

# Assessing sensitivity to change in desert ecosystems – a stable isotope approach

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## 14.1 Introduction

Growth and gas exchange of plants in arid zones are driven primarily by periodic pulses of moisture and nutrient availability. Both seasonal and inter-annual changes in precipitation occur in response to long-term weather cycles causing direct impacts on productivity, competitive displacement, and mortality (Comstock and Ehleringer, 1992; Ehleringer, 1993c; Smith *et al.*, 1997). Deviations from mean climatic conditions might be expected to increase under predicted climate change scenarios, particularly given the disequilibrium between terrestrial and oceanic regions as radiative forces increase (Rind *et al.*, 1990). Surface disturbance caused by land-use change has resulted in significant changes in soil nitrogen levels of aridland ecosystems (Belnap, 1995; Evans and Belnap, 1998) and this may be further exacerbated by variations in monsoonal precipitation patterns.

In this chapter, we explore how analyses of stable isotope ratio patterns in arid land soils and plants help us better understand ecosystem dynamics in response to changes in moisture and nitrogen availability. Arid land ecosystems on the Colorado Plateau in the western United States provide an opportunity to examine plant response to the potential sensitivity of ecosystem components to variations in summer and winter moisture inputs along moisture clines, while at the same time exploring the impact of different land-use patterns on nitrogen availability.

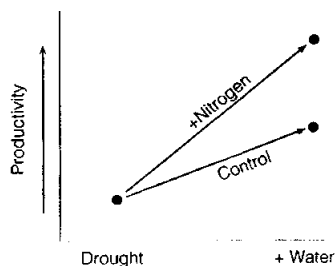
To facilitate modelling approaches for estimating productivity it would be ideal if all vegetation components responded equally to seasonal variations in resource input. More realistically, it would be reasonable to expect that different vegetation components could be aggregated into functional groups, such as by life form, with members of the same life form responding similarly to seasonal pulses in moisture and nitrogen. While stable isotopes may not contribute directly to estimating productivity, stable isotope studies will contribute directly to understanding mechanistic aspects of the constraints on productivity in different species and/or functional groups, thereby

complementing more traditional approaches (Ehleringer *et al.*, 1993). Carbon isotopes in organic material provide an estimate of the extent to which different gas exchange components affect productivity (Farquhar *et al.*, 1989). Hydrogen and oxygen isotopes in xylem waters contribute directly to quantifying use of monsoonal and winter water sources (Ehleringer and Dawson, 1992). Nitrogen isotope ratios provide a quantitative estimate of the balance between nitrogen inputs and losses from the soils and species-specific patterns of nitrogen use, particularly in response to disturbance (Evans and Ehleringer, 1993, 1994; Evans and Belnap, 1998). Together stable isotopes provide an opportunity to assess ecosystem dynamics and the sensitivity of these vegetation components to change and to complement more traditional gas exchange and biomass-assessment approaches.

## 14.2 Deserts as pulse-driven ecosystems

Desert ecosystems are generally characterised by low resource levels, with water representing the single most limiting resource constraining primary productivity through its influence on plant water status and soil nutrient availability (Noy Meir, 1973). Moisture in the upper soil layers is available as a series of brief pulses following intermittent precipitation events. High potential evapotranspiration during the growing season means that soil moisture does not persist long in the upper soil layers, irrespective of the extent of vegetative cover. The amount of plant-available nitrogen in soils is closely tied to these pulses of moisture because nitrogen mineralization is most rapid following precipitation (Burke, 1989; Evans and Ehleringer, 1994; Matson *et al.*, 1991; Zaady *et al.*, 1996). Productivity in deserts can then be thought of as a series of pulse events controlled primarily by soil moisture, and secondarily by nutrient availability following precipitation events (Figure 14.1). The high temporal variability between rainfall events on both an interannual and seasonal bases amplifies the impact of pulses of soil moisture availability on ecosystem dynamics (Noy Meir, 1973).

