

Plant–soil interactions in deserts

WILLIAM H. SCHLESINGER^{1,2,*} & ADRIENNE M. PILMANIS¹

¹Department of Botany, Duke University, Durham, N.C. 27708, USA; ² Division of Earth and Ocean Sciences, Nicholas School of the Environment, Duke University (* Corresponding author: schlesin@acpub.duke.edu)

Key words: aridisols, desertification, erosion, geostatistics, *Larrea tridentata*, nitrogen, phosphorus, *Prosopis glandulosa*, soil heterogeneity

Abstract. Geostatistical analyses show that the distribution of soil N, P and K is strongly associated with the presence of shrubs in desert habitats. Shrubs concentrate the biogeochemical cycle of these elements in ‘islands of fertility’ that are localized beneath their canopies, while adjacent barren, intershrub spaces are comparatively devoid of biotic activity. Both physical and biological processes are involved in the formation of shrub islands. Losses of semiarid grassland in favor of invading shrubs initiate these changes in the distribution of soil nutrients, which may promote the further invasion and persistence of shrubs and cause potential feedbacks between desertification and the Earth’s climate system.

Introduction

Where arid environments are dominated by shrub 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’ characterize desert habitats on all continents, but they are particularly well described in the American Southwest. Recently, Schlesinger et al. (1996) used geostatistics to compare the scale of soil heterogeneity in arid habitats dominated by shrubs and in adjacent areas of semiarid grassland. A near-random distribution of extractable nitrogen was found in grassland soils, but in deserts dominated by *Larrea tridentata*, the distribution of soil N was markedly autocorrelated at a scale close to the average size of shrubs (Figure 1).

Patchy distributions of microbial biomass (Mazzarino et al. 1991; Gallardo & Schlesinger 1992; Smith et al. 1994; Herman et al. 1995), nematodes (Freckman & Mankau 1986), and microarthropods (Santos et al. 1978) reflect the heterogeneous distribution of soil nutrients in deserts. The patchy habitat created by shrubs also determines the biodiversity of animals at higher trophic levels, including lizards and birds (Pianka 1967; Naranjo & Raitt 1993). Indeed, most ecosystem function in shrub deserts is localized under vegeta-

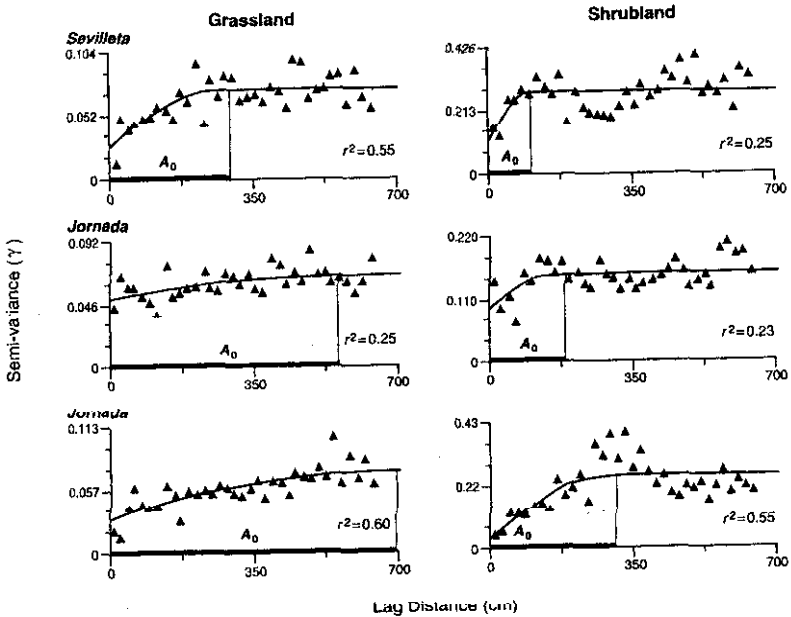


Figure 1. Spherical model semivariograms for the distribution of available N in grassland and desert soils at the Sevilleta National Wildlife Refuge ($n = 1$ each) and the Jornada Experimental Range ($n = 2$ each), in the Chihuahuan Desert of New Mexico. The range of spatial dependence or autocorrelation is designated as A_0 in each panel. From Schlesinger et al. (1996).

tion, while the adjacent shrub interspaces are comparatively devoid of biotic activity.

Origins of islands of fertility in desert shrublands

Despite widespread observations of shrub islands in deserts, we have only a limited understanding of their dynamics – including processes leading to their formation and degradation. Biotic processes, such as the deposition of plant litter beneath the shrub canopy, are certainly involved, but the potential contributions of abiotic processes, such as soil erosion, are less frequently investigated. Coppinger et al. (1991) examined the distribution of ^{137}Cs in a semiarid steppe, concluding that wind erosion redistributes soil materials across the landscape, where they are caught by shrub canopies and accumulate in the soil mounds beneath shrubs. Working in an area of southeastern Arizona where grasslands have recently been invaded by shrubland, Parsons et al. (1992) suggested that differential rainsplash, mediated by the dissipation of raindrop energy in the shrub canopy, resulted in a net transport of soil fines from interspaces to shrub mounds. Under many of the larger shrubs, the soil

mound contained remnants of the surface (A) horizon of the former grassland soil. Between the shrubs, the A-horizon had been eroded when the grassland was replaced by shrubland. Thus, the large mounds were partly erosional and partly depositional features (Abrahams & Parsons 1991; Abrahams et al. 1995).

Biotic processes leading to the development of islands of fertility include plant uptake of essential nutrients, followed by the deposition of litter in the localized areas beneath shrubs. In some areas, shrubs appear to 'mine' nutrients from the soils of the interspace (Garner & Steinberger 1989), where the bare soils may support a cryptobiotic crust of algae, fungi and soil bacteria that fix nitrogen (West 1990). Some desert shrubs, such as acacia (*Acacia* spp.) and mesquite (*Prosopis glandulosa*) maintain symbiotic nitrogen-fixing bacteria in their rooting system, contributing to the accumulation of nitrogen beneath their canopy (Gerakis & Tsangarakis 1970; Garcia-Moya & McKell 1970; Tiedemann & Klemmedson 1973; Virginia & Jarrell 1983; Lajtha & Schlesinger 1986; Wright & Honea 1986). A number of desert shrubs also funnel nutrient-rich stemflow waters to the soil beneath their canopy (Návar & Bryan 1990; Mauchamp & Janeau 1993; Martinez-Meza & Whitford 1996; Whitford et al. 1997). Digging by rodents, especially kangaroo rats, 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 (Mun & Whitford 1990; Chew & Whitford 1992; Whitford 1993).

