P/ET < 0.03$), arid zone ($P/ET 0.03-0.20$), semi-arid zone ($P/ET 0.20-0.05$) and subhumid zone ($P/ET 0.50-0.75$). The majority of studies summarised in this chapter were conducted in arid and semi-arid zones with mean annual precipitation ≤ 300 mm.

The low precipitation and high temperature regimes characteristic of dryland regions result in low annual rates of organic matter decomposition, nutrient cycling and primary productivity (Noy-Meir 1973). While biogeochemical fluxes are small in drylands over the course of a year, relative to temperate or tropical ecosystems, "hot spots" or "hot moments" of biological activity occur, initiating pulses of nutrient flow. These patches or events of biological activity are driven by rainfall and linked to movement of water across the landscape (Belnap et al. 2005). The high degree of spatial and temporal variability in rainfall and associated biological activity that drive nutrient cycling in dryland ecosystems complicate efforts to compile annual nutrient budgets for these ecosystems. Never-

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theless, nutrient budgets are useful tools to identify gaps in current knowledge of dryland biogeochemical cycles.

10.2 Nitrogen Cycle

10.2.1 Nitrogen Inputs from Biological Fixation

Nitrogen (N) as it occurs in the atmosphere cannot be used by vascular plants or other eukaryotic organisms as a nutrient source. Gaseous dinitrogen (N_2) must be reduced or “fixed” to ammonia (NH_3) by either lightning or prokaryotic organisms (e.g. eubacteria and cyanobacteria). These organisms can be found free-living in soils as autotrophs or heterotrophs, lichenised by fungi, or as symbionts with some species of vascular plant (see also Chapter 2 by McNeill and Uncovich, this volume).

Nitrogen fixation rates in dryland ecosystems have long been assumed to be low due to high temperatures and low soil moisture, providing less than optimal conditions for N fixation to occur. This assumption has been supported by using a mass balance approach to identify levels of ecosystem N inputs; biogeochemical model results suggest that soil N levels may be fully accounted for by atmospheric N deposition alone, resulting in little or no inputs via fixation in dryland ecosystems (see CENTURY results in Cleveland et al. 1999). In contrast, field measurements of N fixation can be quite high when conditions are optimal. The length of time over which optimal conditions occur within a year, however, is limited, resulting in low N_2 fixation annually. This will be a recurring theme throughout this chapter. In this section, we review the knowledge of N_2 -fixing organisms and rates in dryland ecosystems and outline the major uncertainties in estimating N_2 fixation in these ecosystems.

Many species of cyanobacteria found in drylands fix N_2 (e.g. *Nostoc*, *Scytonema* and *Schizothrix*). These species can be free-living within the soil, as epiphytes on the surface of lichens, mosses and vascular plants (Belnap 2003), or as part of soil lichens. Much of the research on N_2 fixation in dryland ecosystems has focused on cyanobacteria present in biological soil crusts (Tables 10.1, 10.2, 10.3). Heterotrophic bacteria can also fix N_2 in bulk soil and in the root zone of plants (Table 10.4). The most well-known genera, *Azotobacter*, *Clostridium*, *Azospirillum*, *Streptomyces* and *Spirilla* occur worldwide (West 1991); however, most reported values of N_2 fixation by heterotrophic bacteria are extremely low. Heterotrophic soil bacteria can also live inside the cyanobacteria sheath. In these cases, the heterotrophs often scavenge oxygen, thereby creating anaerobic microzones and thus facilitating N_2 fixation in the cyanobacteria. The hetero-

Table 10.1 Nitrogen fixation estimates for biological soil crusts in United States drylands

Location	Crust type	Converted rates (nmol cm ⁻² h ⁻¹)	Laboratory/ field	Incubation conditions	Reference
Chihuahuan Desert	Cyanobacteria-lichen	0.001	Laboratory	12 h, 25°C	Hartley and Schlesinger 2002
	<i>Microcoleus, Nostoc, Scytonema</i>	0.5–1.5	Laboratory	1 h, 24°C	Yeager et al. 2004
Colorado Plateau	<i>Microcoleus, Nostoc, Scytonema, Collema</i>	0.002–0.98	Laboratory	4 h, 26°C	Belnap 1996, 1999, 2002; Evans and Belnap 1999; Belnap et al. 2004
	<i>Microcoleus, Nostoc-Scytonema</i>	0.3–1.0 0.2, 2.0 0.7, 4.8	Field Laboratory Laboratory	1 h, 32°C 1 h, 24°C No data	Barger 2003 Yeager et al. 2004 Johnson et al. 2005
Great Basin Desert	<i>Microcoleus, Nostoc, Scytonema, Collema</i>	11–12 0.3–5.4 11–21	Laboratory Laboratory Laboratory	96–144 h, 23°C 24 h, 21°C 23°C	Jeffries et al. 1992 Terry and Burns 1987 Skujins and Klubek 1978
	Cyanobacteria-lichen	22–27; 141–178	Field; laboratory	18–20°C; 12 h, 26°C	Rychert and Skujins 1974
Mojave Desert	Cyanobacteria-lichen	1.2–3.3	Laboratory	24 h, 30°C	Billings et al. 2003
Sonoran Desert	Cyanobacteria-lichen	6.4, 11	Laboratory	48 h, 5–30°C	Eskew and Ting 1978
	Cyanobacteria Cyanobacteria	12, 18 78	Laboratory Laboratory	520 days 38°C	Mayland et al. 1966 ^a MacGregor and Johnson 1971

^aMayland et al. 1966 used ¹⁵N to estimate nitrogen fixation; all other studies used the acetylene reduction assay (ARA)

Table 10.2 Nitrogen fixation estimates for biological soil crusts in drylands in Africa and the Middle East ^a

Location	Crust type	Converted rates (nmol cm ⁻² h ⁻¹)	Laboratory/ field	Incubation time/ temperature	Reference
Kalahari Desert, Botswana	Light cyanobacteria	60	Laboratory	9–22 days at 27.5°C	Skarpe and Henriksson 1987
	<i>Nostoc-Scytonema</i>	680			
Maasai Mara, Kenya, 45 sites	Cyanobacteria	0.1–12	Laboratory	4 h at 26°C	J. Belnap, unpublished data
Sahel Desert, Niger	Cyanobacteria	3.5–4.2	Laboratory	2–163 h at 30°C	Issa et al. 2001

^a All Studies used ARA**Table 10.3** Nitrogen fixation estimates for free-living *Nostoc commune* sheets in dryland ecosystems ^a

Location	Crust type	Converted rates (nmol cm ⁻² h ⁻¹)	Laboratory/ field	Incubation time/ Temperature	Reference
Chihuahuan Desert, USA	<i>N. commune</i> sheets	8.2	Laboratory	4 h at 26 °C	Barger 2003
Chihuahuan Desert, USA	<i>N. commune</i> sheets	44.6	Laboratory	4 h at 26 °C	J. Belnap, unpublished data
Inner Mongolia, China	<i>N. commune</i> sheets	2.8	In situ field	4 h at 26 °C	J. Belnap, unpublished data
Vestfold Hills, Antarctica	<i>N. commune</i> sheets	0–5.0	Field	2 h at –20 to 10 °C, throughout summer	Davey and Marchant 1983

^a All Studies used ARA

Table 10.4 Heterotrophic nitrogen fixation estimates for dryland ecosystems ^a

Location	Vegetation	Converted rates	Laboratory/ field	Incuba- tion time/ Temperature	Reference
Mojave desert, USA	<i>Larrea tridentata</i> , <i>Lycium</i> spp., <i>Pleuraphis rigida</i>	0.3–1.9 nmol cm ⁻² h ⁻¹	Laboratory, glucose added	24 h at 30°C	Billings et al. 2003
Great Basin Desert, USA	<i>Artemisia</i>	27.6 ng N (g soil) ⁻¹ h ⁻¹	Laboratory	21 days at 22°C, in the dark	Klubek and Skujins 1980
	<i>Ceratoides</i>	21.4 ng N (g soil) ⁻¹ h ⁻¹			
	<i>Atriplex</i>	34.7 ng N (g soil) ⁻¹ h ⁻¹			
Egypt	Non- or low saline soils	17–19 mg N (100 ml) ⁻¹	Laboratory	7 days at 30°C	Mahmoud et al. 1978
	Saline alkaline soils Moderate-strongly saline	13 mg N (100 ml) ⁻¹			

^a All Studies used ARA

trophs also fix N_2 themselves. Such a relationship has been demonstrated for the cyanobacteria *Microcoleus vaginatus* (Steppe et al. 1996).

