Long-term C Accumulation in Cold Deserts: Role of Shrub 'Islands' and Soil Moisture

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Summary

Arid and semi-arid ecosystems comprise 30-40% of Earth's terrestrial biomes and 32% of California; however, within these ecosystems little is known regarding patterns of soil carbon (C) accumulation, decomposition of specific litter types, and impacts of soil moisture depletion and hydraulic redistribution by shrub roots on decomposition. We quantified C accumulation across a 3,000-year chronosequence and investigated effects of naturally varying soil moisture, other soil properties, microbial communities, and root-soil water relations on decomposition in a California cold desert ecosystem.

Accumulation of soil organic C (SOC) in cold desert soils is rapid for at least two centuries after freshly exposed substrate is colonized by shrubs. After three centuries of ecosystem development, SOC is in approximate steady state. More than 30% of total SOC was found at depths >1m, illustrating the magnitude of root system inputs in this ecosystem. As expected, we documented that shrub-island soils were significantly drier than interspace soils, and this soil moisture heterogeneity influences decomposition as well as provides the driving force for hydraulic redistribution by plant roots. While the drier, shrub-island soils have high concentrations of SOC, more total SOC is stored in interspaces at the landscape scale because of their large relative area. This counter-intuitive result illustrates the need to sample even apparently barren interspace microsites to quantify landscape-scale SOC pools and further emphasizes the importance of root inputs to total SOC in this ecosystem. Hydraulic redistribution occurred in soils under shrubs, but the presence of roots resulted in more extracted water than replaced through hydraulic redistribution processes. Nevertheless, decomposition of litter associated with roots was more rapid than expected in such dry soils. Diel re-hydration of rhizosphere soil by hydraulic redistribution stimulated litter decomposition in shrub-island soils.

These results will: 1) benefit management of "old growth" deserts, 2) guide rehabilitation of anthropogenically degraded desert soils, 3) provide understanding of C sequestration in spatially heterogeneous desert environments, and 4) stimulate reexamination of plant ecophysiological processes as drivers of soil C dynamics in this ecosystem.

Objectives

This research at the Mono Basin Ecosystem Research Site (MBERS), Mono County, California, embraces both the temporal (different aged biogenic dunes along a chronosequence ranging from 49 to approximately 3,000 years since exposure by lake recession) and the spatial (landscape position along the chronosequence and shrub-island / interspace) scales associated with C dynamics in desert ecosystems. In this cold desert ecosystem, we quantified long-term C accumulation and variation in C-cycling processes at multiple spatial and temporal scales.

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C storage and decomposition at two spatial scales.

We hypothesized that storage of C in a California cold desert ecosystem is a function of spatiotemporal variation at the landscape scale (across the chronosequence) and at the smaller spatial scale of shrub islands and interspaces. Further, we hypothesized that soil moisture variation at these scales and shrub root-soil water relations are primary factors governing C loss and soil organic C accumulation during decomposition of various litter inputs, including woody and fine materials.

These hypotheses were addressed through the following objectives:

- Describe patterns of C accumulation over time by inventorying major C pools in *Sarcobatus vermiculatus* shrub-islands and adjacent barren interspaces across MBERS.
- Quantify aboveground and belowground C pools: shrub biomass as stems, leaves, roots and standing dead biomass; total soil organic C and total soil inorganic C; microbial biomass; coarse and fine litter.
- Determine total accumulation and turnover rates of each C pool and predict total amount of C that may be sequestered in a cold desert ecosystem.
- Characterize the influence of soil characteristics, especially soil moisture, on the decomposition of four major litter pools (leaves, woody stems, fine roots, woody roots) in *Sarcobatus vermiculatus* shrub-islands and adjacent barren interspaces across MBERS.
- Determine if soil moisture relationships, as suggested in the literature for deserts, are the primary factor governing litter decomposition across MBERS.

We expanded our initial objectives to include deeper soil profiles (to 2 m) because of the large amount of SOC found in deep sampling trials and also to include more detailed characterization of SOC components and soil microbial communities.

Effects of roots and soil moisture on decomposition.

We hypothesized that increased soil moisture due to hydraulic redistribution (HR) by roots of *Sarcobatus vermiculatus* and *Artemisia tridentata* increases decomposition rate of leaf and fine root litter. These two shrub species have consistently demonstrated hydraulic redistribution (Richards and Caldwell 1987; Caldwell et al. 1998; Donovan et al. 2003).