Development of horizontal pattern in desert soils

Schlesinger et al. (1996) attempted to distinguish the importance of biotic versus abiotic processes leading to the formation of shrub islands by comparing the spatial pattern of various elements in the surface horizon of desert soils. If biotic processes were solely responsible, then only the elements essential to biochemistry should be concentrated under shrub canopies, while non-essential elements, such as Na, Li, Sr, and Cl, should be distributed randomly (cf. Garner & Steinberger 1989). Support for this hypothesis was equivocal: extractable N, P and K were strongly concentrated under shrubs in all desert habitats, but so was Cl in 4 of 6 cases. Sodium, Rb, Li, and Sr were frequently more concentrated in the soils *between* shrubs, suggesting that physical processes lead to localized accumulations of some non-essential elements in deserts – in this case in the intershrub spaces.

Frequency distributions for the occurrence of soil nutrients at the Sevilleta National Wildlife Refuge in New Mexico show that N, P, K and Cl are concentrated in shrub islands at levels above those found in adjacent grasslands, so that the 'islands of fertility' are not simply a lag deposit left by erosion

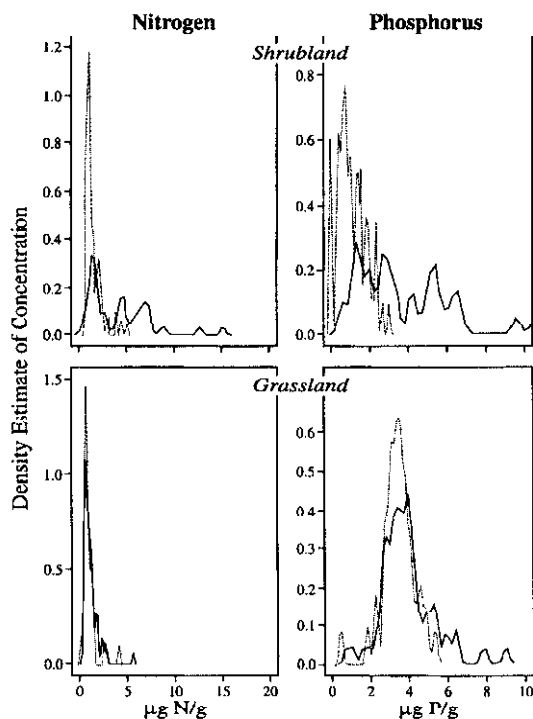


Figure 2. Frequency histogram for the concentration of available N and water-soluble P in soils from adjacent grassland and shrubland sites at the Sevilleta National Wildlife Refuge, New Mexico. In each graph, the solid line is for samples taken under vegetation and the dashed line is for samples taken between vegetation. From the data reported by Schlesinger et al. (1996).

(Figure 2). Although islands of fertility are well developed for N and P in nearly all shrublands, Schlesinger et al. (1996) found that localized patches of high Cl concentration were more striking in shrub islands in the Mojave desert, where shrubs have persisted for 1000s of years, than in the Chihuahuan desert, where shrubs have invaded recently. Compared to the rapid accumulation of N and P by biotic processes, the accumulation of Cl in shrub islands may occur relatively slowly, perhaps carried passively in the mass-flow of water driven by plant transpiration. Working in an *Artemisia* shrubland in Idaho, Ryel et al. (1996) found that seasonal changes in the spatial autocorrelation for soil nitrogen, the most limiting soil nutrient in their ecosystem, were greater than for P and K, which were more abundant in the soil.

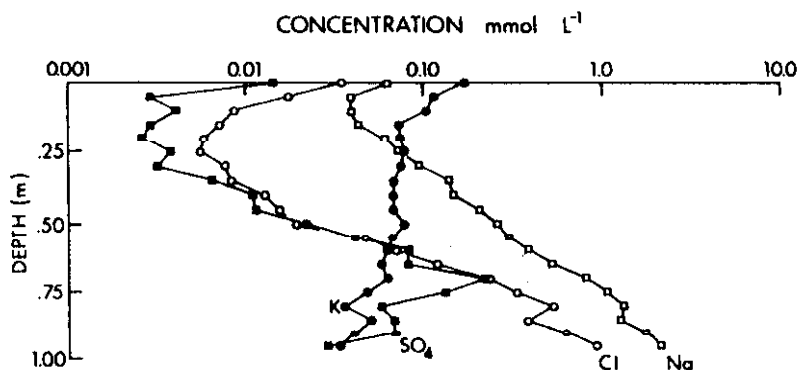
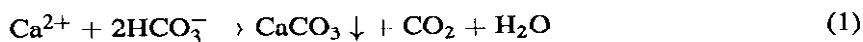


Figure 3. Depth distribution of K, Na, Cl and SO_4 at 5-cm intervals in a soil profile sampled in the southern Mojave Desert. From Schlesinger et al. (1989).

Development of vertical pattern in desert soils

Vegetation also has a strong effect on the vertical dimensions of the soil profile in deserts. Concentrations of nutrients in the 'islands of fertility' are greatest at the soil surface and attenuate with depth (Nishita & Haug 1973; Charley & West 1975; West & Klemmedson 1978; Rostagno et al. 1991). High surface concentrations of K have been attributed to the deposition of illite in aeolian materials (Singer 1989), but this process is undoubtedly enhanced by nutrient cycling and mineral weathering under shrubs (Rostagno et al. 1991; Kelly et al., this volume). In contrast, the concentrations of non-essential ions (e.g., Na and Cl) or non-limiting elements (e.g., Ca and SO_4^{2-}) tend to increase with depth (Yaalon 1965, Figure 3).

At some depth, usually related to mean maximum infiltration of rainfall, Ca is deposited as calcium carbonate in calcic horizons, informally known as caliche in many arid soils (Arkley 1963). The process is enhanced by the removal of soil water by plant roots and retarded by the maintenance of high CO_2 in the soil atmosphere due to respiration of roots and soil microbes (Marion et al. 1985). The relevant equation is:



Carbonate is precipitated most rapidly during seasonal periods of drought which simultaneously lower both soil moisture and root activity (Schlesinger 1985). The precipitation of calcite may be inhibited by the presence of dissolved organic compounds that lower the ion activity of calcium in the soil solution (Reynolds 1978; Suarez & Rhoades 1982; Inskeep & Bloom 1986; Reddy et al. 1990; Marion et al. 1990). Calcic horizons are found at

greater depth beneath the soil mounds of desert shrubs than in the shrub interspaces (Wallace & Romney 1972, p. 308), and at greater depth in semiarid grasslands compared to arid shrublands (Hallmark & Allen 1975).