Many dryland plants have root nodules containing N_2 -fixing bacteria or actinomycetes. The bacteria found in leguminous plants are either *Rhizobium* or *Bradyrhizobium* spp. (Farnsworth et al. 1976; Whitford 2002). In arid and semi-arid ecosystems, the main N_2 -fixing plant species include the shrubs *Acacia*, *Prosopis*, *Pterocarpus* and *Pericopsis* and the herbaceous *Lupinus*, *Dalea*, *Astragalus* and *Lotus*. Many non-leguminous dryland plants also have nodules. These nodules are most often occupied by the actinomycete *Frankia*. These plant families include, but are not limited to Asteraceae, Scrophulariaceae, Zygophyllaceae, Poaceae, Cactaceae, Krameriaceae, Casuarinaceae, Rosaceae and Rhamnaceae (Farnsworth et al. 1976; Redell et al. 1991).

Estimates of biological soil crust and heterotrophic N_2 fixation measured by the acetylene reduction assay (ARA) are highly variable, ranging from 0 to $680 \text{ nmol C}_2\text{H}_4 \text{ cm}^{-2} \text{ h}^{-1}$ (Tables 10.1, 10.2). Although these rates differ by several orders of magnitude, approximately 85% of the reported acetylene reduction rates were $<20 \text{ nmol cm}^{-2} \text{ h}^{-1}$. There are few reported values for symbiotic N fixers in unamended non-agricultural dryland soils due to the difficulty in measuring in situ N fixation rates. However, N inputs by symbiotic N fixers may be quite high. Rundel et al. (1982) estimated that *Prosopis* woodlands in the Sonoran Desert fixed N_2 at rates of $25\text{--}30 \text{ kg ha}^{-1} \text{ year}^{-1}$. There are several factors that may contribute to the large range of N_2 fixation rates reported in the literature. In this next section, we review key factors that influence measurements of N_2 fixation in dryland ecosystems and provide suggestions on how to standardise N_2 fixation methodology for future studies.

10.2.1.1

Methodological Considerations

A basic understanding of N_2 fixation methodology is essential to the interpretation of this body of work. Researchers estimate N_2 fixation by measuring the incorporation of $^{15}N_2$ into the soil directly, or by measuring nitrogenase activity using the acetylene (C_2H_2) reduction assay (ARA). In the latter case, ARA rates must then be converted back to an estimate of the amount of N_2 fixed. Although most studies report nitrogenase activity, and not actual N_2 fixation, we use these terms interchangeably throughout this chapter. Most studies use the theoretical ratio of 3:1 to convert from ethylene (C_2H_4) produced to N_2 fixed (six electrons are required for N_2 reduction, but only two electrons for the reduction of C_2H_2). However, there are many conditions that alter this theoretical ratio. Values from 3 to 4 appear to hold for lichens and N_2 -fixing plants; however, values for free-living soil cyanobacteria range from 0.1 to 6.1 and can change seasonally (reviewed in Belnap 2001a, 2001b). There is no information on conversion ratios for heterotrophic N_2 fixation. Since conversion ratios may be flexible, ARA must be calibrated with $^{15}N_2$ for each site and organism of interest if ARA is to be used effectively as an estimate of N_2 fixation.

10.2.1.2

Environmental Controls on Cyanobacterial N₂ Fixation

Environmental conditions experienced by the organisms before and during the measurements, although often not reported and seldom standardised, strongly influence N₂ fixation rates. In addition, nitrogenase activity is not linear through time, resulting in N₂ fixation rates that may vary depending on incubation time. Here, we review the environmental controls of cyanobacterial N₂ fixation.

Cyanobacteria and bacteria are physiologically active only when water is available; consequently, N₂ fixation is controlled primarily by moisture (Kershaw 1985; Nash 1996). Liquid water is required for carbon (C) fixation in cyanobacteria (Lange 2003) and, because N₂ fixation requires the products of photosynthesis, availability of water also ultimately determines the amount of N₂ fixed. Most dryland soil cyanolichens require a water content of at least 80% dry weight for initiation of net C fixation activity (Lange et al. 1998). Moisture needed to initiate and optimise N₂ fixation varies widely among species, ranging from 6% of dry weight to total saturation (reviewed in Belnap 2003). Nitrogenase activity in *Microcoleus-Collema* soil communities, common in dryland ecosystems, drops rapidly at soil water potentials below -0.33 kPa, with a 50% reduction by -100 kPa (Rychert et al. 1978).

Time from initial wetting to the initiation of C and N₂ fixation is critical in drylands, as high temperatures can cause soils to dry so rapidly that organisms may be unable to accumulate the C needed to support N₂ fixation activities. Upon rewetting, nitrogenase activity generally does not begin for 10–60 min, depending on the species and past and current environmental conditions. Time to maximal fixation ranges from 1 to 36 h (reviewed in Belnap 2003). Time since the last wetting event can also influence time to nitrogenase activity initiation (Dodds et al. 1995; Kershaw and Dzikowski 1977). The lag time between wetting and nitrogenase activity probably reflects the amount of C, nitrogenase enzymes, and ATP in the cell.

Nitrogen fixation rates are also limited by temperature extremes. Most nitrogenase activity occurs at -5 °C to 30 °C, with the optimum at 20 – 28 °C for most drylands (e.g. Lange et al. 1997, 1998). Minimum air temperatures for nitrogenase activity have been recorded at -7.6 °C (Horne 1972), although some species show no activity at 0 °C (Isichei 1980). Freezing can damage nitrogenase and thus substantially reduce nitrogenase activity (Scherer et al. 1984). Low temperatures can reduce photosynthetic rates and thus reduce available ATP and reductant pools, creating a lag time after freezing before N₂ fixation is initiated (Kershaw 1985). Once above the minimum temperature for a species, N₂ fixation rates show a strong, positive response to increasing air temperature until an upper limit is reached, after which rates quickly decline.

Light optima vary among species and places, depending on the distribution and concentrations of photosynthetic and UV-screening pigments, soil characteristics, and the distribution of cyanobacteria within the substrate, colony, or thallus (e.g. Dodds et al. 1995; Garcia-Pichel and Belnap 1996). Light levels required for maximum nitrogenase activity in cyanobacteria are generally low

(100–150 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetically active photon flux density; Garcia-Pichel and Belnap 1996). Below this level, nitrogenase activity is greatly reduced, presumably due to a lack of photosynthetic products to support N_2 fixation (Kershaw 1985). Although depression of N_2 fixation at high light levels has been reported (e.g. Rychert et al. 1978), high temperatures and low moisture content could also explain these results.

Soil properties such as pH, salinity and nutrient content in drylands vary with topographic position or management practices. Dryland soils in low lying areas tend to be more alkaline and saline compared to up-slope soils (James et al. 2004). Intensive irrigation and fertilisation in agricultural dryland soils increase salt and nutrient contents. All of these factors influence N_2 fixation rates. Growth and nitrogenase activity in soil cyanobacteria are greatest above pH 7 (Brock 1973), although some depression of nitrogenase activity has been seen at pH 8–10 (Granhall 1970). Depression of nitrogenase activity at high pH may be due to lower P availability in Ca-rich soils (Lajtha and Schlesinger 1988b; see Sect. 10.3.2), whereas depression of nitrogenase activity at low pH is likely due to reduced photosynthetic capacity (Shapiro 1973) or reduced concentration of nitrogenase enzymes (Stewart et al. 1977).

Salinity effects on nitrogenase activity in dryland soils are not studied frequently and show mixed results. In Utah, N_2 -fixing cyanobacteria preferred soils with high electrical conductivity (70 dS m^{-1} ; Anderson et al. 1982). In contrast, experimental addition of NaCl to cyanobacterial lichen crusts in the Chihuahuan desert inhibited nitrogenase activity (Delwiche and Wijler 1956).

Nutrient effects on nitrogenase activity vary in dryland ecosystems depending on the element. Elevated soil ammonium (NH_4^+) depresses nitrogenase activity, whereas mixed results have been obtained with elevated nitrate (NO_3^-). NH_4NO_3 amendments inhibited nitrogenase activity in cyanobacterial lichen crusts in the Chihuahuan desert (Hartley et al. 2002). Phosphorus and potassium additions can stimulate cyanobacterial nitrogenase activity, perhaps through a stimulation of ATP synthesis (e.g. Dodds et al. 1995). Low amounts of zinc (Zn), cobalt (Co), molybdenum (Mo) and iron (Fe) can stimulate cyanobacterial nitrogenase activity, whereas high levels of the same have adverse effects (e.g. Granhall 1981; Dodds et al. 1995). Field studies did not demonstrate a positive effect of P or micronutrients (Mo, Fe or Co) on Chihuahuan Desert cyanobacterial crusts (Hartley et al. 2002). The absence of enhancement by P or Mo may occur because these elements bind to Ca in CaCO_3 -rich soils, making them unavailable to microbes or plants (Kabata-Pendias and Pendias 1992).

