Chapter 9 | Decomposition and Nutrient Cycling

9.1 NUTRIENT LIMITATIONS

There is no question that water availability limits productivity in deserts. That is intuitively obvious even to the casual observer. Because of the overriding importance of water, many investigators have tended to pass off potential nutrient limitations as unimportant. In arid regions nutrient limitations to productivity and general ecosystem functioning may be important only under low probability climates, e.g. a succession of years of above average rainfall. However, nutrient limitations may also occur at other times when water availability is high even if only for short time periods.

The nutrient most frequently cited as limiting productivity is nitrogen. Charley and Cowling (1968) were among the first ecologists to suggest that nitrogen and other nutrients may be limiting productivity in semiarid ecosystems. They reported that primary production was reduced during prolonged wet periods and attributed that reduction to less available nitrogen. Ludwig and Flavill (1979) reported a similar response in productivity in the northern Chihuahuan desert, and Floret et al. (1982) suggested that nitrogen limitation was the factor limiting production in the Tunisian desert during wet periods. In an extensive study in the Sahel, a group of scientists from Wageningen, the Netherlands, documented that at rainfall amounts above approximately $200 \ mm \ yr^{-1}$ nitrogen availability limited production (Penning de Vries and Djiteye, 1982).

In the northern Chihuahuan desert, Ettershank et al. (1978) reported large increases in net above ground production in the creosotebush, *Larrea tridentata* and a perennial grass, fluff-grass, *Erioneuron pulchellum*, in response to fertilization with ammonium nitrate. When fertilizer was applied at a low rate, only the shallow-rooted grass responded, probably because the grass sequestered the N before leaching carried it to the root zone of the shrubs. The nitrogen limitation–water relationships studied in a series of water supplementation–fertilization studies in the Chihuahuan desert has documented that nitrogen availability affects biomass production of perennial and annual plants and the species composition of annual plant communities (Gutierrez and Whitford, 1987; Fisher et al., 1988; Gutierrez et al., 1988). Nitrogen fertilization does not result in increased productivity of long-lived perennial desert grasses. Irrigation resulted in higher biomass production in black-grama, *Bouteloua eriopoda,* and also affected flowering,

tiller mortality, and insect damage. Nitrogen fertilization reduced the root lengths of the grass clumps. Productivity in the *B. eriopoda* desert grassland appears to be closely linked to rainfall with no temporal lags due to nitrogen immobilization (Stephens and Whitford, 1993). These findings present a real dichotomy in the way that dominant plant species affect the ecosystem responses to rainfall.

Nitrogen fertilization and irrigation experiments demonstrated that nitrogen availability limits productivity if moisture availability is high for a complete plant growth cycle (James and Jurinak, 1978; Romney *et al.*, 1978). Nitrogen fertilization plus supplemental moisture increased in new shoot growth and/or leaf nitrogen content above that of unfertilized plants and in some but not all species of shrubs. Biomass production of several species of annual plants was increased by nitrogen fertilization (Romney *et al.*, 1978). Fertilization studies of native vegetation in the Sahel documented the importance of nitrogen and phosphorus in these semiarid systems. 'The low fertility of the soils, especially in nitrogen and phosphates, is often much more a limiting factor than the low irregular rainfall' (Penning de Vries and Djiteye, 1982). Soil N and P levels were relatively constant moving from north to south with the result that the quality of the vegetation decreased along a north to south gradient. The data of Penning de Vries and Djiteye (1982) suggested that productivity in the southern Sahara–Sahel was water limited at average precipitation of about 150 mm yr^{-1} and by nutrients at greater average rainfall amounts (Fig. 9.1).

Nutrient limitation of productivity is well documented in the semiarid and arid areas of Australia. Charley and Cowling (1968) found nutrient deficiencies, especially nitrogen, limited primary production saltbush desert areas of New South Wales (Charley and Cowling, 1968). They emphasized the importance of nitrogen availability in that system. Several nutrients were found to be potentially limiting in Central Australian ecosystems. In Mitchell grassland, open woodland, and mulga shrubland, nitrogen and phosphorus were found to limit grass production. Other nutrients were deficient and affected productivity in one or more of the ecosystems studied, e.g. sulfur (Freidel *et al.*, 1980). Freidel *et al.* (1980) pointed out two adaptations that are common in ecosystems of low fertility: (1) conservation of nutrients within living plant material and (2) rapid external cycling of nutrients through litter fall. It is important to keep these generalizations in mind as we examine the details of nutrient cycling processes in deserts. In addition to the direct evidence of increased production with application of fertilizer, other studies have invoked nutrient limitations to account for reduction in productivity despite adequate soil moisture availability (Ludwig and Flavill, 1979; Floret *et al.*, 1982). Of the potential long list of nutrients that could be limiting productivity in one or more arid ecosystems, nitrogen and phosphorus are most likely to be limiting in most desert ecosystems. Despite the differences in origin (atmospheric pool vs. rock weathering) both nutrients are processed by complex biological interactions in the soil. Because phosphorus is a product of rock weathering it is in lower concentration in the ancient shield-platform deserts than in the more recent basin and range deserts. Despite these differences, the biological processes and interactions with climate are likely to be similar in all subtropical deserts.
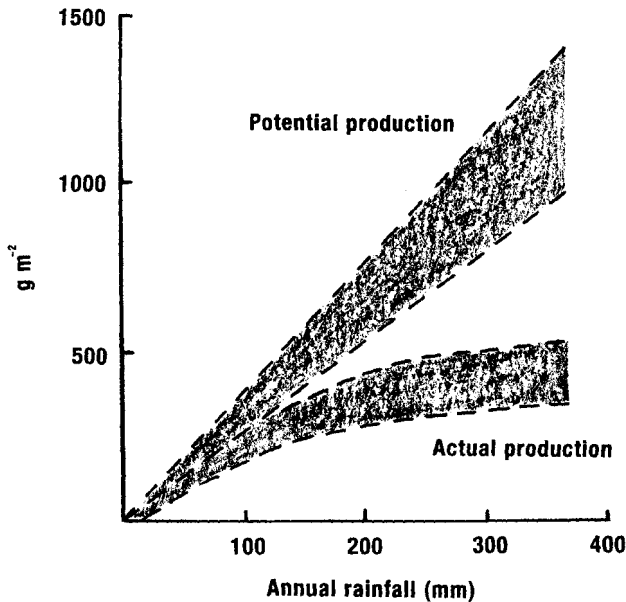
Figure 9.1   Relationship between rainfall and potential and actual primary production. The difference in the curves is due to nutrient limitations. Figure based on Penning de Vries, F. W. T. and Djiteye, M. A. (eds) 1982. La productivite des pasturages saheliens. Reproduced with permission of Backhuys Publishers B. V.

9.2 DECOMPOSITION

Decomposition is the process that releases nutrient materials held in the structure of plant and animal tissues to the soil solution where the nutrients are once again potentially available to plants. Since most nutrient elements cycle from soil solution to plant and back to the soil solution via decomposition, decomposition processes are key features of nutrient cycles. Studies in subtropical deserts have called attention to a number of striking differences in decomposition processes between moist temperate and subtropical arid and semiarid systems.

The decomposition process can be subdivided into two related processes: fragmentation and mineralization. Fragmentation results from abiotic forces that weaken and mechanically fragment large pieces of dead material or from biological activities such as comminution (chewing and passing through the gut) and lysis by enzymes. In mesic systems biological fragmentation is most important. However, in arid and semiarid ecosystems, fragmentation by abiotic means appears to be more important than biological activity. Mineralization processes involve the conversion of litter fragments into microbial biomass and the eventual death and breakdown of that microbial biomass. The breakdown of carbon compounds to CO_2 and H_2O is a mineralization process as is the deamination of

protein and excretion of ammonia. Some mineralization occurs at the same time that biological fragmentation is occurring.

The spatial and temporal linkage between fragmentation and mineralization processes is tight in mesic systems: i.e. both processes occur simultaneously in these systems. In desert ecosystems, fragmentation and mineralization may be separated both temporally and spatially. This separation has profound implications for nutrient cycling processes and ultimately for soil characteristics in desert ecosystems. Both processes of decomposition are affected by biotic and abiotic parameters but to different extents and abiotic effects may be both direct or indirect. Wind, water, heat, and light may interact to effect mineralization of some plant compounds (Pauli, 1964).

In temperate mesic ecosystems there are a number of variables that have been shown to affect decomposition. In mesic systems decomposition rates vary directly as a function of actual evapotranspiration and inversely with lignin concentration (Meentemeyer, 1978). Plant materials with low C:N ratios decompose more rapidly than those with high C:N ratios. Soil arthropods accelerate decomposition by transporting spores and inoculating litter with microbial spores, and comminution (chewing into small fragments) (Swift *et al.*, 1979). Decomposition processes in deserts differ from mesic systems in terms of these variables. A general model for decomposition in deserts requires evaluation of the process with respect to each of the variables identified as important for mesic ecosystems.

9.2.1 Sources and Characteristics of Decomposable Material

Leaves of most desert plants are small and many have a waxy cuticle. Since most desert vegetation is composed of a mixture of drought deciduous, seasonally deciduous and evergreen shrubs or trees plus grasses and herbaceous plants, there is a continuous, but variable quantity of litter input in most desert ecosystems. The chemical and physical characteristics of the dead plant material are variables that affect the decomposition process. However, some of the structural correlates with decomposition rate like lignin content and carbon–nitrogen ratio of the plant material do not apply to deserts (Schaefer *et al.*, 1985). The leaves of desert plants frequently have high concentrations of waxes, volatiles, saponins and especially phenolics in the cuticular and epidermal cells. Lignin content of leaves of desert plants that have been assayed varied between 7.9% and 14.6% (Schaefer *et al.*, 1985; Steinberger and Whitford, 1988) which is low compared to oak leaves and conifer needles in which lignin content varied between 21% and 30% (Swift *et al.*, 1979). The leaves and stems of temperate mesic grasses had lignin contents between 11% and 14%. Carbon-nitrogen ratios of leaves of six desert plants varied between 16 and 52 (Schaefer *et al.*, 1985). Carbon–nitrogen ratios of the roots of two annual plants were 65 and 70 and for the shrubs, *L. tridentata* and *Zinnia acerosa* were 21 and 52, respectively (Whitford *et al.*, 1987). Carbon–nitrogen ratios of four standing dead desert grasses ranged from 71.5 to 115.4 (Montana *et al.*, 1988). These data indicate the considerable variablity in chemical and structural composition of desert plant structures.

The ultimate location of plant litter is probably of greater importance as a factor affecting decomposition than is the physical–chemical structure of the litter. Because of the generally small size and high surface to mass ratio of dead leaves, stem fragments, dead floral parts, etc., these materials are easily moved by the wind. As a consequence, litter tends to accumulate under shrubs, and in depressions (DeSoyza *et al.*, 1997). Because of wind transport, a significant fraction of the litter input is buried as small accumulations in shallow pits and depressions. The quantities buried vary seasonally as a function of digging activities of animals, wind, and litter fall (Steinberger and Whitford, 1983). Litter buried in depressions etc. is exposed to lower temperatures, protected from intense solar radiation and is in an evaporation-retarding environment. The decomposition of buried litter and dead roots, therefore, takes place in a more benign microenvironment than surface litter. Physical location thus has a dramatic effect on the mechanisms of decomposition.

Roots are the main source of carbon inputs into desert soils. Roots of annual plants enter the decomposable material pool in pulses following periods of annual plant production. The distribution of most annual plants is patchy, hence decomposing annual plant roots are concentrated in patches. The rates of turnover of roots of perennial plants are unknown in deserts. We can assume that during periods of rapid growth there is production of fine roots that die and decompose. Quantitative data on root turnover in perennials is difficult to obtain but may represent a significant fraction of the materials being cycled in an ecosystem in a year.