On the Colorado Plateau, precipitation comes either from winter storms generated in the Gulf of Alaska or from summer convection storms generated by the Arizona monsoon system. Understanding the current seasonal and regional patterns of precipitation inputs into an ecosystem has ramifications at several levels: on carbon and mineral cycling at the ecosystem level, on biodiversity at the community level, and on productivity and adaptation at the population and species levels. The interior deserts of Arizona, Nevada, and Utah represent the driest regions of western North America, resulting from a combination of rainshadow effects and either the southern limits of winter moisture input, the northern limits of summer moisture input, or both



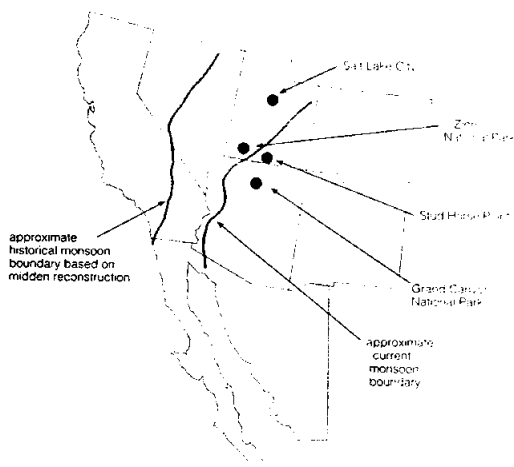
*Figure 14.1. A hypothetical relationship of how water and soil nitrogen influence productivity in desert ecosystems, which are pulse driven.*

(Comstock and Ehleringer 1992; Houghton 1979). Shifts in strengths of storm-generating conditions in the Pacific and in the Gulf influence both the magnitude and seasonality of soil moisture availability (Bryson and Lowry 1955; Mitchell 1976) and therefore constrain periods of primary productivity activity in these aridland ecosystems (Caldwell, 1985; Dobrowolski *et al.*, 1990). One major consequence predicted by global climate change scenarios is a change in monsoonal (summer) precipitation (Schlesinger and Mitchell, 1987; Mitchell *et al.*, 1990); it will increase in some areas and decrease in others. A second is increased soil temperatures and increased interior drought associated with ocean-land temperature disequilibrium (Rind *et al.*, 1990).

Southeastern portions of Utah (northwestern portions of the Colorado Plateau) form a broad northern border for the region influenced by the Arizona monsoonal system (Figure 14.2). Annual precipitation across Colorado Plateau ecosystems ranges from 100 to 400 mm (Houghton 1979), with these ecosystems experiencing low precipitation due to rain-shadow effects from winter-generated storms and the northern limits of monsoonal systems generated in the summer months. While on average approximately half the annual moisture is from summer moisture events, the year-to-year variability is high and depends on the intensity of the Arizona monsoon system that develops in a particular year (Adang and Gall, 1989; Houghton, 1979; Moore *et al.*, 1989). Pack rat midden data indicate that central and northern Utah had an extensive summer-precipitation climate several thousand years ago (Betancourt *et al.*, 1990; Cole, 1990), but the onset of regional summer drought is less clear. Variations in the intensities and predictability of summer rain should have significant impacts on primary productivity in these aridland ecosystems (Ehleringer and Mooney, 1983; Hadley and Szarek, 1981; Noy Meir, 1973; Smith and Nowak, 1990).

### 14.3 Water uptake patterns by aridland plants

Given that soil moisture levels limit productivity in deserts, how do plants respond to the pulses in moisture input? In particular, how do plants respond to variations in



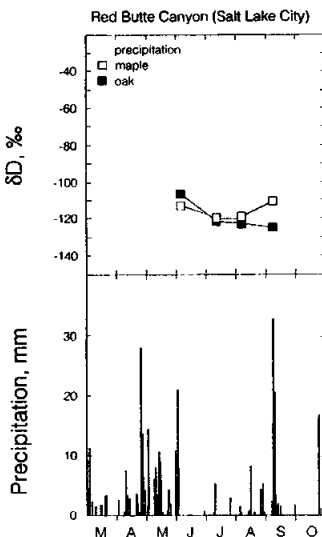
**Figure 14.2.** The current and historical distribution limits of the Arizona monsoon system in western North America. Also shown are major sites referred to in this chapter.

summer moisture events? Our initial hypothesis was that perennial plants would extract moisture from surface layers when it was available and then switch to moisture from deeper soil layers in between summer-precipitation pulses.