10.2.1.3

Environmental Controls on Heterotrophic N_2 Fixation

Heterotrophic N_2 fixation in dryland ecosystems is influenced by soil temperature, moisture, pH and carbon (Rychert et al. 1978; West and Skujins 1978); however, very few studies have been done on these influences. Experiments show

that heterotrophic nitrogenase activity increases with glucose additions, suggesting that carbon sources are essential (Billings et al. 2003; Rychert et al. 1978). Klubek and Skujins (1980) reported a 15–60% increase in nitrogenase activity in Great Basin desert soils supplemented with 2% glucose. Glucose additions boosted nitrogenase activity in Chihuahuan desert soil crusts, presumably due to heterotrophic activity (Hartley et al. 2002). Because heterotrophic N_2 fixers rely on external C sources, it is expected that most heterotrophic fixation takes place close to or within surface autotrophic organisms and in rhizosphere of vascular plants (Rychert et al. 1978; West and Skujins 1978). Binet (1981), Mahmoud et al. (1978), and Stewart (1966) report that optimal heterotrophic N_2 fixation requires a soil temperature of 28 °C, soil moisture >10%, a pH of 6.5–9.5, low salinity (<0.8 g NaCl kg⁻¹ for non-salt-tolerant isolates, <1 g kg⁻¹ for salt-tolerant isolates), and low soil N. Suppression of N_2 fixation by plant leachates (exudates) was observed by Rychert et al. (1978), and this may be due to suppression of both heterotrophic and autotrophic fixers. Plant root exudates have also been shown to reduce growth of *Azotobacter* and *Rhizobium* (Rice 1964).

10.2.1.4

Environmental Controls on Higher Plant N_2 Fixation

There is limited information on the environmental controls of symbiotic N_2 fixation in drylands. Binet (1978) reports that *Rhizobium* nodule formation on *Zygophyllum* is favoured by low soil moisture and high soil temperatures, but no specific values were given. Nodule formation is limited when soil pH and N levels are high (Pepper and Upchurch 1991; Zahran 1999). Stress from high salt (EC >7.5 dS m⁻¹), high temperature (>40 °C), high pH (>9), or high water deficit reduces nitrogenase activity (Pepper and Upchurch 1991). Species that commonly nodulate in other environments do not always do so under dryland conditions (Virginia et al. 1992; West and Skujins 1978); even with nodules, nitrogenase activity rates are low, as soils underneath leguminous shrubs often are not higher in nitrogen than soils underneath non-leguminous shrubs (Garcia-Moya and McKell 1970; West 1991). It appears that only *Prosopis glandulosa*, and then only when its roots can reach permanent water, fixes appreciable amounts of N in dryland ecosystems (Pepper and Upchurch 1991; West 1991). In addition, legumes are rare or even absent in most dryland areas (West and Skujins 1978), being generally concentrated in a few specific habitats.

Similarly to the rhizobia, the nodulation, growth, and N_2 fixation of *Frankia* are reduced by high soil N, high temperatures (>30 °C), high water stress (–0.5 to –0.8 MPa), high salt (>100 mM), pH (>7), and low levels of soil nutrients other than N (e.g. Fe, Mn, Cu and Zn) (Redell et al. 1991). However, there are few studies on a small number of species, and thus it is difficult to assess the importance of *Frankia* associations in drylands.

Overall, any study of N_2 fixation at the very minimum should closely document the environmental conditions (i.e. moisture, temperature, light, soil char-

acteristics) at which the measurements were taken. If N_2 fixation rates are to be scaled to an annual estimate, measurements must be collected across a range of moisture and temperature regimes in order to allow more accurate estimation of the actual input.

10.2.1.5

Species Considerations

Rates of N_2 fixation vary widely among species of free-living cyanobacteria and cyanolichens; for example, *Microcoleus vaginatus* has lower nitrogenase activity rates than *Nostoc-Scytonema* combinations, and free-living *Nostoc* has lower rates than lichenised *Nostoc* (in *Collema*; Table 10.1). As few studies report the proportion of the different cyanobacterial species present or the biomass/cover of cyanobacteria or lichens in the test material; it is therefore impossible to directly compare reported rates.

10.2.2

Nitrogen Losses

10.2.2.1

Nitrogen Gas Losses

During the last two decades, advances in measuring trace N gases such as nitric oxide (NO) nitrous oxide (N_2O) and dinitrogen (N_2) from soils have resulted in an ever-widening body of literature on N gas loss from a range of ecosystems. Few of these studies have been conducted in dryland ecosystems (Davidson and Kinglerlee 1997). Due to the importance of these gases in atmospheric chemistry, most research in trace N gas production has focused on identifying the major terrestrial sources of NO and N_2O (Davidson and Kinglerlee 1997). An understanding of pathways of N loss in drylands may be critical to identifying the processes that underlie losses of soil fertility associated with desertification.

Because very little research effort has focused on trace N gas production from dryland soils, it begs the question, based on what we know of controls of nitrification and denitrification processes, whether dryland soils could be a major source of trace N gases. In a review of NO losses from a range of ecosystems, tropical dry forest ecosystems were a major source of NO globally (Davidson and Kinglerlee 1997), which suggests that trace N gas losses from aridland ecosystems may also be significant.

NO, N_2O and N_2 are produced in soil via microbially mediated pathways in nitrification and denitrification (see also Chapter 2 by McNeill and Uncovich, this volume). In nitrification, both NO and N_2O production may occur in the

oxidation of NH_4 to NO_3^- along a two step pathway (NH_4^+ to NO_2^- , NO_2^- to NO_3^-). Primary controls of nitrification rates are availability of NH_4^+ and O_2 partial pressure, soil pH, soil moisture, and soil temperature (Firestone and Davidson 1989; Paul and Clark 1996).

NH_4^+ availability in dryland soils is low relative to other ecosystems. Along a precipitation gradient in South America, Austin and Sala (2002) showed that NH_4^+ availability was more than 100-fold higher in a *Northofagus* forest soils as compared to desert scrub soils. Although soil NH_4^+ concentrations are low, environmental factors such as temperature and moisture may favour nitrification of the available NH_4^+ pool.

Optimum temperatures for denitrification range between 30 and 35 °C, temperatures common in dryland soils during the warmer months. Saturated soil conditions limit diffusion of O_2 into soils, which is essential for nitrifiers, therefore the generally low moisture content in dryland soils should favour nitrification. Ammonium: NO_3^- ratios in dryland soils are often <1 (Barger et al. 2006; Hartley and Schlesinger 2000; Mummey et al. 1997), which suggests that available NH_4^+ is rapidly nitrified.

Denitrification is the biological process that occurs under reducing conditions where NO_3^- is used by denitrifying bacteria (primarily heterotrophic bacteria) in the absence of O_2 as an electron acceptor (see also Chapter 2 by McNeill and Uncovich, this volume). NO_3^- is converted to NO , N_2O and N_2 along a reduction pathway. Factors regulating denitrification rates are low O_2 partial pressure, available NO_3^- to serve as an oxidant, and organic C as an energy source for heterotrophic bacteria (Williams et al. 1992). Previously, it was thought that denitrification in dryland ecosystems would be low because anaerobic conditions should rarely occur in arid environments. However, the presence of anaerobic microsites within dryland soils is not as rare as previously believed. Garcia-Pichel and Belnap (1996) reported oxygen levels near zero in the surface 4 mm of a biological soil crust. A large portion of the microbial community resides in the top few millimetres of dryland soils; thus, a pulse in microbial activity after a rain event may quickly reduce soil oxygen levels.

Denitrification rates reported from several western United States drylands are highly variable ranging from 0.65 to 322 $\text{ng N}_2\text{O-N m}^{-2} \text{ s}^{-1}$, with an average of 55 $\text{ng N}_2\text{O-N m}^{-2} \text{ s}^{-1}$ (Table 10.5). The upper end of these short-term denitrification rates is comparable to those observed in forest and agricultural soils (Barton et al. 1999; Ullah et al. 2005). Much of the variability in published rates may be attributed to experimental design. Across studies, denitrification rates were positively correlated with the amount of water added, with the simulated rain event explaining 99% of the variability in denitrification rates (Fig. 10.1). The simulated rain event of 31 mm used by Schlesinger and Peterjohn (1991) is in the range of a 10-year precipitation event for these sites (<http://hdsc.nsw.noaa.gov/hdsc/pfds/>) and far higher than the typical summer rain event, which is generally less than 2 mm. As a result, soil moisture values that rarely occur in these soils were used to generate estimates of annual denitrification rates, which may have resulted in overestimation of denitrification from these soils.

