Structure and Function of Chihuahuan desert Ecosystem
The Jornada Basin Long-Term Ecological Research Site
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Nutrient Cycling within an Arid Ecosystem

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Low quantities of soil nitrogen limit plant growth in the Chihuahuan Desert (Ettershank et al. 1978; Fisher et al. 1988; Lajtha and Whitford 1989; Mun and Whitford 1989) and in other deserts of the world (Wallace et al. 1980; Breman and de Wit 1983; Sharifi et al. 1988; Link et al. 1995). Indeed, although deserts are often regarded as water-limited systems, colimitation by water and N may be the more general rule (Hooper and Johnson 1999; Austin and Sala 2002). In a broad survey of desert ecosystems, Hooper and Johnson (1999) found evidence for colimitation by water and N even at the lowest levels of rainfall. In arid ecosystems, water is delivered in discrete events separated by drier periods, which restrict biological activity and uncouple plant uptake of nutrients from decomposition. Local variations in net primary production in arid and semiarid ecosystems are largely determined by processes that control the redistribution of water and soil nutrients across the landscape (Noy-Meir 1985; Schlesinger and Jones 1984; Wainwright et al. 2002; see also chapter 11). In this chapter we focus on the N cycle in different plant communities of the Jornada Basin with the recognition that after water, N is the most likely resource to determine the plant productivity of this ecosystem.

Where arid environments are dominated by shrubby vegetation, the distribution of soil properties is markedly patchy with strong accumulations of plant nutrients under shrubs and relatively infertile soils in the intershrub spaces (Noy-Meir 1985). These islands of fertility are particularly well described in the Chihuahuan Desert and other areas of the American Southwest. Local accumulations of nutrients under vegetation are also documented for desert habitats on

other continents, including Europe (Gallardo et al. 2000), Africa (Gerakis and Tsangarakis 1970;

Belsky et al. 1989; Wezel et al. 2000), Australia (Tongway and Ludwig 1994; Facelli and Brock

2000), and South America (Rostagno et al. 1991; Mazzarino et al. 1991, 1998; Gutierrez et al.

1993). In the Jornada Basin, Schlesinger et al. (1996) used geostatistics to compare the scale of

soil heterogeneity in arid habitats dominated by shrubs and in adjacent areas of arid grassland. A

nearly random distribution of extractable N was found in grassland soils, but in areas dominated

by creosotebush (*Larrea tridentata*) the distribution of soil N was patchy at a scale close to the

average size of shrubs (figure 6-1). <<COMP: insert figure 6-1 about here>>

The patchy habitat created by shrubs also determines the biodiversity of animals at higher

trophic levels, including lizards and birds (Pianka 1967; Naranjo and Raitt 1993). Patchy

distributions of soil microbial biomass (Mazzarino et al. 1991; Gallardo and Schlesinger 1992;

Kieft 1994; Smith et al. 1994; Herman et al. 1995), nematodes (Freckman and Mankau 1986),

and microarthropods (Santos et al. 1978) reflect the heterogeneous distribution of soil nutrients

in desert shrublands. Indeed, most ecosystem function in shrub deserts is localized under

vegetation, whereas the adjacent shrub interspaces are comparatively devoid of biotic activity.

Greater microbial activity under shrubs is manifest in high rates of N mineralization and

nitrification (Charley and West 1977; Mazzarino et al. 1991; Smith et al. 1994). These microbial

processes have the potential to produce gaseous by-products—NH_3, NO, N_2O and N_2—that are

lost to the atmosphere. In some deserts, the emission of these gases is an important part of the

biogeochemical cycle (West and Skujms 1977; Westerman and Tucker 1979; Virginia et al.

1982), but in most cases, the shrubs act to conserve N by its immobilization in the litter and

microbial biomass of soil mounds (Peterjohn and Schlesinger 1991; Schlesinger and Peterjohn

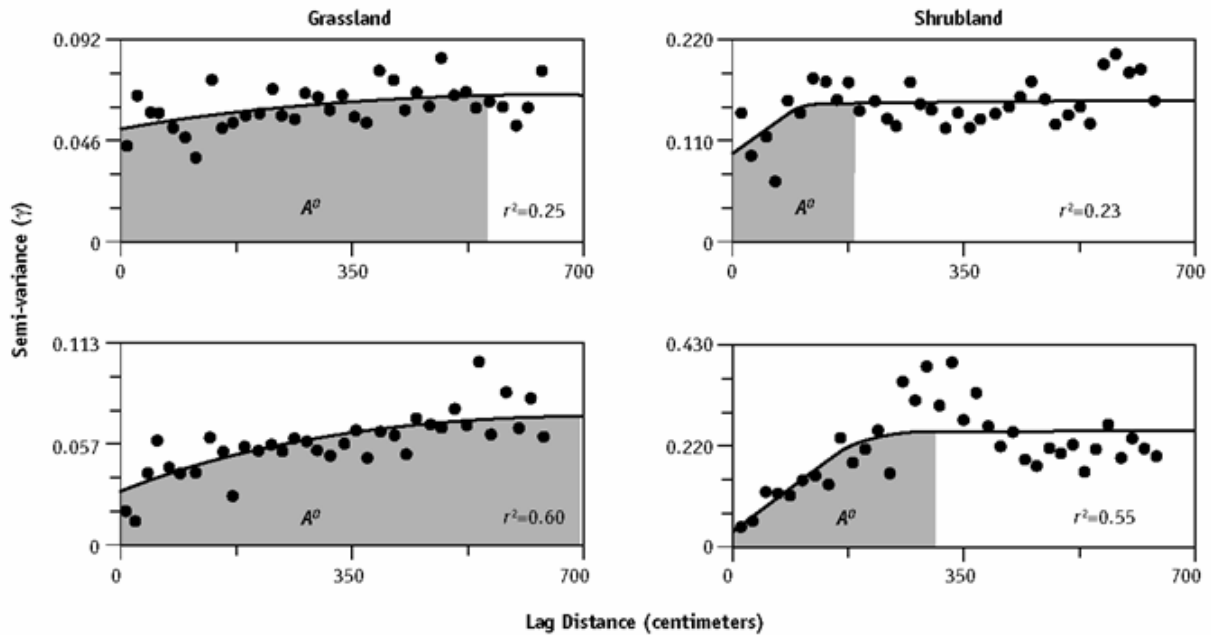1991; Gallardo and Schlesinger 1992; Zaady et al. 1996). Indeed, the local nutrient accumulation

Fig. 6-1. Spherical model semivariograms for the distribution of available N in grassland and desert soils at the Jornada Experimental Range *(n = 2 each)* in the Chihuahuan Desert of New Mexico. The range of spatial dependence or autocorrelation is designated as Ao in each panel (modified from Schlesinger et al. 1996).

under shrubs may exceed the original nutrient concentrations in grassland soils that the shrubs have invaded (Kieft et al. 1998; Cross and Schlesinger 1999).