Because CO_2 in the soil pore space is derived from plants, the isotopic composition of the carbon in pedogenic calcite is easily traced to a photosynthetic origin. Changes in the isotopic ratio of soil carbonates can be used to record the past distribution of C-3 versus C-4 plants in arid lands (Amundson et al. 1989; Quade et al. 1989a). The oxygen isotope composition in calcite is related to the $\delta^{18}\text{O}$ in incident rainfall and the proportion of water that is lost from the soil profile by evaporation vs. plant transpiration (Cerling 1984; Quade et al. 1989b).

The deposition of pedogenic calcite also affects the availability of phosphorus in arid soils, where much of the P may be bound to calcium minerals (Lajtha & Bloomer 1988; Marion & Babcock 1977). In response to potential phosphorus deficiency, desert plants appear to have special adaptations to extract P from these soils (Lajtha & Schlesinger 1988) and to retranslocate P efficiently from senescent foliage (Lajtha 1987). A small amount of phosphorus held in organic forms may be critical to the biogeochemical cycle of phosphorus in arid soils (Cross 1994). Often, organic- and bicarbonate-extractable P – forms easily available for plant uptake – are concentrated beneath the canopy of shrubs, while Ca-bound P is greatest in the shrub interspace (Charley & West 1975; Cross 1994).

Changes in soil nutrients with desertification

The 1994 United Nations Convention on Desertification defines desertification as 'land degradation in arid, semiarid, and dry subhumid areas, resulting from various factors including climatic variations and human activities.' In southern New Mexico, desertification is associated with the loss of semiarid grassland, dominated by black grama (*Bouteloua eriopoda*) and the invasion of desert shrubs, primarily mesquite (*Prosopis glandulosa*) and creosotebush (*Larrea tridentata*) (Buffington & Herbel 1965). Here, 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).

Our emphasis on the heterogeneous pattern of soil nutrients in shrub deserts is not to say that the distribution of soil nutrients in semiarid grasslands is homogeneous, but rather that the scale of patchiness in grasslands is much smaller than that seen in desert shrublands (Hook et al. 1991; Tongway & Ludwig 1994). Working at the Jornada Experimental Range in southern New Mexico, Pilmanis and Schlesinger (1998) sampled soil nitrogen at four sites in a grassland showing progressive invasion by mesquite, and they applied

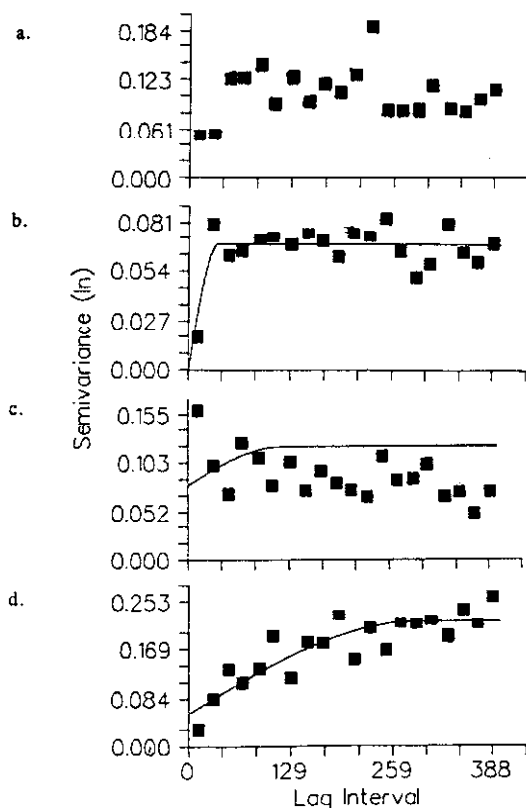


Figure 4. Spherical model semivariograms for available nitrogen at 4 sites representing a gradient from grassland (A) to a mesquite-dominated shrubland (D) at the Jornada Experimental Range in southern New Mexico. From Pilmanis and Schlesinger (1998).

geostatistics to deduce the scale of patchiness in each habitat. At the scale of their sampling, a random distribution of available nitrogen was found in the grassland (Figure 4). With the invasion of shrubs, the distribution of soil nitrogen became patchy, showing a progressive autocorrelation of values at distances in a range of 20 to 260 cm – typical of the mean diameter of mesquite in these shrublands. Over 70% of the total variance in soil nitrogen was associated with the presence of shrub islands. Thus, the invasion of shrubs changed the scale of patchiness from a fine-grained pattern in grasslands to a coarse-grained pattern in shrublands.

Allogenic factors, for instance kangaroo rats and grazing cattle, that lead to the development of patches of fertility in grasslands may promote the invasion of shrubs (Afzal & Adams 1992; Chew & Whitford 1992), since local areas of high fertility are likely to be favored sites for shrub regeneration. A reduction in the density of grass or the formation of a gap in the grass canopy seem

essential for *Prosopis* to establish (Bush & Van Auken 1989, 1995). Once established, however, the shrubs enrich the nutrient content of soils beneath their canopy through autogenic, biological processes that may help to ensure the persistence and regeneration of the shrub ecosystem (Schlesinger et al. 1990).

Degradation of shrub islands

In study plots near Portal, Arizona, Jim Brown and his colleagues have removed kangaroo rats from plots of desert scrub since 1977. While the shrubs persist, these areas have been invaded by an annual grass, *Aristida adscensionis*, and an exotic perennial bunchgrass, *Eragrostis lehmanniana* (Brown & Heske 1990; Heske et al. 1993). In the summer of 1994, we sampled these plots, and adjacent control areas, with the geostatistical design used by Schlesinger et al. (1996) to see if the removal of kangaroo rats and the associated invasion of grasses affected the distribution of soil nutrients. As in other areas of desert scrub, extractable N, P and Cl were significantly more concentrated under the canopy of shrubs in control plots (Table 1) and autocorrelated at a range of values (51 to 262 cm) similar to the range of shrub diameters. The removal of kangaroo rats and the invasion of grasses had little effect on the distribution of soil N, but the concentrations of P and Cl became random or autocorrelated over very large distances (>300 cm), clearly not associated with shrubs. Thus, the removal of kangaroo rats and the appearance of grasses acted to disperse these nutrients from a local patchy distribution in surface soils.