9.2.2 Rates and Mechanisms of Mass Loss (Surface Litter)

As pointed out above, the fate of dead plant material varies as a function of its physical–chemical composition and its physical location in the environment. Most studies of decomposition focus on litter on the soil surface. Conventional wisdom holds that surface litter in deserts should decompose slowly in brief pulses following rains. However, decomposition rates of a variety of litter types in several of the world's deserts demonstrate that this is not the case. Several investigators have suggested that decomposition rates are regulated by actual evapotranspiration (AET) and can be predicted from AET. Other factors that are included in general models of decomposition include C/N and C/P ratios, lignin concentrations, and lignin/N and lignin/P ratios. At a global scale (excluding data from desert regions) climate expressed as AET was the best predictor for decomposition constants (k values) (Aerts, 1997). In the semiarid Mediterranean region, the lignin/N ratio was the best chemical predictor of litter decomposition.

Decomposition rates in mesic environments can be predicted by a regression model that incorporates actual evapotranspiration and lignin content (Meentemeyer, 1978). That model has the form

$$Y_1 = 1.31369 + 0.05350X_1 + 0.18472X_2$$

where Y_1 is mass loss (%), X_1 is actual evapotranspiration (mm) and X_2 is actual evapotranspiration (mm) divided by lignin content in percent dry mass.

The AET model markedly underestimates mass loss in deserts. That underestimate was attributed to the relative independence of desert soil fauna from constraints imposed by dry, hot surface environments (Whitford *et al.*, 1981). There was a slight positive *not* negative correlation between lignin content and mass loss and no relationship between AET and mass loss. High mid-day temperature and intense ultraviolet radiation characteristic of high elevation desert regions may have combined to produce photooxidation of lignins and other complex molecules (Schaefer *et al.*, 1985).

The earliest suggestion that the high temperatures and intense ultraviolet light could be significant in the breakdown of organic matter in deserts was by Pauli (1964). Sunlight at wavelengths of 280–400 nm has sufficient energy to catalyze oxidations and reductions, especially of cyclic compounds like phenolics. Approximately 15% mass loss was measured in grass leaves and shrub leaves treated with mecuric chloride to eliminate all biota in short grass prairie and Chihuahuan desert respectively (Vossbrinck *et al.*, 1979; MacKay *et al.*, 1994). Photooxidation of structual materials which weakens leaves produces conditions where raindrop inpact will shatter pieces from the leaves. This scenario is consistent with the results of several studies of mass losses of materials on the soil surface in a desert (Moorhead and Reynolds, 1989). The contribution of abiotic factors such as high temperatures and sunlight is supported by data on grass decomposition rates which were relatively constant over time and independent of temperature and moisture. Litter C:N ratios remained constant during the study when mass losses were 40% and 80% for the grasses *Sporobolus airoides* and *Hilaria mutica* respectively (Montana *et al.*, 1988).

Photodegradation and fragmentation by intermittent rainfall can produce the high decomposition rates reported for mass loss from surface litter in deserts (Table 9.1). There is a growing body of evidence that photodegradation can be a major factor in the decomposition of plant materials. A recent empirical study reported that UV-B decreased the proportion of lignin in plant residues, suppressed microbial respiration, and changed the decomposer fungal community structure (Gehrke *et al.*, 1995). High amounts of UV-B radiation reach the soil surface in low- and mid-latitude deserts and that radiation combined with the high surface temperatures makes the abiotic breakdown hypothesis a reasonable explanation of the high rates of decomposition recorded in such deserts. This also explains the high *negative* correlation between decomposition rates and initial lignin content reported by Schaefer *et al.* (1985).

Correlations of surface litter disappearance and rainfall (Strojan *et al.* 1987) are partially the result of biological activity but also the result of raindrop impact fragmenting the material after the structural lignin has been broken down by photodecomposition. Rainfall causes fragmentation of structurally weakened material (Steinberger and Whitford, 1988). Thus the mechanisms involved in surface litter breakdown involve photchemical lysis of lignin followed by physical

Table 9.1
Annual Rates of Decomposition of Plant Litter and Roots in Various Landscape Positions, and Deserts Around the World

Material	Location	Mass loss	Reference
Larrea tridentata (shrub) leaf litter	Buried, bajada, New Mexico	60%[b]	Santos and Whitford (1981)
Shrub and grass mixed	Flooded ephemeral lake, New Mexico watershed	55% 1 mo.[b]	MacKay *et al.* (1992)
Larrea tridentata leaf litter (buried)	Mojave Desert, southern Nevada	38% 6 mo.[b]	Santos *et al.* (1984)
Larrea tridentata leaf litter (buried)	Colorado Desert, California and Sonoran Desert, Arizona	43–48%[b]	Santos *et al.* (1984)
Larrea tridentata leaf litter (shrub)	Chihuahuan Desert watershed	47–58%[a]	Cepeda-Pizarro and Whitford (1990)
Larrea tridentata leaf litter (shrub)	Mojave Desert bajada	43%[a]	Strojan *et al.* (1987)
Ambrosia dumosa above-ground litter (shrub)	Mojave Desert bajada	58%[a]	Strojan *et al.* (1987)
Larrea tridentata leaf litter (shrub)	Chihuahuan Desert, basin	93%[a,c]	Elkins *et al.* (1982)
Quercus harvardii leaf litter (shrub)	Chihuahuan Desert coppice dunes	20%[a]	Elkins *et al.* (1982)
Salsola inermis whole plant (annual) buried	Negev Desert, Israel	85%[b]	Steinberger and Whitford (1988)
Hamada scoparia litter (shrub) buried	Negev Desert, Israel	40%[b]	Steinberger and Whitford (1988)
Salsola inermis whole plant – surface	Negev Desert, Israel	25%[a]	Steinberger and Whitford (1988)
Hamada scoparia litter	Negev Desert, Israel	35%[a]	Steinberger and Whitford (1988)
Stipa capensis litter (annual grass)	Irrigated – control various locations on watershed, Negev Desert	20–35%[a]	Steinberger and Whitford (1988)
Ambrosia dumosa litter (shrub)	Mojave Desert bajada	58%[a]	Strojan *et al.* (1987)
Larrea tridentata litter	Mojave Desert bajada	43%[a]	Strojan *et al.* (1987)
Lycium pallidum leaf litter (shrub)	Mojave Desert bajada	63%[a]	Strojan *et al.* (1987)
Tridens (Erioneuron) pulchella (grass) (foliage)	Upper bajada, New Mexico	62%[a]	Cepeda-Pizarro and Whitford (1990)
Baileya multiradiata (annual) stems and leaves	Mid-slope bajada, New Mexico	58%[a]	Cepeda-Pizarro and Whitford (1990)
Prosopis glandulosa (shrub) leaves	Lower-slope bajada, New Mexico	46%[a]	Cepeda-Pizarro and Whitford (1990)
Larrea tridentata litter (shrub)	Five locations – watershed, New Mexico	53–65%[a]	Cepeda-Pizarro and Whitford (1990)
Panicum obtusum litter (perennial grass)	Ephemeral lake basin, New Mexico	38%[a]	Cepeda-Pizarro and Whitford (1990)
Yucca elata leaves (perennial monocot)	Bajada, Chihuahuan Desert	64%[a]	Schaefer *et al.* (1985)
Chilopsis linearis litter (riparian shrub)	Ephemeral stream margin, New Mexico	77%[a]	Schaefer *et al.* (1985)

Table 9.1 – *continued*

Material	Location	Mass loss	Reference
Prosopis glandulosa litter (shrub*)*	Bajada, New Mexico	31%[a]	Schaefer *et al.* (1985)
Larrea tridentata litter	Bajada, New Mexico	35%[a]	Schaefer *et al.* (1985)
Flourensia cernua litter (shrub*)*	Bajada, New Mexico	41%[a]	Schaefer *et al.* (1985)
Annual plant litter	Bajada, New Mexico	62%[a]	Schaefer *et al.* (1985)
Zinnia acerosa (subshrub) roots	Bajada, New Mexico watershed	45%[b]	Whitford *et al.* (1987)
Larrea tridentata (shrub) roots	Bajada, New Mexico watershed	45%[b]	Whitford *et al.* (1987)
Baileya multiradiata (annual) roots	Bajada, New Mexico watershed	89%[b]	Whitford *et al.* (1987)
Dithyrea wislizenii (annual) roots	Bajada, New Mexico watershed	87%[b]	Whitford *et al.* (1987)
Panicum obtusum (grass) roots	Ephemeral lake, buried	20%[b]	Mun and Whitford (1998)
Bouteloua eriopoda (grass) roots	Piedmont toe slope, buried	38%[b]	Mun and Whitford (1998)
Tridens (Erioneuron) pulchella (grass) roots	Various locations on watershed	21–31%[b]	Mun and Whitford (1998)
Sporobolus airoides (grass)	Drainage basin	50%[a]	Montana *et al.* (1988)
Wheat straw	Desert plain, Judean Desert, Israel	16–22%[a]	Steinberger *et al.* (1990)
Gutierrezia sarothrae (subshrub) roots	Various locations on watershed, New Mexico	23–43%[b]	Mun and Whitford (1998)
Atriplex repanda (shrub)	Bajada – Chile	18%[a]	Cepeda-Pizarro (1993)
Atriplex semibaccata (shrub)	Bajada – Chile	11%[a]	Cepeda-Pizarro (1993)
Atriplex nummularia (shrub)	Bajada – Chile	16%[a]	Cepeda-Pizarro (1993)
Avena sterilis litter – buried (annual)	Judean Desert, Israel	60–65%[b]	Hamadi *et al.* (2000)
Avena sterilis litter	Judean Desert, Israel	20%-40%[a]	Hamadi *et al.* (2000)

[a] Decomposition rates of litter on the soil surface.

[b] Decomposition of buried litter.

[c] Litter consumed by termites during a 3-month period at the end of the growing season.

fragmentation by rainfall. Breakdown by microbial enzymes is obviously limited to those brief periods when litter and soil are moist and soil temperatures are moderate. Biological decomposition of surface materials is therefore sporadic and brief.

Measurement of mass loss cannot distinguish between fragmentation and mineralization. However, if mass loss is a function of biological activity, there should be a relationship between frequency and duration of litter wetting and mass loss since growth and activity of microorganisms requires moist environments. Experiments designed to examine this question by providing supplemental water by sprinkler irrigation have shown that there is no clear relationship between quantity and frequency of rainfall and mass loss (Whitford *et al.*, 1986; Mackay *et al.*, 1987; Steinberger and Whitford, 1988). Adding 305 mm yr^{-1} to the 230 mm annual total had no significant effect on mass losses nor did frequent pulses (Whitford *et al.*, 1986). When litter was placed in the field during an extended dry period, irrigated litter lost mass faster than nonirrigated litter. The rates, however, were equal thereafter (Fig. 9.2). Further insights into this process were gained in irrigation experiments in the Negev, Israel. In the Negev, the probability of rainfall in the summer months of May–September is essentially zero. Although
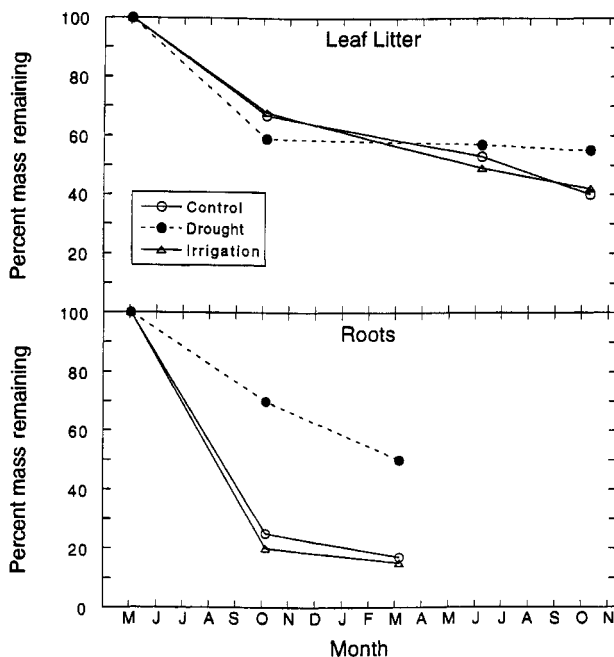

Figure 9.2 The effect of artificial drought and irrigation on decomposition of surface litter and buried roots in a cresotebush, *Larrea tridentata*, shrubland. (From Whitford *et al.*, 1995.) With kind permission from Kluwer Academic Publishers.

irrigation added considerable water and kept soils and litter wet for longer periods, there were no detectable irrigation effects during the normal winter–spring 'rainy period'. Irrigation increased mass losses during the rainless summer (Steinberger and Whitford, 1988).