The spatial heterogeneity of biotic activity in shrublands controls movements of water and soil materials in desert ecosystems. Total ground cover is the most important variable influencing runoff and sediment production on desert rangelands in southern New Mexico (Wood et al. 1987) and other arid and semiarid regions (Zobisch 1993). In the Jornada Basin, vegetation aerial cover can be up to 50–60% in grasslands versus 30% in creosotebush and mesquite (*Prosopis glandulosa*) shrublands (Schmidt unpublished data). When shrubs replace grasslands, the rate of erosion increases and the surface soil materials are progressively lost from the barren shrub interspaces, especially for sand textured soils (Bull 1979; Abrahams et al. 1994,

1995; Gutierrez and Hernandez 1996; see also chapter 9). When shrubs are widely spaced, the

barren intershrub soils are also subject to wind erosion that redistributes soil materials across the

landscape (Snow and McClelland 1990; Stockton and Gillette 1990; Okin and Gillette 2001).

Losses of soils and soil nutrients are closely tied to the degradation and desertification of desert

grasslands in southern New Mexico and other arid and semiarid regions of the world.

Nutrient Cycling in the Jornada Basin

Simultaneous limitation of plant growth by water and N (response to water added alone and to N

added alone) is common in the Chihuahuan Desert (Ettershank et al. 1978; Gutierrez and

Whitford 1987a). For example, Fisher et al. (1988) found that the growth of creosotebush nearly

doubled with experimental additions of 100 kg N/ha, with the greatest plant growth seen when N
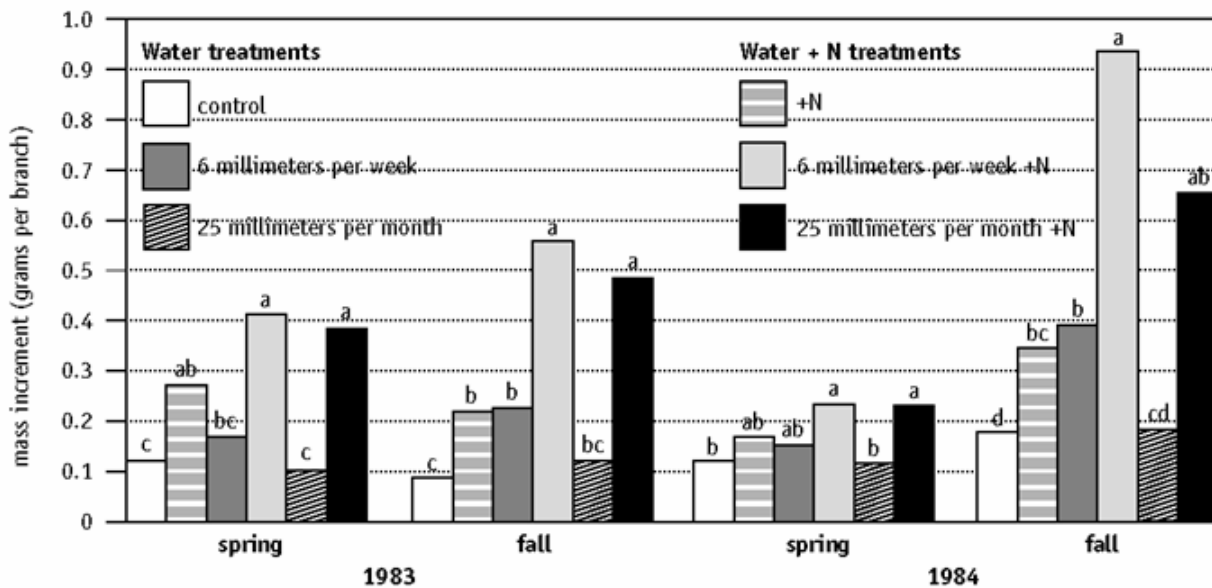
and water were added together (figure 6-2).

Fig. 6-2. Effects of nitrogen fertilization and two patterns of irrigation on seasonal mass increments in vegetation in creosotebush *(Larrea tridentate)* shrubs in the Jornada Basin. Within each year and season, significant differences between treatments are indicated by different letters (modified from Fisher et al. 1987).

Depending on the site and circumstances, pulses of primary production related to variable rainfall may shift between water and nutrient limitation of plant growth (Mun and Whitford 1989). During years of high winter rainfall in the Jornada Basin, the decomposition of an abundant growth of spring annuals can immobilize soil N, leading to deficiencies that subsequently limit the growth of creosotebush during the summer (Parker et al. 1984a). These interactions between water and N may contribute to the poor correlation between annual net primary production and recent precipitation in semiarid habitats worldwide (Le Houerou et al. 1988; see also chapter 11).

Intersystem Nutrient Flux

N inputs from the atmosphere average around 2.5 kg/ha/yr in the Jornada Basin (Schlesinger et al. 2000) with about half as NH_4^+ and half as NO_3^-. Deposition of N in rainfall dominates over the deposition of N in dust and particles. The N in atmospheric deposition is supplemented by rather meager inputs, mostly < 1 kg N/ha/yr, from asymbiotic N-fixing bacteria in soil crusts (Loftis and Kurtz 1980; Hartley and Schlesinger 2002). In the Jornada Basin, the only appreciable rates of soil fixation, ranging up to 10 kg N/ha/yr, are found in tarbush (*Flourensia cernua*) communities, especially in soils with a low N/P ratio (Hartley and Schlesinger 2002). Herman et al. (1993) also report N-fixing bacteria in the rhizosphere of black grama (*Bouteloua eriopoda*), but their contribution to the N economy of the grassland habitats remains unknown. Field experiments show that most asymbiotic N fixation appears to be due to heterotrophic soil bacteria, and the rate of fixation is stimulated by experimental additions of carbon and water (Hartley and Schlesinger 2002). The low rate of N fixation in Jornada desert soils contrasts sharply with high inputs by this process in the cold desert steppe of the Great Basin (West and Skujms 1977; Belnap 2002) but compares favorably to the results of Rundel and Gibson (1996),

who report similar low rates of asymbiotic fixation in creosotebush habitats in the Mojave Desert of southern Nevada.