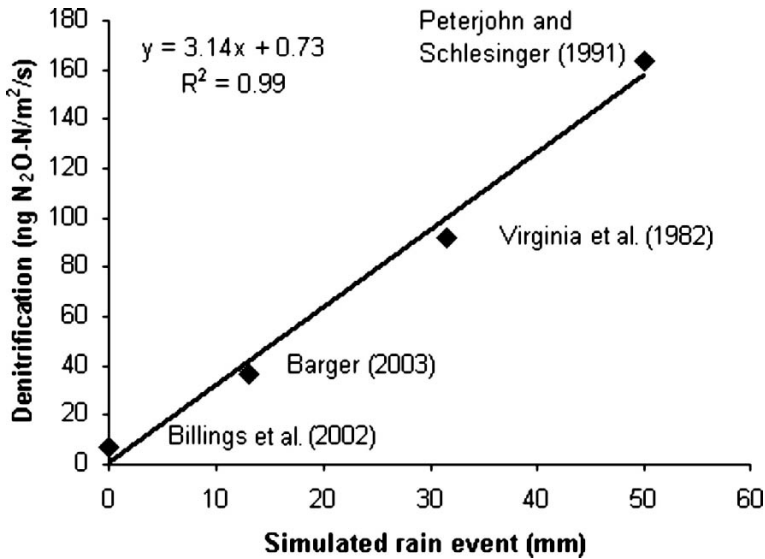


Fig. 10.1 Denitrification rates as a function of simulated rain event. The amount of water added in the simulated rain event explained 99% of the variability in denitrification across four desert sites

Table 10.5 Denitrification N losses from desert soils

Location	Vegetation	Rates (ng N m ⁻² s ⁻¹)	Rates (kg N ha ⁻¹ year ⁻¹)	Reference
Chihuahuan Desert, USA	<i>Bouteloua eriopoda</i> grassland, <i>Larrea</i> <i>tridentata</i> shrubland, playa grassland	92	7.2	Peterjohn and Schlesinger 1991
Colorado Plateau, USA	Biological soil crust	38	0.7	Barger 2003
Great Basin Desert, USA	Salt desert shrub	–	19	West and Skujins 1977
Mojave Desert, USA	Desert scrub	2	–	Billings et al. 2002
Sonoran Desert, USA	<i>Prosopis</i> Interspace	322 6	–	Virginia et al. 1982

The first effort to create an annual N gas loss budget for a desert ecosystem was conducted during the US/International Biological Program Desert Biome effort in the 1970s. These early estimates of annual N gas loss were high, i.e. 20 kg N ha^{-1} , of which $19 \text{ kg N ha}^{-1} \text{ year}^{-1}$ was attributed to denitrification (West and Skujins 1977), rates that are comparable to fertilised agricultural and forested ecosystems (Barton et al. 1999; Davidson and Kingerlee 1997). More recent experiments have shown that annual N gas loss from dryland soils is far lower than early estimates, which may be partially explained by differences in methodology. Denitrification rates from soils were estimated from a laboratory ^{15}N addition study of decaying biological soil crusts maintained at high moisture contents. Over a 10-week period 75% of the added ^{15}N was not recovered, which was then assumed to have been lost via denitrification. Estimates of annual N_2 fixation by biological soil crusts in this study were $25 \text{ kg N ha}^{-1} \text{ year}^{-1}$. Of the N fixed by biological soil crusts, 75% was assumed to be lost via denitrification based on the laboratory incubations, yielding an annual denitrification rate of $19 \text{ kg N ha}^{-1} \text{ year}^{-1}$ (West and Skujins 1977). However, the laboratory conditions under which the biological soil crusts were incubated optimised N_2 fixation rates in these soil crusts, most likely resulting in an overestimation of denitrification rates.

Three of the five studies listed in Table 10.5 scaled up short-term denitrification rates to an annual loss rate. Estimates of annual N loss rates via denitrification were highly variable, which may have been due to a number of factors. The study by Barger (2003) was conducted on biological soil crusts in plant interspaces. Plant interspaces tend to have lower denitrification rates relative to soils beneath plants (Billings et al. 2002; Virginia et al. 1982), resulting in lower annual N loss estimates. Annual N gas loss via denitrification from a Chihuahuan desert site was high, with estimates of denitrification at $7.2 \text{ kg N ha}^{-1} \text{ year}^{-1}$ (Schlesinger and Peterjohn 1991). In scaling to an annual denitrification loss rate in this study, the assumption was made that soils were wet for 3 months or approximately 90 days per year. However, soil moisture data collected over a 3-year period near Canyonlands National Park on the Colorado Plateau showed that soils only maintain adequate soil moisture for microbial activity ($>1\%$ volumetric water content) for approximately 10 days during the summer monsoon (J. Belnap, unpublished data). Although the largest proportion of annual precipitation falls during the summer in the Chihuahuan Desert, one would not expect the number of hours available for denitrification from soils to be 9-fold higher in the Chihuahuan desert compared to the Colorado Plateau. Thus, denitrification rates from the Peterjohn and Schlesinger (1991) study most likely overestimate annual losses.

Nitrous oxide fluxes from dryland soils ranged from -1.6 to $7.3 \text{ ng N}_2\text{O-N m}^{-2} \text{ s}^{-1}$, much lower than denitrification rates, which suggests that a large proportion of the N gas loss in denitrification is lost as N_2 and not N_2O (Table 10.6). In the study by Barger (2003), denitrification rates ($\text{N}_2\text{O} + \text{N}_2$) were 30-fold higher than N_2O losses alone, which further supports the idea that much of N gas being lost is in the form of N_2 . In the studies that estimated annual N_2O losses, rates ranged from 0.15 to $0.48 \text{ kg N}_2\text{O-N ha}^{-1} \text{ year}^{-1}$.

Table 10.6 Nitrous oxide emissions from desert soils

Location	Vegetation	Rates (ng N m ⁻² s ⁻¹)	Rates (kg N ha ⁻¹ year ⁻¹)	Water addition	Reference
Colorado Plateau, USA	Biological soil crusts	1.2	–	Yes	Barger 2003
Great Basin, USA	<i>Artemisia</i> shrub-steppe	7.0	0.15	Yes	Mummey et al. 1994
	<i>Artemisia</i> shrub-steppe	1.5	0.48	Yes	Mummey et al. 1997
Mojave Desert, USA	<i>Larrea-Ambrosia-Lycium</i> scrub	0.51	–	No	Billings et al. 2002
	<i>Larrea-Ambrosia-Lycium</i> scrub	0.001–13	–	Yes	Schaeffer et al. 2003
Sonoran Desert, USA	<i>Syderoxylon</i> spp., <i>Larrea tridentata</i> , <i>Parkinson aculeate</i> overstory	–1.6–7.3	0.40	No	Guilbault and Matthias 1998

Table 10.7 Nitric oxide emissions from desert soils

Location	Vegetation	NO-N (ng N m ⁻² s ⁻¹)	NO-N (kg N ha ⁻¹ year ⁻¹)	Water addition	Reference
Chihuahuan Desert, USA	Grassland	3.0	0.15–0.38	Yes	Hartley and Schlesinger 2000
	Shrubland	0.3			
	Creosote	3.4			
	Tarbush	1.7			
Colorado Pla- teau, USA	Biological soil crust	4.4	0.02–0.16	Yes	Barger et al. 2006

There have been few published studies of NO loss from dryland ecosystems. Of the two studies listed in Table 10.7, NO loss rates after a simulated rain event ranged from 0.3 to 4.4 ng NO-N m⁻² s⁻¹. When scaled to an annual loss rate, NO losses were similar to N₂O losses and in the range of 0.02 to 0.38 kg N ha⁻¹ year⁻¹. In the Barger et al. (2005) study, NO fluxes were measured only from biological soil crust communities in plant interspaces, which partially explains the lower rates compared to Hartley and Schlesinger (2000), where NO fluxes were measured in a variety of plant communities. Although NO losses may be due to both nitrification and denitrification processes, losses from arid soils are more often associated with nitrification (Hartley and Schlesinger 2000; Martin et al. 2003; Smart et al. 1999). In a study of NO fluxes in a creosotebush community in the Chihuahuan desert, net nitrification rate explained 89% of the variability in NO fluxes, and fluxes were controlled by soil moisture and NH₄⁺ availability (Hartley and Schlesinger 2000).

Ammonia (NH₃) volatilisation occurs with the deprotonisation of NH₄⁺ and subsequent formation of NH₃ gas (see also Chapter 2 by McNeill and Uncovich, this volume). Unlike N gas loss in denitrification and nitrification pathways, NH₃ volatilisation is not a microbially mediated N loss pathway, thus temperature and moisture have less impact on NH₃ volatilisation rates. Dryland soils, however, do provide optimal conditions for ammonia volatilisation, since rates are positively correlated with soil pH, CaCO₃ and total salt content, but negatively correlated with organic matter content, cation-exchange capacity (CEC) and clay content (Duan and Hongland 2000). The range of ammonia volatilisation rates from dryland soils are similar to N gas losses as NO and N₂O and range from 0.06 to 2.2 ng NH₃-N m⁻² s⁻¹ (Table 10.8).

