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FINAL REPORT TO THE

DEPARTMENT OF ENERGY

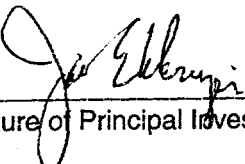For

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Water Use, Productivity and Interactions Among Desert Plants

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1. Overview and Background of Originally Proposed Research

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 or the northern limits of summer moisture input or both (Houghton 1979, Comstock and Ehleringer 1992). 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; Caldwell and Richards, 1989; Dobrowoski 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).

This PER project focused on the influence of variations in summer moisture input on structure-function relationships within a cold desert ecosystem on the Colorado Plateau. Our primary field sites were located at Stud Horse Point, Utah, located on the Utah-Arizona boundary in the Glen Canyon National Recreation Area and at the Arizona monsoon boundary region.

2. Report on the Research Conducted

During the past three years of this project, we have focused on several key areas as described in the original proposal. **This section that follows is written as a review, providing both the background and interpretation associated with our recent contributions. The references in italics at the end of each section refer to the specific publications in section 3 that have been published from this DOE research.**

Southeastern portions of Utah (northwestern portions of the Colorado Plateau) form a broad northern border for the region influenced by the Arizona monsoonal system (Bryson and Lowry 1955, Mitchell 1976). Annual precipitation across Colorado Plateau ecosystems ranges 100-400 mm (Houghton 1979). 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 (Houghton 1979, Adang and Gall 1989, Moore et al. 1989). Variations in the intensities and predictability of summer rain should have significant impacts, since water is the single most important factor influencing primary productivity in these aridland ecosystems (Ehleringer and Mooney, 1983; Smith and Nowak, 1990). 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.

There is also evidence indicating pronounced fluctuating climates over the past several hundred years - shifts in both the amount and timing of precipitation events; the consequences have been both increases and decreases in precipitation from current conditions. Stine (1994) observed that two extended droughts of 140-200 years occurred in the western US earlier in this millennia. He suggested that the Pacific High Pressure may have been located farther north than at present, diverting northward winter storm systems. A more northward position for the Pacific High may have allowed summer monsoonal moisture to move farther north into the Intermountain West. Rose and Lindstrom (1994) have confirmed

these patterns in other lakes of the Sierras, as well as indicating that similar patterns on a smaller scale have occurred since the 1300's. Feng and Epstein (1994) reported a shift in the hydrogen isotope ratios of bristlecone pine tree rings several hundred years ago that is consistent with a reduction in summer precipitation in Sierra Nevada Range. Coltrain (1994) reported that corn, once common, disappeared from the diet of native Americans living on the eastern shores of the Great Salt Lake approximately 700 years ago. Lack of corn could indicate a loss of summer precipitation. *Quercus turbinella* is a common shrub oak, whose northern distribution is limited by its dependence on summer precipitation (Nielsen and Wullstein, 1983; Ehleringer and Phillips, 1995). While its current northern distribution limit is in southern Utah, hybrids with *Q. gambelii* can be found as far north as Salt Lake City (Cottam et al., 1959), nearly 500 km farther north; this migration may have been in response to a decrease in summer monsoon incursions. Lastly, Lanner (1974) reported relict *P. edulis* in the northern portions of the Wasatch Range 200 km north of the main northern distribution limit. These patterns suggest a relatively recent loss of reliable summer moisture in the northern habitats leaving only the relictual populations in isolated sites. Using tree-ring chronologies Taylor and Rose (1992) reconstructed climatic conditions on the Colorado Plateau and observed recurring 20-80 year drought cycles over the past two millennia. These drought cycles are of long enough duration to influence aridland vegetation composition, especially the dynamics of herbaceous perennial vegetation components, which tend to be shorter-lived.

Water sources of plants and climate change

Plants do not fractionate against D or ^{18}O during water uptake, and therefore the isotopic composition of water in roots and suberized stem tissues is an integrated measure of the water uptake patterns of the roots (White et al., 1985, Dawson and Ehleringer, 1991; Dawson and Ehleringer, 1993). The analysis of stable isotope ratios of xylem sap then provides a quantitative measure of the water sources currently used by plants. This approach has been used to describe short-term, temporal patterns of water uptake by species as well as the differential use of soil moisture resources by species in a habitat (reviewed by Ehleringer and Dawson, 1992; Ehleringer, Hall, and Farquhar, 1993).