Symbiotic N fixation is largely confined to habitats dominated by mesquite . At the Jornada, Jenkins et al. (1988) report nodules on mesquite roots from 13 m depth, complicating attempts to estimate overall N inputs to this ecosystem. Based on studies in other ecosystems, we might expect N fixation in mesquite habitats to range from 40 (Rundel et al. 1982) to 150 kg N/ha/yr (Johnson and Mayeux 1990), depending on plant cover. From measurements of $\delta^{15}N$ in its foliage, Lajtha and Schlesinger (1986) estimated that mesquite in the Jornada Basin obtains 48% of its N from symbiotic fixation, accounting for about 20 kg N/ha/yr.

In the face of these inputs of N, the Chihuahuan Desert persists in an N-deficient state, owing to soil erosion by wind and water and to the microbial production and loss of N-containing gases to the atmosphere. Wind erosion may remove up to 14 kg N/ha/yr from mesquite habitats, assuming a soil N concentration of 0.1% (Gallardo and Schlesinger 1992) and a net soil loss of 1,400 g/m^2/yr (chapter 9). Additional losses of 1–5 kg N/ha/yr are associated with the suspended and bedload sediments carried in runoff waters. Only a small fraction of the runoff loss occurs in forms that are available to plants. For instance, Schlesinger et al. (2000) report runoff losses of dissolved N totaling 0.15 kg N/ha/yr in black grama grasslands and 0.33 kg N/ha/yr in creosotebush shrublands. A surprising fraction of the dissolved N loss, nearly 70% on bare soils, is carried in dissolved organic forms (DON). Relatively little N is lost to groundwater in the Chihuahuan Desert, in contrast to large apparent losses of NO_3^- to groundwater in other North American deserts (Peterjohn and Schlesinger 1991; Jackson et al. 2004; Seyfried et al. 2005). Volatilization of NH_3 to the atmosphere is rather small (0.03–0.35 kg

N/ha/yr) (Schlesinger and Peterjohn 1991), and losses of nitric oxide (NO) associated with

nitrification (figure 6-3) range from 0.15 to 0.38 kg N/ha/yr (Hartley and Schlesinger 2000).
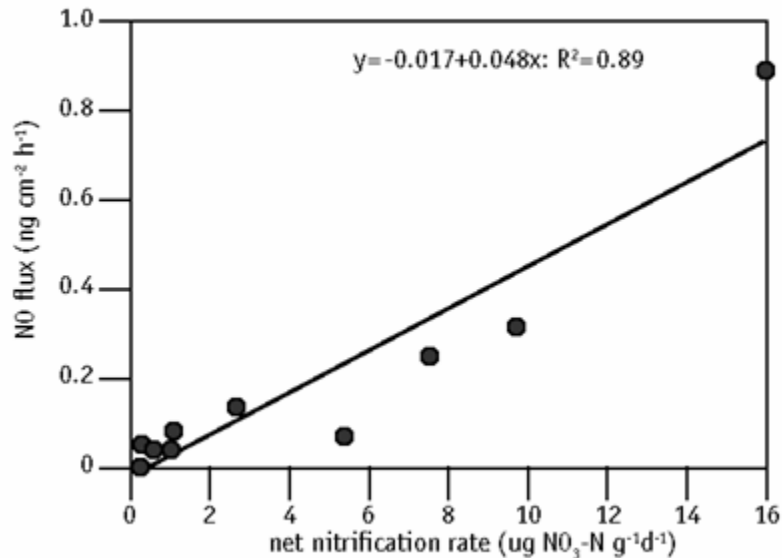

Fig. 6-3. Relationship between soil NO emission and potential net
nitrification rates, measured in the laboratory, in a variety of soils from the
Jornada Basin (from Hartley and Schlesinger 2000).

Peterjohn and Schlesinger (1991) report bursts of denitrification after wetting events, potentially

leading to losses of 7.2 kg N/ha/yr from these ecosystems. A significant fraction of this loss may

occur as N_2O, which Hartley (1997) estimated to return up to 3.9 and 6.2 kg N/ha/yr to the

atmosphere from grasslands and shrublands, respectively. By comparison, Guilbault and

Matthias (1998) report the loss of 0.4 kg N/ha/yr as N_2O from soils of the Sonoran Desert.

In summary, new inputs of N are limited and a variety of processes lead to the loss of N

from desert soils and to a deficiency of N for plant growth, especially in wet years in the Jornada

Basin. Nutrient losses from shrubland habitats exceed those from grasslands, but much of the

apparent loss may simply result in a local redistribution of soil nutrients on the landscape.

Intrasystem Nutrient Cycling

Plant Nutrition

Plant nutrient uptake by Chihuahuan Desert shrubs is closely tied to the availability of soil water.

In watering experiments, creosotebush showed a rapid uptake of soil N, whereas mesquite

showed little response (BassiriRad et al. 1999). This difference may result from the relatively

shallow rooting system in creosotebush and a greater reliance by mesquite on N-fixation at depth

(Lajtha and Schlesinger 1986; Ho et al. 1996). In fourwing saltbush (*Atriplex canescens*) Sisson

and Throneberry (1986) found the highest levels of leaf nitrate reductase during the seasonal

periods of greatest leaf water potential, consistent with patterns of soil N availability, which

show a dominance of NO_3 over NH_4 during the summer wet season. Creosotebush shows a

distinct preference for NO_3 as a N source, consistent with its growth during the summer

(BassiriRad personal communication). That plant uptakes affect soil N dynamics is clearly

evident in the greater accumulations of plant-available N that are found in the soils of rainfall-

exclusion experiments (Reynolds et al. 1999a).