This hypothesis was addressed through the following objectives:

- Identify how HR by desert shrubs *S. vermiculatus* and *A. tridentata* influences the magnitude and duration of soil moisture depletion and fluctuations at one site (300year-old dunes) at MBERS.
- Determine if soil moisture fluctuates through HR by *S. vermiculatus* and *A. tridentata* to stimulate decomposition of leaf and fine root litter.
- Test if water augmentation alone stimulates decomposition in *S. vermiculatus* and *A. tridentata* island soils to the same extent or more than that by HR.

Initially only one shrub species, *S. vermiculatus*, was included. We included another Great Basin Desert shrub species (*A. tridentata*) known to conduct extensive HR (Richards and Caldwell 1987; Caldwell *et al.* 1998) in this objective to make the results more general and thus more useful for understanding cold desert C cycling processes.

Approach and Procedures

Soil sampling to 2-m depth under shrubs and in interspaces was completed at four landscape locations across the Mono Basin Ecosystem Research Site (MBERS) chronosequence. The four landscape positions represent biogenic dune complexes developed on shorelines of Mono Lake after lake recession. These locations have been available for shrub colonization and soil development for 48 (Shadow Dunes), 86 (Transverse Dunes), ~300 (Diverse Dunes), and ~3,000 (Old-growth Dunes) years. At each location, replicate shrubs (8) and interspaces (5-8) were sampled for C (and N) inventory, soil organic matter chemistry, and microbial communities. Soil inorganic and organic C was fractionated and quantified using standard procedures. Soil water content was quantified with a neutron probe 4-5 times each growing season (2004-2006) and soil water potential and temperature were quantified with soil thermocouple psychrometers and data loggers recording hourly measurements. Details on all soil analyses are provided in Shuldman (2006) and Aanderud (2006).

Results and Discussion

Soil and plant carbon accumulation across a dune chronosequence.

Although productivity in deserts is low, dry soils and long-lived shrubs could result in significant amounts of stored soil C over long time scales. We inventoried biologically derived C in a California cold desert ecosystem at two scales: 1) landscape, along a 3.5-km-long space-for-time chronosequence of four shoreline dune complexes ranging in age from 48 to ~3,000 years; and 2) microsite, *Sarcobatus vermiculatus* shrub islands and barren interspaces typical of desert ecosystems. We determined the amount of C derived from biogenic inputs (i.e., shrubs and microbes; to 2-m soil depth) by using direct excavation of shrub island and interspace soils, soil cores, and canopy harvests to determine the components of soil and plant C pools.

We found that C pools varied between dune complexes across the landscape, as expected, and that fine carbon (FC; carbon not distinguishable as litter) was the largest C pool at all sites, ranging from 62 to 99% of the total belowground organic C. Total belowground organic C and total landscape-scale organic C increased over time with the youngest dune complexes storing significantly less C than the oldest dune complex (*table 1*). As a result of belowground accumulation, landscape-scale total organic carbon accumulation rose to reach an apparent plateau by 300 years and was in steady state after that. Although much less carbon storage is involved than in forests, these data suggest that cold desert ecosystems, like forests, require several centuries of ecosystem and soil development without disturbance to reach steady state in C accumulation and to achieve a state that can be characterized as an 'old-growth' ecosystem.

Although concentrations of organic C were much higher in shrub-island soils than in interspace soils, at each location across the chronosequence, the amount of C in interspaces represented more than 50% of total ecosystem C because of the much greater relative cover of interspaces. This counter-intuitive result illustrates the need to sample even apparently barren interspace microsites to quantify landscape-scale organic C pools and emphasizes the importance of root inputs to total organic C in this ecosystem. The magnitude of root inputs is also illustrated after discovering that more than 30% of belowground organic C was found at depths greater than 1 m. Sampling surface soils is inadequate to characterize ecosystem C pools in cold-desert ecosystems with deep-rooted plant species. While these data do not explain mechanisms of C dynamics through time, they indicate that modeling soil C pool dynamics at the spatial and temporal scales represented by the chronosequence would help develop understanding of drivers of C storage and release in the Mono Basin, and in arid ecosystems in general. Such basic inventories are essential to understand mechanisms and processes governing the storage and flow of carbon pools in soils that support one of California's most extensive ecosystems.