In other experiments, in which shrubs have been removed by cutting, herbicides or fire, the islands of fertility have shown variable rates of degradation. Tiedemann and Klemmedson (1986) reported a significant loss of soil N from former shrub islands, 13 years after the removal of mesquite, but there were no significant changes in P or S over the same interval. At the Jornada Experimental Range, Virginia (unpublished) also observed a degradation of the nitrogen pool in shrub islands 15 years after spraying mesquite with herbicides. Burke et al. (1987) found that 14 years after the removal of sagebrush (*Artemisia tridentata*) from a semiarid rangeland in Wyoming, the rate of nitrogen mineralization was similar among samples located beneath the 'skeletons' of former shrubs and in areas of former shrub interspace. Halvorson et al. (1997) reported that the high concentrations of total and mineralizable nitrogen under former *Artemisia* had largely disappeared one decade after burning of a site in southern Washington. In each of these cases, a loss of the local biogeochemical cycle associated with shrubs has allowed physical processes to disperse soil nutrients across the landscape.

Table 1. Comparison of the concentration and spatial distribution of soil elements in 'control' and kangaroo-rat removal plots ($n = 2$ each) near Portal, Arizona.

Element	Ratio of mean concentration under vs. between shrubs		Range of autocorrelation in spherical semivariogram (cm)	
	Control	Removal	Control	Removal
N _{avail}	1.98*	1.60	259	87
	1.71*	2.30*	262	264
PO ₄	2.08*	1.28	150	>300
	1.33*	2.01	108	>300
Cl	2.88*	1.27	237	>300
	1.44*	1.69	51	>300
Na	0.79	1.42	>300	>300
	1.52	0.85	>300	>300
Li	0.80*	0.92	>300	>300
	0.95	0.82	65	201

* difference between under vs between shrub positions is significant ($P < 0.05$) using a t -test.

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 soils as on 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 & Shachak 1994). Otherwise, plant succession on these lands can be extremely slow (e.g., McAuliffe 1988; Carpenter et al. 1986; *New York Times*, April 21, 1992 p. B9).

Shrub islands and ecosystem function

The spatial heterogeneity of soil fertility associated with shrubs controls the movement and transformations of water, nitrogen, and other nutrients in arid ecosystems. Despite occasional observations of hydrophobic layers in the soils under shrubs, including *Larrea tridentata* (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 & Qashu 1969; Bach et al. 1986; Rostagno 1989). When shrubs replace semiarid

grasslands, the rate of erosion increases as the surface soil materials are progressively lost from the barren shrub interspaces (Bull 1979; Abrahams et al. 1994, 1995; Gutierrez & Hernandez 1996). Wood et al. (1987) concluded that total ground cover was the most important variable influencing infiltration and sediment production on desert rangelands in southern New Mexico. When shrubs are widely spaced, the barren intershrub soils may be subject to wind erosion that redistributes soil materials across the landscape (Snow & McClelland 1990; Stockton & Gillette 1990).

Higher levels of microbial biomass are found under shrubs compared to barren shrub interspaces (Gallardo & Schlesinger 1992; Kieft 1994; Herman et al. 1995). Greater microbial activity is manifest in high rates of nitrogen mineralization and nitrification under shrubs (Charley & 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 nitrogen-rich desert soils, the emission of these gases is a dominant part of the biogeochemical cycle (West & Skujins 1977; Westerman & Tucker 1979; Virginia et al. 1982), but in many cases, the shrubs may act to conserve nitrogen by its immobilization in the litter and microbial biomass of soil mounds (Peterjohn & Schlesinger 1991; Schlesinger & Peterjohn 1991; Gallardo & Schlesinger 1992; Zaady et al. 1996). In areas of southern New Mexico, where semiarid grasslands have been invaded by shrubs, the proportional loss of soil organic matter exceeds that for soil nitrogen, so that soil C/N ratios decrease and carbon becomes limiting for microbial biomass as desertification proceeds (Gallardo & Schlesinger 1992, 1995).

The redistribution of soil nutrients that accompanies shrub invasion of grasslands is not so much associated with a loss of biotic activity as with its reconfiguration on the landscape. At the Jornada Experimental Range, the total ecosystem content of organic carbon differs little between grassland and shrubland habitats; when shrubs invade grasslands, the organic carbon that is lost from the soils is roughly balanced by the organic carbon that accumulates in shrubs (Table 2). Huenneke et al. (in prep.) report similar levels of NPP in grassland and shrubland communities, with much higher spatial variation in the distribution of NPP and biomass in shrublands (Phinn et al. 1996). 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 (Schlesinger et al. 1990, 1996; Pilmanis & Schlesinger 1997).

Table 2. Net ecosystem carbon balance at the Jornada Experimental Range, 1858–1963, excluding carbon held as soil carbonates.

Vegetation type	Biomass carbon (g C m ⁻²) ^a		Soil organic carbon (g C m ⁻²) ^{b,e}	Total ecosystem carbon (g C m ⁻²) ^b	Areal extent ^f (× 10 ⁴ m ²)		Regional carbon pool (× 10 ¹⁰ g)	
	Aboveground ^c	Total ^d			1858	1963	1858	1963
Grassland	131	190	2,112	2,302	33,800	0	77.8	0
Mesquite shrubland	129	235	1,804	2,039	15,500	37,000	31.6	77.1
Creosote shrubland	102	159	1,929	2,088	400	7,500	0.8	15.7
Tarbrush shrubland	82	119	4,824	4,943	8,700	13,100	43.1	64.8
Total					58,400	58,400	153.3	157.6

^a Dry plant biomass is assumed to contain 50% carbon.

^b To one meter depth.

^c Mean peak annual aboveground biomass in 3 sites of each type during 1989–1992 (Huenneke, in prep).

^d Aboveground biomass was converted to total biomass using root/shoot ratios of 1.45 for black grama from J. Baggs (pers. comm) and data for shrubs given by Ludwig et al. (1975).

^e Mean soil nitrogen in 49 samples in 3 sites of each type (Virginia et al., unpublished data), converted to carbon using a bulk density of 1.45 g/cm³ and the C/N ratios of Gallardo and Schlesinger (1992).

^f Community grouping based on species dominance. From Buffington and Herbel (1965).

Global feedbacks

The changes in soils that accompany the invasion of semiarid grasslands by desert shrubs extend well beyond the local redistribution of plant nutrients. Barren lands and barren soils between shrubs are subject to wind erosion, contributing to aerosols in the atmosphere (Fryrear 1995). Arid lands are a significant source of tropospheric dust, and human disturbances of arid-land soils may have increased wind erosion by a factor of 50% globally during the past century (Schütz 1980; Tegen et al. 1996). Terrestrial dusts exert negative radiative forcing – i.e., they cool the atmosphere – over the oceans. Mineral aerosols appear to have variable forcing on the atmosphere over land [see Ackerman and Chung (1992) versus Sokolik and Toon (1996)]. In any case, an increasing flux of desert dust offers a potential feedback between desertification and future global climate as predicted by general circulation models (Tegen & Fung 1995).