Although some desert plants have been reported to have especially high leaf N contents

(El-Ghonemy et al. 1978), the N content of plants in the Jornada Basin is not significantly

different from that of many forest species (Killingbeck and Whitford 1996). As for most plants,

photosynthesis in creosotebush is positively correlated to leaf N content (figure 6-4), but N-use

efficiency declines significantly with increasing leaf N contents (figure 6-5; Lajtha and Klein

1988). N-use efficiency is inversely correlated to water-use efficiency, so both C acquisition and

water conservation are greater in desert plants with high leaf N contents (Lajtha and Whitford 1989).
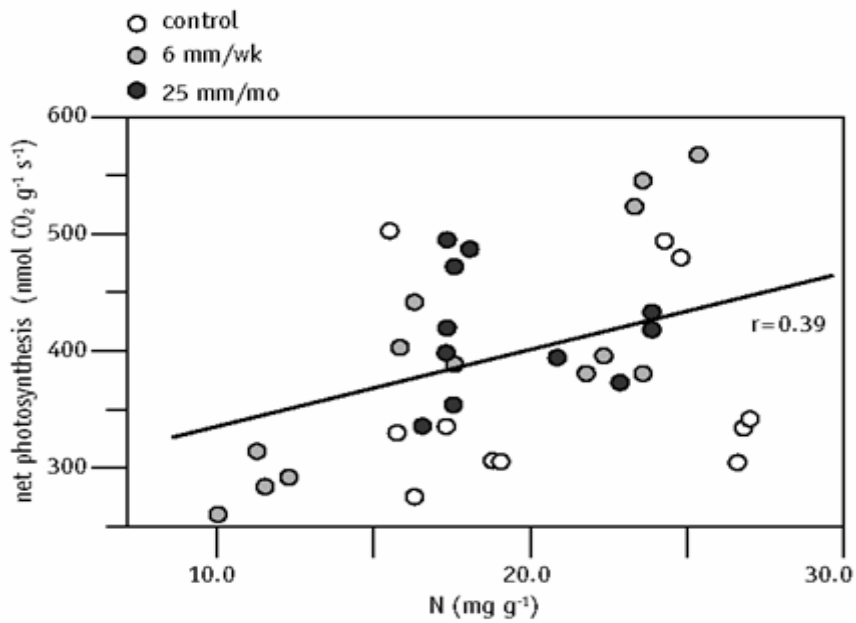

Fig. 6-4. Relationship between net photosynthesis and leaf N in creosotebush (*Larrea tridentata)* in the Jornada Basin, among shrubs receiving different irrigation treatments (from Lajtha and Whitford 1989).
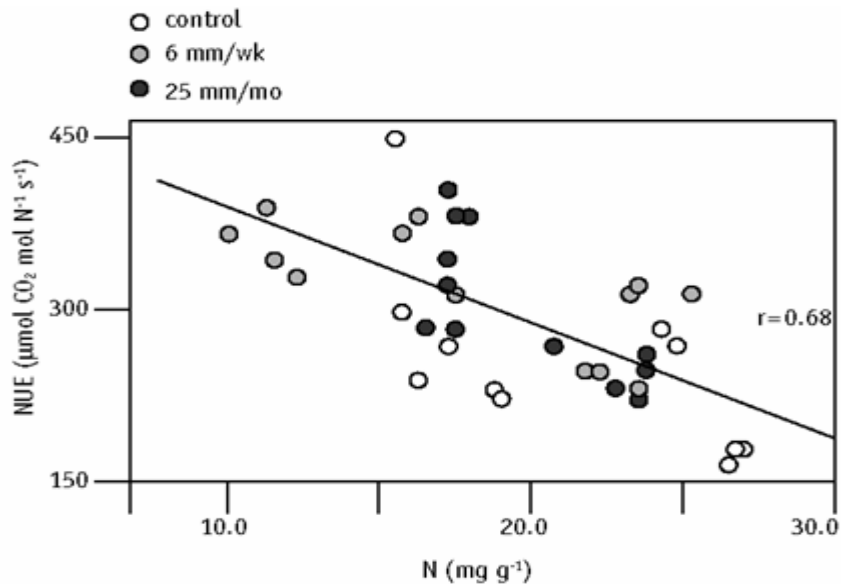

Fig. 6-5. Relationship between leaf nitrogen-use efficiency and leaf N concentration in creosotebush (*Larrea tridentata)* (from Lajtha and Whitford 1989).

However, plants with high leaf N contents are also more attractive to insect and mammalian herbivores, who enhance the return of N to the soil through their feeding (Lightfoot and Whitford 1989, 1990; Day and Detling 1990; Frank and Evans 1997).

Mycorrhizae may contribute to the nutrient-uptake capacity of many species in the Jornada Basin (Herman 2000). Abundant fungal endophytes with mycorrhizal traits have been found on fourwing saltbush (Barrow et al. 1997) and black grama (Barrow 2003) in the Jornada Basin, and creosotebush is reported to harbor mycorrhizae in the deserts of southern California (Bethlenfalvay et al. 1984). The mycorrhizae on fourwing saltbush are dark septate fungi with the ability to solubilize rock phosphate (Barrow and Osuna 2002).

Mycorrhizal production of oxalic acid may be particularly important to phosphorus mobilization in high carbonate soils (Jurinak et al. 1986). The widespread deposition of pedogenic calcite in arid soils affects the availability of phosphorus, and much of the total P pool in the soil is bound to calcium minerals (Marion and Babcock 1977; Lajtha and Bloomer 1988). Lajtha and Schlesinger (1988) report decreased uptake of inorganic P in creosotebush in response to experimental additions of $CaCO_3$ to soils. In the Chihuahuan Desert only a small amount of phosphorus is found in organic forms, which may be of special importance to plant phosphorus nutrition (Cross and Schlesinger 2001). Often, organic and bicarbonate-extractable P (forms easily available for plant uptake) are concentrated beneath the canopy of shrubs, whereas Ca-bound P is greatest in the shrub interspace (Charley and West 1975; Cross and Schlesinger 2001).

In creosotebush, resorption of N and P before leaf abscission is positively related to the nutrient status of foliage (Lajtha 1987; Lajtha and Whitford 1989). For creosotebush, especially high resorption efficiencies for phosphorus (72–86%) may be a response to limited P availability

in the high carbonate soils of the Jornada Basin (Lajtha 1987). For comparison, N-resorption

efficiency in creosotebush is about 50–60% (Lajtha 1987; Lajtha and Whitford 1989), not unlike

the global mean for terrestrial plants (Aerts 1996). The N-resorption efficiency of mesquite is

exceptionally low (36%), perhaps reflecting its reliance on N fixation as a source of N

(Killingbeck and Whitford 2001).

Soil Processes

Whitford et al. (1981b) noted that the rate of decomposition of plant litter in the Chihuahuan

Desert was greater than predicted by the simple correlation with actual evapotranspiration, as

promulgated by Meentemeyer (1978) in his seminal study comparing decomposition in various

terrestrial biomes. Later, Schaefer et al. (1985) found that lignin content, C/N ratio, and the

lignin/N ratio in plant litter also failed to predict decomposition in the Jornada Basin, despite the

success of these variables as predictors of decomposition in a variety of other ecosystems

(Melillo et al. 1982). Unexpected high decomposition rates of surface litter were thought to be

related to its photo-oxidation by ultraviolet light and to the abundant activity of microfauna and

termites (*Gnathamitermes*) in desert soils. Despite several attempts to demonstrate high rates of

photo-oxidation of surface litter materials, the importance of this process remains equivocal

(Moorhead and Reynolds 1989a; MacKay et al. 1994). Meanwhile, the importance of soil

microfauna to litter decomposition and soil N content has been clearly demonstrated by using

insecticides to inhibit their activity in litterbags (Santos and Whitford 1981; Santos et al. 1981;

Brown and Whitford 2003). Johnson and Whitford (1975) found that termites consumed about

50% of the surface litter in creosotebush and mesquite communities (see also Whitford et al.