There is niche differentiation with respect to soil moisture use in Utah aridland and semi-arid woodland ecosystems. Not all perennial species respond equally to summer moisture inputs. Ehleringer et al. (1991) showed that following summer rains several of the woody perennial shrub species in a Colorado Plateau desert scrub ecosystem were not using that moisture input. Other woody perennials in this ecosystem derived 20-70% of their transpiration water from the upper soil layers wetted by summer rains. The CAM, annual, and herbaceous perennial components of the ecosystem relied on moisture derived from summer rains. Similar water-source partitioning has been shown to occur in the pinyon-juniper woodland (Flanagan et al., 1994; Evans and Ehleringer, 1994), sagebrush steppe (Donovan and Ehleringer ,1994), and oak-maple woodland (Phillips and Ehleringer, 1995). If monsoonal boundaries move, then it is particularly important to know if the dominant species located on the boundaries will be sensitive to this change. Based on field observations, Ehleringer et al. (1991) suggested a differential sensitivity among vegetation components, implying possible long-term instability in current species composition with a shift in precipitation input patterns.

We established field experimental systems with which to examine mechanistic aspects and ecological consequences of variation in the capacity to take up summer moisture on plant performance. These included an experimental watering system in southern Utah for looking at naturally-established plants, a community-level system in southern Utah which included all of the dominant species, and an individual field container system at the University of Utah which focused on key species. All three designs included systems with the ability to add isotopically-labeled water in a manner analogous to natural precipitation. At the University of Utah site, this also includes the possibility to introduce labeled water at different soil depths. Over a 2-year period, we conducted a field irrigation experiment to quantify timing and ability to

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take up moisture from summer rain events. We simulated a 25-50 mm increase in summer rains during July and September on five dominant perennials. We took advantage of the fact that the stable isotope ratios of precipitation at our study site differed between winter and summer precipitation events (Fig. 1). By isotopically enriching the hydrogen isotope ratio of artificial rain events, we could distinguish among deep soil (winter-recharge water source) and our artificial summer rain event that wetted the upper 20-50 cm, or combinations thereof as the water source used by a plant (Fig. 2). These results confirm that some dominants, such as *Atriplex*, did not uptake moisture from the upper 20-50 cm, despite the observations that live roots were present in those soil layers. Instead *Atriplex* continued to use moisture from deeper soil layers. In contrast, *Coleogyne* derived a significant fraction of its moisture from the upper layers wetted by a summer rain.

Although soil moisture from upper soil layers may not have been used equally by all species (Line et al., 1996), there were significant changes in leaf carbon isotope discrimination (Δ), indicating that "set point" acclimation for gas exchange [see next section for explanation] had occurred during the summer. However, because there were parallel changes in Δ within each plant as resource levels changed, the rankings of set points among genotypes and species remained constant as predicted (Fig. 3) (Ehleringer, 1993a, 1994). As higher Δ values tend to indicate less photosynthetic stomatal limitation, it is likely that herbaceous perennials had greater rates of carbon gain than did the woody perennials.

For all species, the capacity to take up moisture from the surface layers was greater in September, a cooler month, than it was in July. We find it quite interesting that these woody perennials would differ in their capacities to take up summer moisture at different times during the summer [some species increased summer rain uptake from 16% to 52% between July and September]. The suggestion that soil temperature may play a role in water uptake has received limited attention in the literature. Ehleringer et al. (1991) observed that woody and nonwoody perennials had the same capacity to take up moisture during the winter-spring months; it is only during the summer months that we see this life-form distinction. One possible explanation is that many of these woody perennials do not maintain surface roots for water uptake during the summer. Root excavation studies, however, showed that all of these species had some live roots in the upper soil layers (Phillips and Ehleringer, unpublished obs.). Perhaps these upper layer roots were involved in nutrient uptake. Flanagan et al (1992) had investigated summer moisture uptake in a nearby pinyon-juniper woodland over a two-year period. Consistent with our observations, they observed less summer moisture uptake by *Juniperus osteosperma* in 1989 (a warm summer) than in 1990 (a cooler summer). Ehleringer and Dawson (1992) hypothesize that woody perennials in these ecosystems may be allocating carbon belowground to those rooting zones most likely to have the greatest likelihood of moisture on a long-term basis. As such, if the probability of summer moisture in the upper soil layers is sufficiently low, the amount of water uptake through time per carbon invested in roots may be greater to the plant if available carbon was allocated to roots in deeper soil layers.

