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Successional processes in hanging gardens:
response of hanging garden flora and biota to fire

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Introduction

Very little is known about the establishment of hanging garden ecosystems, recruitment of plant species, immigration of vertebrates and invertebrates, or interactions among species during succession (Nebeker et al. 1977, Malanson 1980, Malanson and Kay 1980, Welsh and Toft 1981). Natural disruption of hanging garden communities is limited primarily to rock falls crushing vegetation, sloughing of vegetation and colluvium off the footwall, and herbivory. Under these circumstances, succession is typically a cyclic process; the crushed or sloughed vegetation is replaced by the same species following the physical change in the system (Welsh and Toft 1981).

The Knowles Cañon hanging garden is in a side cañon off the main stem of Knowles Cañon, at an elevation of 1160m, in Navajo Sandstone. It was classified as a Class IV hanging garden (Welsh 1983, unpub. data). The garden is two-tiered, the upper level is a wide, shallow alcove with backwall and detrital slope components, and a lower level of cliff-face vegetation ending at the plunge basin in the cañon floor. Fairly large *Quercus gambelii*, and *Cercis occidentalis* grew around the periphery of the upper garden, on slopes at the ends of the alcove, and along the lower ledges between the alcove and the lower cliff face.

On 4 July 1989, the Knowles Cañon garden burned after visitors ignited fireworks in the area. The aboveground vegetation on the upper terrace was completely destroyed, although rootstocks of some species survived. Portions of the lower garden vegetation was also burned. The fire was very hot, with flames as high as 15-20m, causing rock slabs to spall off the alcove roof. Most of the organic material in the soil of the garden was burned, and there is no soil structure remaining in most of the garden. A few patches of dense litter, mostly leaves and seed pods of *Cercis*, or packrat midden material remain, but most of the "soil" consists of very dry, powdery ash, and sand derived from the sandstone. The rock that fell off the roof covers a significant portion of the dry areas on the alcove floor, some individual pieces cover more than 2m².

Dr. Stanley Welsh visited Knowles Canyon in 1983, and made plant species lists for a number of hanging gardens in the canyon, including the one that burned (Welsh 1983). This represents the extent of pre-fire knowledge of the hanging garden. Photo points were established, and photos taken of the garden in March 1990. I visited the site in May 1992 prior to designing this study.

Post-fire vegetation patterns in the Knowles garden appear to be driven by two factors: surviving rootstocks and soil moisture. Vegetation is limited to herbaceous species growing in the wettest areas and sprouting rootstocks of perennials, primarily *Cercis occidentalis*, *Quercus gambelii*, *Phragmites australis*, and *Juncus balticus*, scattered throughout the garden (Figure 1). There is some encroachment of desert annuals around the periphery in dry ash (e.g. *Eriogonum cernuum*, *Bromus rubens*, and *B. tectorum*). The trees have experienced vigorous growth, some are over 2m tall. Herbaceous species covered approximately 10% of the alcove, but plant cover is 100% in some patches. The rest of the alcove is covered by dry, rocky soil and ash.

Fire generally lowers microbial biomass and respiration, the degree of reduction depends on heat and duration of the fire (Fritze et al. 1993, 1994, Bisset and Parkinson 1980, Pietikainen and Fritze 1993, Raison and McGarity 1980). Recovery rates also depend on how hot the fire was, how much ash is deposited, and the degree of vaporization of soil carbon (Raison 1979, Bisset and Parkinson 1980, Fritze et al. 1994).

Soil fertility and plant growth depend on the soil microbial community to make nutrients available to plants (Fritze et al. 1994). Soil communities can influence plant succession by differentially affecting growth rates of different plant species (Chapman et al. 1988, Blair et al. 1990). Soil community structure may be indicative of the seral stage of the plant community as well (Insam and Domsch 1988, Insam and Haselwandter 1989). The significance of changes in soil community structure is not known relative to hanging garden succession. Given the importance of healthy soil communities for maintenance of other plant communities, successful regeneration of the Knowles Cañon hanging garden is expected to require the re-establishment of the soil community. Nothing is known about soil communities in hanging gardens. Monitoring the soil community over time in the burned garden will provide at least correlative data on how soil and plant communities change over time in hanging gardens following devastating disturbances. Linking plant and soil community changes can enhance management of these ecosystems,

knowing how the two communities interact will enable resource managers to protect and/or restore hanging gardens more effectively.

Fire involves changes in physical, chemical, and biological conditions. The successional response by a hanging garden community to fire may be different from its response to rock fall. This event, while unfortunate, has provided the National Park Service with an opportunity to study successional processes in the unique hanging garden habitat. The objectives of this study are to document successional changes in plant communities of the hanging garden over time, and determine if and when the garden reaches a relatively stable stage. This study will have two facets: 1) comparisons of plant community structure over time in each habitat of the burned garden; and 2) documentation of changes in the soil communities of the burned garden habitats.