1982; Silva et al. 1985; Whitford 1991; see also chapter 12). Photo-oxidation of litter appears

more important in the Patagonian steppe of Argentina where termites are less abundant (Austin personal communication).

Because much of the plant litter in the Jornada Basin is processed by the activities of termites, rainfall timing and amount is not as strong a predictor of decomposition in the Chihuahuan Desert (Santos et al. 1984; Whitford et al. 1986; Kemp et al. 2003) as it is in other desert ecosystems (Strojan et al. 1987). Because surface litter is subject to rapid drying after rainfall, the rate of decomposition of litter in local patches where it accumulates, such as under shrubs, is greater than in adjacent areas of lesser accumulation where it dries quickly (Whitford et al. 1980b, 1982; Parker et al. 1984a). For most species the decomposition of buried litter and roots, largely mediated by microarthropods (Santos et al. 1984), is faster than the rate of disappearance of surface litter, which shows large fluctuations in moisture content (Schaefer et al. 1985).

Litter quality, especially N content, appears to play only a limited role in determining rates of decomposition in desert habitats of the Jornada Basin (Schaefer et al. 1985) and elsewhere in the American Southwest (Murphy et al. 1998). Experimental additions of N had little effect on the decomposition of black grama or creosotebush litter (MacKay et al. 1987a; see also Mun and Whitford 1998).

Among habitats of the Jornada Basin, soil microbial biomass is related to the content of soil organic carbon and extractable N ($NH_4 + NO_3$) (Gallardo and Schlesinger 1992). Fertilization with N increases microbial biomass in grassland soils, whereas additions of C have little effect. In shrublands, fertilization by C increases microbial biomass and decreases extractable N and P, which are immobilized during microbial growth (Gallardo and Schlesinger 1995). In many areas of the Jornada Basin, where shrubs have invaded upland grasslands, the

proportional net decrease of soil organic C exceeds that for soil N, so that soil C/N ratios

decrease and C becomes limiting for microbial biomass as desertification proceeds (Gallardo and

Schlesinger 1992, 1995; Kieft 1994).

Completing the nutrient cycle, the release, or "mineralization," of N from soil organic

materials is closely tied to fluctuations in soil moisture. Fisher et al. (1987) found that small,

frequent experimental applications of simulated precipitation (6 mm/week) caused greater rates

of N mineralization than a larger, infrequent event (25 mm/month), followed by periods of

drought. The mineralization of NH_4^+ proceeds even at relatively low soil water potentials,

presumably due to fungi and bacteria whose activity may extend to soil water potentials of –6 to

–8 MPa (Whitford 1989). Nitrifying bacteria are particularly sensitive to drought (Wetselaar

1968), so the concentration of soil NH_4^+ builds up during the dry season with rapid conversion to

NO_3^- when the summer rains begin (Fisher and Whitford 1995; Mazzarino et al. 1998; Reynolds

et al. 1999a; Hartley and Schlesinger 2000). In wet soils, nitrifying bacteria can deplete the pool

of NH_4^+ more rapidly than it is restored by mineralization, so the nitrification rate, as measured

by NO production, declines with repeated watering (Hartley and Schlesinger 2000).

N mineralization, approximated from estimates of plant uptake, ranges from 28 to 64 kg

N/ha/yr in creosotebush habitats (Whitford and Parker 1989) and where net primary production

(NPP) averages about 139 g/m^2/yr (chapter 11). This estimate of N mineralization is

considerably higher than 6.5 kg N/ha/yr reported for a sparsely vegetated creosotebush desert in

Nevada, where NPP ranges from 20 to 60 g/m^2/yr (Rundel and Gibson 1996). Our estimate of N

mineralization is much lower than 149 kg N/ha/yr reported for habitats dominated by

creosotebush in Argentina (Mazzarino et al. 1991).

Nutrient Budgets for the Jornada Basin

Comparative N budgets for representative plant communities in the Jornada Basin are shown in
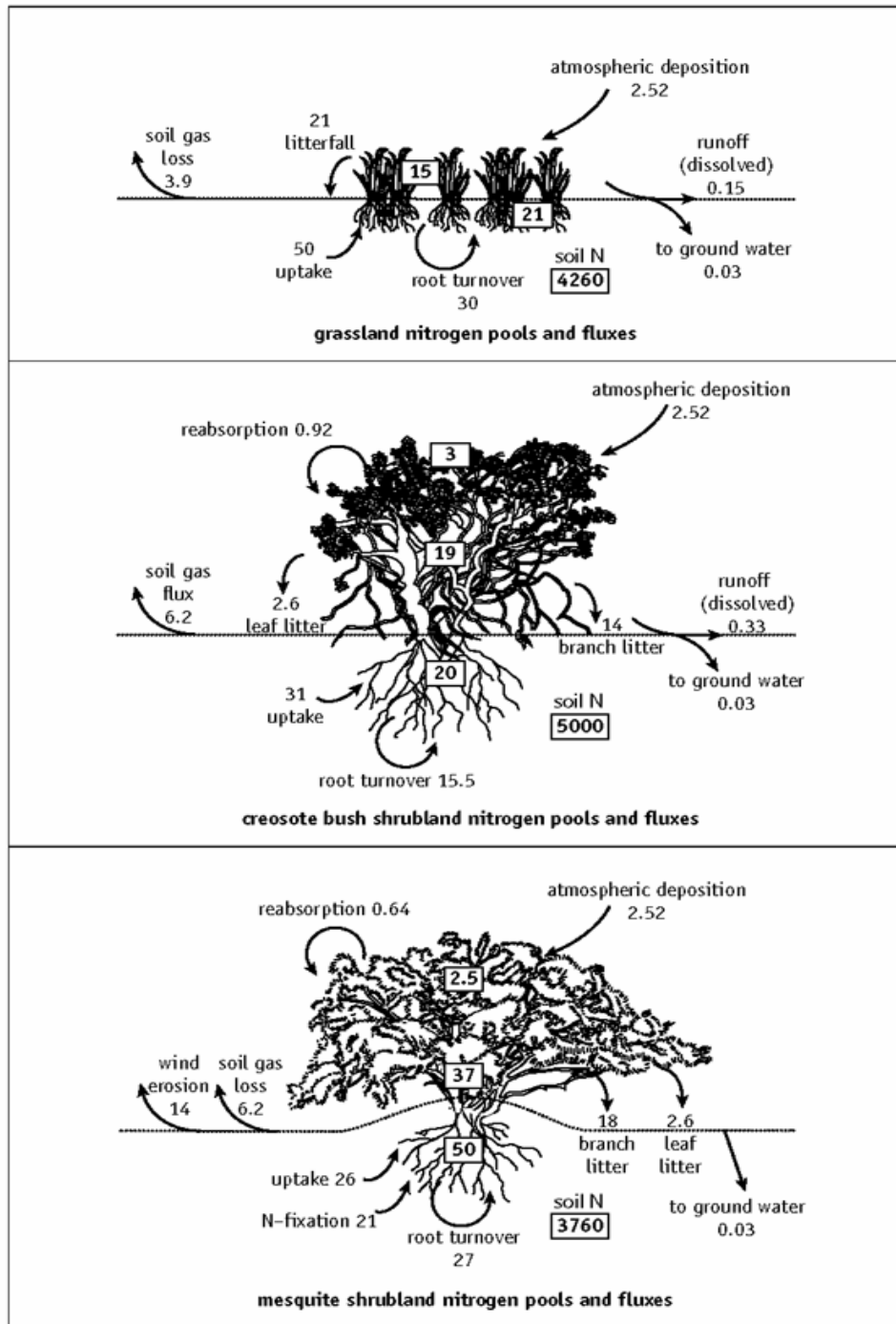
figure 6-6.