Although rainfall supplementation experiments provide some insights into how climate variation affects decomposition, imposition of drought is essential to really understand climate–decomposition relationships. 'Rain-out' shelters constructed of steel frames with greenhouse plastic roofs were used in several studies in the Chihuahuan Desert. These studies demonstrated that the imposition of drought resulted in a marked decrease in average litter inputs (45 g per trap compared to 83 g per trap in year 1, and 72 g per trap compared to 112 g per trap in year 2 in droughted plots and controls, respectively). Imposition of drought had no effect on the rates of decomposition of creosotebush leaf litter on the soil surface (Fig. 9.2). However, decomposition rates of roots of a perennial herb were significantly reduced by imposed drought but not by irrigation (Fig. 9.2).

9.2.3 Spatial Variation

Variation in microclimate and physicochemical soil properties resulting from topographic position and vegetative cover can produce different patterns of decomposition, mineralization and soil organic matter accumulation (Seastedt, 1984). In a study of surface litter decomposition at several locations on a desert watershed, there were no differences in initial rates of mass loss (k_1) across the range of locations on the watershed. There were differences in average rates of mass loss among locations in the second phase of decomposition (k_2). Highest rates of decomposition were recorded for a run-on area at the base of the watershed. The lowest rates of decomposition were recorded in the dry lake basin on fine textured clay soils (Cepeda-Pizarro and Whitford, 1990). The high rates of decomposition in the run-on area were attributed to partial or complete burial of the litter bags by water-transported soil. The low rates of decomposition measured in the dry lake basin were attributed to the extremely low infiltration of water into those soils and shading by the dense grass cover.

In contrast to surface litter, decomposition of roots on the same watershed yielded no significant differences among sites, except for the dry lake basin, on the same watershed where the surface litter studies were conducted. There were no significant differences in decomposition rates of roots in nitrogen fertilized soils and in unfertilized soils (Mun and Whitford, 1998). The spatial differences in mass loss rates in the dry lake were attributed to the high clay content soils of the lake basin which reduced water availability and to the absence of termites in the lake basin. Therefore, it appears that topographic position and soil textural characteristics have little effect on decomposition processes except when landscape position results in litter burial or where fine texture soils affect the composition of the soil fauna.

9.2.4 Decomposition of Buried Litter and Roots

Litter that is buried in the soil decomposes more rapidly than surface litter and is primarily a biological process (Santos *et al.*, 1981; Elkins and Whitford, 1982; Parker *et al.*, 1984). Decomposition rates of buried litter varies inversely with initial lignin content and C:N ratio. The chemical changes in decomposing buried litter are the same as those reported for forest litter (Berg *et al.*, 1984). The early stages of buried litter decomposition involves losses of soluble materials and holocellulose but essentially no change in the lignin. Nitrogen immobilization occurs in the early stages of buried litter decomposition as the microbial biomass growing on the litter increases (Parker *et al.*, 1984).

The biotic regulation of decomposition of buried materials was clearly documented in studies in the hyperarid Namibian sand sea, southwestern Africa. Decomposition of cellulose (cotton cloth and filter paper) buried at 10 cm depth occurred in pulses following rain events. About 84% (range 64.7–97.2%) of the original mass was lost following rains of 9 mm or greater (Jacobson and Jacobson, 1998). Mass loss during a dry period was only 8.2% (range 0–16.7%). Most substrates were colonized by fungi. Termites and tenebrionid beetle larvae were recorded as feeding on the fungus-colonized substrates. In hyperarid systems where soils are too dry to support growth of fungi and activity of microarthropods, rainfall is the trigger that stimulates episodic periods of high rates of decomposition. The episodic pulses of decomposition result from rapid growth of fungi and activity of soil mesofauna and macrofauna that feed on fungi and fungal modified cellulose.

Considering that the recalcitrant materials in surface litter are rapidly destroyed by photodecomposition and that only a fraction of the litter is buried, it is obvious that the largest contribution to the recalcitrant soil organic carbon pool is that of decomposing roots. Roots vary considerably in initial lignin content (approximately 17% for roots of an annual plant, 24% for roots of a woody shrub, and 27–29% for roots of several grasses. Decomposition rates of roots were inversely related to the initial lignin content and also to the initial nitrogen content which were lower in the roots of grasses than in the other species examined (Mun and Whitford, 1998).

Decomposition rates of roots in the Chihuahuan Desert were equal to or higher than those reported for decomposing roots in mesic ecosystems (Whitford *et al.*, 1988). Rates of decomposition of roots of woody shrubs and of herbaceous annuals were not affected by supplemental irrigation. The absence of an irrigation effect was attributed to the relatively 'average' rainfall during the time that decomposition was measured. Average annual mass losses from woody roots (40%) were considerably lower than the average annual mass losses from roots of herbaceous annuals (85–90%) which was related to the lignin content of the roots and to the susceptibility of herbaceous roots to attack by subterranean termites. Simulated drought reduced the mass loss from roots of an herbaceous perennial from an average mass loss of 80% to an average mass loss of 50% (Whitford *et al.*, 1995; Fig. 9.3). The roots of the woody shrubs retained relatively constant C:N ratios through the experiment indicating little if any nitrogen immobilization. The C:N ratios of the roots of
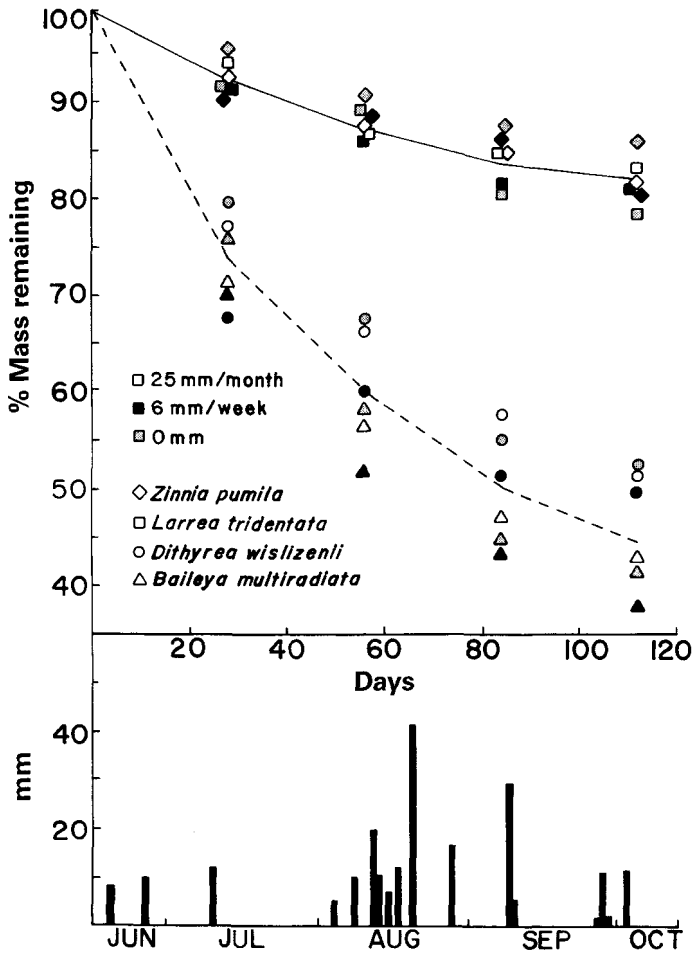
Figure 9.3   Comparison of effects of irrigation on the decomposition of buried roots (From Whitford *et al.*, 1988.) With permission of Springer-Verlag GmbH & Co KG.

annuals decreased by an average of 28 after 4 months indicating that microbial biomass on the roots of the annuals had immobilized a large amount of soil nitrogen.

The changes in carbon chemistry of decomposing roots in a desert are similar to those of decomposing roots in mesic forests and in mesic grasslands (McClaugherty *et al.*, 1984). The percentage composition of nonpolar compounds and water-soluble compounds in decomposing roots of all species dropped to approximately 20% of their original concentration within the first year (Mun and Whitford, 1998). The rapid decrease in these compounds is probably the result of rapid colonization of roots by bacteria and fungi and the subsequent rapid metabolism of these easily metabolizable compounds. The acid-soluble compounds are more recalcitrant than

the nonpolar and water-soluble compounds and these decreased by only 10% of their original concentration at the end of the first year and to between 10% and 25% (depending on the species) after 42 months of decomposition. The relative concentration of lignin increased during the decomposition of roots and there were marked increases in the relative concentration of nitrogen in the roots of an annual but nitrogen immobilization in decomposing roots of woody plants did not occur until after 24 months of decomposition (Mun and Whitford, 1998). The evidence from changes in chemistry of decomposing roots and of buried litter supports the conclusion that decomposing roots are the principal source of recalcitrant carbon in desert soils.

9.2.5 The Role of Microfauna in Decomposition and Mineralization

The soil microfauna have been shown to play a major role in decomposition processes in mesic temperate ecosystem (Swift *et al.*, 1979; Seastedt, 1984). The soil microfauna in arid systems is nearly as diverse as the soil microfauna of mesic soils (Wallwork, 1982). In order to adequately address the role of soil biota in decomposition, it is necessary to distinguish between the plant litter, dung, wood, etc., exposed to the intense light and heat of the soil surface and the litter, litter fragments and dead roots at varying depths below the soil surface.

Organic materials on the soil surface have microclimatic conditions conducive to microbial growth and activity of soil microflora for brief periods at night and for slightly longer periods following rains (Whitford, 1989). However, the micro-mesofauna appear to have virtually no effect on the rates of mass loss from surface litter (Silva *et al.*, 1985; MacKay *et al.*, 1987).

Some plant litter is buried in pits produced by animals and an unknown fraction of the surface leaf litter is mixed into the surface soil as small fragments. The microclimate in the soil, even as shallow as 1 cm depth, is very much modified compared to surface conditions. The moderate soil temperatures and high humidity in the soil interstices, produces microclimates that allow some microarthropods to remain active even in soils with water potentials lower than −6.0 MPa (Whitford, 1989). In soils with water potentials lower than −3.0 MPa most of the soil protozoans are encysted, the nematodes are in a state of anhydrobiosis as are the collembolans and some of the soil acari. The active mesofauna in dry soils are soil acari. There are some species of soil acari that remain active in soils as dry as −6.0 MPa and some species that enter a cryptobiotic (inactive) state in dry soils (Whitford, 1989). In desert soils the complete soil micro- and mesofaunal community is involved in decomposition and mineralization only during periods when the soil is moist. Rainfall regulates decomposition and mineralization in arid ecosystems by stimulating rapid growth of fungi and activating the soil fauna. Rainfall-induced pulses of activity are observed most clearly in hyperarid systems where rainfall events are separated by sufficient time periods for soil to dry between events (Jacobson and Jacobson, 1998).