We had intended to also compare plant and soil communities in the burned garden with communities in an undisturbed garden that appeared similar in terms of size, aspect, topography, and geology if we could find one. We were not able to find a suitable undisturbed garden to use as a control, so this aspect of the study, which would only have become meaningful after a number of years as the burned garden approached equilibrium, will not be addressed.

Methods

Nested frequency (Hironaka 1985, Mosley et al. 1986, 1989, Smith et al. 1987), and cover, as cover classes modified from Daubenmire (1959) for rock, bare ground, litter, and each plant species were estimated in 20 permanent plots randomly located in each habitat (Figure 2). The number of seedlings in each permanent plot was recorded, and seedlings were identified to species where possible. The longest canopy diameter, and longest diameter perpendicular to that diameter were measured for individual *Cercis* to estimate canopy cover of these trees. Different sized plots were sampled in the different habitats because they covered different sized areas. The dry habitats were sampled with 0.25m² plots, the central area with 0.1m² plots, and 0.05m² plots were sampled in the backwall habitat.

Frequency is the probability of finding a particular species or soil character if a quadrat is placed randomly in an area (Hironaka 1985). It indicates presence/absence of a plant or soil character within each plot, and thus

provides a relative indication of abundance. Frequency values are highly dependent on plot frame size as well as plant density and distribution (Hironaka 1985, West 1985). For this reason, a series of nested plots is generally used (Hironaka 1985). Nested frequency uses a plot frame subdivided into 4 quarters, with plots of decreasing size considered to be nested within the actual frame used (Figure 3). Nested frequency values are obtained for each plant species rooted within the plot frame, as well as rock, gravel, bare ground, cryptobiotic crust components, and litter. The nested plots are considered sequentially, and the frequency score is recorded as the plot frame in which the plant first occurs. Thus, a plant found in the first plot (A of Figure 2) occurred in all four plots, and is given a value of 4; a plant in the second plot (B) occurred in three plots, and is scored a 3, C is scored a 2, and if a plant doesn't occur until the entire plot frame is considered (D), it is scored a 1. Frequency values for the area sampled are calculated by summing the nested frequency values across the plots for each species, then dividing by the number of plots (usually 20 in this study), and multiplying by 100. Frequency values using this method range from 0-400. Chi square analysis will be used to determine if frequency values for a species differs from one year to the next (Hironaka 1985).

Plant cover is estimated as the percent of the entire plot frame covered by each species, and is recorded as a cover class (Table 1). Cover is estimated for all plant species occupying space in or above the plot, whether the plant is rooted in the plot or not. Cover of soil characters are also estimated in each plot (Table 3).

Absolute cover for a species is estimated by multiplying the mid-point of each cover class (Table 1) by the number of plots cover for the species was assigned to that cover class. The resulting cover estimates are summed, and the total divided by the number of plots to get percent absolute ground cover for that species.

Percent cover and frequency were totalled for each species, and for rock, litter, and bare ground in each area. Plant cover values were summed to obtain an absolute plant cover value for each area. Canopy cover (CC) was estimated for each tree as: $CC = \pi * [(d_1 + d_2) / 4]$. Canopy cover was summed and average canopy cover for trees was calculated.

Soil samples were collected in each habitat area from random points (Figure 2). Four samples were collected from backwall and central seep habitats, and six were collected in each dry habitat. Soil samples consisted of cores, 5cm in diameter, and 15cm deep, except in the backwall habitat where the soil was only 3-10cm deep.

The backwall samples represent the entire soil column at each site. Samples were collected 13 July 1993, just before we left Knowles Cañon, sealed in zip lock bags, and shipped the next day to the Soil Microbial Biomass Service, Oregon State University, for analysis. Soil moisture was measured in each sample by subtracting the weight of dry soil from wet soil weight. Soil moisture is reported as the weight of water that would be associated with one gram of dry soil. Active bacteria, active and total fungi, nematode numbers, and trophic and guild composition of the nematode community were determined. Soil samples were analyzed as described in Ingham et al. (1989) and Coleman et al. (1990).

Results and Discussion

Vegetation

The hanging garden appeared to have changed little between May 1992 and July 1993. Most of the ledge is still devoid of any vegetation; colonization appears to be occurring as vegetative expansion from established areas. Essentially no plants are rooted in the large dry areas on either side of the central drip line. The central area had expanded some along its edges, although there is still a bare patch within the area where a small *Cercis occidentalis* burned (it has not re-sprouted). Revegetation of the backwall is also proceeding slowly. *Adiantum capillus-veneris* is the most abundant species along the backwall, but its distribution is quite patchy as shown by the amount of bare ground recorded in the transect. Although total ground cover is still sparse, the area occupied by *Phragmites* had expanded since our 1992 visit.