The global transport of desert dust is implicated as a source of P and Fe for the growth of marine phytoplankton (Talbot et al. 1986; Duce & Tindale 1991) and tropical rainforests (Swap et al. 1992). Alkaline soil dusts and NH_3 volatilized from arid soils control the acidity of rainfall in the regions downwind of deserts (Loye-Pilot et al. 1986; Young et al. 1988; Gillette et al. 1992; Schlesinger & Hartley 1992; Roda et al. 1993; Sequeira 1993). Changes in the flux of desert dust between glacial and interglacial periods may have affected a large number of global biogeochemical properties, including the uptake of carbon dioxide by the oceans (Martin 1990; Coale et al. 1996) and changes in the global water cycle (Yung et al. 1996). If the area of deserts expands globally, as a result of lower mid-continental precipitation (Rind et al. 1990), the flux of dust from barren desert soils is also likely to increase during the next century (Reheis & Kihl 1995).

Losses of plant cover that accompany the transition between semiarid grasslands and shrublands affect other aspects of the Earth's climate system. The albedo of barren soil exceeds that of vegetation, so increasing albedo typically accompanies the loss of vegetation cover in desertified grasslands (Wendler & Eaton 1983; Dirmeyer & Shukla 1996; Aguiar et al. 1996). The loss of cover is also associated with an increasing flux of sensible vs. latent heat from the Earth's surface, since the plant transpiration of water is lower in shrub deserts than in grasslands (Cable 1980; Aguiar et al. 1996). Thus, despite their greater albedo, barren desert soils are warmer and air temperatures are typically higher in shrub deserts than in grasslands (Courel et al. 1984; Balling 1988; Bryant et al. 1990). Nasrallah and Balling (1994) attribute nearly half of the recent climatic warming in the Sahel to the spread of deserts in that region. The largest difference in soil temperature between

grasslands and shrublands is seen during seasonal droughts, which minimize the surface evaporation in both communities (Balling 1989).

Conclusions

In desert ecosystems dominated by shrubby vegetation, the distribution of soil nutrients and the surface expression of other soil properties are strongly affected by vegetation. Plant nutrients are concentrated in 'islands of fertility' beneath desert shrubs. The establishment of shrub vegetation stimulates the processes leading to the formation of soil islands, allowing the persistence and regeneration of shrubs and a positive feedback to further desertification (Schlesinger et al. 1990). Many models of future global climate predict an expansion of desert ecosystems during the transient phases of global warming (Rind et al. 1990; Chahine 1995). As the area of semiarid grasslands diminishes in favor of shrub deserts and barren soils, we can expect an increasing flux of dust and a higher surface albedo from desert ecosystems. Thus, characteristics of the soil surface in deserts have strong feedbacks to the global climate system.

Acknowledgements

We thank Heavin Bortz, Anne Cross, Qinfeng Guo, Anne Hartley, Jane Raikes, and Beth Thomas for help in field and laboratory work. Jim Brown encouraged us to sample at his study site near Portal, Arizona, and graciously made it available to us. In this and several projects, Michael Lavine has provided important insights to the statistical analysis of our data, and Jim Reynolds and Athol Abrahams provided helpful comments on earlier drafts of this paper. The investigations reported in this paper are a contribution to the Jornada Long Term Ecological Research (LTER) program funded by NSF Grants DEB 92-40261 and 94-11971.

References

- Abrahams AD & Parsons AJ (1991) Relation between infiltration and stone cover on a semiarid hillslope, southern Arizona. *Journal of Hydrology* 122: 49–59
- Abrahams AD, Parsons AJ & Wainwright J (1994) Resistance to overland flow on semiarid grassland and shrubland hillslopes, Walnut Gulch, southern Arizona. *Journal of Hydrology* 156: 431–446
- Abrahams AD, Parsons AJ & Wainwright J (1995) Effects of vegetation change on interrill runoff and erosion, Walnut Gulch, southern Arizona. *Geomorphology* 13: 37–48

- Ackerman SA & Chung H (1992) Radiative effects of airborne dust on regional energy budgets at the top of the atmosphere. *Journal of Applied Meteorology* 31: 223–233
- Adams S, Strain BR & Adams MS (1970) Water-repellent soils, fire, and annual plant cover in a desert scrub community of southeastern California. *Ecology* 51: 696–700
- Afzal M & Adams WA (1992) Heterogeneity of soil mineral nitrogen in pasture grazed by cattle. *Soil Science Society of America Journal* 56: 1160–1166
- Aguiar MR, Paruelo JM, Sala OE & Lauenroth WK (1996) Ecosystem responses to changes in plant functional type composition: An example from the Patagonian steppe. *Journal of Vegetation Science* 7: 381–390
- Amundson RG, Chadwick OA, Sowers JM & Doner HE (1989) The stable isotope chemistry of pedogenic carbonates at Kyle Canyon, Nevada. *Soil Science Society of America Journal* 53: 201–210
- Arkley RJ (1963) Calculation of carbonate and water movement in soil from climatic data. *Soil Science* 92: 239–248
- Bach LB, Wierenga PJ & Ward TJ (1986) Estimation of the Philip infiltration parameters from rainfall simulation data. *Soil Science Society of America Journal* 50: 1319–1323
- Balling RC (1988) The climatic impact of a Sonoran vegetation discontinuity. *Climatic Change* 13: 99–109
- Balling RC (1989) The impact of summer rainfall on the temperature gradient along the United States-Mexico border. *Journal of Applied Meteorology* 28: 304–308
- Boeken B & Shachak M (1994) Desert plant communities in human-made patches – implications for management. *Ecological Applications* 4: 702–716
- Brown JH & Heske EJ (1990) Control of a desert-grassland transition by a keystone rodent guild. *Science* 250: 1705–1707
- Bryant NA, Johnson LF, Brazel AJ, Balling RC, Hutchinson CF & Beck LR (1990) Measuring the effect of overgrazing in the Sonoran desert. *Climatic Change* 17: 243–264
- Buffington LC & Herbel CH (1965) Vegetational changes on a semidesert grassland range from 1858 to 1963. *Ecological Monographs* 35: 139–164
- Bull WB (1979) Threshold of critical power in streams. *Bulletin of the Geological Society of America* 90: 453–464
- Burke IC, Reiners WA, Sturges DL & Matson PA (1987) Herbicide treatment effects on properties of mountain big sagebrush soils after fourteen years. *Soil Science Society of America Journal* 51: 1337–1343
- Bush JK & Van Auken OW (1989) Soil resource levels and competition between a woody and herbaceous species. *Bulletin of the Torrey Botanical Club* 116: 22–30
- Bush JK & Van Auken OW (1995) Woody plant growth related to planting time and clipping of a C4 grass. *Ecology* 76: 1603–1609
- Cable DR (1980) Seasonal patterns of soil water recharge and extraction on semidesert ranges. *Journal of Range Management* 33: 9–15
- Carpenter DE, Barbour MG & Bahre CJ (1986) Old field succession in Mojave desert scrub. *Madrono* 33: 111–122
- Cerling TE (1984) The stable isotope composition of modern soil carbonate and its relationship to climate. *Earth and Planetary Science Letters* 71: 229–240
- Chahine MT (1995) Observations of local cloud and moisture feedbacks over high ocean and desert surface temperatures. *Journal of Geophysical Research* 100: 8919–8927
- Charley JL & West NE (1975) Plant-induced soil chemical patterns in some shrub-dominated semi-desert ecosystems of Utah. *Journal of Ecology* 63: 945–964
- Charley JL & West NE (1977) Micro patterns of nitrogen mineralization activity in soils of some shrub-dominated semi-desert ecosystems of Utah. *Soil Biology and Biochemistry* 9: 357–365
- Chew RM & Whitford WG (1992) A long-term positive effect of kangaroo rats (*Dipodomys spectabilis*) on creosotebushes (*Larrea tridentata*). *Journal of Arid Environments* 22: 375–386