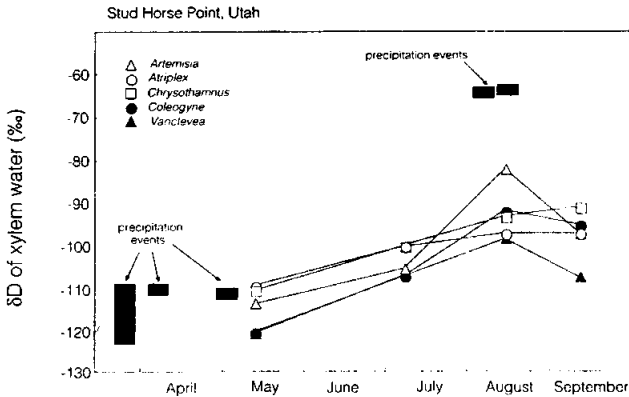
Stable isotopes in xylem water have been particularly useful in quantifying soil layers from which plants extract water, since roots do not fractionate during water uptake (reviewed in Ehleringer and Dawson, 1992; see Chapter 11). Moisture derived in winter, often as snow, penetrates to deeper layers because cold temperatures constrain biological activities. When the upper layers dry out in the spring and summer, moisture in the upper layers is recharged by precipitation events during the growing season. Differences in cloud temperatures during winter and summer precipitation events result in contrasting stable isotope ratio values in the precipitation (Figure 14.3). As a consequence, there is a layering of water in the soil profile with different stable isotope ratios. Analysis of xylem waters then allows us to quantify the extent to which species are using moisture derived from one zone to another and of the dynamics in switching between these two contrasting moisture zones.

Contrary to initial expectations, *Acer grandidentatum* and *Quercus gambelii* in the xeric woodlands north of the monsoon boundary did not use moisture in the upper layers at any point during the growing season (Figure 14.3). Instead, these dominant shrubs appeared to use winter-derived moisture that had penetrated to deeper soil depths. When monsoonal moisture fell in the latter part of the summer, neither species used appreciable amounts of this surface water source.

In the desert ecosystem of the Colorado Plateau, perennial plants used only a limited fraction of the summer moisture input (Figure 14.4). Moderate precipitation events in the early spring charged the profile and served as the water source from spring through early summer. The strong evaporative demand in this desert ecosystem resulted in some evaporative enrichment within the soil profile that was reflected in the isotopic composition of xylem water in early summer (July). Following strong



**Figure 14.3.** Upper diagram, The hydrogen isotope ratio of precipitation in Salt Lake City (grey) and of xylem water from *Acer grandidentatum* (open square) and *Quercus gambelii* (closed square) for plants in Red Butte Canyon during the course of the year. Lower diagram, The seasonal dynamics of daily precipitation. Modified from Phillips and Ehleringer (1995).



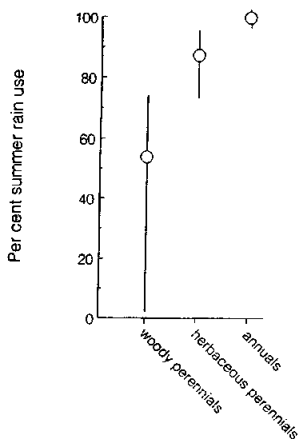
**Figure 14.4.** The seasonal dynamics of hydrogen isotope ratio of water in xylem sap for five common desert shrubs in a Colorado Plateau desert ecosystem at Stud Horse Point, Utah. The species are *Artemisia filifolia*, *Atriplex canescens*, *Chrysothamnus nauseosus*, *Coleogyne ramosissima* and *Vanclevea stylosa*. Also shown are the hydrogen isotope ratios of precipitation events. Data are modified from Lin *et al.* (1996).

precipitation events in early August (~60 mm), there were moderate changes in the xylem water isotopic composition of these shrubs, indicating a limited uptake of the moisture retained in the upper soil layers.