Twenty six species were recorded in the garden during relevés by John Spence (Table 2). Of these, 18 species occurred in at least one permanent plot in one of the habitat patches. Many of the other species (e.g., *Quercus gambelii*, *Tamarix ramosissima*, *Cirsium rydbergii*, *Astragalus* cf. *zionis*, etc.) were either rare (usually 1 plant) or were growing outside the study area, usually along the foot slope below the main burned part of the garden, or in the lower garden. Figure 4 shows the accumulation of species detected in sampling vs. the total area sampled for each of the four habitat patches (species/area curves). The percent of the total number of species observed in each habitat that occurred in sample plots are indicated at the end of each line. Table 3 presents frequency and cover estimates from plots in each habitat patch.

The total area of each dry habitat is estimated to be about 200m². To facilitate placement of permanent plots in the dry habitats, a 50m² (5m X 10m) quadrat was established in the center of each dry area (Figure 2). A total of 5m² was sampled in each dry area (20 0.25m² plots). This represents 10% of the quadrat, but only about 2.5% of the total area of each dry habitat. Some plots fell completely or mostly on large boulders, which will not show evidence of succession for many years. Substitute plots will be located in 1994 so that the area sampled represents habitat that could be colonized in ecological time. The dry areas were adequately sampled given the lack of plants growing in them now, but an additional 20 plots will be established in each dry habitat area in 1994 in anticipation of eventual colonization by plants.

There were almost no plants rooted in the dry areas, but in both areas, there are plants encroaching via vegetative growth (*Juncus arcticus* and *Panicum acuminatum* on the west, *Phragmites australis* on the east). Seven species were present on the east side (Table 2). Two species were found outside the defined study area, *Quercus gambelii* below the study area on the lower footslope, and *Cercis occidentalis*, found along the periphery of the dry area above and below the study quadrat (Figure 1). Six species (Table 2) were used in calculating species-area sampling efficiency (Figure 4). *Cercis occidentalis* was included because some trees had canopies hanging over the dry area. Three species occurred in at least one vegetation plot; 50% of the species present in the study area were detected. Total vegetation cover in the east dry area was estimated at 5.8% (Table 3).

No species were rooted in the west quadrat, but nine species were found around the edges of the 50m² sampling plot (Table 2). Single plants of *Astragalus zionis* and *Eriogonum cernuum* were found at the western edge of the garden, near the dry slope outside the alcove. *Brickellia longifolia*, *Tamarix ramosissima*, and *Panicum acuminatum* were found along the upper backwall edge of the west study area, while *Q. gambelii*, *Bromus rubens*, and *Juncus balticus* were found at the lower edge of the study area, extending down onto the lower footslope (Figure 1). *Cercis occidentalis* is present at both upper and lower edges of the west dry study area. Five species were considered in species-area calculations, only one species (20%) occurring within the defined west dry study area was detected in the 20 quadrats sampled (Figure 4). Vegetation cover in the 50 m² sampling plot was only 0.15% (Table 3).

The backwall habitat was sampled as a strip transect at the base of the wall, 0.5m wide. Sampling along the backwall was designed to monitor herbaceous vegetation only, thus the shrub and tree species (e.g., *Cercis*, *Brickellia*, and others) were not recorded, even though their canopies did hang over some plots. These species were not included in calculating percent of the total number of species present that were detected in plots. Eleven herbaceous species were found along this wall (Table 2), only five of which (45.5%) occurred in the 20 sample plots (Figure 4, Table 3). Plants covered only 42.2% of the backwall ledge, and 18.9% of the ledge soils remained unvegetated, four years after the fire even though most of the backwall was quite moist (Table 3). Vegetation was dominated by *A. capillus-veneris*, with estimated cover of 41.3% (97.9% relative plant cover), and a frequency of 255 (Table 3). The backwall habitat is very heterogenous, with high species richness and patchy vegetation cover.

The central seep area is the most heavily vegetated patch of the garden. Vegetation was estimated to cover 70.1% of the ground in this habitat. Much of the patch actually has 100% vegetation and/or litter cover. There were 18 plant species present (Table 2), 11 of which (61.1%) were recorded in plots (Figure 3, Table 3). Four of the unrecorded species were present as single individuals. *Adiantum capillus-veneris* (cover 29.6%, frequency 150) and *Polypogon semiverticillata* (cover 28.2%, frequency 280) dominated central seep vegetation (Table 3). These two species accounted for 83.6% of the cover of vegetation in the central seep study area.