The importance of the soil microarthropod fauna in mass loss of buried litter in deserts has been well documented (Santos and Whitford 1981; Santos *et al.*,

1981; Elkins and Whitford, 1982; Parker *et al.*, 1984). In desert ecosystems, the activity of soil microarthropods (primarily soil acari), accounted for 30% of the initial mass losses. Despite the fact that the amount of soil respiration that can be attributed to all soil animals is 10% or less than the total amount (Reichle, 1971). The soil fauna directly or indirectly influence the soil microflora by their feeding activities. The effects of soil acari on decomposition in arid ecosystems appear to be indirect. The common soil acari that are active at high soil water potentials are small prostigmatid mites that feed on fungi and on nematodes. In the initial stages of decomposition of buried creosotebush leaf litter, microarthropods controlled the population densities of bacterial feeding nematodes. Where microarthropods were excluded, the high nematode populations reduced the bacterial biomass resulting in reduced rates of mass loss (Santos *et al.*, 1981) (Fig. 9.4).
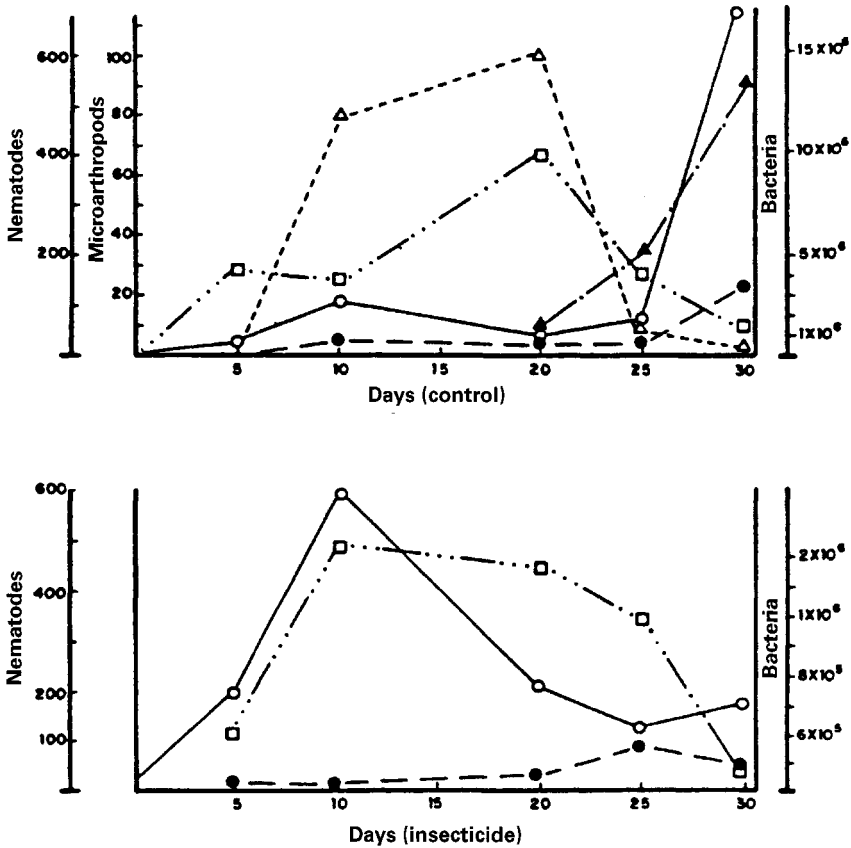

Figure 9.4   The effects of excluding soil microarthropods on the populations of soil nematodes and on decomposition rates in the Chihuahuan Desert. ○, Bacteriophagous nematodes; ●, fungivorous nematodes; △, Tydeidae; ▲, Pyemotidae; □, bacteria. (Data from Santos *et al.*, 1981.) With permission by The Ecological Society of America.

Whereas soil bacteria dominate the early stages of buried leaf litter decomposition, the later stages are dominated by fungi (Parker *et al.*, 1984). The microarthropods that are most abundant in buried decomposing litter or around decomposing roots are small fungal feeding mites. Although microarthropods have very little effect on mass losses during the later stages of decomposition, i.e. after the first 90 days they do directly affect rates of nitrogen mineralization.

9.2.6 The Role of Termites

Termites are abundant in the soils of most subtropical, arid, and semiarid regions of the world (Lee and Wood, 1971). Although large above-ground mounds are an impressive indication of the presence of these animals, the majority of termite species live below the soil surface. Based on the distribution of termites and the limited studies of the quantities of dead plant parts and other organic materials consumed by these animals, it is clear that these insects have a significant effect on nutrient cycling and nutrient availability in arid and semiarid systems. Termites are responsible for removing a large fraction of certain species of litter (Silva *et al.*, 1985; MacKay *et al.*, 1987). Soil moisture and temperature affect termite activity, hence mass loss from litter species consumed by termites shows a strong positive correlation to rainfall (MacKay *et al.*, 1987).

Materials such as grass leaves and annual plant leaves and stems that are preferred foods by Chihuahuan Desert termites are harvested during periods when soil moisture and temperature allows termites to forage on surface litter (Whitford *et al.*, 1982; MacKay *et al.*, 1986). For example, *Gnathamitermes tubiformans* cease foraging at soil moisture less than -5.4 ± 0.2 MPa and hence are capable of feeding in litter accumulations for much of the year when soil temperatures are higher than 5°C (MacKay *et al.*, 1986).

In southeastern Australia, termites were harvesting or directly consuming grass leaves and fragments, shrub and tree leaves and phyllodes, sheep and kangaroo dung, dead wood, fungal modified stem bark, and dead roots (Whitford *et al.*, 1992). In southern Somalia, litter decomposition was rapid (95% disappeared in one year) and not correlated with rainfall because termites were active throughout the dry season (Thurow, 1989). In the northern Chihuahuan Desert, mass loss from plant litter on plots from which termites had been chemically excluded were compared to mass loss from plant litter on plots with termites present. These studies demonstrated that a large fraction of dead plant parts and dung were consumed by termites (Whitford *et al.*, 1982, 1988) (Fig. 9.5). Materials ingested by termites are mineralized by the symbionts within the gut of the termite. The breakdown of materials within the termite gut includes not only the cellulosic compounds, but also lignins (Lee and Wood, 1971).

The small quantities of fecal material produced by termites are generally used in the cementing materials of gallery walls and nest chamber walls. The mineral nutrients in the food material are largely retained in the biomass of the colony and are returned to the ecosystem only via predators of the workers and reproductives
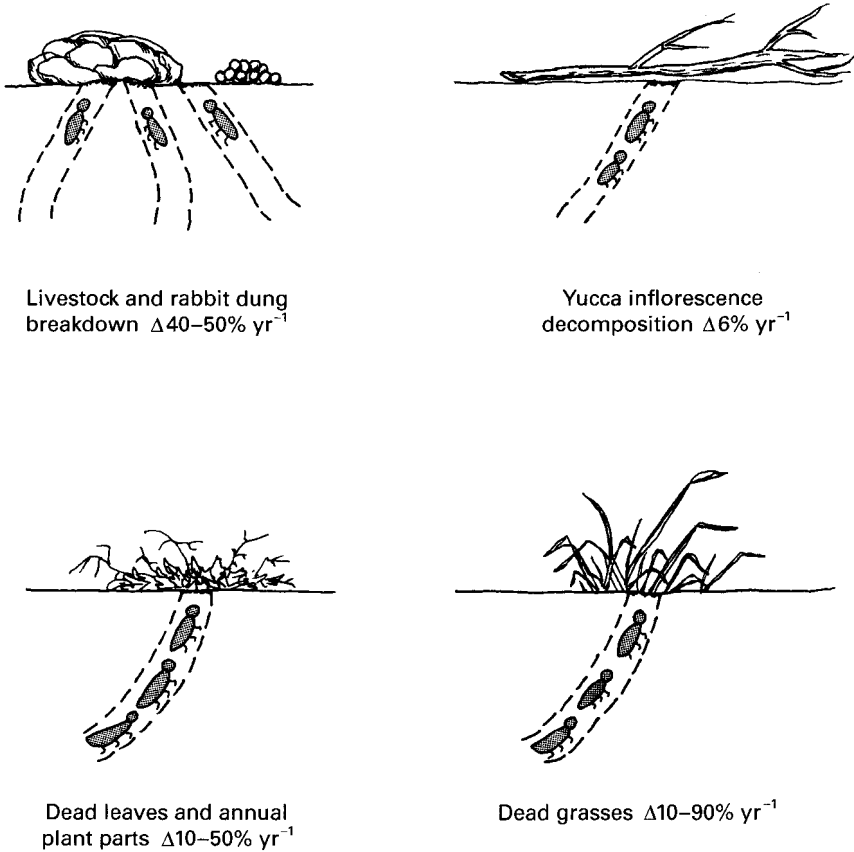
Livestock and rabbit dung
breakdown Δ40–50% yr^{-1}

Yucca inflorescence
decomposition Δ6% yr^{-1}

Dead leaves and annual
plant parts Δ10–50% yr^{-1}

Dead grasses Δ10–90% yr^{-1}

Figure 9.5   The keystone role of subterranean termites on decomposition processes and ecosystem function in Chihuahuan Desert ecosystems.

(Schaefer and Whitford, 1981). Because so much of the decomposition of organic matter in arid ecosystems occurs within the guts of termites, there appears to be a negative correlation between termite abundance and soil organic matter or soil nutrients. On a Chihuahuan Desert watershed where measurements of termite abundance and activity and soil organic matter were made at 30 m intervals over a 2 km transect, there was a highly significant correlation, $r = -0.97$ between termite abundance and soil organic matter (Nash and Whitford, 1995). The absence of a pattern of regularly increasing soil organic matter from the top to bottom of the watershed added further support to the contention that subterranean termites were primarily responsible for the variations in soil organic matter on that watershed. The most important macro-nutrient, nitrogen, tends to vary directly with soil organic matter (Whitford *et al.*, 1987). The negative relationship between termites and soil organic matter suggests that soil fertility varies inversely with termite

abundance. However, the importance of termites as producers of macropores and their effects on infiltration of water is probably more important for sustaining the productivity of desert ecosystems than their effect on reducing the nitrogen content of desert soils.

9.2.7 Conceptual Model of Decomposition Processes in Deserts

The following conceptual model is proposed to account for the relationships among variables that have an effect on the decomposition processes in deserts. Initial high rates of mass losses from litter on the surface result from leaching of low-molecular-weight materials from leaf surfaces and by the breakdown of lignins by photochemical decomposition. This accounts for the direct correlation between initial lignin content and decomposition. At low light intensities and low sun angles, mass loss rates are low and occur primarily from low level activity of microorganisms. At high light intensities, photooxidation of complex structural molecules results in fragmentation by wind or water drops. The small fragments are transported into the soil by water where they are then decomposed by biological activity of the microflora during periods when soils are moist. This is the source of elevated CO_2 production measured when soil and litter are moist (Parker *et al.*, 1983).

A major component of the high rates of decomposition of surface litter is the consumption of many of these materials by termites. Termites consume more than 50% of the total surface litter and may consume up to 70–80% of the litter and most of the animal dung. Materials consumed by termites are virtually completely converted into carbon dioxide and water because the symbiotic gut flora of many termites is capable of processing recalcitrant organic molecules such as lignins. Thus litter falling to the surface of the soil in deserts contributes little to the soil organic carbon pool and minerals in litter are returned to the soil in a mineralized state largely through the feces of animals that prey on termites.

A variable quantity of the litter input in a desert ecosystem may be blown into soil pits and buried. The process of decomposition of buried litter and dead roots is very different from that of surface litter in arid environments. The moderate environment of the soil affects both decomposition rates and patterns of decomposition. Buried litter accumulates moisture and remains moist even in dry soils. The moderate temperature and moisture content of buried litter is conducive to growth of microflora and microfauna. Dead roots encounter the same moderate conditions in soil and serve as ready substrates for growth of the microflora. Increasing populations of microflora on decomposing materials attract microfloral grazers (protozoans, nematodes, and microarthropods), which in turn attract predators (predatory nematodes and nematophagous mites). Complex food webs are quickly established around moist roots and buried litter accumulations. The extracellular enzymes of the microflora rapidly decompose the water-soluble and nonpolar compounds (sugars, fats, waxes, starches, and cellulose). The complex acid-soluble compounds are slowly attacked by a small subset of the microbial

heterotrophs. Decomposition of buried litter and roots is primarily a biological process.

9.3 LANDSCAPE PATTERNS OF NUTRIENT DISTRIBUTION

One of the best-documented spatial patterns of nutrient distributions in arid ecosystems are the 'islands of fertility' associated with shrubs and trees (Garcia-Moya and McKell, 1970; Charley and West, 1975, 1977; Barth and Klemmedson, 1978; Parker *et al.*, 1982; Virginia and Jarrell, 1983; Schlesinger *et al.*, 1996). The accumulation of nutrients in the surface soil beneath shrubs and the lower nutrient levels in soil between shrubs results from a whole suite of processes: plant-nutrient uptake, litter fall, dust interception, soil-erosion, soil deposition, soil biota-mineralization, decomposition, animal decomposition, fecal decomposition, and predation. The relationship between shrub morphology and spatial pattern on below-canopy litter accumulation has been documented for one species but undoubtedly applies to a number of other species of shrubs (DeSoyza *et al.*, 1997). In landscapes composed of patches with a variable mix of shrubs, grasses, and perennial herbs, the nitrogen stores in the soil are related to the characteristics of the patch. Available nitrogen was considerably higher in soils from complex patches, intermediate in simple shrub–grass patches and lowest in patches of bare soil (Mazzarino *et al.*, 1996).