Ehleringer *et al.* (1991) had reported similar results for water uptake by different shrubs within this desert ecosystem. In that study, roots of annual and herbaceous species fully utilised the moisture in the upper soil layers (Figure 14.5). In contrast, there was a wide variation in the response of woody perennial shrubs to summer moisture inputs. On average, 54% of the xylem water in woody perennial plants was derived from summer precipitation, but within individual species this value ranged from 1% to 79% summer-derived moisture use.

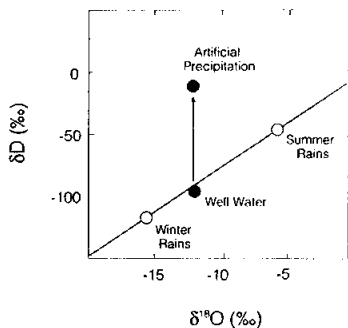
In a follow-up study, Lin *et al.* (1996) used stable isotopes to follow uptake of moisture from artificial summer rain events of different magnitudes (Figure 14.6). Plants were monitored following the artificial precipitation events to see how long it took for moisture to be taken up. Typically, 2 to 3 days was required for maximum uptake. Since moisture in the uppermost soil layers only persists for 5–10 days following rain, a large fraction of this moisture is lost by evaporation and is not used by plants. Lin *et al.* (1996) observed that desert perennial shrubs differed in the extent to which they responded to monsoonal moisture inputs. On average, for a 25-mm precipitation event, less than 20% of the plant moisture was derived from the saturated upper soil layers (Figure 14.7). A greater response was seen in some species following a 50-mm precipitation event, but in no case did this upper-layer moisture account for more than 42% of the xylem water. Several of the species (*Atriplex canescens* and *Chrysothamnus nauseosus*) did not respond appreciably to either a 25-mm or a 50-mm precipitation event, with summer-derived moisture accounting for 7% or less of the water being taken up by the plants. Based on isotope ratio gradients within the soil profile, Thorburn and Ehleringer (1995) had concluded that these desert perennials were deriving most of their summer moisture from a depth of ~0.6 m.

Summer rain use in August by different plants in a Colorado Plateau desert shrub community (data from Ehleringer et al. 1991)

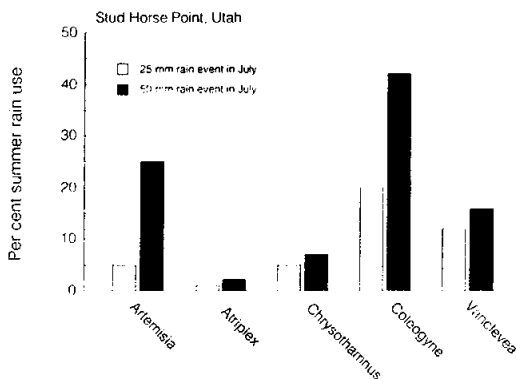


**Figure 14.5.** The per cent usage of summer rains by woody perennials, herbaceous perennials, and annuals in a Colorado Plateau desert ecosystem at Stud Horse Point, Utah. Circles represent the mean for each life form and the vertical bars represent the entire range of values for different species within that life form. Based on data in Ehleringer et al. (1991).

Some species at sites on the monsoon boundary show year-to-year variation in the extent to which they take up summer moisture. For example, Gregg (1991) reported that *Juniperus osteosperma*, a dominant tree of pinyon-juniper woodlands did not take up appreciable amounts of summer rain on sites north of the Arizona monsoon boundary. At Coral Pink (just east of Zion National Park and on the monsoon boundary), she reported that junipers did not take up summer moisture. Flanagan *et al.* (1992) working at the same Coral Pink site reported that junipers did not take up summer rain in one year, but did so in the following year. Evans and Ehleringer (1994) also working at Coral Pink observed that some juniper individuals did take up summer rains in yet a different year, but that others did not. At Tintic (north of the monsoon boundary), Donovan and Ehleringer (1994) reported that junipers did not respond to summer rain, specifically following a 21-mm summer precipitation event. *Artemisia tridentata*, a widespread shrub whose distribution spans the monsoon boundary, has been shown to take up summer moisture, irrespective of the location (Donovan and



**Figure 14.6.** The meteoric water line for Stud Horse Point, Utah, showing the mean values for winter precipitation, summer precipitation, well water, and the deuterium-spiked water used for irrigation studies. Modified from Lin *et al.* (1996).