A second possible explanation is that high soil temperatures during the summer, combined with late spring drought before the monsoon rains arrive, had inactivated the shallow-depth roots and prevented root regrowth in these upper soil layers. Caldwell and colleagues have shown a seasonal progression of fine root production into deeper soil layers for shrub and grass species in nearby sagebrush steppe ecosystems (Fernandez and Caldwell, 1975; Caldwell, 1985; Caldwell and Richards, 1986) where summer rains are uncommon. Perhaps when summer moisture was applied in our experiments, the soils were then too warm to reactivate the fine surface roots in some species. This would provide a simple mechanism for why some species responded to rain in spring and in late summer, but not in midsummer. There is evidence to suggest that this may be the case. In a study of fine root mortality in sugar maples, Hendrick and Pregitzer (1993) observed that higher root mortality in the upper soil layers was associated with warmer soil temperatures. However, several of the species in our study also commonly occur in more southerly habitats with a greater fraction of the annual rains from summer monsoons. It may well be that there is substantial population-level variability in the response to summer rains. Ehleringer and Dawson
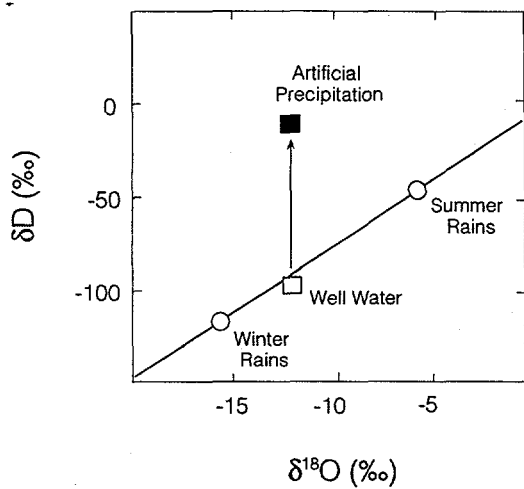
Figure 1. The relationships between hydrogen and oxygen isotope ratio for summer rains, winter rains, well water, and the enriched water used for irrigation experiments. From Lin et al. (1995)
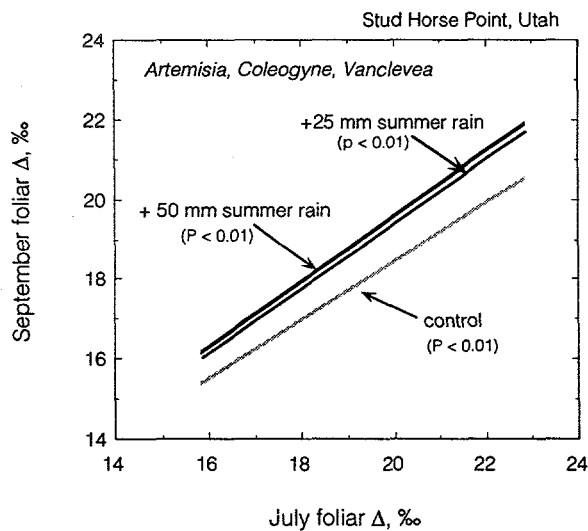

Figure 3. Effects of summer rain increase in July 1993 on foliar carbon isotope discrimination of four C3 species measured in September at Stud Horse Point, Utah. Each point represents the mean and standard error of the measurements on five plants, and the significance level is for the comparison of the mean between the control plants and the plants receiving either 25 mm or 50 mm summer rain treatment. From Lin et al. (1995)