Although the activity of subterranean termites may be enhanced by the presence of leaf litter and the moderating effect of the canopy on soil temperature, shrub and tree leaves rank low on the food preference scale of most termite species. Tree and shrub leaf litter, therefore, provides the energy and nutrient source for the soil microbiota, resulting in nutrient enrichment. Another factor affecting the nutrient enrichment of the subshrub soil is the activity of animals like lizards. Many lizards move quickly from shrub to shrub spending most of their time foraging or simply sitting in the more benign subcanopy environment (Creusere and Whitford, 1982; Peterson and Whitford, 1987). In the northern Chihuahuan Desert, lizards are the most important predators of subterranean termites. In other arid regions, e.g. Australia and the Kalahari of southern Africa, lizards are the most important termite predators. Many lizards feed almost exclusively on termites (Pianka, 1985; James, 1991). In these deserts, lizards use clumps of vegetation as shelter and as foci for their foraging activities thereby contributing to the 'islands of fertility'. Given the abundance of termites and lizards in arid and semiarid regions, it is likely that this linkage between detritivore–predator and spatial nutrient pattern is generally important in all such systems. The general pattern of nutrient distribution with high concentration in center to mid-canopy soils decreasing rapidly from mid-canopy to canopy edge and into the intershrub space, is characteristic not only of shrubs, but also of perennial grass clumps and small trees. Nutrients are accumulated where soil organic matter is elevated either by debris accumulation or turnover of fine roots.

Fossorial mammals, burrowing mammals, mammals and lizards that dig for invertebrate prey contribute to the nutrient heterogeneity of soils in arid regions. Foraging pits fill with litter, frass, dung, and seeds creating small nutrient-rich 'hot spots'. Burrow systems that are occupied by successive generations of central place foragers, e.g. banner-tail kangaroo rats, hairy-nosed wombats, harvester ants, and mound building termites) gradually accumulate nutrients in the mound soils and eventually develop into nutrient rich patches (Fig. 9.6). Fossorial mammals turn over soil and leave patches that are rich in organic matter in storage chambers and defecation sites (Whitford and Kay, 1999; Whitford, 2000). The abundance, species composition, and behavior of those animals that disturb soil or accumulate organic materials in burrows are important variables to consider when assessing the patterns of nutrient distribution across the landscape.

The spatial distribution patterns, morphologies, and physiological characteristics of dominant plant species clearly affect the richness of the below canopy 'islands of fertility'. However, when the frame of reference is moved from the local patch to the landscape scale there are many other variables that affect the nutrient status of soils and nutrient cycling in the ecosystems that make up a landscape. One of the most important variables that affect both nutrient status and the temporal characteristics of nutrient cycling is the spatial distribution of different root systems in a landscape. There are some generalizations about root systems
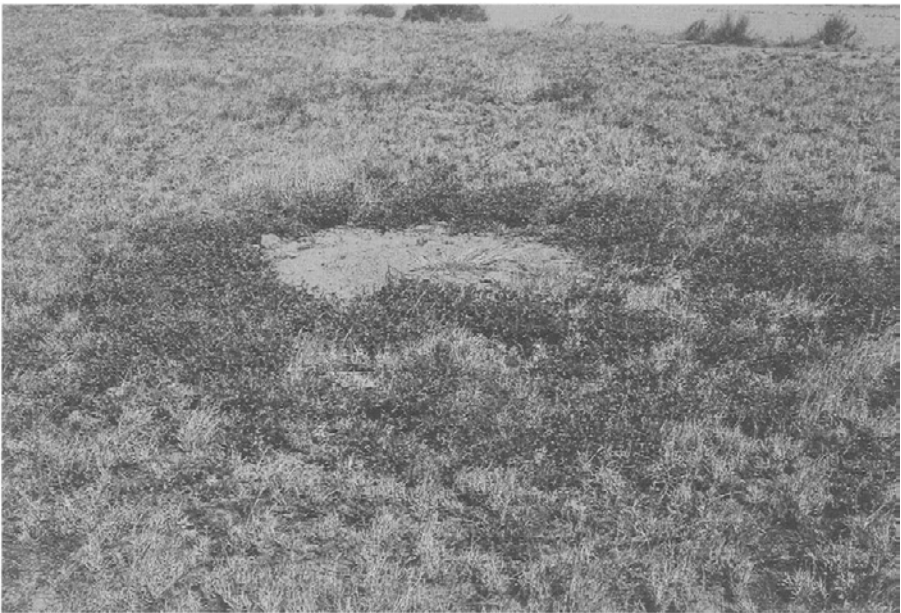

Figure 9.6   Vigorous growth of a herbaceous annual, *Erodium texanum*, in a corona around the nest of a central place forager – seed-harvesting ants, *Pogonomyrmex rugosus*. Nitrogen concentrations in the soils of the corona were double that of the surrounding soil.

that can be inferred from the above-ground life form of the vegetation. Perennial grasses tend to produce a dense but relatively shallow mat of roots below the basal area of the plant. The root system of some species may occupy an area somewhat larger than the canopy crown of the grass but few grasses have spatially extensive root systems. Some species of grasses have physiological characteristics that result in complex rhizosheaths of mucilages and mucigels, and microbes (Wullstein *et al.*, 1979). In some species the mucilages and mucigels secreted from the roots of grasses serve to attract and support free-living nitrogen fixing bacteria in the rhizosheath (Mandimba *et al.*, 1986; Reinhold *et al.*, 1986).

The root systems of most herbaceous annuals may consist of a main tap root with fine roots emerging from the bottom third or of three or more roots that extend from the root crown. Herbaceous annuals that germinate during the growing season may have shallow root systems and root:shoot ratios as low as 0.2. In herbaceous annuals that germinate during the nongrowing season (i.e. winter–spring annuals in North American deserts), the rooting depth and root biomass is dependent on the depth of the wetting front and the length of time that the deeper soil profile remains moist. During cool periods when above-ground growth does not occur, the roots of the rosettes continue to grow. This can produce root:shoot ratios as high as 1.2 at peak above-ground biomass production. The root biomass of annual plants can vary both temporally and among species.

Perennial herbaceous plants are generally but a small fraction of the cover and biomass of desert vegetation. Some perennial herbaceous species are clonal and may occur in dense patches. Usually there is more below-ground biomass of herbaceous perennials than above-ground biomass. The root systems are generally fleshy (storage organs) with fine roots emanating from the actively growing segments.

Most desert shrubs and small trees have diffuse, relatively deep (> 1 m) woody roots systems. Many desert trees and shrubs also have extensive shallow root systems in addition to the deep roots (Gile *et al.*, 1998). In most desert soils, nitrogen is concentrated in the upper 10 cm of soil. The growth responses of a nitrogen-limited desert shrub and small rain events suggest that the shallow roots contribute most of the nitrogen uptake and allow the shrub to respond rapidly to relatively small rain events (Fisher *et al.*, 1987).

Plants with symbiotic nitrogen fixers are common in arid landscapes. Many species of small tree and shrub legumes have nodules containing the nitrogen-fixing *Rhizobium* spp. Not all legumes host symbiotic nitrogen fixers on the root system. Several species of legumes have increased in abundance and cover in areas where domestic stock grazing has modified the environment, e.g. *Acacia caven* (in Chile), *Prosopis* spp. (in North America) and *Acacia* spp. (in Africa). These species produce leaves with lower C:N values than those of other non-leguminous species even in those plants with root systems devoid of nodules. Even when a legume is removed, there is a residual elevation in soil nitrogen levels (Klemmedson and Tiedeman, 1986). This has important implications for

the patchiness of vegetation, species composition of the vegetation and the productivity of arid areas in which woody legumes dominate the landscape. The abundance and spatial distribution of such species affects soil nitrogen levels and productivity of grasses and other plants that grow under the canopies of woody legumes (Weltzin and Coughenour, 1990). Nutrient enrichment of soils under legume canopies can result in production values that are twice those measured in the between-canopy space (Weltzin and Coughenour, 1990).

Herbaceous nitrogen-fixing legumes are a relatively minor component of the vegetation. Some of the nitrogen-fixing legumes are ephemeral plants, e.g. species such as *Astragalus* spp. in North America. Most of the herbaceous nitrogen-fixing legumes are perennial. However, perennial herbaceous legumes accounted for only a fraction of one percent of the vegetative cover on most locations on a desert watershed (Whitford *et al.*, 1987). It is unlikely that herbaceous legumes contribute much to the nitrogen economy of desert ecosystems.

There is a clear correlation between soil organic matter and nutrient availability in desert ecosystems. This is not a surprising correlation because the primary source of nutrients in soils is from the decomposition and mineralization of organic materials. In a study using nitrogen mineralization potential as a measure of nutrient availability to plants, Whitford *et al.* (1987) found good correlations between mean soil organic matter and mineralized N (Fig. 9.7). The spatial distribution of soil organic matter in deserts is determined by (1) location and relative abundance of termites, (2) run-off, run-on patterns, (3) resistance of the vegetation to wind transport of litter and (4) structure of the vegetation mosaic. There is a positive relationship between soil organic matter, total nitrogen and nitrogen mineralization potential (the rate of nitrogen mineralization under defined conditions of soil incubation). This relationship is well documented in the northern Chihuahuan Desert (Fig. 9.7). As the data for the dry lake bed soils show, the direct positive relationship may be somewhat modified by soil texture.

Total N–organic matter relationships are also affected by the genetic physiological characteristics of the vegetation. For example, the total soil N is elevated in mesquite coppice dune soils because of the lower C:N ratio of *Prosopis glandulosa* leaves in comparison to other shrubs and grasses in the area. Another important consideration affecting the spatial variability of soil nutrients is the negative relationship between soil organic matter and subterranean termites. Soils that are unfavorable for termites will tend to have higher levels of soil organic matter and higher nutrient concentrations. The spatial pattern of termite colonies and their foraging patterns will certainly affect the variability in nutrient availability across an arid landscape. The morphology and physiology of the dominant plants also affect the variability and the relative importance of various processes. For example, in plants with canopies shaped as inverted cones, accumulation of dust on the leaves may contribute greatly to nutrient concentration around the root crown because of effective stem flow (DeSoyza *et al.*, 1997). Perennial species with symbiotic N fixers may produce nitrogen rich patches, but the concentrations of other nutrients may not be proportioned to the N concentration.
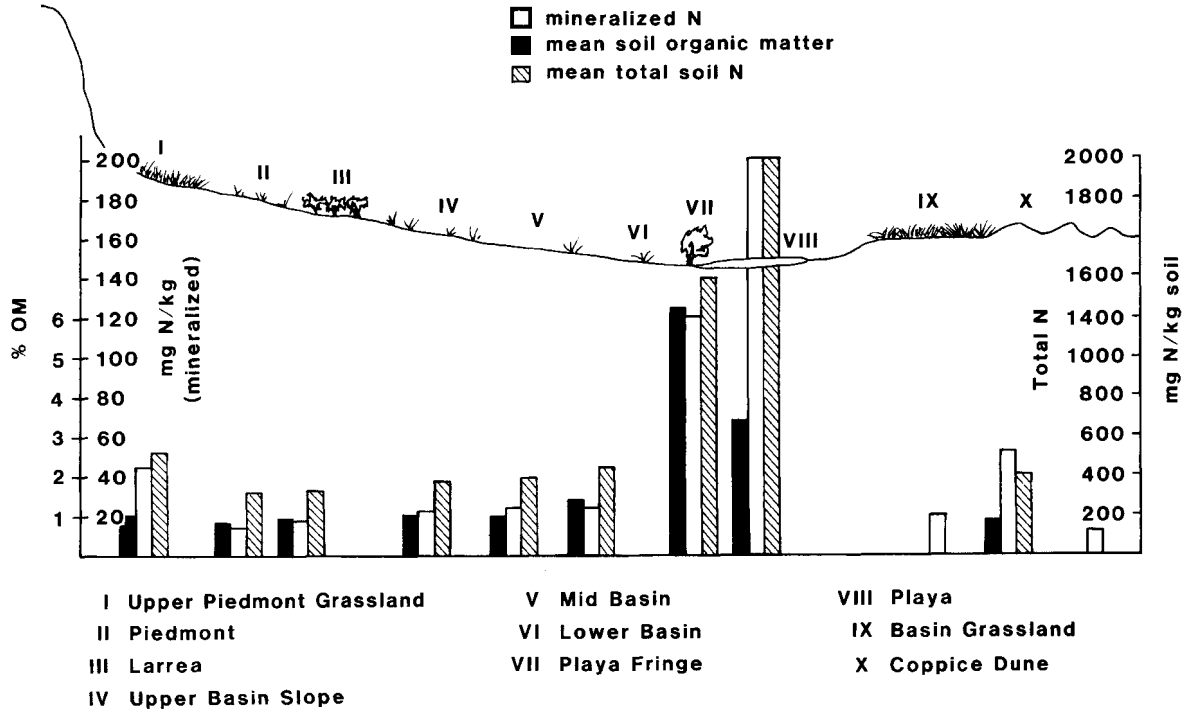
Figure 9.7   The distribution of nitrogen, soil organic matter (OM), and nitrogen mineralization potential across a Chihuahuan Desert landscape. (From Whitford *et al.*, 1987).