- Coale KH, Johnson KS, Fitzwater SE, Gordon RM, Tanner S, Chavez FP, Ferioli L, Sakamoto C, Rogers P, Millero F, Steinberg P, Nightingale P, Cooper D, Cochlan WP, Landry MR, Constantinou J, Rollwagen G, Trasvina A & Kudela R (1996) A massive phytoplankton bloom induced by an ecosystem-scale iron fertilization experiment in the equatorial Pacific ocean. *Nature* 383: 495–501
- Connin SL, Virginia RA, Chamberlain P, Huenneke L, Harrison K & Schlesinger WH (1997) Dynamics of carbon storage in degraded arid land environments: A case study from the Jornada Experimental Range, New Mexico (USA). In: Squires VR (Ed) *Drylands and Global Change in the Twenty-First Century*. University of Arizona Press, Tucson
- Coppinger KD, Reiners WA, Burke IC & Olson RK (1991) Net erosion on a sagebrush steppe landscape as determined by cesium-137 distribution. *Soil Science Society of America Journal* 55: 254–258
- Courel MF, Kandel RS & Rasool SI (1984) Surface albedo and the Sahel drought. *Nature* 307: 528–531
- Cross AFS (1994) Biogeochemistry at the Grassland-Shrubland Boundary: A Case Study of Desertification in the Northern Chihuahuan Desert of New Mexico. Ph.D. Dissertation, Duke University, Durham, NC
- Dirmeyer PA & Shukla J (1996) The effect on regional and global climate of expansion of the world's deserts. *Quarterly Journal of the Royal Meteorological Society* 122: 451–482
- Duce RA & Tindale NW (1991) Atmospheric transport of iron and its deposition in the ocean. *Limnology and Oceanography* 36: 1715–1726
- Freckman DW & Mankau R (1986) Abundance, distribution, biomass and energetics of soil nematodes in a northern Mojave desert ecosystem. *Pedobiologia* 29: 129–142
- Fryrear DW (1995) Soil losses by wind erosion. *Soil Science Society of America Journal* 59: 668–672
- Gallardo A & Schlesinger WH (1992) Carbon and nitrogen limitations of soil microbial biomass in desert ecosystems. *Biogeochemistry* 18: 1–17
- Gallardo A & Schlesinger WH (1995) Factors determining soil microbial biomass and nutrient immobilization in desert soils. *Biogeochemistry* 28: 55–68
- Garcia Moya E & McKell CM (1970) Contribution of shrubs to the nitrogen economy of a desert-wash plant community. *Ecology* 51: 81–88
- Garner W & Steinberger Y (1989) A proposed mechanism for the formation of 'fertile islands' in the desert ecosystem. *Journal of Arid Environments* 16: 257–262
- Gerakis PA & Tsangarakis CZ (1970) The influence of *Acacia senegal* on the fertility of a sand sheet ('goz') soil in the central Sudan. *Plant and Soil* 33: 81–86
- Gillette DA, Stensland GJ, Williams AL, Barnard W, Gatz D, Sinclair PC & Johnson TC (1992) Emissions of alkaline elements calcium, magnesium, potassium, and sodium from open sources in the contiguous United States. *Global Biogeochemical Cycles* 6: 437–457
- Gutierrez J & Hernandez II (1996) Runoff and interrill erosion as affected by grass cover in a semi-arid rangeland of northern Mexico. *Journal of Arid Environments* 34: 287–295
- Hallmark CT & Allen BL (1975) The distribution of creosotebush in West Texas and Eastern New Mexico as affected by selected soil properties. *Soil Science Society of America Proceedings* 39: 120–124
- Halvorson JJ, Bolton H & Smith JL (1997) The pattern of soil variables related to *Artemisia tridentata* in a burned shrub-steppe site. *Soil Science Society of America Journal* 61: 287–294
- Herman RP, Provencio KR, Herrera-Matos J & Torrez RJ (1995) Resource islands predict the distribution of heterotrophic bacteria in Chihuahuan desert soils. *Applied and Environmental Microbiology* 61: 1816–1821
- Heske EJ, Brown JH & Guo Q (1993) Effects of kangaroo rat exclusion on vegetation structure and plant species diversity in the Chihuahuan desert. *Oecologia* 95: 520–524
- Hook PB, Burke IC & Lauenroth WK (1991) Heterogeneity of soil and plant N and C associated with individual plants and openings in North American shortgrass steppe. *Plant and Soil* 138: 247–256