**Figure 14.7.** The per cent usage of summer rains by five common woody perennials in a Colorado Plateau desert ecosystem at Stud Horse Point, Utah. Plants were provided with either a 25-mm rain event or a 50-mm rain event and then 3–5 days following this the xylem sap was sampled to determine the extent of the summer rain usage. The species are *Artemisia filifolia*, *Atriplex canescens*, *Chrysothamnus nauseosus*, *Coleogyne ramosissima*, and *Vancleavea stylosa*. Modified from Lin *et al.* (1996).

Ehleringer, 1994; Evans and Ehleringer, 1994; Flanagan *et al.*, 1992). In contrast to *J. osteosperma* with a widespread distribution, *Pinus edulis* (the other common tree in the piñon-juniper woodland) does not occur north beyond the monsoon boundary. Both Flanagan *et al.* (1992) and Evans and Ehleringer (1994) reported that *Pinus edulis* at Coral Pink used summer moisture inputs and was consistently more responsive than *J. osteosperma* to summer rain events. The factors contributing to a year-to-year variability in moisture uptake by plants along the monsoon boundary are unclear, but previous soil moisture stress, soil temperature, and the magnitude of the summer precipitation event are likely to be contributing factors.

#### 14.4 Stomatal limitations as inferred from carbon isotope ratios

Long-term estimates of the ratio of intercellular to ambient  $\text{CO}_2$  concentrations ( $C_i/C_a$ ) in  $C_3$  species can be derived from leaf carbon isotope ratios (Farquhar *et al.*, 1989). Ehleringer (1993a, b) proposed that the  $C_i/C_a$  ratio reflected a metabolic set point, reflecting tradeoffs in the relative rates of  $\text{CO}_2$  supply through stomata versus photosynthetic demand for that  $\text{CO}_2$ . Variations in the  $C_i/C_a$  ratio negatively correlate with plant longevity. On the basis of structure, species in these arid land ecosystems can be classified into four functional groups (tree, woody perennial shrub, herbaceous perennial, and annual) with carbon isotope discrimination negatively correlated with plant longevity (Ehleringer, 1993a,b; Ehleringer and Cerling, 1995; Ehleringer and Cooper, 1988; Schuster *et al.*, 1992). These patterns suggest that stomatal limitations in gas exchange become most prominent in long-lived functional groups. One possible trade-off is that an increased stomatal constraint on gas exchange is associated with the reduced likelihood of xylem cavitation during drought periods. In response to increased resource levels from summer irrigation, all plants responded equally and as a result carbon isotope

discrimination differences among species were maintained (Lin *et al.*, 1996). Changes in carbon isotope discrimination by  $C_3$  and  $C_4$  species closely parallel resource availability in both winter and summer-monsoon precipitation seasons, with carbon isotope discrimination increasing with stress in  $C_4$  plants and decreasing with stress in  $C_3$  plants (Evans and Ehleringer, 1994; Flanagan *et al.*, 1992; Lin *et al.*, 1996).

### 14.5 Nitrogen sources

Cryptobiotic crusts are biological soil crusts composed of cyanobacteria, lichens, mosses, green algae, and fungi. They are found in mesic environments, tropical and temperate deserts, and in polar regions (Eldridge and Greene, 1994), but they reach their best development in arid regions where they are ubiquitous on undisturbed arid and semi-arid soils. The absence of fire and grazing by large mammals has allowed the cryptobiotic crusts of the Colorado Plateau and Great Basin to become especially well developed (Mack and Thompson, 1982). The crusts can be as great as 10 cm deep and approach 100 % coverage in undisturbed ecosystems (Harper and Marble, 1988; Kleiner and Harper, 1972). The cryptobiotic crust is held together by cyanobacteria that exude a gelatinous sheath which binds soil particles and organisms (Campbell *et al.*, 1989; Belnap and Gardner, 1993). Surface disturbance disrupts the cohesiveness of the cryptobiotic crust causing loss of nitrogen fixation (Belnap, 1996; Belnap *et al.*, 1994). The consequences of surface disturbance are uncertain because the relative importance of nitrogen assimilated by the crust versus that deposited by atmospheric deposition is not known (West, 1990).