The patterns of nitrogen mineralization and soil organic matter across a Chihuahuan Desert landscape reflect these variables. The inverse correlation between termite relative abundance and soil organic matter has been well established for a Chihuahuan Desert watershed. In deserts where termites are more abundant, soil nutrient levels may be considerably lower than the concentrations recorded in North American deserts. The pattern of nitrogen mineralization on a watershed also reflected the run-off, run-on patterns of organic materials. The dry lake basin where the highest nitrogen mineralization and highest total soil N were recorded is not only enriched by organic matter run-on but is also an area where the fine textured soils and infrequent inundation eliminate termites. The relationships between soil organic matter and landscape position, soil characteristics, and nitrogen mineralization are probably applicable to most arid and semiarid landscapes.

9.4 RESORPTION

An important variable that affects decomposition and mineralization is the resorption of nutrients from foliage prior to leaf abscission. In the process of resorption, nutrients are mobilized from senescing leaves and transported to other plant tissues. Nutrients that are resorbed are conserved by the plant for use in primary production in the next growing season. Nutrient resorption is especially important for plants growing in nutrient poor environments (Aerts, 1996). In a review of nutrient resorption in perennial plants, Aerts (1996) reported that mean nitrogen resorption efficiency was significantly lower in evergreen trees and shrubs (47%) than in deciduous trees and shrubs (54%). Phosphorus resorption efficiency was essentially the same for evergreen (51%) and deciduous (50%) shrubs and trees.

Nutrient resorption patterns in desert plants differ from the general patterns for mesic species. Resorption of phosphorus in creosotebush (*L. tridentata*) was very high (72–86%) (Lajtha, 1987). However, the nitrogen resorption values for creosotebush fell within the range of values for evergreen trees and shrubs (Lajtha and Whitford, 1989). Mean resorption efficiencies calculated on the data for desert shrubs for nitrogen and phosphorus were 57% and 53%, respectively. There was a large intersite and interyear variation in resorption efficiencies of ocotillo, *Foquieria splendens*, suggesting that the regulation of resorption efficiencies in desert shrubs may be quite complex.

Winter-deciduous shrubs growing on the margins of ephemeral stream channels exhibited nutrient resorption patterns related to their status as facultative or riparian species. Nitrogen and phosphorus resorption efficiencies of obligate riparian species (*Brickellia laciniata* and *Chilopsis linearis*) (N = 63%, P = 58%) were substantially higher than in facultative riparian species (*Fallugia paradoxa*, *Rhus microphylla*, *Prosopis glandulosa*, and *Flourensia cernua*) (N = 46%, P = 46%). The species resorbing the least nitrogen from the leaves was mesquite, *P. glandulosa*; a species known to harbor nitrogen-fixing symbionts on the roots

(Killingbeck and Whitford, 2001). It has been hypothesized that plant species with nitrogen-fixing root symbionts will resorb less foliar nitrogen than other species in the same environment. In the Sonoran Desert, no resorption of nitrogen was reported in senescing leaves of *P. glandulosa* (Rundel *et al.*, 1982).

9.5 NITROGEN CYCLE

9.5.1 Nitrogen Fixation

Of all of the soil nutrients required for plant growth, nitrogen appears to be the most important limiting nutrient in semiarid and arid ecosystems. Despite the huge atmospheric pool of nitrogen, that pool represents a nonusable form of nitrogen for use in photosynthesis. The biologically active forms of nitrogen are ammonium and nitrate which can be used to produce amino acids and other nitrogen-containing organic molecules. The fate of fixed nitrogen is complex (Fig. 9.8) and involves a variety of microorganisms, soil microfauna, plus plants and animals.

The fixation of atmospheric nitrogen (N_2) is an energy-expensive reduction to ammonium (NH_4) that occurs in some cyanobacteria, in nodules on the roots of legumes by *Rhizobium* spp. bacteria, and in some free-living N-fixing bacteria

Atmosphere (N_2)

↓

_____**Soil**_____

N_2 fixation (Symbiotic bacteria (*Rhizobium & Frankia*) cyanobacteria (*Nostoc* etc.) free living bacteria (*Azobacter, Clostridium, Azospirillum*) $N_2 + 4H^+ \rightarrow NH_4^+$

↓

Nitrification $NH_4^+ + 2O_2 \rightarrow NO_3^-$ (*Nitrosomonas and Nitrobacter*) (plant uptake of NH_4^+ and NO_3, incorporation into plant proteins)

↓

Dead plant parts, animal feces (decomposition and mineralization) $NH_3 \rightarrow$ nitrification and/or plant uptake

Nitrogen Losses from Organic Pool

Ammonia Volatilization $NH_4^+ + OH^- \leftrightarrow NH_3\uparrow + H_2O$

Denitrification $NO_3 \rightarrow N_2O \rightarrow N_2\uparrow$ (*Pseudomonas, Achromobacter*)(requires anaerobic or extremely low soil oxygen concentration)
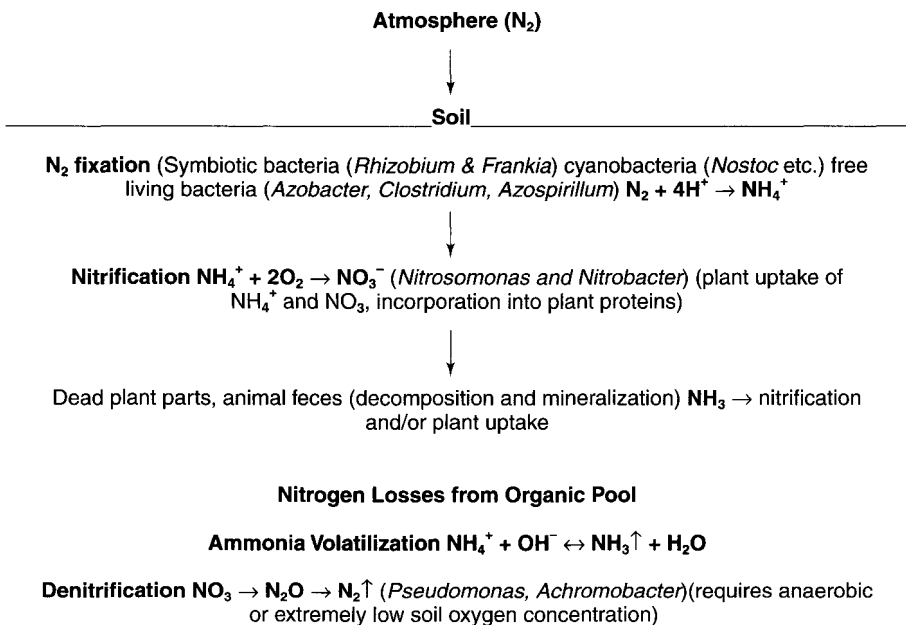
Figure 9.8   A general nitrogen cycle applicable to desert ecosystems.

such as *Azobacter* spp. Some other genera of free-living bacteria such as *Azospirillum* sp. may fix atmospheric nitrogen but there is conflicting evidence concerning these organisms as N-fixers.

Cyanobacteria are widely distributed as components of the algal–lichen (cryptogamic) crusts that are common in many deserts (Fig. 9.9). Cyanobacteria also occur in some desert soils where microphytic crusts appear to be absent. In areas with well-developed cyanobacterial crusts, atmospheric N-fixation may contribute significant amounts of nitrogen to the soils. Soils with cyanobacterial and lichen crusts had nitrogen contents 4 to 7 times higher than soils with no lichen or algal crusts (Shields, 1957). Nitrogen fixation in desert algal crusts, measured by uptake of isotopically labeled nitrogen, was rapid after initial wetting of the crusts. Cyanobacterial and lichen crusts leak the fixed nitrogen to the soil, usually in the form of ammonium, thereby increasing soil nitrogen levels (Mayland and McIntosh, 1966).

Nitrogen fixation is not the only influence of cyanobaterial and lichen crusts on soil nutrient enrichment. The concentrations of the elements N, P, K, Ca, Mg, and Fe, were significantly higher in a grass, *Festuca* spp. growing on cryptogamic (algal and lichen) crusted soil than on soil with no cryptogamic crust (Belnap and Harper, 1995). They reported that cryptogamic crusts fixed considerable nitrogen, which becomes available to vascular plants via decomposition and mineralization of the cryptogams or by cellular secretion in the living cryptogams. In deserts, the

Figure 9.9   Cryptogamic crusts covering bare patches in a tabosa grass, *Pleuraphis mutica*, swale in the northern Chihuahuan Desert, New Mexico.

nutrient enrichment of soils by cyanobacterial and lichen crusts is rainfall depend-
ent. In an area with 15% surface cover of algal crusts, up to 1.3 g N ha^{-1} h^{-1} was
added to the soil during the daylight hours for the first 24 hours after a rainfall
(Loftis and Kurtz, 1980).

Symbiotic nitrogen fixation in desert plants may be by *Rhizobium* nodules or
nodules containing actinomycetes. One of the important tree species in the tem-
perate and tropical semiarid zone of Australia is *Casuarina cunninghamiana,*
which harbors actinomycete symbionts (*Frankia* spp.) in nodules on its roots.
Frankia spp. on the roots of this tree fixed considerable nitrogen at soil tempera-
tures between 20°C and 30°C (Reddell *et al.*, 1985). Actinomycete symbionts
may be important in nitrogen fixation in other woody plant species in arid regions
but there is insufficient information on most species to evaluate this possibility.

Tree and shrub legumes are abundant in most arid and semiarid regions of the
world. Many of the most common genera harbor *Rhizobium* spp. or
Bradyrhizobium spp., symbiotic, nodule-forming, nitrogen-fixing bacteria.
Among the common genera confirmed to have nodulation and nitrogenase activ-
ity are *Acacia*, *Prosopis*, *Pterocarpus*, and *Pericopsis* (Shearer *et al.*, 1983;
Hogberg, 1986). Studies using nitrogen abundance ratios (N^{15}/N^{14}) confirmed
symbiotic nitrogen fixation in *Prosopis* at six of seven sites in the Sonoran Desert.
Nitrogen fixation was also reported in other Sonoran Desert legumes of the sub-
family Papilionoideae: *Lupinus*, *Dalea*, *Astragalus* and *Lotus* (Shearer *et al.*,
1983). An abundant shrub (*Psorothamnus spinosus*) growing in the low nitrogen
environment at the margins of ephemeral streams obtained approximately one-
third of its nitrogen from symbiotically fixed N. From the limited available data,
it appears that most of the woody legumes and a large portion of the herbaceous
legumes obtain fixed atmospheric nitrogen from symbiotic *Rhizobium* or
Bradyrhizobium species. Nitrogen fixation by root symbionts is probably the
primary source of nitrogen in the fertile islands that develop under the canopies
of leguminous trees and shrubs.