Table 1. *Landscape-scale organic C pools across the chronosequence. Amount of C in each microsite (shrub island or interspace) was multiplied by the proportion of each microsite's area and summed to estimate landscape-scale amounts. Values are back-transformed LS means with the upper SE in parentheses (n = 8). Within column significant differences are indicated by different superscript letters. Aboveground C includes leaves, live stems and dead stems and belowground C includes buried wood (including woody roots), fine roots, large litter, small litter and FC. Total landscape-scale C is equal to aboveground plus belowground.*

	Aboveground C kg C m^{-2}	Belowground C kg C m^{-2}	Total landscape C kg C m^{-2}
Shadow Dunes (49 yr)	1.1 (0.2)^{ab}	4.1 (0.1)^{c}	5.2 (0.3)^{c}
Transverse Dunes (87 yr)	0.7 (0.1)^{b}	13.2 (0.5)^{b}	13.9 (0.6)^{b}
Diverse Dunes (~300 yr)	1.2 (0.1)^{ab}	14.3 (0.5)^{ab}	15.5 (0.5)^{ab}
Old-growth Dunes (~3000 yr)	1.8 (0.3)^{a}	15.3 (0.6)^{a}	17.1 (0.6)^{a}

Relationships among soil organic matter, C and N stable isotopes, and humification.

In deserts where shrub vegetation dominates, soil organic matter (SOM) accumulates more in soils beneath shrubs than in barren interspaces between shrubs. However, little is known concerning the distribution of individual SOM fractions as dunes develop or of humification processes in these ecosystems. To explore these dynamics, the distribution and stable C and N isotope values of dissolved organic C (DOC), and light (LF) and heavy (HF) fractions (all included in fine carbon (FC) mentioned above) were evaluated and related to soil C and N mineralization rates across the MBERS chronosequence. Further, the contribution of shrubs to the accumulation of SOM fractions and humification was also identified by comparing shrub-island and interspace soils at four soil depths (0-10, 30-40, 90-100, and 160-170 cm).

In shrub-island soils at all depths, N concentrations in HF were on average six-times greater than in LF, while concentrations of C in HF and DOC were 5 and 15 times greater than in LF, respectively. Accumulations of C and N in all fractions were localized in the top 40 cm of soil and more than 86 years of dune development was required to accumulate substantial amounts of relatively permanent long-term C stores as HF. Depletion of ^{13}C in shrub soils was greater in HF than in LF and DOC and this reflected humification by microorganisms preferentially degrading more ^{13}C-enriched labile compounds while preserving more ^{13}C-depleted recalcitrant macromolecules. Based on $\delta^{13}C_{LF}$ and $\delta^{13}C_{DOC}$, LF and DOC may occupy similar biogeochemical roles, except in a few instances where total soil organic C was less than 3 mg C kg^{-1} soil. After ≈3,000 years of dune development, enrichment of ^{13}C from surface to deepest subsurface soils under *S. vermiculatus* was 2.3‰ for DOC and 1.5‰ for HF. Differences in isotopic values and mineralization between shrub and interspace soils indicated that greater depletion of ^{13}C in DOC and LF in shrub soils was attributed to higher N and C mineralization. There were no consistent trends in $\delta^{15}N$ for any fraction during humification or with depth.

These results provide new insight into the distribution of DOC, LF, and HF, feasibility of using $\delta^{13}C$ in describing humification, and importance of DOC and LF in C and N cycling during dune development and in desert soils beneath shrub species.

Shrub-interspace dynamics alter relations between microbial community composition and belowground ecosystem characteristics.

Microbial community composition in most terrestrial ecosystems is regulated primarily by organic C quality and quantity and secondarily by physiochemical stresses and soil moisture. In deserts, however, it is unclear which ecosystem characteristics influence microbial community composition or if these characteristics shift across the landscape or with shrub-island development. To evaluate how ecosystem characteristics relate to microbial community composition, shifts in phospholipid fatty acid (PLFA) profiles in soil beneath shrubs and in interspaces were related to 34 belowground characteristics at two soil depths (0-10 cm = surface and 30-40 cm = subsurface) across the MBERS chronosequence.