Fig. 6-6 Nutrient budgets (pools in kg/ha; flux in kg/ha/yr) for grassland, creosotebush *(Larrea tridentate)* shrubland and mesquite shrubland, as synthesized from the data in this chapter and other sources.

Preparation of these budgets is complicated by the different scales of spatial heterogeneity in biomass and soil characteristics in each community and the need to extrapolate to landscape-scale values using assumptions about the relative cover of vegetation and bare ground. The data in these diagrams are compiled from many sources and constrained to yield a mass balance for the annual intrasystem cycle of the plant community. These should be regarded as rough estimates of nutrient cycling in the Jornada Basin and an impetus for future work.

In all habitats, the pool of N in vegetation is dwarfed by that held in the upper meter of the soil profile with percentages in vegetation ranging from 0.8% in grassland to 2.3% in mesquite shrublands. Despite inputs from N fixation, the soil N pool under mesquite (3,760 kg N/ha) is less than that in grassland (4,260 kg N/ha), whereas that in creosotebush is slightly higher (5,000 kg N/ha). In grassland and creosotebush habitats, the intrasystem cycling of nutrients dominates over new inputs of nutrients from outside the system. For instance, the internal cycle in grasslands provides about 50 kg N/ha/yr for plant uptake versus new inputs of < 3 kg N/ha/yr. In contrast, in mesquite the input of N from N fixation provides 48% of the N uptake (Lajtha and Schlesinger 1986). If estimates of N uptake by plants are used as a proxy for mineralization rates, grasslands have a mineralization rate that is roughly double that of the shrubland habitats that have replaced them over much of the Jornada Basin. Mesquite, through its reliance on N fixation, is less dependent on N derived from soil microbial mineralization and shows the lowest rate of N uptake from the soil.

The rapid rate of N mineralization in grasslands is associated with a higher rate of biomass turnover in grasslands than in the shrubland habitats. Overall, the biomass turnover is quite rapid in Chihuahuan Desert ecosystems, with mesquite having the longest mean residence time for N in biomass—about two years. In all habitats, turnover of N in roots is greater than or equal to that of aboveground components, and the percentage turnover of N in roots is greatest in grasslands where

the mean residence time for N in roots is < 1 year. In each habitat, only a small fraction of the total annual demand for N is satisfied by internal plant cycling (i.e., nutrient resorption) which increases nutrient-use efficiency.

The budgets presented in figure 6-6 reflect the local geomorphology that typically characterizes each community. For example, creosotebush tends to dominate coarse soils on the bajada slopes of the Jornada Basin, so estimates of the runoff losses of N are derived from field studies in plots located on those slopes (Schlesinger et al. 2000). Runoff losses are also included for adjacent plots in grassland, but many of the grasslands in the Jornada Basin are found on relatively flat ground with little long-distance overland flow. The budget for mesquite does not include a runoff component because mesquite dunelands normally show only a local redistribution of materials between shrub mounds and the local shrub interspace (Parsons et al. 2003). Eolian losses of N are shown only for mesquite, which is the only major habitat showing net removal of materials by wind in the Jornada Basin (chapter 9,).

Given similar topography, there is greater N loss through runoff in shrub-invaded systems (Schlesinger et al. 2000). These systems are more susceptible to runoff because there is less total plant cover to intercept rainfall and to prevent erosion and scouring by wind and water. With larger plants and gaps between plants, flow paths are connected over longer distances (Howes and Abrahams 2003). There are also greater gaseous losses of N in shrublands through higher denitrification rates (Peterjohn and Schlesinger 1991; Hartley 1997). Thus our comparison of the N cycle in shrubland and grassland communities shows that areas invaded by shrubs have greater N losses even though shrubland landscapes appear to sequester equivalent or greater amounts of soil N (Jackson et al. 2002). Desertified areas may be more sensitive to further disturbance and nutrient loss

because the ability of shrubs to conserve nutrients is reduced compared to that of the uninvaded

grassland.

Desertification of Grasslands and Remediation of Shrublands

Redistribution of Soil Nutrients with Desertification

In southern New Mexico, desertification is associated with the loss of grassland, dominated by black

grama, and the invasion of desert shrubs, primarily mesquite and creosotebush (Buffington and

Herbel 1965; see also chapter 10). Huenneke et al. (2002) report similar levels of NPP in grassland

and shrubland communities but much higher spatial variation in the distribution of NPP and biomass

in shrublands (chapter 11). On a landscape-scale, the mass of soil nutrients in shrublands is similar

or higher than that in grasslands (Kieft et al. 1998; Cross and Schlesinger 1999; Hibbard et al. 2001;

Jackson et al. 2002), but the spatial distribution of the soil nutrients contrasts strongly between these

communities. Table 6-1 shows only a minor (4%) change in the estimated N pool of the Jornada

Basin ecosystem between 1858 and 1963.