Although nitrogen fixation in *Rhizobium* nodules benefits the host plant with
the nitrogen enrichment most of the nitrogen gain does not enter the ecosystem
until the N-rich leaves decompose. The published estimates of quantities of fixed-
N relative to the quantities of N incorporated into growing plant tissues are not
particularly reliable. In desert ecosystems, the relative importance of the various
N fixation processes can probably be assessed by the presence and cover of
cyanobacterial crusts, cover of legumes known to support *Rhizobium* nodules, and
distribution and cover of vegetation life forms that provide rhizospheres con-
ducive to the growth of free-living N-fixers.

Some desert grasses and herbaceous perennials produce rhizosheaths of soil
particles bound together and to the root surface by mucilages and other complex
carbohydrates (Fig. 9.10). Rhizosheaths surrounding root surfaces are several
times the diameter of the root that secreted the complex carbohydrates (Rougier
and Chaboud, 1985). Rhizosheaths provide an ideal habitat for a variety of soil
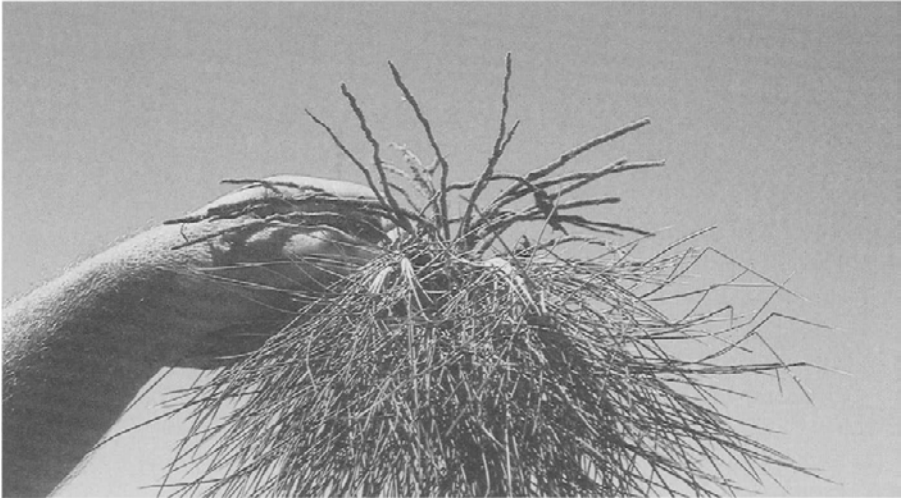microorganisms. Some of the microorganisms inhabiting rhizosheaths are species

Figure 9.10   The rhizosheath on the roots of a porcupine grass, *Triodia pungens*, north-western New South Wales, Australia.

of bacteria that are free-living nitrogen fixers (*Clostridium* spp., *Azotobacter* spp., and *Azospirillum* spp.) (El Shahaby, 1988). In plants that produce rhizosheaths, there appears to be stimulation of nitrogen fixation. The relationship between root secretion and nitrogen fixation by rhizosheath bacteria is an example of associative nitrogen fixation. Associative nitrogen fixation is a loose symbiosis in which the energy supplied by the plant supports nitrogen fixing bacteria that supply nitrogen to the plant. Studies of associative free-living nitrogen fixation in the rhizospheres of grasses from a desert watershed showed peak nitrogen fixation during the vegetative growth stage and seed production phenophase of the grasses (El Shahaby, 1988). Grasses grown in sterile quartz sand inoculated with bacterial cultures of species isolated from grass rhizosheaths in the field, exhibited growth related to the inoculum. Grasses grown in sterile quartz sand inoculated with either *Azotobacter* spp. or *Azospirillum* spp. exhibited higher growth rates than grasses grown with a balanced nutrient solution minus nitrogen. Grasses grown with an inoculum of both species exhibited considerably higher growth than grasses grown with a single species of N-fixer (El Shahaby, 1988). The growth stimulation produced by associative rhizosheath bacteria may be produced by growth factors (hormones or hormone-like compounds) released in addition to nitrogen.

In addition to N_2 that is fixed by biological fixation, there are atmospheric inputs of nitrogen in the form of dust. Dryfall inputs to desert ecosystems vary considerably depending on the proximity of the desert area to industry and population centers. In the Mediterranean region of southern Europe, long-distance transport of polluted air masses increased atmospheric wet nitrogen input by at

least a factor of 1.6 (Loye-Pilot *et al.*, 1990). In the northern Chihuahuan Desert there were high values of calcium, sulfate, nitrate, and total nitrogen in dryfall during the growing season. The growing season values of sulfate and nitrogen were nearly double the annual average values. These values were attributed to the differences between directional movement of air masses during the winter months and variable direction of air masses during the season of convectional storms (growing season). Air masses passing over metropolitan areas pick up nitrogen, sulfur, and other minerals that are deposited in rainfall or as dryfall. The concentrations of nitrate and total nitrogen in dry fall ranged between 4.4 ± 2.7 and 1.4 ± 0.9 ppm in dry fall and averaged 0.23 ppm in bulk precipitation (Whitford *et al.*, 1997). Rainfall inputs of NO_3–N that averaged 39 g ha^{-1} cm^{-1} rainfall were measured in the Chihuahuan Desert in west Texas (Loftis and Kurtz, 1980). In the semiarid chaparral of southern California, precipitation and dryfall resulted in mean annual deposition of Ca, K, NH_4^+–N, NO_3^-–N, Na, Mg, and SO_4^{2-}–S equal to or more than equal to annual losses reported in run-off from these ecosystems (Schlesinger *et al.*, 1982).

9.5.2 Nitrogen Losses

Ammonia volatilization and denitrification are mechanisms of loss of nitrogen from soil pools back to the atmosphere. Ammonia volatilization occurs in soils with a pH of 7.0 or greater. Since many desert soils are basic, there is a large potential for ammonia volatilization from desert landscapes. Ammonia is formed by the loss of a proton from NH_4 by the following reaction:

$$NH_4 + OH^- \Rightarrow NH_3 \Uparrow + H_2O$$
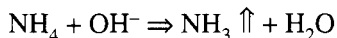
Ammonia is very soluble in water, therefore volatilization from moist soils is minimal. The loss of ammonia is greatest from coarse, dry soils with limited cation exchange capacity (Fleisher *et al.*, 1987). Ammonia volatilization measured in three habitats on a Chihuahuan Desert watershed demonstrated that wetting soils increased the rates of nitrogen mineralization and of ammonia volatilization (Schlesinger and Peterjohn, 1991). Another study found that irrigation decreased nitrogen mineralization which would have the effect of decreasing ammonia volatilization (Fisher *et al.*, 1987). The differences in results of these studies emphasizes the importance of long-term studies for understanding ecosystem processes in arid ecosystems. The studies by Schlesinger and Peterjohn were short-term incubations of soils enclosed in PVC pipe into which water and/or chemicals were added. The studies by Fisher *et al.* (1987) were conducted in the field over several years and incorporated 'droughted plots' under 'rain-out shelters', irrigated, and unmanipulated plots. The relationship between ammonia volatilization and nitrogen mineralization is affected by the effects of rainfall on development of the ephemeral plant community. In shrub-dominated systems, irrigation stimulates growth of dense stands of ephemerals. The decomposition of the dead roots of those plants results in nitrogen immobilization and reduction in

mineralization rates with irrigation in the following year (Fisher and Whitford, 1995). Thus the relative importance of ammonia volatilization in desert ecosystems is dependent on climate patterns as well as spatial variability.

Denitrification is another avenue of loss of nitrogen from the soil pool back to the atmospheric pool. Denitrification results from the microbial reduction of nitrate (NO_3) or nitrite (NO_2) to either N_2O or dinitrogen (N_2). There are many species of heterotrophic soil bacteria that are capable of denitrification. Factors that have been shown to affect the rate of denitrification include: pH, temperature, available carbon, available nitrogen and the partial pressure of oxygen in the soil (Firestone, 1982). Desert soils are notoriously low in carbon and nitrogen, are frequently basic, and subject to extremes in temperature. Most desert upland soils are coarse textured and well aerated thus not good environments for denitrification.

In most desert watersheds, losses of nutrients in litter and plant debris transported into ephemeral streams is a spatial phenomenon, i.e. concentration of organic materials at the watershed terminus. Nutrient losses from desert watersheds only occur in those few watersheds that are drained by perennial streams. Thus in most desert landscapes, denitrification is the most important means of loss of this nutrient. In a nitrogen budget developed for the Great Basin Desert in the western US, it was estimated that denitrification accounted for 95% of the annual nitrogen losses and 65% of the total N inputs (West and Skujins, 1977). Estimates of denitrification rates in the cold Great Basin Desert in North America (19 kg N ha^{-1} yr^{-1}) were approximately equal to 65% of the nitrogen inputs. Other studies in the Great Basin estimated denitrification losses equal to approximately 80% of the nitrogen fixed by cryptogamic crusts and of added ^{15}N-labeled ammonium (Klubek and Skujins, 1981). In the Sonoran Desert, high rates of denitrification were measured in wet soil under nitrogen-fixing mesquite tree canopies (Virginia *et al.*, 1982). Denitrification was estimated to account for > 77% of the N inputs in the desert regions of the US (Peterjohn and Schlesinger, 1990). The content of denitrifying enzymes in upland desert soils was associated with indices of N and C availability. However, wet desert soils provided optimal conditions for the several variables that affect denitrification (Peterjohn and Schlesinger, 1991). In the Chihuahuan Desert denitrification rates were affected by water availability and the C/N ratio of the soil. Highest rates were measured in desert grassland and there were no 'fertile island' effects on denitrification rates in shrubland soils. Annual rates of denitrification on a Chihuahuan Desert watershed were estimated at 2.3 kg N ha^{-1} yr^{-1} on piedmont grassland soils, 4.3 kg N ha^{-1} yr^{-1} in creosotebush (*L. tridentata*) shrubland soils, 10.5 kg N ha^{-1} yr^{-1} in basin grassland soils, and 3.5 kg N ha^{-1} yr^{-1} in ephemeral lake soils. The differences in rates of denitrification in soils from various locations on the watershed were attributed to soil textural differences that affect soil water potentials (Peterjohn and Schlesinger, 1991).

These studies suggest that denitrification is probably an important process in the ecosystems of most desert regions. However, caution must be applied when extrapolating the results of studies of denitrification, based on irrigated soil cores, to desert regions of the world. In incubations used to measure denitrification of

soils, cores were flooded with the equivalent of a 31.5 mm rain (Peterjohn and Schlesinger, 1990). Rains of that intensity have a return time of less than one storm per 20 years in the area where these studies were conducted (Fisher and Whitford, 1995). Since low oxygen tensions are characteristic of supersaturated soils, measures of denitrification under such conditions clearly optimize denitrification. Although the spatial variation and ratio of soil carbon and nitrogen are important variables affecting desertification, rates of denitrification are probably considerably lower, with water inputs equivalent to an average rainfall event of 10–15 mm, than those reported in the literature based on saturated soil incubations.

Most of the available nitrogen in the soil comes from the mineralization of organic nitrogen. Available soil nitrogen is affected by the relative rates of mineralization and immobilization. Immobilization of nitrogen occurs when ammonia or nitrate are incorporated into microbial biomass. Microbial biomass can change very rapidly under suitable conditions of substrate (available organic matter) and soil moisture. In desert ecosystems there appears to be an increase in microbial biomass, an increase in soil carbohydrates, and a decrease in extractable soil nitrogen in response to irrigation (Gallardo and Schlesinger, 1995). In desert grassland soils, fertilization with nitrogen increased microbial biomass but addition of carbohydrate increased microbial biomass only when accompanied by nitrogen fertilization. In shrub-dominated ecosystems, addition of carbohydrate resulted in increased microbial biomass and decreased extractable nitrogen and phosphorus (Gallardo and Schlesinger, 1995). Thus increases in microbial biomass requires different conditions in desert grasslands in comparison to desert shrublands.