Microbial community composition differed between shrub and interspace soils in surface and subsurface soils (*fig. 1*). These communities were differentiated by bulk density, NO_3^-, pH, presence of roots, and total C soil, and to a lesser extent by gravimetric water content at time of harvest, Ca, and soil texture. Interspace communities in surface and subsurface soils were related to total soil C and NO_3^- while shrub communities in subsurface soils were related to the presence of roots. When microbial communities were compared within shrub soils, surface communities and subsurface communities were specific to shrub species and highlighted community differences between halophyte (*Sarcobatus vermiculatus*) and non-halophyte (*Tetradymia tetrameres*, and *Artemisia tridentata* ssp. *tridentata*) shrub soils. In shrub surface soils, communities were influenced by NO_3^- and NH_4^+ concentrations, pH, and silt, while subsurface soils communities were related to Cl and P concentrations, total N soil, and NO_3^- concentrations. These interactions reflected differences in soil characteristics created by specific shrub species and/or the similar importance of soil stresses in structuring shrub and microbial communities alike. Microbial community composition in interspace soils varied across the landscape with community differences primarily associated with B concentration followed by Cl concentration and soil texture. Distributions of Gram-positive bacteria and fungi distinguished shrub versus interspace soils while Actinobacteria and fungi highlighted community differences within shrub soils. Across the chronosequence microbial communities in shrub and interspace soils of younger dunes were primarily associated with soil stresses and this trend declined as soil stresses were alleviated during dune development. These results emphasize the heterogeneity of belowground characteristics across desert landscapes and highlight how fundamental physiochemical differences between interspace and shrub soils, as well as during dune development, influence microbial community composition with expected impacts on soil processes of decomposition and nutrient mineralization.

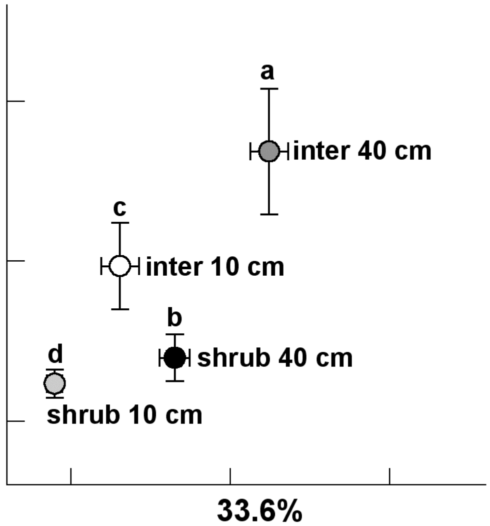

Figure 1. Ordination plot of correspondence analysis results of PLFA microbial community fingerprints from shrub soils, including all shrub species, and interspace soils across MBERS at two depths. Values are means (*n* = 4-5) with standard errors of the means of axis 1 and 2 scores. Different letters indicate significant differences ($P \leq 0.05$) between groups along axis 1.

Hydraulic redistribution stimulates litter decomposition.

Hydraulic lift or redistribution (HR) creates diel drying-rewetting cycles in the rhizosphere in proximity to decomposing roots and buried litter. Since decomposition is often constrained by soil moisture and C cycling is stimulated by drying-wetting cycles, we hypothesized that diel drying-rewetting via HR would allow decomposition of root litter to continue in soils that would be otherwise too dry. This process would be most pronounced in dry shrub-island soils in summer associated with large magnitude HR diel drying-rewetting cycles. We did not expect to find such an effect in spring when HR is nearly absent. We further hypothesized that artificial monthly drying-rewetting through water additions would increase decomposition rates of litter not only in summer, as with HR, but also in spring. We quantified the decomposition of root litter from two desert shrubs, *Artemisia tridentata* ssp. *tridentata* and *Sarcobatus vermiculatus*, in intact soil cores in the field where roots were present and could produce HR cycles (HR Treatment), in similar cores with no roots and no HR cycles (NHR Treatment), and in similar cores with no roots but which received a monthly dose of water to generate artificial drying-rewetting cycles (RW Treatment). The experiments were conducted over two years at the Diverse Dunes site on the MBERS chronosequence.