Although NH₃ volatilisation rates from dryland soils were in the same range as NO and N₂O losses, there is reason to believe that these rates are strongly underestimated due to problems with current methods used to measure NH₃ volatilisation from soils. In all of the studies listed in Table 10.8, a static chamber method was used to measure the amount of NH₃ volatilised from soils. In this method, a soil sample is placed in a sealed container along with a vial of strong acid that captures the volatilised the NH₃. In contrast, the dynamic chamber actively pumps chamber gases through the acid trap. In a study that calibrated the dynamic chamber method against the static method, only 5% of the NH₃ volatilised was captured using the static method as compared to the dynamic method (Frank and Zhang 1997). As a result, studies based solely on the static chamber method may result in vastly underestimated NH₃ volatilisation rates.

10.2.2.2

Nitrogen Leaching Loss

Nitrogen leaching losses have long been thought to be an insignificant N loss pathway in dryland ecosystems (Peterjohn and Schlesinger 1990; West and

Skujins 1977) due to low mean annual precipitation, which limits water and associated element movement to deeper soil layers. Not surprisingly, most of the work on leaching of N compounds through the soil profile has been conducted in irrigated agricultural systems and regions such as tropical and temperate forests that receive plentiful rainfall. However, a recent study examining nitrate (NO_3^-) reservoirs across several deserts in the western United States showed that the vertical flux of NO_3^- in dryland soils may be higher than previously believed. Estimates of NO_3^- leaching from surface soils to sub-soils were in the range of 0.09 to 1.17 kg NO_3^- -N ha^{-1} year $^{-1}$ (Table 10.9, Walvoord et al. 2003). These rates were highly variable across different deserts, which may be attributed to differences in climate, vegetation type, land use history, and soil type (Walvoord et

Table 10.8 Ammonia loss from dryland soils

Location	Vegetation	Rates (ng NH_3 -N m^{-2} s^{-1})	Rates (kg NH_3 -N ha^{-1} year $^{-1}$)	Water addition	Reference
Chihuahuan Desert, USA	Grassland	0.64	–	Yes	Schlesinger and Peterjohn 1991
	Shrubland				
	Playa				
Colorado Plateau, USA	Biological soil crust	0.2	–	Yes	Evans and Johansen 1999
	Bare soil	0.06	–		
	Biological soil crust	2.2	–	Yes	
Great Basin, USA	<i>Artemisia</i> shrub-steppe	–	1.0	Yes	West and Skujins 1977
Mojave Desert, USA	Desert scrub	2.0	–	No	Schaeffer et al. 2003
	Desert scrub	1.3	–	No	
				No	Billings et al. 2002

Table 10.9 Nitrate leaching to subsoils (to 1 m depth) in three desert environments (Walvoord et al. 2003)

Site	NO_3^- flux (kg ha^{-1} year $^{-1}$)
Mojave Desert, USA	0.09–1.17
Chihuahuan Desert, USA	0.02
Sonoran Desert, USA	0.13–0.76

al. 2003). These estimates also do not include other forms of dissolved N such as organic N, which often make up a large fraction of the dissolved N flux (Hedin et al. 1995; Oyarzún 2004; Pregitzer 2004). As a result, N leaching losses to deeper soils in these regions may be largely underestimated.

10.2.2.3

Erosional Losses of Nitrogen

Nitrogen may be lost during water erosion as dissolved N in runoff and N bound to eroded sediments. Runoff amount is determined by soil infiltration capacity, which is affected by soil porosity and residence time of water on the soil surface. Sediment yield in water erosion is affected by energy of incoming rainfall or rainfall intensity.

Total dissolved N losses in rainfall simulation experiments ranged from 0.11 to 1.17 mg N m⁻² min⁻¹ (Table 10.10). Dissolved organic nitrogen (DON) made up a large proportion of the total N flux, ranging from 40% to 78%. Interestingly, the range in total dissolved N loss did not vary strongly across sites even though there were large differences in experimental conditions. Of these studies, only one reported sediment-bound N losses, which ranged from 0.06 to 0.63 g N m⁻² min⁻¹ from biological soil crusts (Barger et al. 2006). Sediment-bound N in this study was ≥98% of the total N flux (dissolved + sediment).

Estimating annual N losses in water erosion is difficult due to the low frequency of natural runoff events in dryland environments. In some sites several years may pass without generating a runoff event. As a result, there is very little data available on annual N loss from natural precipitation events for dryland ecosystems. Thus, the available data on N loss in water erosion were generated in rainfall simulation experiments. Where a number of factors, such as size of rainfall simulation plot and intensity and duration of the simulated rain events affect N loss calculations.

The spatial scale of the study will often determine whether a net loss or accumulation of N is observed. For example, in a study of N in runoff with a natural precipitation event at the watershed scale at a Sonoran desert site, Fisher and Grimm (1985) reported net N accumulation (N inputs in rainfall exceeded outputs in runoff) (Table 10.11). However, all small plot studies listed in Table 10.10 exhibited net N loss (N outputs exceed inputs). Wilcox et al. (2003) examined runoff and erosion dynamics at several spatial scales in a semi-arid woodland and showed that runoff decreased by 50-fold from the microplot (1–3 m²) to the hillslope (2,000 m²) scale. Patterns in erosion losses in that same study were similar to runoff dynamics. Sediment losses from the microplot scale ranged from 1,000 to 4,000 kg ha⁻¹, but decreased to <100 kg ha⁻¹ at the hillslope scale. Thus, small plot studies are more likely to represent nutrient redistribution within the watershed rather than a net loss of N from the watershed.

Rainfall intensity of a simulated rain event also impacts N loss in runoff and sediments. In rainfall simulation experiments conducted in a California grass-

Table 10.10 Dissolved N losses in water erosion from rainfall simulation experiments. DON Dissolved organic nitrogen

Site	Vegetation	NH ₄ ⁺ (mg m ⁻² min ⁻¹)	NO ₃ ⁻ (mg m ⁻² min ⁻¹)	Inorganic N (mg m ⁻² min ⁻¹)	DON (mg m ⁻² min ⁻¹)	Total dis- solved N (mg m ⁻² min ⁻¹)	Plot size (m ²)	Rainfall intensity/ duration	Reference
Colorado Plateau, USA	Dark crust	0.03	-0.002	0.014	0.15	0.19	0.5	228 mm h ⁻¹	Barger et al. 2006
	Light crust	-0.01	0.03	0.02	0.07	0.11		10 min	
Chihuahuan Desert, USA	Grassland	Not reported	Not reported	0.42	0.55	0.98	2.0	90 mm h ⁻¹	Schlesinger et al. 1999
	Shrubland			0.33	0.42	0.76			
	Intershrub			0.18	0.41	0.59		30 min	
Chihuahuan Desert, USA	Mesquite- nabkha	0.08	0.08	0.16	0.22	0.54	1.0	144 mm h ⁻¹	Parsons et al. 2003
	Interdune	0.06	0.24	0.30	0.87	1.17		15 min	

Table 10.11 Dissolved N losses in water erosion from natural precipitation events

Site	Vegetation	NH ₄ ⁺ (kg N ha ⁻¹ year ⁻¹)	NO ₃ ⁻ (kg N ha ⁻¹ year ⁻¹)	Inorganic N (kg N ha ⁻¹ year ⁻¹)	DON (kg N ha ⁻¹ year ⁻¹)	Plot size	Reference
Chihuahuan Desert, USA	Creosotebush	0.10	0.41	0.51	0.06	4 m ²	Schlesinger et al. 2000
	Grassland	0.08	0.05	0.13	0.03		
Sonoran Desert, USA	Lower Sonoran desert scrub	-0.02	-0.08	-0.10	-0.008	Watershed	Fisher and Grimm 1985

land, Fierer and Gabet (2002) showed that sediment N loss increased linearly with increasing rainfall intensity. The relationship between dissolved N in runoff and rainfall intensity was less clear in this study. Nitrate loss increased with increasing rainfall intensity, but no relationship existed between rainfall intensity and NH_4^+ and organic N loss. Of the three studies listed in Table 10.10, rainfall intensities range from 90 to 228 mm h^{-1} , but there was no clear relationship between dissolved N flux and rainfall intensity across the studies.

The duration of simulated rainfall also affects calculations of N loss in water erosion. In many rainfall simulation experiments, rainfall intensity must be high in order to generate runoff and to obtain a steady-state runoff rate. Using precipitation frequency estimates for the site, investigators are able to choose over what time period to calculate N losses. For example, in Schlesinger et al. (1999), N losses were calculated over a 30-min rainfall simulation at an hourly intensity of 90 mm. Over the 30-min period 45 mm was applied, which, according to precipitation frequency estimates, occurs every 50–100 years in this region (Precipitation Frequency Data Server, <http://hdsc.nws.noaa.gov/hdsc/pfds/>). If investigators were interested in N losses in a 5-year precipitation event, then calculations would be done over the first 10 min of the precipitation event. These, calculations over different time periods of a rainfall simulation may yield different information on N loss and how it relates to precipitation frequency data for a given site.