- Huenneke LF, Anderson J, Muldavin E & Schlesinger WH (in prep.) Spatial and temporal variation in aboveground biomass and net primary production in Chihuahuan desert ecosystems. Manuscript
- Inskip WP & Bloom PR (1986) Kinetics of calcite precipitation in the presence of water-soluble organic ligands. *Soil Science Society of America Journal* 50: 1167–1172
- Kelly EF, Chadwick OA & Hilinski TE (1998) The effect of plants on mineral weathering. *Biogeochemistry*, this issue
- Kieft TL (1994) Grazing and plant-canopy effects on semiarid soil microbial biomass and respiration. *Biology and Fertility of Soils* 18: 155–162
- Lajtha K (1987) Nutrient reabsorption efficiency and the response to phosphorus fertilization in the desert shrub *Larrea tridentata* (DC.) Cov. *Biogeochemistry* 4: 265–276
- Lajtha K & Bloomer SH (1988) Factors affecting phosphate sorption and phosphate retention in a desert ecosystem. *Soil Science* 146: 160–167
- Lajtha K & Schlesinger WH (1986) Plant response to variations in nitrogen availability in a desert shrubland community. *Biogeochemistry* 2: 29–37
- Lajtha K & Schlesinger WH (1988) The effect of CaCO_3 on the uptake of phosphorus by two desert shrub species, *Larrea tridentata* (DC.) Cov. and *Parthenium incanum* H.B.K. *Botanical Gazette* 149: 328–334
- Loye-Pilot MD, Martin JM & Morelli J (1986) Influence of Saharan dust on the rain acidity and atmospheric input to the Mediterranean. *Nature* 321: 427–428
- Ludwig JA, Reynolds JF & Whitson PD (1975) Size-biomass relationships of several Chihuahuan desert shrubs. *American Midland Naturalist* 94: 451–461
- Lyford FP & Qasbi HK (1969) Infiltration rates as affected by desert vegetation. *Water Resources Research* 5: 1373–1376
- Marion GM & Babcock KL (1977) The solubilities of carbonates and phosphates in calcareous soil suspensions. *Soil Science Society of America Journal* 41: 724–728
- Marion GM, Schlesinger WH & Fonteyn PJ (1985) CALDEP: A regional model for soil CaCO_3 (caliche) deposition in southwestern deserts. *Soil Science* 139: 468–481
- Marion GM, Schlesinger WH & Fonteyn PJ (1990) Spatial variability of CaCO_3 solubility in a Chihuahuan desert soil. *Arid Soil Research and Rehabilitation* 4: 181–191
- Martin JH (1990) Glacial-interglacial CO_2 change: The iron hypothesis. *Paleoceanography* 5: 1–13
- Martinez-Meza E & Whitford WG (1996) Stemflow, throughfall and channelization of stemflow by roots in three Chihuahuan desert shrubs. *Journal of Arid Environments* 32: 271–287
- Mauchamp A & Janeau JL (1993) Water funnelling by the crown of *Flourensia cernua*, a Chihuahuan desert shrub. *Journal of Arid Environments* 25: 299–306
- Mazzarino MJ, Oliva L, Abril A & Acosta M (1991) Factors affecting nitrogen dynamics in a semiarid woodland (Dry Chaco, Argentina). *Plant and Soil* 138: 85–98
- McAuliffe J (1988) Markovian dynamics of simple and complex desert communities. *American Naturalist* 131: 459–490
- Mun H-T & Whitford WG (1990) Factors affecting annual plants assemblages on banner tailed kangaroo rat mounds. *Journal of Arid Environments* 18: 165–173
- Naranjo LG & Raitt RJ (1993) Breeding bird distribution in Chihuahuan desert habitats. *Southwestern Naturalist* 38: 43–51
- Nasrallah HA & Balling RC (1994) The effect of overgrazing on historical temperature trends. *Agricultural and Forest Meteorology* 71: 425–430
- Návar J & Bryan R (1990) Interception loss and rainfall redistribution by three semi-arid growing shrubs in northeastern Mexico. *Journal of Hydrology* 115: 51–63
- Nishita H & Haug RM (1973) Distribution of different forms of nitrogen in some desert soils. *Soil Science* 116: 51–58
- Noy-Meir I (1985) Desert ecosystem structure and function. In: Evenari M et al. (Eds) *Hot Deserts and Arid Shrublands* (pp 93–103). Elsevier Science Publishers, Amsterdam

- Parsons AJ, Abrahams AD & Simanton JR (1992) Microtopography and soil-surface materials on semi-arid piedmont hillslopes, southern Arizona. *Journal of Arid Environments* 22: 107–115
- Peterjohn WT & Schlesinger WH (1991) Factors controlling denitrification in a Chihuahuan desert ecosystem. *Soil Science Society of America Journal* 55: 1694–1701
- Phinn S, Franklin J, Hope A, Stow D & Huenneke L (1996) Biomass distribution mapping using airborne digital video imagery and spatial statistics in a semi-arid environment. *Journal of Environmental Management* 47: 139–164
- Pianka ER (1967) On lizard species diversity: North American flatland deserts. *Ecology* 48: 333–351
- Pilmanis AM & Schlesinger WH (1998) Spatial Assessment of Desertification in Terms of Vegetation Pattern and Available Soil Nitrogen. In: *Proceedings of the 5th International Conference on Desert Development*. Texas Tech University, Lubbock
- Quade J, Cerling TE & Bowman JR (1989a) Development of Asian monsoon revealed by marked ecological shift during the latest Miocene in northern Pakistan. *Nature* 342: 163–166
- Quade J, Cerling TE & Bowman JR (1989b) Systematic variations in the carbon and oxygen isotopic composition of pedogenic carbonate along elevation transects in the southern Great Basin, United States. *Geological Society of America Bulletin* 101: 464–475
- Reddy KJ, Lindsay WL, Workman SM & Drever JI (1990) Measurement of calcite ion activity products in soils. *Soil Science Society of America Journal* 54: 67–71
- Reheis MC & Kihl R (1995) Dust deposition in southern Nevada and California, 1984–1989: Relations to climate, source area, and source lithology. *Journal of Geophysical Research* 100: 8893–8918
- Reynolds RC (1978) Polyphenol inhibition of calcite precipitation in Lake Powell. *Limnology and Oceanography* 23: 585–597
- Rind D, Goldberg R, Hansen J, Rosenzweig C & Ruedy R (1990) Potential evapotranspiration and the likelihood of future drought. *Journal of Geophysical Research* 95: 9983–10004
- Roda F, Bellot J, Avila A, Escarre A, Pinol J & Terradas J (1993) Saharan dust and the atmospheric inputs of elements and alkalinity to Mediterranean ecosystems. *Water, Air and Soil Pollution* 66: 277–288
- Rostagno CM (1989) Infiltration and sediment production as affected by soil surface conditions in a shrubland of Patagonia, Argentina. *Journal of Range Management* 42: 382–385
- Rostagno CM, del Valle HF & Videla L (1991) The influence of shrubs on some chemical and physical properties of an aridic soil in north-eastern Patagonia, Argentina. *Journal of Arid Environments* 20: 179–188
- Ryel RJ, Caldwell MM & Manwaring JH (1996) Temporal dynamics of soil spatial heterogeneity in sagebrush-wheatgrass steppe during a growing season. *Plant and Soil* 184: 299–309
- Santos PF, DePree E & Whitford WG (1978) Spatial distribution of litter and microarthropods in a Chihuahuan desert ecosystem. *Journal of Arid Environments* 1: 41–48
- Schlesinger WH (1985) The formation of caliche in soils of the Mojave desert, California. *Geochimica et Cosmochimica Acta* 49: 57–66
- Schlesinger WH & Hartley AE (1992) A global budget for atmospheric NH_3 . *Biogeochemistry* 15: 191–211
- Schlesinger WH & Peterjohn WT (1991) Processes controlling ammonia volatilization from Chihuahuan desert soils. *Soil Biology and Biochemistry* 23: 637–642
- Schlesinger WH, Fonteyn PJ & Reiners WA (1989) Effects of overland flow on plant water relations, erosion, and soil water percolation on a Mojave Desert landscape. *Soil Science Society of America Journal* 53: 1567–1572
- Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA & Whitford WG (1990) Biological feedbacks in global desertification. *Science* 247: 1043–1048