Figure 2. Changes in δD values (before and after irrigation) of stem xylem sap from five dominant perennial species of a Colorado Plateau cold desert community after receiving simulated summer rain having a δD value of -10 ‰ in July and September. Each bar represents the mean and standard error of the measurements on five plants, and the significance level is for the comparison of the mean between the control plants and the plants 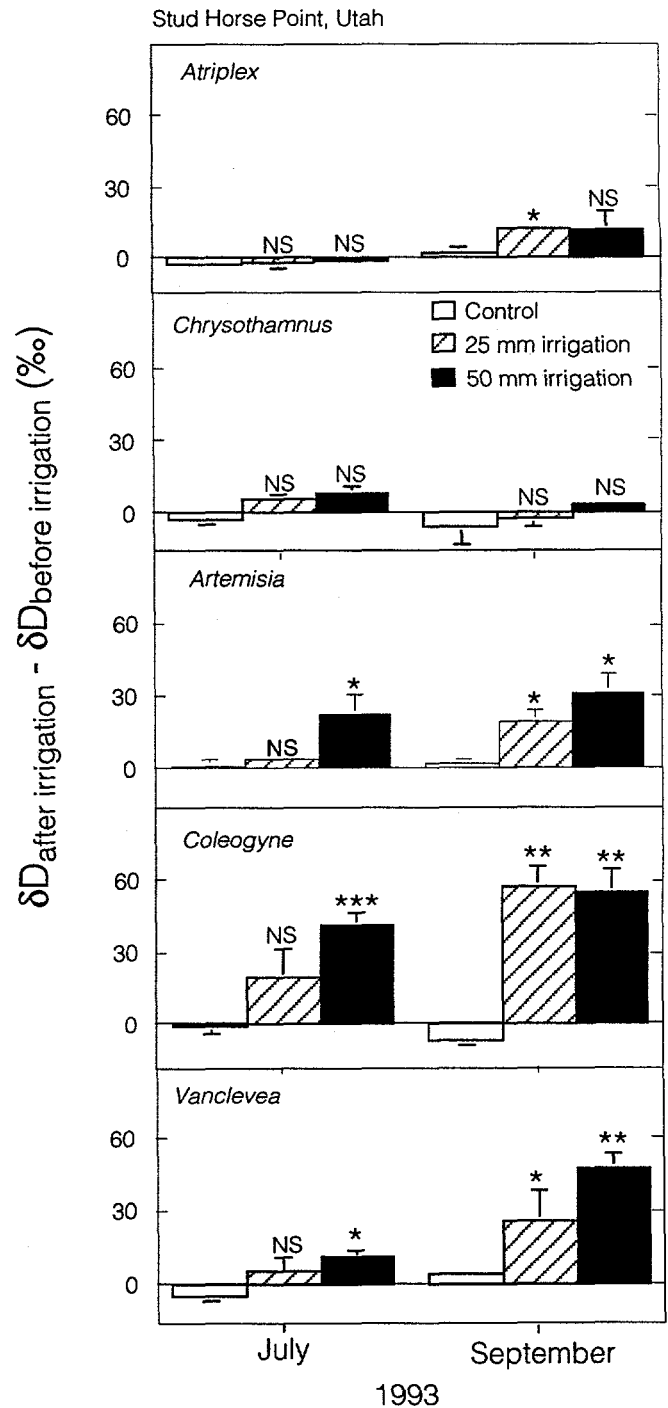receiving either 25 mm or 50 mm summer rain treatments (n=5): NS, not significant, P>0.05; *, significant at P<0.05; **, significant at P<0.01 and ***, significant at P<0.001 (t- test). From Lin et al. (1995).

(1992) cite juniper data showing a latitudinal-gradient response to summer rains. Williams and Ehleringer (1996) have also shown similar population-level differences in the response to summer rains for *Pinus edulis* and *Juniperus osteosperma*. We hypothesize that temperature differences may be the major factor responsible for such difference in uptake of summer rain by desert shrubs between July and September.