10.2.2.4

Aeolian Losses

Arid and semiarid systems typically have sparse and variable cover. Due to the size and connectivity of unvegetated gaps in these regions, abiotic transport processes are able to move nutrient-rich sediments. Short-distance transport of nutrients by wind and water is an important factor in the development of islands of fertility common in drylands, especially from bare interspaces to nearby sub-canopy areas (Okin et al. 2001b; Schlesinger et al. 1990). Long-range transport of sediments and their associated nutrients can lead to the overall loss of nutrients from the landscape (Leys and McTainsh 1994; Schlesinger et al. 1996; Schlesinger et al. 2000).

Aeolian transport can account for observed redistribution and losses of nutrients from the soil surface, as well as disrupt nutrient cycling in deserts in other ways. Aeolian transport is initiated when the wind shear velocity exceeds the threshold shear velocity. The threshold of particle transport in the absence of vegetation, the soil erodibility, can be impacted by several factors such as soil texture (Alfaro and Gomes 2001; Leys and McTainsh 1996), mineralogy (Gillette 1997) and moisture (Ravi and D'Odorico 2005). Above the threshold shear velocity, three aeolian transport processes observed by Bagnold (1941) govern the fundamental erosion and movement of mineral dust aerosols: suspension, saltation and creep.

Saltation is initiated when the lift provided by wind exceeds the forces of gravity and cohesion holding the particle to the surface (Cornelis and Gabriels 2003). The most efficient saltators, those with the lowest threshold shear velocity, have a diameter of about 70 μm , but most saltation sized particles are 50 to 500 μm (Raupach and Lu 2004). Due to their size, saltation-sized particles have low surface area. As a result, they likely have low concentration of adsorbed plant-available inorganic nutrients. Particles that are ejected from the surface are entrained by saltation bombardment. Larger particles move by creep when they are nudged by impacting saltators.

Saltating sediments carry the bulk of the kinetic energy and momentum flux in aeolian transport. As a result, saltation has an important effect on vegetation in areas undergoing wind erosion. The abrasion and damage of plant tissue within the saltation layer, usually less than 1 m above the surface, can be a critical control on plant productivity and longevity. Cleugh et al. (1998) have reviewed the mechanical impacts of sandblasting for crops. Okin et al. (2001a) observed that, even for endemic shrub species, sandblasting can destroy cambium, strip leaves, and bury plants. This physical damage likely results in diminished net primary productivity and high mortality of young plants while their soft tissue is within the saltation layer (Okin and Gillette 2001). Thus, though saltation particles are themselves poor in plant-available nutrients, they can disrupt nutrient cycling in drylands by reducing the growth and establishment rates of plants, thus reducing the amount of organic matter (C, N and P) added to the soil in litter.

Saltation also leads to the emission of suspended material, dust, by sandblasting the surface (Alfaro and Gomes 2001; Gillette et al. 1997). Saltating particles bombard the surface, imparting kinetic energy to small particles that cannot be ejected by aerodynamic forces alone (i.e. particles with diameter <50 μm). Small mineral particles ejected in this way have high surface area and therefore high cation- and anion-exchange capacities. Low-density particles composed of organic material from the decomposition of plant litter are also ejected from the surface by this mechanism. In addition to having high CEC, these organic particles are also long-term reservoirs of organic nutrients.

The loss of nutrient-rich mineral and organic particles by dust emission has important consequences for the fertility of arid regions (Leys and McTainsh 1994). Okin et al. (2001a, 2001b) have shown that aeolian transport can lead to a reduction of nearly two-thirds of plant-available N and P on the 10-year timescale. More recent results from field experiments have supported this estimate and shown that this effect, when coupled with the removal of grasses, may be an important mechanism in the conversion of grasslands to shrublands observed throughout the world's drylands (Li and Okin 2004; J. Li et al. manuscript submitted).

Because plants serve as a barrier for wind and aeolian sediment flow, vegetation canopies can serve as the loci of deposition in partially vegetated areas. Coarse-grained particles travel short distances and therefore are often moved from plant interspaces to adjacent regions underneath plant canopies. Fine-grained particles that are suspended in the wind can also be intercepted by plant

canopies and deposited within the plant canopy (Okin et al. 2006). Thus, transport and emission from interspaces likely leads to the depletion of soil nutrients in these areas, whereas deposition within canopies of wind-transported material likely contributes to the accumulation of nutrients here. This redistribution of nutrients is vital in the formation and maintenance of islands of fertility in dryland ecosystems.

10.2.3

Summary of N Budgets in Dryland Ecosystems

To date, efforts to close N budgets in dryland ecosystems have met with very little success, due primarily to the spatial and temporal variability in N pools and fluxes. Not surprisingly, in this review of N fluxes the results were highly variable across dryland sites and are strongly influenced by experimental conditions. Most experiments reviewed in this section were conducted in the laboratory under optimal conditions or in the field with water added to capture the short-term fluxes of N, which in many cases were comparable to rates observed in forested and agricultural ecosystems. Great care must be taken in scaling these results up to an annual flux. In drylands, there are very limited periods within a year when these optimal conditions occur, especially for the microbially mediated processes. For example, we know from studies on the Colorado Plateau that conditions for N gas loss are optimal during only 9–25 days each year (Barger et al. 2005). As a result, in future experiments of N cycling in drylands it is critical to couple N fluxes to measured data on soil moisture and temperature throughout the year in order to constrain an annual N budget. Problems also arise when processes do not occur on an annual basis. For example, runoff events are extremely episodic, and N loss in water erosion may only occur once every few years. Thus, rainfall simulation experiments must be coupled with data on rainfall intensity data to adequately estimate N losses in water erosion. Overall, this review suggests that dryland soils have a high potential to fix or lose N, and short-term rates can be extremely high but scaling these rates to estimate annual fluxes remains a challenge.

10.3

Phosphorus

Several studies report P as limiting to plants in drylands Schlesinger et al. (1990) in the Chihuahuan Desert. In a lab experiment, Lajtha and Schlesinger (1988b) observed that *Larrea tridentata* seedlings grown in the highest P treatment produced more biomass, had higher P concentrations in roots and whole seedlings, higher total uptake of N and P, and higher final root and shoot N and P contents

than plants grown in the lower P treatments. In the same study, *L. tridentata* seedlings grown in soils amended with CaCO₃ had higher root:shoot and tissue N:P ratios, and lower specific absorption rates of P than control plants without CaCO₃, which suggests that CaCO₃ reduces P availability.

10.3.1 Phosphorus Inputs

Weathering of primary minerals such as apatite is the major source of phosphorus in soils (see also Chapter 3 by Bünemann and Condron, this volume). Data on chemical weathering rates of P are sparse for terrestrial ecosystems, but published values from temperate ecosystems range from 0.01 to 1 kg P ha⁻¹ year⁻¹ (Newman 1995; no dryland estimates listed). Rock weathering rates are estimated using a mass balance approach on a catchment scale (Schlesinger 1997). This method has limited applications in dryland ecosystems; for example, inputs or losses of elements other than P by erosion or weathering can affect the estimate of the relative percentage of P in the remaining material (Lajtha and Schlesinger 1988a).

Phosphorus inputs from the atmosphere are assumed to be negligible; however, organic and inorganic P can be added as wet and dry deposition, i.e. deposited in rainfall or in particulate form. Methodological challenges associated with measurements of atmospheric P deposition are described in Newman (1995). In this review of terrestrial ecosystems, total inputs of P in wet or wet+dry deposition ranged from 0.07 to 1.2 kg ha⁻¹ year⁻¹; however, none of these studies were from dryland ecosystems. Using global dust deposition models, Okin et al. (2004) have estimated global P deposition in desert dust. Estimates of dust-borne P deposition rates for drylands vary over several orders of magnitude depending on proximity to the world's largest dust sources in North Africa, the Middle East and northwestern China.

10.3.2 Geochemical and Biological Controls on Phosphorus Availability

Because of the geological origin of P in terrestrial ecosystems and the fact that secondary minerals in soils regulate P availability, P is considered to be geochemically controlled. As parent material weathers chemically and soil forms, P is leached and lost from the system or it may remain in the soil in either occluded, non-occluded or organic fractions of the total P pool (Walker and Syers 1976; see also Chapter 3 by Bünemann and Condron, this volume). Non-occluded P is bound to hydroxides of Al and Fe or CaCO₃. The presence of these secondary minerals in dryland soils, CaCO₃ in particular, strongly influences availability of P (Cross and Schlesinger 2001; Lajtha and Bloomer 1988). The

above model of P weathering was developed for soils derived from igneous rock. Neff et al. (2006) propose that in dryland soils derived from sedimentary rock, the majority of P weathers from Fe and Al oxide forms rather than primary minerals. Fe oxide minerals appear to regulate P availability more than Ca in some areas near Canyonlands National Park (Utah; Neff et al. 2006).