Table 6-1. Net Nitrogen balance at the Jornada Experimental Range by vegetation type, 1858-1963.

Vegetation Type	Biomass Nitrogen (kgN/ha)	Soil Nitrogen (kgN/ha)[a]	Total Ecosystem Nitrogen (kgN/ha)	Year	Areal Extent (ha)[b]		Regional N Pool (10^8 kg)	
					1958	1963	1958	1963
Grassland	36	4260	4300		33800	0	1.45	0
Mesquite Shrubland	90	3760	3850		15500	37800	0.6	1.45
Creosotebush Shrubland	42	5000	5040		400	7500	0.02	0.38
Tarbush Shrubland	82	7870	7950		8700	13100	0.69	1.04
Total					58400	58400	2.76	2.87

[a] To one meter depth
[b] from Buffington & Herbel (1965)

Thus, desertification is not so much associated with a loss of biotic productivity as with the redistribution of soil resources on the landscape (Schlesinger et al. 1990, 1996) that increases the scale of patchiness (Hook et al. 1991; Tongway and Ludwig 1994). Lower NPP is the expected and traditional outcome of arid land degradation, but changes in the spatial distribution of soil resources may be a more effective index of desertification.

Resource islands develop as a function of shrub age (Facelli and Brock 2000; Shachak and Lovett 1998). Large shrub mounds are partly erosional and partly depositional features (Abrahams and Parsons 1991; Abrahams et al. 1995). In the Jornada Basin, ^{137}Cs profiles reveal that soil has accumulated under mesquite shrubs and been removed from interdune areas. In grasslands, the ^{137}Cs data show much less soil redistribution (Ritchie et al. 2003). In an area recently invaded by shrubs in southeastern Arizona, the soil mound contained buried remnants of the surface (A) horizon of the former grassland soil and between the shrubs, the A horizon had been eroded (Parsons et al. 1992). Rainsplash, mediated by the dissipation of raindrop energy in the shrub canopy, results in a net transport of soil fines from interspaces to shrub mounds (Parsons et al. 1992). Wind erosion also redistributes soil materials across the landscape where they are caught by shrub canopies and accumulate in the soil mounds beneath shrubs (Coppinger et al. 1991). Digging by rodents, especially kangaroo rats (*Dipodomys*), redistributes soil materials in desert landscapes, leading to patches of fertility that may become preferred sites for the establishment of annual plants and shrub seedlings (Moorhead et al. 1988; Mun and Whitford 1990; Chew and Whitford 1992; Whitford 1993; Ayarbe and Kieft 2000). The capture of soil particles adds C and N to the soil mounds that develop beneath desert shrubs (Shachak and Lovett 1998).

Once established, shrubs further enrich the nutrient content of soils beneath their canopy through autogenic, biological processes that help ensure the persistence and regeneration of the

shrub ecosystem (Schlesinger et al. 1990). Biotic processes leading to the development of islands of

fertility include plant uptake of essential nutrients from the soils of the interspace followed by the

deposition of litter in the localized areas beneath shrubs. Thus shrubs appear to "mine" nutrients

from the soils of the interspace (Garner and Steinberger 1989), which may support a cryptobiotic

crust of algae, fungi, and soil bacteria that fix N (West 1990; Evans and Johansen 1999). Shrubs,

such as acacia (*Acacia* ssp.) and mesquite, which maintain symbiotic, N-fixing bacteria in their

rooting system, directly contribute to the accumulation of N beneath their canopy (Garcia-Moya and

McKell 1970; Gerakis and Tsangarakis 1970; Tiedemann and Klemmedson 1973; Virginia and

Jarrell 1983; Lajtha and Schlesinger 1986; Wright and Honea 1986). Despite occasional

observations of hydrophobic layers in the soils under shrubs, including creosotebush (Adams et al.

1970), infiltration rates are typically higher under desert shrubs as a result of better soil crumb

structure and a lower impact energy of raindrops (Lyford and Qashu 1969; Bach et al. 1986;

Rostagno 1989; Shachak and Lovett 1998; Schlesinger et al. 1999; Wainwright et al. 1999a, 2000;

see also chapter 5). A number of desert shrubs also funnel nutrient-rich stem flow waters to the soil

beneath their canopy (Navar and Bryan 1990; Mauchamp and Janeau 1993; Martinez-Meza and

Whitford 1996; Whitford et al. 1997; see also chapter 8).

In the Jornada Basin, extractable N, P, and K are strongly concentrated under creosotebush

shrubs, whereas Na, Li, and Sr are more concentrated in the soils between shrubs, suggesting that

physical processes, such as runoff, lead to localized accumulations of some nonessential elements in

intershrub spaces and biological processes are more important in concentrating biologically essential

elements under shrubs (Schlesinger et al. 1996). In similar Chihuahuan Desert habitats at the

Sevilleta National Wildlife Refuge, 300 km north of the Jornada Basin, Cross and Schlesinger

(1999) found no spatial variations in the concentration of various soil nutrients in grassland habitats

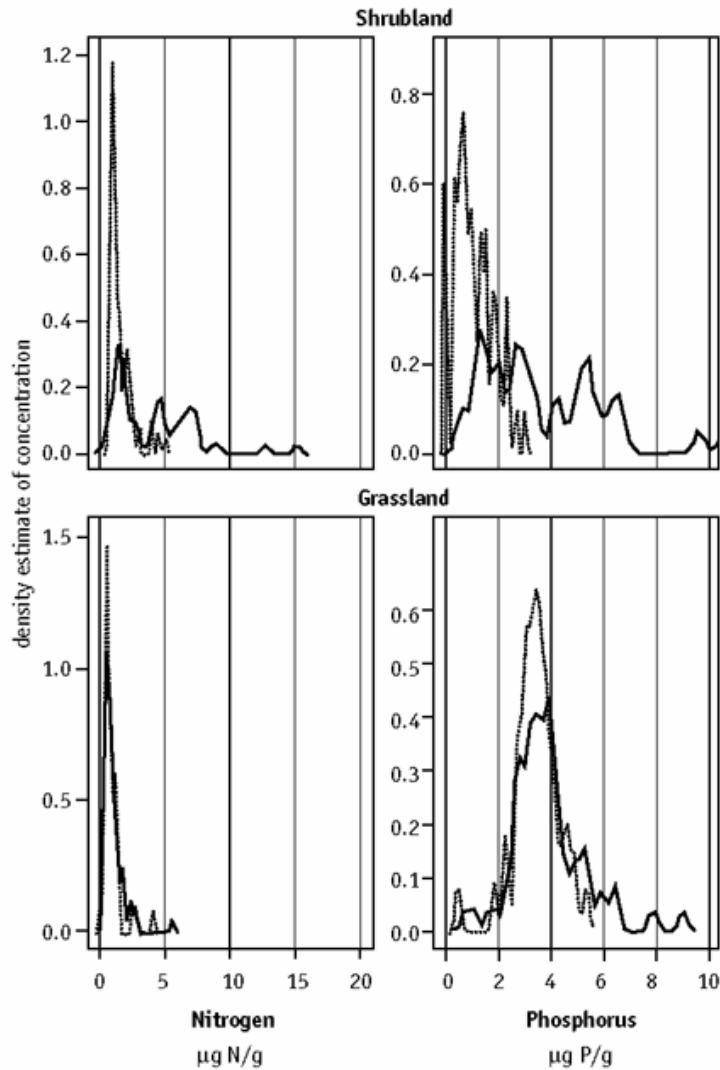but strong accumulations of N, P, and K under creosote bushes (figure 6-7).