Elevated soil temperatures and an inhibition of root activity in the upper layers are likely to play a significant role in determining species interactions and competition for water, especially since arid lands of the Colorado Plateau represent a convergence of flora from different regions and evolutionary histories. We hypothesize that the degree to which plants shift to deeper soil layers for moisture during the summer will be proportional to soil temperature in the upper soil layers. A mechanistic approach to understand what environmental factors increase a plant's sensitivity to stress will be critical if we want to predict the sensitivity of these ecosystem components to change. Woody perennials also differed in summer water uptake in a way that is consistent with the hypothesis that soil temperature may play a direct role in the capacity to take up surface moisture. Consistent with this is the recent observation that altered soil temperature plays a direct role in shifting life-form dominance within a community (Harte and Shaw, 1995). This area of research is likely to shed new insights into why some perennial species are extremely sensitive to temperature, which may ultimately result in their being out-competed by other perennial and/or weedy species that are able to take up soil moisture from the upper layers.

[Publications arising from research on this topic are 162, 180, 190, 194, 197, 198]

Mechanistic basis for variation in carbon isotope discrimination

We continued to examine the general hypothesis that leaf intercellular carbon dioxide is a measure of the metabolic set point in plants and its ramifications for response to climate-induced stresses (Ehleringer, 1993, 1994). This parameter is measured most easily in an integrated manner through carbon isotope discrimination. This concept for integrating plant behavior continues to be supported by our field experiments. Plants irrigated increase their carbon isotope discrimination as predicted by our models (most recent is Ehleringer, 1994). This approach has been adopted by a number of other laboratories who find that stable isotopes provide a valuable approach for scaling physiological processes to the population and ecosystem levels. We have also examined the isotopic composition of respired carbon dioxide, to insure that leaf-level measurements adequately reflect the gas exchange processes (Lin and Ehleringer, 1996). This parameter does not necessarily tell you direct information on the absolute metabolic rate, but rather tells you of the constraints imposed by integration among metabolic components. In the case of plants, this is the interactions between those structural components involved in water flux (uptake, transport, loss) and those components involved in carbon dioxide flux (light-harvesting structure, enzymatic activity, gas diffusion). Our efforts at understanding tradeoffs between productivity and water stress tolerance among components of the ecosystem appear to fit this broader picture.

A major assumption of the models linking carbon isotope discrimination to the intercellular carbon dioxide concentration is that there is no major secondary fractionation after the first photosynthetic carboxylation event. One possible pathway for fractionation that had not been examined was dark respiration. We have just completed a study looking at the possible steps in mitochondrial respiration (Lin and Ehleringer 1996). We can detect no carbon isotope fractionation during respiration using a variety of substrates in both C_3 and C_4 plants. Whole-leaf experiments also suggest that there is no fractionation during dark respiration. Thus, it would appear that we are safe in our assumption that fractionation by RuBP carboxylase is the primary discrimination step in plant carbon isotope discrimination.

[Publications arising from research on this topic are 163, 164, 168, 170, 171, 172, 174, 176, 179, 191,

Nutrient cycling in arid zones

Cryptobiotic soils composed of cyanobacteria, lichens, and mosses occur throughout arid ecosystems. The cryptobiotic crust can be as thick as 10 cm and is held together by cyanobacteria that exude a gelatinous sheath binding both microorganisms and soil together (Belnap and Gardner, 1993). Undisturbed soils of the Colorado Plateau are dominated by these cryptobiotic crusts (Harper and Marble, 1988; West, 1990; Belnap and Gardner, 1993). Disturbance through trampling by cattle and man disrupts function of this fragile soil component. Much of the uncertainty surrounding ecosystem nitrogen inputs into arid ecosystems concerns the potential contribution of nitrogen-fixing organisms within the crust to the total nitrogen inputs (West, 1990). While the dominant cyanobacteria and the common lichen *Collema* are capable of nitrogen fixation, their contribution to the nitrogen pools has been recently questioned (West, 1990). Evans and Ehleringer (1993) used nitrogen isotope ratios to show that these organisms were the primary nitrogen sources into Colorado Plateau ecosystems. Furthermore, they showed that disruption of the crust resulted in a net loss of nitrogen from the ecosystem with the remaining soil nitrogen and its nitrogen isotope ratio linearly related as predicted by Raleigh distillation. Thus, nitrogen isotope ratios of soils were strongly correlated with nitrogen mineralization rates and the vegetation nitrogen isotope ratios become a reliable estimator of soil nutrient quality (Evans and Ehleringer, 1994).