Erosional losses of P are important in arid and semiarid regions. Okin et al. (2001b) have shown that wind erosion can dramatically reduce the concentration of plant-available P in surface soils. Runoff studies (Schlesinger et al. 1999, 2000) have shown that runoff is not a significant cause of P loss from soils.

The extent to which P remains available for uptake by organisms depends on soil chemical properties, which in turn are determined by the degree of weathering, soil development and erosion. In aridisols with an argyllic (clay-rich) A horizon, phosphorus sorbs to Fe- and Al-oxides and precipitates out of solution as $\text{AlPO}_4 \cdot 2\text{H}_2\text{O}$ and $\text{FePO}_4 \cdot 2\text{H}_2\text{O}$ as soil pH falls below ~ 6.0 – 6.5 . Below the argyllic A horizon or at the surface if the argyllic horizon has eroded, P binds to calcium (Ca) and precipitates out of solution as $\text{Ca}_3(\text{PO}_4)_2$ as the pH rises above 7.0 (Lindsay and Vlek 1977). High levels of Ca^{2+} and HCO_3^- can reduce or prevent the dissolution of carbonate and Ca-P compounds, making P unavailable. Phosphorus can also complex with other elements (e.g. Mn or Zn).

The predominance of geochemical controls has been documented in drylands around the world. In an analysis of a soil chronosequence in the Chihuahuan Desert (New Mexico), Lajtha and Schlesinger (1988a) found negligible accumulation of organic P, but increasing inorganic P storage in calcium carbonate layers. Integrated over time, dryland vegetation appears not to conserve and store P as other ecosystems do. Even direct inputs of organic P do not increase inorganic P availability. Soil column experiments showed negligible net P mineralisation rates even in moist Kalahari Desert soils amended with cattle dung (Dougill et al. 1998). The authors suggest that microbial immobilisation or inorganic fixation of P to minerals occurs in these relatively Ca- and Fe-rich soils.

A few studies suggest that biological processes exert strong local influences on P availability. Leaf P in wild populations of an indigenous Kalahari desert tree *Vangueria infausta* increased with both the percentage of arbuscular mycorrhizal (AM) colonisation of roots and the P concentration in the soil (Bohrer et al. 2001). *V. infausta* seedlings inoculated with local strains of AM fungi depleted soil mineral P concentrations and increased seedling size (Bohrer et al. 2003). The mechanism used by mycorrhizal fungi to mediate P uptake for its desert hosts is not yet understood. Ectomycorrhizal and arbuscular mycorrhizal fungi occur throughout aridlands in the United States (Great Basin, Southern California deserts; Allen et al. 1996) but, unlike their counterparts in forest ecosystems, these symbionts do not appear to produce oxalate or phosphatase that could facilitate P uptake by their desert hosts (Jurinak et al. 1986).

Climate can interact with biotic processes to affect P availability in dryland ecosystems. The rate of H_2CO_3 formation in soil is partially controlled by soil water content and the solubility of CO_2 in water (Krauskopf and Bird 1995). Solubility of CO_2 in soil solution increases in cold temperatures. Because both abiotic CO_2 solubility and biotic CO_2 production vary relative to soil tempera-

ture and soil moisture, but in the opposite direction to each other, maximum H_2CO_3 production occurs with increasing soil temperature and decreasing soil moisture (Seastedt and Knapp 1993). Assuming most P in these soils is present as CaHPO_4 , P availability should also be highest at this maximum as CaHPO_4 is solubilised by H_2CO_3 in favour of the formation of CaCO_3 . This scenario is supported by several studies. *Bromus* shows high levels of winter root growth when soils are cold and moist (Harris 1967). Under the above scenario, winter would be the time when P would be most available in dryland soils. Root growth would also contribute respiratory CO_2 , facilitating the acquisition of carbonate-bound nutrients. In situ resin bags near our Colorado Plateau sites also show an increase in soil P availability during cold, moist conditions found in winter (Miller 2000). *Bromus* growth rates were greatest at these sites in winter, and were positively correlated with P/Ca and inversely correlated with above-ground N and P. Lajtha and Schlesinger (1988b) also found that in situ resin bag P concentrations peaked in cool winter conditions in the Chihuahuan desert. Magid and Nielsen (1992) showed that laboratory extractions performed at 4 °C recovered significantly more P than those at 25 °C. In general, lower diffusion rates at lower temperatures partially counteract the increase in available soil P. However, the situation may be different in calcareous soils, as diffusion rates may actually increase with decreasing temperatures (but above freezing), as H_2CO_3 generation facilitates carbonate dissolution and the transition of solid-phase P to solution-phase P (Jungk and Claassen 1997).

10.4

Other Nutrient Cycles

Potassium (K) is an essential nutrient for plants. Plants require a fairly large quantity of K and can often use more than is available in soils (Troeh and Thompson 1993). Most K is derived from the micas muscovite and biotite, the feldspars orthoclase and microcline, and evaporative deposits found in dryland climates (Day and Ludeke 1993; Troeh and Thompson 1993). In soil, K generally occurs in mineral structures or as hydrated ions either in solution or adsorbed onto the negatively charged sites on clays and organic matter. Hydrated K ions are the same size as ammonium ions and held with about the same strength, whereas they are weakly held relative to calcium (Ca) and magnesium (Mg) ions. Therefore, K ions are readily exchangeable. Plant roots can easily obtain K if they reach the adsorption site; however, K moves very slowly through soils. Potassium is more soluble in calcareous than non-calcareous soils, due to the effect of carbonic acid in the calcareous soils. It is also more easily exchanged with other cations in calcareous soils compared to non-calcareous soils. In general, K is not easily leached from soils, even over long periods of time, due to K fixation and sorption to the cation-exchange sites in soils. In drylands, K accumulates at

the surface due to upward transport by plants and accumulation of K in plant litter (Jobbágy and Jackson 2001; Schlesinger and Pilmanis 1998; and references therein). Higher K concentrations in surface soils are also attributed to illite deposition in aeolian materials (Singer 1989).

Most K in soils is in a non-exchangeable form, with only about 1% occurring in an exchangeable form. The transformations of non-available K to available K forms are facilitated by wet-dry, freeze-thaw, and warming-cooling cycles that accelerate mineral weathering. However, high soil moisture and freezing temperatures occur only rarely in dryland regions, which results in low rates of weathering and K transformations. Despite the importance of K to plants and the low transformation rates and thus availability in drylands soils, there have been only a few studies on how K may influence vascular plant distribution or productivity in these regions.

Crooke and Knight (1962) and Scott and Billings (1964) were the first to note that dryland soils with high K/Mg ratios were dominated by annual plants, whereas soils with a low K/Mg ratio were dominated by perennial plants. Harner and Harper (1973), Pederson and Harper (1979), and Woodward et al. (1984) all corroborated these earlier findings. Crooke and Knight (1962) and Gray et al. (1953) found that K uptake by plants was highly correlated with plant root CEC and that annual plants, especially grasses, generally had higher root CECs than perennial plants. Annual grasses have also been found to have higher tissue concentrations of K than adjacent native perennial plants (Blank et al. 2002), as well as higher root CECs (Belnap et al. 2006). This may also indicate that annual grasses have a higher requirement for K than native perennial plants (Tilman 1982). Belnap et al. (2006) found that annual grasses in south-east Utah are found only in soils with higher K, K/Mg and K/Ca. Traditionally, agriculture has regarded soils with less than 140 mg kg⁻¹ of available K to be deficient in K. However, this standard may be too high, with K deficiency occurring at less than 70 mg kg⁻¹ (Leigh and Storey 1991). If the standard of 70 mg K kg⁻¹ is used, many soils in western United States drylands are K limited (Belnap et al. 2006).

There are several reasons why K may be important to dryland plants. Osmoregulation in plants is mediated by K (e.g. Mäser et al. 2002; Wang et al. 2002). The high Na levels of many dryland soils can be toxic to many plants, and there are multiple studies showing that K ameliorates Na toxicity in plants (e.g. Mäser et al. 2002) as well as in other organisms such as bacteria (e.g. Kraegeloh and Kunte 2002). The preferential transport of K over Na is especially pronounced in actively photosynthesising organs such as young leaves and developing seeds (Wang et al. 2002). The extent to which plants utilise K to avoid Na stress varies among species (Mäser et al. 2002). In addition, K has been implicated in plant adaptation to water stress (Xu et al. 2002). Multiple studies support the observations that high levels of Mg and Ca can restrict plant uptake of K in both the laboratory and the field (Epstein 1961; Sinanis et al. 2003).