Fig. 6-7. Frequency histogram for the concentration of available N and
water-soluble P in soils from adjacent grassland and shrubland sites at the Sevilleta
National Wildlife Refuge, New Mexico. In each graph, the solid line is for samples
taken under vegetation

Frequency distributions for the occurrence of soil nutrients at the Sevilleta show that N and P are concentrated in shrub islands at levels above those found in adjacent grasslands so that the islands of fertility are not simply a remnant left after erosion (see Kieft et al. 1998).

Concentrations of nutrients in the islands of fertility are greatest at the soil surface and attenuate with depth (Nishita and Haug 1973; Charley and West 1975; West and Klemmedson 1978; Rostagno et al. 1991). High surface concentrations of K have been attributed to the deposition of illite in eolian materials (Singer 1989), but surface accumulations of K are undoubtedly enhanced by nutrient cycling and mineral weathering under shrubs (Rostagno et al. 1991; Kelly et al. 1998). In contrast, the concentrations of nonessential ions (e.g., Na and Cl) or nonlimiting elements (e.g., Ca and SO_4^{2-}) tend to increase with depth due to periodic leaching (Yaalon 1965; Schlesinger et al. 1989). The depth to the peak concentration of various solutes in desert soils follows the global pattern reported by Jobbágy and Jackson (2001) from shallowest to deepest in the order $P < K < Ca < Mg < SO_4 = Na = Cl$. This vertical pattern mirrors the horizontal pattern extending from shrubs to the shrub interspaces (Schlesinger et al. 1996).

When shrubs are removed by cutting, herbicides, or fire, N, P, and other soil nutrients are lost from former islands of fertility. Elimination of the local biogeochemical cycle associated with shrubs allows physical processes to disperse soil nutrients across the landscape. The redistribution of N seems to be more rapid than that of P, likely due to more rapid gaseous and soluble losses of N and retention of P by adsorption to soil minerals. Thirteen years after the removal of mesquite there was a significant loss of soil N from former shrub islands, but there were no significant changes in P or S over the same period (Tiedemann and Klemmedson 1986). Similarly, in Australia, Facelli and Brock (2000) found that P-rich spots persisted for 50 years after the death of Western myall (*Acacia papyrocarpa*), but N was lost rapidly from former shrub islands. At the JER, Virginia (unpublished

data) observed a degradation of the N pool in shrub islands within 15 years after spraying mesquite with herbicides.

Recovery of desert shrub vegetation on cleared areas is most rapid when the original soil conditions, such as the islands of fertility, remain intact. Wallace et al. (1980) found more than twice as much shrub biomass regenerated on bare, undisturbed desert soils compared to plowed, disked, or scraped soils after 20 years of plant succession in the Mojave Desert. When land managers wish to reestablish shrub-dominated vegetation on soils that have been homogenized by human activities, such as cultivation or construction, they must consider creating heterogeneity in soils by artificial means (Boeken and Shachak 1994; Shachak and Lovett 1998). Similarly, conversion of shrubland to grassland involves consideration of redistributing resources into finer scale patchiness. Otherwise, transitions of shrub-dominated states on these lands can be extremely slow (e.g., Carpenter et al. 1986; McAuliffe 1988; see also chapter 14).

Conclusions

In the Chihuahuan Desert, water and N limit net primary production. Water is delivered in pulses, interspersed with dry periods, which uncouple soil nutrient cycling processes from plant uptake and allow more opportunity for redistribution or export of nutrients. Water, wind, and animals transport nutrients, creating strong spatial patterns of resources, influenced by the interactions of climate, topography, soils, and vegetation. In desert shrublands, redistribution of resources creates distinct islands of fertility around shrubs, separated by depleted interspaces.

N inputs are relatively small compared to other deserts. Biological soil crusts are poorly developed, but symbiotic N fixation is significant in mesquite shrublands. Outputs of N are relatively large, especially via wind and water erosion from shrublands. Leaching below the root zone is infrequent and much less important than gaseous losses. Plant uptake of nutrients is enhanced by

mycorrhizae and fungal endophytes and controlled by temperature and water availability.

Decomposition is rapid, but not strongly related to water availability or C/N ratio of the substrate.

Termites are especially important in speeding the decomposition of surface litter and some photo-oxidation also occurs. Decomposition of subsurface litter is mainly by fungi and bacteria, mediated by microathropods, and are more strongly influenced by soil moisture.

In grasslands, N cycling is relatively faster with lower outputs and proportionally greater internal fluxes between plants and soil. In contrast, Shrublands have greater aboveground biomass, deeper roots, smaller internal fluxes, and greater outputs. Wind is more important in exporting N from sandy mesquite shrubland, whereas water is more important in exporting N from upslope creosotebush shrubland. N fixation by mesquite reduces dependence on soil N and allows increased N concentration in biomass, providing more opportunity for N accumulation under the shrub and more N export in litter and soil.

Conversion of grassland to shrubland in the northern Chihuahuan Desert is accompanied by redistribution of nutrients at the scale of the plant/interspace, which often promotes increased output of nutrients at the patch scale and sometimes, longer distance transport of nutrients at the landscape scale (chapters 7 and 9). Restoration or remediation of landscapes in the Chihuahuan Desert (Chapter 14) could be improved by understanding, accommodating, and possibly managing the redistribution of resources.