Evans and Ehleringer (1993) used nitrogen isotope ratios to show that these organisms were the primary nitrogen sources into Colorado Plateau ecosystems (Figure 14.8). The relationship between the isotopic composition and nitrogen content of soils followed a Raleigh distillation model (Fustec *et al.*, 1991; Mariotti *et al.*, 1981). Disturbance of the cryptobiotic crust resulted in net loss of nitrogen from the ecosystem causing an increase in soil nitrogen isotope composition (Evans and Ehleringer, 1993). Rates of nitrogen mineralisation depend on the availability of soil organic nitrogen (Binkley and Hart, 1989; Matson *et al.*, 1991) so mineralization potentials were also strongly correlated with soil nitrogen isotope ratios (Evans and Ehleringer, 1994). Fractionation does not occur during uptake of ammonium or nitrate (Evans *et al.*, 1996; Yoneyama and Kaneko, 1989) so plant nitrogen isotope composition becomes a reliable estimator of soil nutrient quality (Evans and Ehleringer, 1994). Plants growing on disturbed sites had higher nitrogen isotope ratios and lower leaf nitrogen contents than those on less disturbed sites (Evans and Ehleringer, 1994).

The sensitivity to change of the Colorado Plateau desert ecosystems, induced by either land-use practices or by shifting monsoonal conditions is great (Figure 14.8). Plant function, decomposition, and cryptobiotic function are all influenced by periodic moisture pulses, whether they come in the summer or in the winter. As with the reduced responsiveness of desert perennials to summer rain events, Belnap (1996) has shown that nitrogen-fixation rates by cryptobiotic crusts are less responsive to summer rain events than they are to winter-spring precipitation events. The long-term vegetation composition in these desert ecosystems will be a function of variation in summer moisture input, land-use pressures which select against some components of the herbaceous vegetation that can use the summer moisture inputs, and the susceptibility of these sites to invasions associated with either disturbance or changes in soil/climatic conditions.

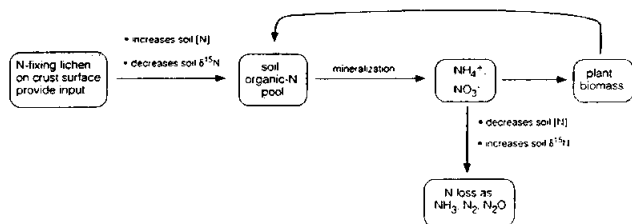


## 30 years of recovery following cryptobiotic soil crust disturbance in Canyonlands National Park

	Undisturbed	Disturbed	Difference
soil $\delta^{15}\text{N}$ (‰)	$3.6 \pm 0.4$	$5.1 \pm 0.3$	1.5 ‰
plant $\delta^{15}\text{N}$ (‰)	$1.1 \pm 0.7$	$2.6 \pm 0.3$	1.5 ‰
soil N (mg/g)	$0.41 \pm 0.01$	$0.27 \pm 0.03$	66 %
plant N (mg/g)	--	--	

Soil crusts with moderate grazing at Coral Pink Sand Dunes State Park  
(data from Evans and Ehleringer 1994)

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

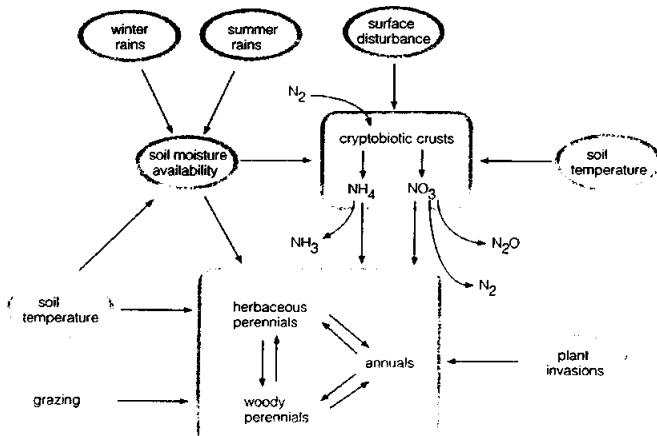


**Figure 14.8.** Changes in the soil and plant nitrogen isotope ratio values for plants growing on soils that have intact or disturbed cryptobiotic crusts in Canyonlands National Park. Shown also is a model to account for the observed variations in nitrogen isotope ratio associated with crust disturbance. Modified from Evans and Ehleringer (1994) and Evans and Behnapp (1998).