Mineralization of nitrogen involves the soil microfauna as well as the soil microflora. As pointed out earlier, much of the organic matter that serves as a source of nutrients for plant growth is in the form of high C:N ratio dead plant roots (especially roots of ephemeral plants). As soon as the roots of annual plants die, they are colonized by heterotrophic bacteria and fungi. In soils where available N is very low, the growth of microbes on the roots is limited by available N. Microbes scavange the available N and convert it into microbial biomass N. The N in microbial biomass is not available to plant roots until the microbial biomass dies and that microbial biomass N is released as inorganic N. When desert soils are wet (less than −0.3 MPa) there is a complex of soil microfauna that graze on the microbial biomass and release mineral N as excretory products. That soil microfauna is composed of protozoans, nematodes, and microarthropods. However, in dry soils, most of the soil microfauna is encysted or anhydrobiotic, leaving only a few taxa of soil mites to graze on the fungal hyphae (Whitford, 1989). During dry periods, some fungi grow slowly on the organic substrates in the soil and there is limited mineralization of N via the grazing activities of the few soil mites. The relative rates of N mineralization and N immobilization, therefore, are determined by the pulses of rainfall and pulses of inputs of organic substrates. Periodic drought results in the death of microbial biomass. Rainfall that ends such drought produces conditions for rapid mineralization of the dead

microbial biomass and competition of the growing microbial biomass and plant roots for available nutrients (Fisher and Whitford, 1995).

The differences in responses of shrubland and desert grassland to nitrogen fertilization appear to be related to the spatial and temporal distribution of ephemeral plants and to the growth characteristics of the dominant plants. In desert grasses the gradual turnover of root biomass and location of nitrogen-fixing organisms in the rhizosheaths of roots of some species produce conditions where nitrogen mineralization rates always exceed rates of nitrogen immobilization (Fig. 9.11) (Whitford and Herrick, 1996). The temporal patterns of mineralization–immobilization on the dead roots of ephemeral plants also explains the temporal variation in productivity of annual plants in shrublands where that productivity is decoupled from rainfall (Guo and Brown, 1997). In the northern Chihuahuan Desert, high production of winter–spring annuals is linked to reductions in production of summer annuals even in years with above-average summer rainfall.

The relationships between rainfall, plant productivity, and the relative rates of nitrogen mineralization to immobilization are complex. Rainfall that initiates growth and establishment of ephemeral plants sets up the potential for an input pulse of decomposable organic matter. Spatial distribution and densities of ephemerals are a function of the morphologies of the dominant vegetation. With C_3 shrubs, a large residual pool of dead roots from the previous growing season

grassland
shrubland with summer ephemerals only
shrubland with ephemerals (summer + winter)
growing season summer C4 grasses
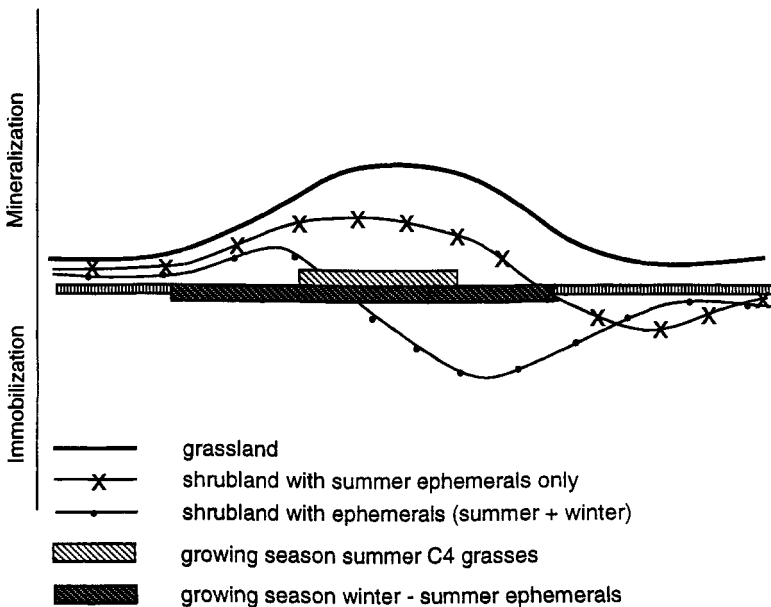growing season winter - summer ephemerals

Figure 9.11   The hypothesized relationships between nitrogen mineralization and nitrogen mobilization in perennial desert grasslands and in desert shrublands. (From Whitford and Herrick, 1995.) With permission from The Society for Range Management.

or a pool of dead roots from the winter–spring ephemerals, establishes conditions for nutrient immobilization and reduction in growth rates of the shrubs. In desert grassland dominated by C_4 grasses, spatial distribution of ephemerals is random and pulses of dead roots do not result in rates of immobilization exceeding rates of mineralization (Whitford and Herrick, 1995) (Fig. 9.11).

9.6 OTHER POTENTIALLY LIMITING NUTRIENTS

Phosphorus is frequently a limiting element in cultivated agricultural systems. In studies on a northern Chihuahuan desert watershed, there was no evidence for P limitation of primary production (Lajtha and Schlesinger, 1988). However, phosphorus may be limiting in deserts with very ancient soils, e.g. Australian, South African arid regions, but there are no quantitative data available to support this supposition. There are also suggestions that other elements may be limiting factors in primary production in arid and semiarid ecosystems but there are no empirical studies that examine this suggestion. Thus for most materials the processes of decomposition and mineralization turn over sufficient quantities of elements for the water-limited plant growth.

9.7 ROLE OF MYCORRHIZAE

Mycorrhizae (literally fungal roots) are fungi that develop mutualistic symbioses with roots of many species of plants. Mycorrhizal fungi are known to enhance the nutrition of the host plant (especially with respect to phosphorus nutrition) and receive benefit from the host plant in the form of useable energy: carbohydrates (Read *et al*., 1985). Mycorrhizae produce nondestructive interfaces with root cells as intercellular hyphae, intracellular coils, arbuscules and vesicals (Fig. 9.12). The external micorrhizal hyphae extend from the root surface into the soil where the hyphae serve as functional extensions of the roots. Some studies have documented mycorrhizal mycelial links between different species of plant (Watkins *et al*., 1996). Most of the research on mycorrhizal associations and the ecological significance of these symbioses has been conducted with agricultural plants or with naturally occurring host plants in mesic environments. Approximately 95% of the world's plant species belong to families that are typically mycorrhizal and most of these families form vesicular–arbuscular endomycorrhizae associations (Trappe, 1981). A survey of the literature on mycorrhizal colonization of roots of arid and semiarid plants revealed that some species in most of the plant families surveyed were colonized by mycorrhizae. Most of the reports were based on single observations but where multiple samples were examined, some samples were mycorrhizal and some were not, e.g. *Atriplex canescens* (Chenopodiaceae) (Trappe, 1981). Arid zone plants that were usually mycorrhizal were members of the Compositae, Gramineae, Leguminosae,
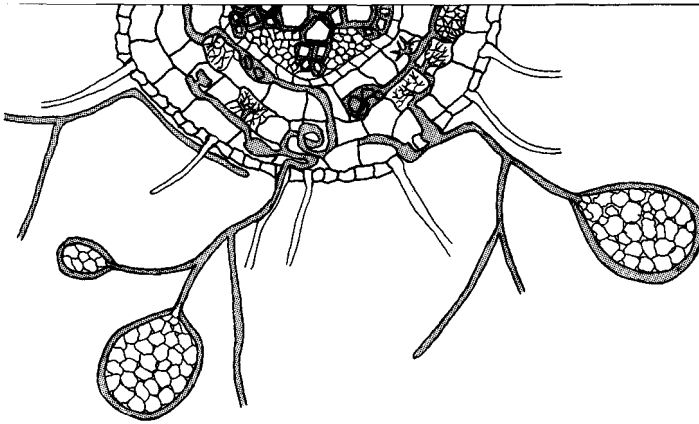
Figure 9.12   Vesicular–arbuscular mycorrhizal structures in a root.

Rosaceae, Salicaceae, and Solonaceae. The Cruciferae and Zygophyllaceae were reported to be largely nonmycorrhizal. Out of 93 species of plants from 37 families in semiarid, open mallee (*Eucalyptus* spp.) 85 were mycorrhizal and most of the mycorrhizae were vesicular–arbuscular (McGee, 1986). Several genera that were not previously known to harbor mycorrhizae were found to be mycorrhizal. Some species of Cactaceae and Chenopodiaceae were mycorrhizal at some times and nonmycorrhizal at other times. Ephemeral species in families that are typically mycorrhizal appear to develop mycorrhizal symbionts as readily as the perennial species in those families.

Vesicular–arbuscular mycorrhizae fruit as single spores in the soil. The concentrations of vesicular–arbuscular spores in the soil vary seasonally, with soil moisture, and probably with the phenological stage of the host plant. Mycorrhizal spores are dispersed by anything that moves soil (wind, water, and animals) (Allen *et al.*, 1989). A variety of arthropods (crickets, grasshoppers, ants, wasps, and other insects) and some small mammals have been found to be spore dispersers (Trappe, 1981). Mycophagous arthropods may adversely affect the symbiosis between vesicular–arbuscular mycorrhizae and plants by grazing on the spores and external hyphae. Some microarthropods may also act as symbiotic mutualists by grazing and disseminating fungal propagules or by stimulating fungal growth and activity by grazing (Moore, 1988). Harvester ants, *Pogonomyrmex occidentalis*, leave high densities of vesicular–arbuscular mycorrhizal fungi in the soils of the nest mounds that assist in the establishment of mutualistic mychorrizal associations after the ant colonies have abandoned the mounds (Friese and Allen, 1993).

The mutualism between mychorrizal fungi and plant roots is one in which the fungus receives carbon from the plant and the plant receives nutrients from the fungus. Mycorrhizal fungi differ in their ability to take-up and metabolize various

carbon sources (Smith and Read, 1998). Vesicular–arbuscular mycorrhizae are totally dependent on photosynthetically derived glucose. The external mycelia of other mycorrhizae can use a greater variety of carbon sources. Root exudation may trigger mycorrhizal colonization but the quantities of exudate are apparently insufficient to support continuous mycorrhizal development. Mycorrhizal colonization may reduce and change the quality of root exudates (Ingham and Molina, 1991).

There is some evidence that mycorrhizal plants are more drought tolerant than non-mycorrhizal species. This is thought to result from the increased soil volume exploited by mycorrhizal plants and not to an increase in uptake of water by the fungi (Ingham and Molina, 1991). The enhancement of growth in mycorrhizal plants is generally attributed to the exploitation of a larger volume of soil by the mycorrhizal mycelia that are external to the root. Increased phosphorus and ammonium uptake and inflow to plant roots has been documented (Read *et al.*, 1985). Direct connection of plant roots of different individuals of the same species or roots of different species by mycorrhizal bridges has also been documented (Robinson and Fitter, 1999). Also, there is evidence for the movement of nutrients from dying roots to living plants via mycorrhizal links between dying and living roots (Newman and Eason, 1989). Experimental evidence for the direct interplant transfer of carbon suggests that mycorrhizal associations may be extremely important for productivity of patches of plants with different rooting depths and phenologies. An immediate supply of carbohydrate could allow shallow-rooted plant species to initiate growth of photosynthetic tissue as soon as soil moisture becomes available.

Mycorrhizal associations may not be the only root–fungus mutualism that improves the growth and survival of desert plants. The roots of dominant grass and shrub species of the arid southwestern United States, were extensively colonized by dark septate fungal endophytes (Barrow *et al.*, 1997). Dark septate fungi were either the only fungi in the root or were found in combination with vesicular–arbuscular mycorrhizae in the same root. The internal morphology of dark septate fungi is different from other mycorrhizal associations. The dark septate hyphae penetrate the root and grow inter- and intracellularly in the root cortex. Dark septate fungi form microsclerotia of various structural configurations over time. These microsclerotia take the form of coils and vesicles. Dark septate fungi are widespread and are abundant in stressed ecosystems suggesting that they are ecologically important (Jumpponen and Trappe, 1998). Dark septate fungal associations with the roots of a desert shrub, *Atriplex canescens*, were found to contain large quantities of lipid during the period of leaf production by the shrub in the early spring. It was hypothesized that the storage of carbon in the dark septate fungi during peak growth periods of the plant could serve as a carbon sink and enhance water retention in the fungal hyphae. From the fungal reservoir, sufficient carbon, water, and nutrients could be supplied to the plant to insure survival during periods of climatic stress (Barrow, 2001). This fascinating fungus–plant association should be the focus of future research on desert plants and nutrient cycling processes.

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