By spring of the second year, a substantial root system had developed in HRT cores with a root length density for *A. tridentata*=26.5 and *S. vermiculatus*=23.8 km root m^{-3} soil. In spring mean soil Ψ_w was lowest in HRT (-0.2 to -0.3 MPa), intermediate in NHRT (-0.1 MPa), highest in the RWT (-0.03 MPa) consistent with water extraction by roots in HRT and water additions in RWT. Litter decomposition rates were correlated with soil Ψ_w and were significantly lower in the HRT cores than in the other two treatments (*fig. 2*). In summer, however, despite very low mean soil Ψ_w (-2.2 MPa beneath *A. tridentata* and -3.7 MPa beneath *S. vermiculatus*) in HRT cores, litter decomposition rates were not significantly different from those in NHRT cores with much higher mean soil Ψ_w (-1.1 to -1.5 MPa) or from those in RWT cores with mean soil Ψ_w of approximately -0.2 MPa (*fig. 2*). The HRT cores had large magnitude diel drying-rewetting cycles caused by HR (0.5-1.1 MPa for *A. tridentata* and 0.5-2.0 MPa for *S. vermiculatus*). These results suggest that the presence of HR diel cycles in HRT cores maintained decomposition processes in soils that would otherwise have been so dry as to strongly inhibit decomposition.

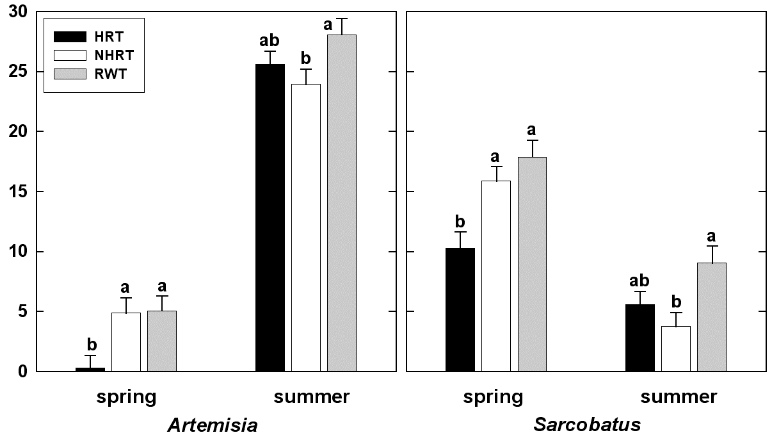

Figure 2. Decomposition rates (%C loss yr^{-1}) of *Artemisia* and *Sarcobatus* root litter exposed to hydraulic redistribution (HRT), no roots or hydraulic redistribution (NHRT) and monthly rewetting treatments (RWT) over spring and summer 2005. Values are means with one standard error (*n* = 12-14). Different letters indicate significant differences ($P \leq 0.05$) within season and shrub species.

Differences in soil temperature, litter chemistry and rhizosphere priming effects between treatments were assessed and did not explain the decomposition results. Thus, these results provide the first field evidence that HR stimulates rhizosphere litter decomposition. Additionally, these results demonstrate the importance of drying-rewetting cycles in arid ecosystems and highlight the need to understand how these cycles will respond to intra- and inter-annual variation in precipitation and future changes in precipitation patterns. Plant root system effects on soil moisture heterogeneity and hydraulic redistribution have important implications for soil carbon storage and cycling in arid ecosystems in California and worldwide.

Overall the results of this research indicate that arid land ecosystems can accumulate soil organic C over centuries, if managed in a way that allows steady state to be approached. Total organic C accumulations per unit ground area are not large, compared with more productive ecosystems. However, when combined with the very extensive distribution of arid land ecosystems in California and worldwide the potential is high for substantial C accumulation. In contrast to much previous work in desert ecosystems, the multi-scale approach used here identified interspace soils as significant reservoirs of soil organic C at the landscape scale, because of the large relative area of interspace microsites. Further, deep soil layers (> 1 m depth) were documented to hold more than 30% of soil organic C, and this suggests that more extensive sampling of deeper soil layers in other ecosystems where deep-rooted species occur (e.g., savannas, chaparral, oak woodlands, etc.) might produce very different estimates of ecosystem C storage than are available at present. The effect of soil moisture heterogeneity, both spatially and temporally, on decomposition processes was investigated. Across the MBERS chronosequence interactions of microbes and plants with soil stresses makes simple correlations of decomposition and soil moisture difficult. For example, the direct effect of hydraulic redistribution on decomposition, shown for the first time here, means that the dry shrub island soils have decomposition rates that are much greater than would be predicted by soil moisture alone. Given the large concentrations of soil organic C (and N) in those microsites, this result has significance for spatial microbial community patterns, for individual shrub nutrition, and for carbon and nutrient cycling in arid ecosystems.

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