- Schlesinger WH, Raikes JA, Hartley AE & Cross AF (1996) On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* 77: 364–374
- Schütz L (1980) Long range transport of desert dust with special emphasis on the Sahara. *Annals of the New York Academy of Sciences* 338: 515–532
- Sequeira R (1993) On the large-scale impact of arid dust on precipitation chemistry of the continental northern hemisphere. *Atmospheric Environment* 27A: 1553–1565
- Singer A (1989) Illite in the hot-aridic soil environment. *Soil Science* 147: 126–133
- Smith JL, Halvorson II & Bolton H (1994) Spatial relationships of soil microbial biomass and C and N mineralization in a semi-arid shrub-steppe ecosystem. *Soil Biology and Biochemistry* 26: 1151–1159
- Snow JT & McClelland TM (1990) Dust devils at White Sands Missile Range, New Mexico. I. Temporal and spatial distributions. *Journal of Geophysical Research* 95: 13707–13721
- Sokolik IN & Toon OB (1996) Direct radiative forcing by anthropogenic airborne mineral aerosols. *Nature* 381: 681–683
- Stockton PH & Gillette DA (1990) Field measurement of the sheltering effect of vegetation on erodible land surfaces. *Land Degradation and Rehabilitation* 2: 77–85
- Suarez DL & Rhoades JD (1982) The apparent solubility of calcium carbonate in soils. *Soil Science Society of America Journal* 46: 716–722
- Swap R, Garstang M, Grcco S, Talbot R & Kallberg P (1992) Saharan dust in the Amazon basin. *Tellus* 44B: 133–149
- Talbot RW, Harriss RC, Browell EV, Gregory GL, Sebacher DI & Beck SM (1986) Distribution and geochemistry of aerosols in the tropical North Atlantic troposphere: Relationship to Saharan dust. *Journal of Geophysical Research* 91: 5173–5182
- Tegen I & Fung I (1995) Contribution to the atmospheric mineral aerosol load from land surface modification. *Journal of Geophysical Research* 100: 18707–18726
- Tegen I, Lacis AA & Fung I (1996) The influence on climate forcing of mineral aerosols from disturbed soils. *Nature* 380: 419–422
- Tiedemann AR & Klemmedson JO (1973) Effect of mesquite on physical and chemical properties of the soil. *Journal of Range Management* 26: 27–29
- Tiedemann AR & Klemmedson JO (1986) Long-term effects of mesquite removal on soil characteristics: I. Nutrients and bulk density. *Soil Science Society of America Journal* 50: 472–475
- Tongway DJ & Ludwig JA (1994) Small-scale resource heterogeneity in semi-arid landscapes. *Pacific Conservation Biology* 1: 201–208
- Virginia RA & Jarrell WM (1983) Soil properties in a mesquite-dominated Sonoran desert ecosystem. *Soil Science Society of America Journal* 47: 138–144
- Virginia RA, Jarrell WM & Franco Vizcaino E (1982) Direct measurement of denitrification in a *Prosopis* (mesquite) dominated Sonoran desert ecosystem. *Oecologia* 53: 120–122
- Wallace A & Romney EM (1972) Radioecology and Ecophysiology of Desert Plants at the Nevada Test Site. Environmental Radiation Division, Laboratory of Nuclear Medicine and Radiation Biology, University of California, Los Angeles
- Wallace A, Romney EM & Hunter RB (1980) The challenge of a desert: Revegetation of disturbed desert lands. *Great Basin Naturalist Memoirs* 4: 216–225
- Wendler G & Eaton F (1983) On the desertification of the Sahel zone. *Climatic Change* 5: 365–380
- West NE & Skujins J (1977) The nitrogen cycle in North American cold-winter semi-desert ecosystems. *Oecologia Plantarum* 12: 45–53
- West NE & Klemmedson JO (1978) Structural distribution of nitrogen in desert ecosystems. In: West NE & Skujins J (Eds) *Nitrogen in Desert Ecosystems* (pp 1–16). Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania
- West NE (1990) Structure and function of microphytic soil crusts in wildland ecosystems of arid to semi-arid regions. *Advances in Ecological Research* 20: 179–223
- Westerman RL & Tucker TC (1979) In situ transformations of nitrogen-15 labeled materials in Sonoran desert soils. *Soil Science Society of America Journal* 43: 95–100

- Whitford WG (1993) Animal feedbacks in desertification: An overview. *Revista Chilena de Historia Natural* 66: 243–251
- Whitford WG, Anderson J & Rice PM (1997) Stemflow contributions to the 'fertile island' effect in creosotebush, *Larrea tridentata*. *Journal of Arid Environments* 35: 451–457
- Wood JC, Wood MK & Tromble JM (1987) Important factors influencing water infiltration and sediment production on arid lands in New Mexico. *Journal of Arid Environments* 12: 111–118
- Wright RA & Honea JH (1986) Aspects of desertification in southern New Mexico, U.S.A.: Soil properties of a mesquite duneland and a former grassland. *Journal of Arid Environments* 11: 139–145
- Yaalon DH (1965) Downward movement and distribution of anions in soil profiles with limited wetting. In: Hallsworth ED & Crawford DV (Eds) *Experimental Pedology* (pp 157–164). Butterworth, London
- Young JR, Ellis EC & Hidy GM (1988) Deposition of air-borne acidifiers in the western environment. *Journal of Environmental Quality* 17: 1–26
- Yung YL, Lee T, Wang C-H & Shieh Y-T (1996) Dust. A diagnostic of the hydrologic cycle during the last glacial maximum. *Science* 271: 962–963
- Zaady E, Groffman PM & Shachak M (1996) Litter as a regulator of N and C dynamics in macrophytic patches in Negev desert soils. *Soil Biology and Biochemistry* 28: 39–46