## 14.6 Sensitivity of Colorado Plateau arid land ecosystems to invasions

The contributions of cryptobiotic crusts to nitrogen input in aridlands and its disruption by anthropogenic activities have important implications for the nitrogen cycle in arid regions (Evans and Ehleringer, 1993). The physical destruction of cryptobiotic crusts through land-use change (Figure 14.9) can eliminate the predominant source of nitrogen input. In the long term, removal of this nitrogen input source, coupled with continuous gaseous losses of nitrogen from the ecosystem, will ultimately decrease the amount of nitrogen available for plant growth. Crust recovery is slow (Behnapp, 1991), and so in effect the nitrogen cycle is broken, with significantly reduced nitrogen inputs but continued and possibly accelerated rates of nitrogen loss from the system (Evans and Ehleringer, 1993). As indicated in Figures 14.8 and 14.10, this degradation leads to decreased fertility and ultimately to degradation of community structure and shifts in composition towards species that are either capable of nitrogen fixation or are tolerant of low nitrogen availability (Schlesinger *et al.*, 1990). Comparative studies of grazed and nearby pristine sites on the Colorado Plateau have already provided evidence for these changes in species composition (Kleiner and Harper, 1972).

Water-limited and nutrient-poor ecosystems are likely candidates for biological invasions (Mooney and Drake, 1986). The Colorado Plateau is no exception, in part due to both cryptobiotic crust damage and by land-use change (Kleiner and Harper, 1972; Loope *et al.*, 1988). Cryptobiotic crust damage makes the ecosystem more susceptible to invasion; one suggestion presented earlier is that disturbed soils may have less nitrogen available to plants than do pristine cryptobiotic soils.



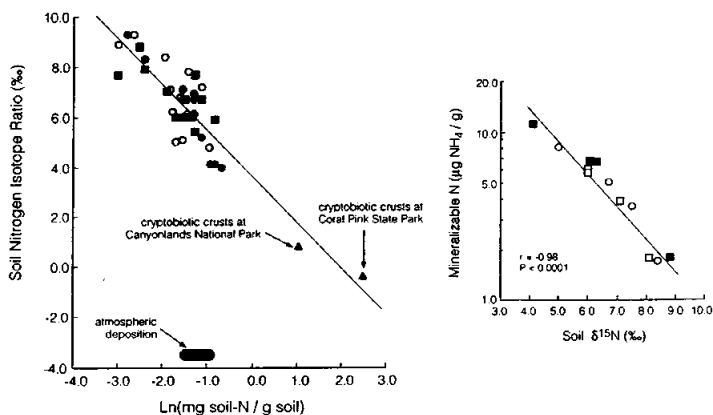
**Figure 14.9.** A model of the impacts of changes in precipitation patterns, soil temperature, grazing, and plant invasions, on the dynamics and interactions between plant components of a Colorado Desert ecosystem and the cryptobiotic crust.

This then raises the question of how much effect the increasing crust disturbance will have on the magnitude of the pulse precipitation event (Figure 14.11). Data from the previous section indicate that both soil and plant nitrogen contents have been decreasing on crust-disturbed ecosystems. Given that photosynthetic capacity is tightly correlated with leaf nitrogen content (Field and Mooney, 1986; Figure 14.11), one would expect that primary productivity by existing species should be decreased on disturbed sites.