The contributions of cryptobiotic crusts to nitrogen input in arid lands 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 livestock trampling (Fig. 4) 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 (Belnap, 1990), 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 Fig. 5, this degradation leads to decreased fertility and ultimately in degradation of community structure and shifts in composition towards species that are either capable of nitrogen fixation or are tolerant of low nitrogen availability.

[Publications arising from research on this topic are 167, 185, 186, 187, and B]

Ecological scaling

Questions of scale predominate ecology, especially in trying to understand the impact of ecophysiological processes at the canopy, ecosystem, and regional levels. In 1993 we finished a volume (Ehleringer and Field, 1993) in which we examined how to scale across various levels of ecological organization, including an examination of what processes are scalable, how the interactions among components change across ecological scales, and the roles of integrating tools such as models and stable isotope analyses. Also in 1993, we published a second volume that further explored the stable isotope components as they relate to ecophysiology and scaling to ecosystem processes (Ehleringer, Hall, and Farquhar, 1993).

[Publications arising from research on this topic are 158, 161, 166, 178, and 191]
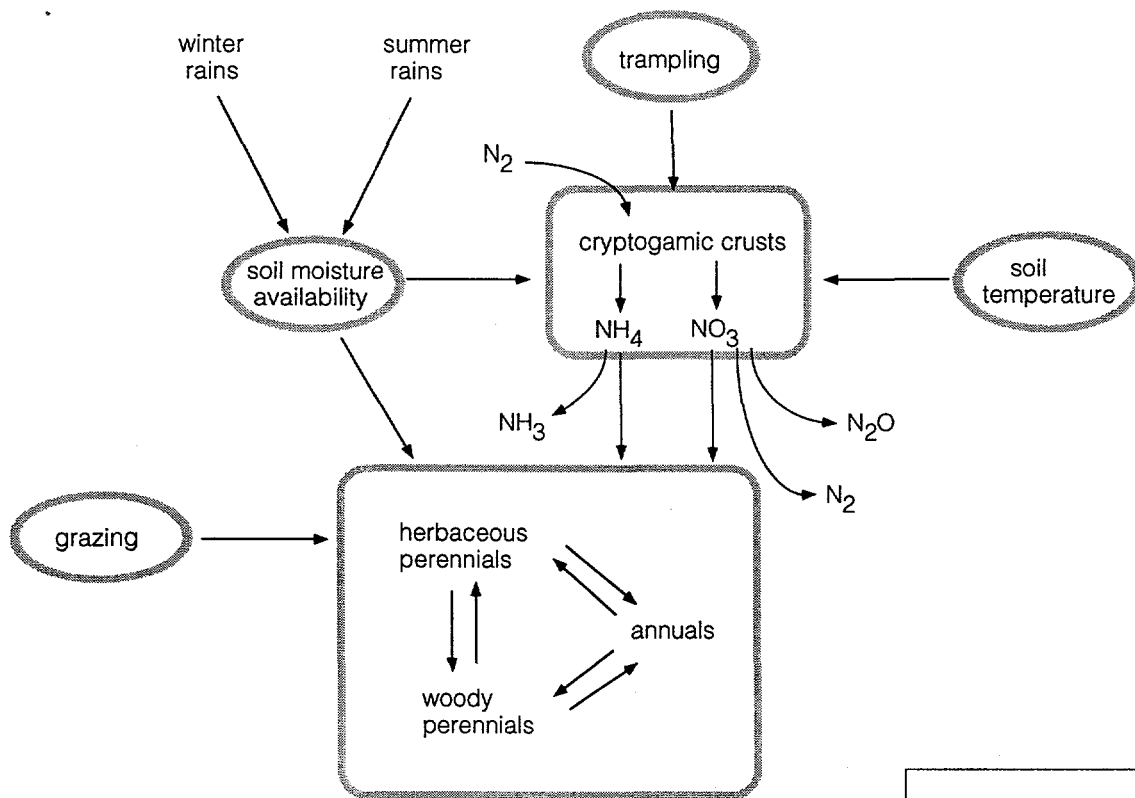
Figure 4. Box-arrow diagram of vegetation-crust-grazing fluxes and interactions with precipitation.
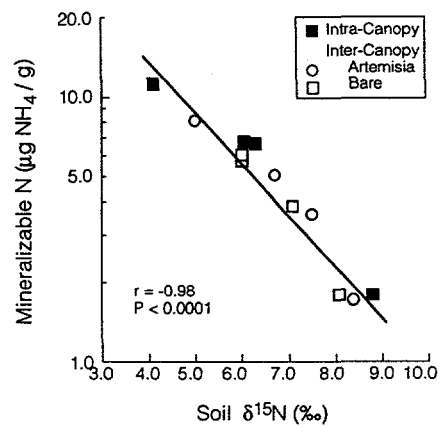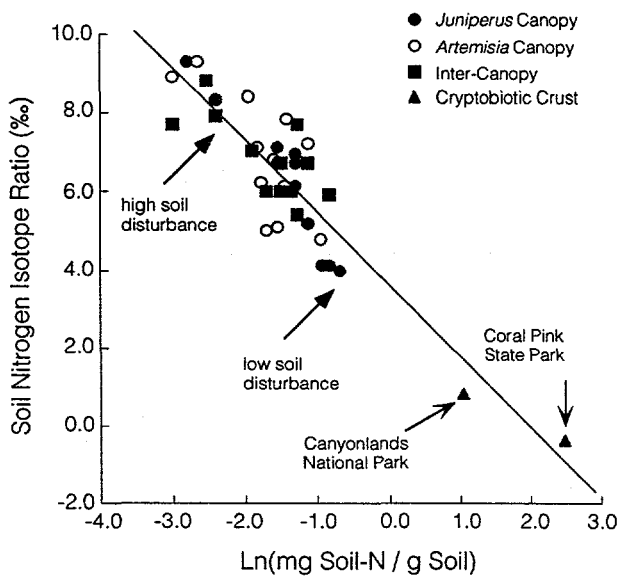