Calcium (Ca) concentrations in dryland soils are generally sufficiently high not to limit plant productivity. Calcium generally occurs in the minerals apatite, plagioclase and hornblende. Because minerals that contain Ca can weather rela-

tively quickly, Ca is subject to leaching. Dryland soils generally have very high levels of Ca, reaching more than 5% of the soil by weight and occupying 75–85% of the CEC sites (Troeh and Thompson 1993). Hydrated Ca ions are relatively small polyvalent ions; thus, they tend to preferentially occupy CEC sites, making Ca less bioavailable than other cations that are held less strongly. The high levels of Ca in dryland soils can have a profound influence on the availability of other nutrients. Excess Ca precipitates as Ca carbonate at the soil depth to which most precipitation infiltrates; this layer can harden (called caliche or calcrete) and block plant roots and water flow. Calcium carbonate is an effective pH buffer maintaining alkaline conditions; however, Ca can bind with other soil nutrients, such as P, Mn, Zn and Mg, making these unavailable to organisms (Troeh and Thompson 1993). In addition, the polyvalent Ca can swamp CEC sites in plant roots. Therefore, the ratio of Ca to other cations can influence plant productivity (Barber 1995; Lajtha and Schlesinger 1988b). Under cold conditions Ca carbonate solubility in water is high (Krauskopf and Bird 1995) and thus these bonds may be broken or weakened when soils are cold and wet.

Magnesium (Mg) is found in igneous rocks, associated with the ferro-magnesium minerals such as olivine, inosilicates and biotite micas. It is also an important component of the sedimentary rock dolomite. Magnesium-containing minerals tend to be relatively easily weathered, and thus soils are depleted of Mg faster than of K or Ca. The Mg ion is much smaller than the Ca ion, being more similar in size to K, and, as with Na and K, is less strongly held to CEC sites than Ca. Generally, Mg occupies 12–18% of the CEC sites. Both Mg and Ca ions are more likely found on CEC sites than in solution. Dryland soils with an excess of Mg (occupying 40–60% of the CEC sites and having a Ca/Mg ratio <1) have sparse plant cover and high erodibility (Burt et al. 2001). Fertiliser trials show that Mg ions interact strongly with other cations, especially the monovalent K and Na, due to the preferential adsorption of the polyvalent Mg ion. Therefore, similar to Ca, the ratio of Mg to other cations can influence plant productivity (see Sect. 10.4).

Sodium (Na) is considered a non-essential element, but is beneficial in small amounts. Sodium levels in soil are almost always sufficient for plant growth. Sodium ions are less tightly held to soil particles than K, Ca or Mg. Therefore, Na is more easily leached from soil than the other cations. However, in dryland soils, low amounts of precipitation limit the amount of downward leaching. In addition, salts (mostly Na salts) move upwards in the soil due to capillary action when the soil surface is drier than underlying layers, forming a white crust on the surface that is almost exclusively sodium chloride (Troeh and Thompson 1993). Thus, much of the alkalinity of dryland soils is due to the presence of Na. The large amount of Na often found in dryland soils can damage soil structure and reduce plant productivity. Many dryland plants have active mechanisms to handle excess soil Na, such as extruding salt onto the leaf surface or storing Na in cell vacuoles to prevent interference with processes in the cytoplasm (Whitford 2002).

Sulphur (S) is an essential plant nutrient. Sulphur is similar to nitrogen in that it occurs in a gaseous and solid form, it is unavailable to plants in its elemental form, and its most common bioavailable form, SO_4^{2-} , is an anion easily leached from the soil (see also Chapter 3 by Bünemann and Condon, this volume). Similarly to N, a considerable amount of S can be added to the soil via rain and the breakdown of organic matter. The presence of Ca limits the solubility of S; thus S generally has low mobility in dryland soils. On the other hand, high pH soils generally have a low anion exchange capacity, and thus anions such as SO_4^{2-} are more easily leached than in soils with lower pH (Troeh and Thompson 1993). Lack of precipitation in dryland regions results in limited overall leaching and dryland soils often have high concentrations of dissolved sulphates. Gypsum (CaSO_4) is common in dryland regions. In addition to occurring in surface soils, it often accumulates just below or in the Ca carbonate layer. Gypsum influences plant distribution in the Mojave Desert (Meyer 1986), due primarily to soil physical factors such as the tendency of indurated surfaces to inhibit seedling establishment, rather than nutrient chemistry.

Most copper (Cu) found in soils is associated with organic matter, but can also be held by cation exchange or bound in Fe-Cu oxides. The cation exchange bond is stronger than that of Ca, making Cu relatively immobile. High pH, calcareous and/or Fe-rich coarse soils, typical soils of dryland areas, have inherently low concentrations of available Cu (Alloway and Tills 1984). Jarrell and Virginia (1989) postulated that Cu may limit plant productivity in dryland regions. Copper deficiency has been linked to suppressed N_2 fixation in vascular plant-*Rhizobium* associations (Cartwright and Hallsworth 1970), and may also limit N_2 fixation for N_2 -fixing lichens. As discussed in the section on N above, soil lichens can be the dominant source of N for many dryland ecosystems. Therefore, low available Cu may have large implications for plant productivity in these regions.

Most iron (Fe) is found in igneous rocks in the ferrous (Fe^{2+}) form. However, Fe can also be found as the highly insoluble ferric Fe (Fe^{3+}) form. Both forms of Fe are less soluble in high pH soils compared to low pH soils; thus, Fe availability is low in calcareous soils. Low temperature also reduces the solubility of Fe compounds (Troeh and Thompson 1993). Iron oxides can adsorb P, making them both unavailable to organisms. The formation of Fe phosphate reduces Fe solubility, so the presence of P can reduce Fe availability. Because Fe and Mn are chemically similar, they can be antagonistic. Similarly, high levels of Zn or Cu can also result in Fe deficiencies (Day and Ludeke 1993), as these other micro-nutrients can act as oxidising agents to convert ferrous to ferric Fe. Iron deficiencies are much more common in dryland regions with high pH soils than in soils with lower pH. Hunter et al. (1980), Nelson and Jolley (1989) and Wallace (1989) all suggest that Fe may limit plant productivity in drylands.

Manganese (Mn) is derived mostly from widespread igneous inosilicate minerals. Concentrations of total Mn in dryland soils can be so high that Mn nodules are found in lower soil horizons (Yaalon et al. 1972). In contrast, exchangeable, available Mn is often low, due to its low solubility in alkaline soils. The

availability of Mn is also reduced with high levels of Na, K, Fe, Cu or Zn (Day and Ludeke 1993). As mentioned above, Mn and Fe have a similar structure, and thus compete with each other. Because many dryland soils contain high levels of Na and Fe, Mn deficiency may be quite common. Bowker et al. (2006) reported that Mn deficiency controls the distribution of the common N₂-fixing lichen *Collema tenax* in the western United States. Therefore, as with Cu, limitation by Mn may reduce N input into dryland ecosystems, thus reducing plant productivity. Belnap et al. (2006) have shown that exotic annual grasses prefer soils high in Mn in cool western deserts in the United States. Cramer and Nowak (1992) report that the addition of Mn stimulates growth in annual grasses, whereas others have noted that Mn deficiency may limit plant productivity in drylands (Jaurequi and Reisenauer 1982; Marschner 1995; B. Blank, personal communication). These studies indicate that Mn may play a large role in dryland ecosystems, which warrants further investigation.

Zinc (Zn) is derived mostly from rock minerals. Total Zn concentrations in soils is generally high, but very little Zn is found in solution, especially in soils with a pH above 6 (Troeh and Thompson 1993). Above a pH of 8.4, Zn can precipitate. Carbonates can also adsorb Zn. Therefore, available Zn in dryland soils is generally low in the western United States (Jarrell and Virginia 1989), and this deficiency is likely common throughout dryland regions of the globe, limiting plant productivity (Hacisalihoglu and Kochian 2003; Jarrell and Virginia 1989; Jaurequi and Reisenauer 1982; Killingbeck 1989; Marschner 1997). Belnap et al. (2006) found that high levels of Zn suppressed annual grass occurrence, which may result from the formation of low solubility of Zn phosphates or the interference of high Zn with P uptake by plants (Sharma et al. 1968). Zinc uptake can also be reduced by high levels of soil Mn, as it is similar in size to Zn and can compete for carrier molecules in the root cells. The solubility and plant uptake of Zn is also reduced in cool soils.

10.5 Conclusions

This chapter reviews a large number of studies on dryland nutrient cycling, many of which were conducted in the western United States. Despite the multitude of studies on nutrient fluxes and stocks, few dryland regions are studied intensively enough to permit the compilation of nutrient budgets even for essential macronutrients like N and P. Nutrients are lost from drylands in wind and water erosion and become unavailable when secondary minerals bind nutrients in soils. Human activity can accelerate nutrient losses; for example, livestock grazing reduces vegetation cover, which leads to more rapid erosion. Satellite imagery documents climate-driven trends in dryland primary productivity and reveals large-scale transport of dust into oceans and other continents, but more

work is needed to quantify the magnitude of nutrient exports. Because nutrient fluxes are highly variable in space and time, more intensive measurements are needed to compile annual budgets and thereby track long-term trends in the nutrient status of dryland ecosystems.

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