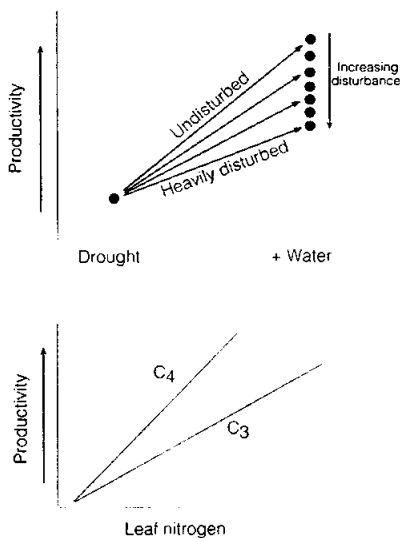
At some point in the deterioration of the nitrogen levels within these desert ecosystems, there may be a shift toward favouring  $C_4$  species over the predominantly  $C_3$  native species. This will arise because  $C_4$  plants are intrinsically more efficient in their nitrogen-use efficiency (NUE) than  $C_3$  plants and can achieve greater photosynthetic rates per unit leaf nitrogen content. In Colorado Plateau deserts, invasive species are increasing in abundance; most of the weedy species are annuals. Winter weeds include the bromes (*Bromus* sp.) and mustards; summer annuals are primarily  $C_4$  chenopods (*Bassia*, *Kochia*, *Halogeton*, *Salsola*). South African  $C_4$  grasses are becoming more aggressive in the southern deserts (Anable *et al.*, 1992; Cox *et al.*, 1988), but thus far have had limited impact thus far on the Colorado Plateau ecosystems. By far the most noxious of the summer-time weeds is *Salsola*; this species appears to become established quickly on disturbed soil. In general, weedy species have a difficult time becoming established on undisturbed cryptobiotic soils.

These invading species are capable of using summer moisture inputs to a greater extent than can the native woody species (Ehleringer *et al.*, 1991; Lin *et al.*, 1996). If greater access to summer moisture results in greater productivity by invading species and greater acquisition of nutrients released by decomposition during periodic summer precipitation events, then invading species may have a competitive advantage over native perennial species in the long run.

## Colorado Plateau desert



**Figure 14.10.** Left diagram. The relationship between soil nitrogen isotope ratio and the concentration of nitrogen in soils in a Colorado Plateau desert ecosystem. Right diagram. The relationship between mineralizable nitrogen and soil nitrogen isotope ratio a Colorado Plateau desert ecosystem. Modified from Evans and Ehleringer (1993, 1994).



**Figure 14.11.** Top diagram. The hypothetical relationship of how water and soil nitrogen influence productivity in desert ecosystems, which are pulse driven, when crust disturbance is incorporated into the ecosystem interactions. Bottom diagram. The relationship between photosynthesis and leaf nitrogen content for C<sub>3</sub> and C<sub>4</sub> species.

## 14.7 Conclusions

Water and nitrogen limitations constrain plant productivity in the desert ecosystems of the Colorado Plateau. Moisture inputs are biseasonal, acting as pulse events with prolonged drought periods between major precipitation periods. There is no clear evidence for niche differentiation with respect to water source by perennial functional

groups in the spring growing season. However, there are clear differences in the capacities of woody life forms to utilise summer moisture inputs. Differences in water source utilisation occur within the same life form, limiting a simplified niche-partitioning approach. Herbaceous annuals (including invasive species) utilise more of the monsoon precipitation than do woody perennials. Temperature may play a role in limiting the uptake of upper-layer moisture by some species, creating an imbalance in the capacities for different life forms to compete for monsoonal moisture input.

Variations in the soil nitrogen isotope ratios and nitrogen contents suggest a progressive loss of nitrogen from soils that fits a Rayleigh relationship. These disturbance-driven patterns are consistent with a decrease in nitrogen-fixing capacity relative to nitrogen loss; cryptobiotic crusts are implied as the primary nitrogen source in these ecosystems. Plant nitrogen isotope ratios then become a strong indicator of the quality of the soil resource following disturbance. Many of the invading species are  $C_4$  plants with a lower intrinsic nitrogen requirement than the native vegetation.

These patterns suggest that the native vegetation of the Colorado Plateau may not fully utilise monsoonal moisture inputs and may be exposed to progressively eroding soil nitrogen availability associated with disturbance. Together these factors imply that such native ecosystems are unlikely to be responsive to changes in monsoonal moisture input (at least in their current composition) and are sensitive to change by invasive species. Fluctuations in the relative contributions of winter and monsoonal moisture and disturbance-driven decreases in soil nitrogen availability would both contribute to this effect.

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