Figure 5. Left. Relationships between nitrogen isotope ratio of the soil and soil nitrogen content (Evans and Ehleringer, 1993). Right. Relationships between nitrogen isotope ratio of the soil and mineralizable nitrogen content (Evans and Ehleringer, 1994).

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3. Publications Arising Totally or in Part as a Result of Department of Energy Support between 1993 and 1996.

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B.   Evans, R.D., A.J. Bloom, S.S. Sukrapanna, and J.R. Ehleringer. Nitrogen isotope composition of tomato (*Lycopersicon esculentum* Mill. cv T-5) grown under ammonium or nitrate nutrition. Plant Cell Environ.

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C.   Leffler, A.J., F. Basha, and J.R. Ehleringer. Salinity increases bundle sheath leakiness in *Atriplex canescens*, a C_4 halophyte. Plant Cell Environ.

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4. Personnel Supported By The Grant and Student Training, 1992 - 1995

Ms. Farhana Basha	Undergraduate Student
Mr. Joshua Leffler	Undergraduate Student
Mr. Michael Lott	Undergraduate Student
Mr. Robert Mack	Undergraduate Student
Ms. Leah Richardson	Undergraduate Student
Mr. Sean Schaeffer	Undergraduate Student
Ms. Lynda Sperry	Undergraduate Student
Ms. Susan Phillips	M.S. Graduate Student and Research Associate
Mr. Darren Sandquist	Ph.D. graduate student
Mr. Peter Thorburn	Ph.D. graduate student
Dr. R. David Evans	Postdoctoral Associate
Dr. Guanghui Lin	Postdoctoral Associate