Sampling the *Phragmites australis* patch is difficult. In 1993, we measured the longest length and width of the patch, without examining cover within the patch. The estimated total size of the patch was calculated by treating the area as a triangle, and area calculated as $BH/2$, where $H = 11.7\text{m}$ and $B = 5.6\text{m}$. The total area was 32.76m^2 , but actual cover of *P. australis* was estimated to be only about 50% of the triangle.

Canopy cover of *Cercis occidentalis* is shown in Table 4. Nine trees were measured in the west dry area, and eight were measured in the east dry area (about 50% of the total canopy cover of this species in each area above the foot slope). Total cover for the 17 trees was 84.5m^2 , average cover per tree was $4.97 \pm 3.67\text{m}^2$. Abundance of redbud was similar in the two areas (19 trees in the west area, 17 trees in the east area), but average canopy cover was significantly different in the two dry areas (Table 4, $t_{d.f.13} = 2.58$, $p = 0.023$). We did not measure trees with overlapping canopies because of the difficulties of determining canopy boundaries.

Soil Community

Soil community analyses indicate extremely variable conditions exist within and between habitats. Table 5 shows soil moisture, active and total fungal biomass, active bacterial biomass, and nematode numbers determined at each sample location. Table 6 is a summary of the data, presenting the average, standard deviation, and range of values for soil community parameters. Soil sample site conditions are given in the Appendix.

Soil moisture

All four samples from the central seep area appeared very moist in the field. Soil moisture ranged from 0.48g to 1.02g water per gram of dry soil. The sample from below the dripline had the highest water content, samples above the drip line contained less water (Table 5). This indicates that much of the water in the latter habitat falls from overhanging rock instead of running down the cliff face and seeping through the soil below the backwall ledge.

In the backwall habitat, water content of soil samples ranged from .06 to 0.24g g⁻¹ dry soil. Soil moisture was significantly lower along the backwall than in the central seep area, additional evidence that much of the water in the central seep habitat falls directly from the overhanging rock.

East dry habitat soil sample water content ranged from 0.02g to 0.16g g⁻¹ dry soil. Three soil samples in the east dry area were moist enough when collected to hold the soil sample in the sampler. Unfortunately, the three dry samples had water leak into their bags during transit (Table 5), so measured soil moisture content does not represent actual field moisture levels. Comparing the appearance of these samples to dry samples from the west dry area indicates that water content was probably $\leq 0.01\text{g g}^{-1}$ dry soil.

The west dry habitat had drier soils than the east side, only 2 of the 6 samples were moist when collected. These 2 samples were contaminated with water in transit, and thus actual soil moisture could not be determined (Table 5). The other 4 samples were all very dry ($\leq 0.01\text{g g}^{-1}$ dry soil).

Soil fungal biomass

Fungal biomass varied within and between habitats (Tables 5 and 6). Regression of active fungal biomass on soil moisture was significant when the data were pooled across habitats (Figure 5a). The relationship to soil moisture was also significant for total fungal biomass (Figure 6a). The influence of soil moisture on active or total fungal biomass within each habitat is not clear, due at least in part because of the small number of samples in each

area (Figures 5b and 6b). The central seep had the greatest fungal biomass, although the backwall sites and 2 sites in the east dry area also had large estimates. Site DE4 was taken in a mat of *Cercis* seed pod and leaf litter, and DE6 was taken in the middle of the *Phragmites* patch. Both were moist at the 10-15cm depth. The highest fungal biomass value in the west dry area also came from a sample taken in seed pod and leaf mat that was moist when collected. Active fungal biomass estimates in Knowles Canyon hanging garden soils were much lower than levels reported for a variety of agricultural soils (91 to 377 $\mu\text{g g}^{-1}$ dry soil) by Sakamota and Oba (1994), but were similar to prairie (0.8 $\mu\text{g g}^{-1}$ dry soil) and meadow (1.2 $\mu\text{g g}^{-1}$ dry soil) soils (Ingham et al. 1989). Ingham et al. (1989) found pine forest soils had much higher active fungal biomass (80 $\mu\text{g g}^{-1}$ dry soil) than any Knowles Canyon hanging garden soils (Tables 5 and 6). Total fungal biomass in Knowles Canyon hanging garden soils followed the same pattern as active fungal biomass (Tables 5 and 6).

Soil bacterial biomass

Active bacterial biomass was greatest in the central seep habitat, but differences between central and backwall areas were small (Table 5). Regression of active bacterial biomass on percent soil moisture across all habitats was significant, but the relationship is weak (Figure 7a). The relationship between soil moisture and active bacterial biomass within habitats show varying results. The backwall had a clear positive relationship, but other regressions were less clear (Figure 7b). In the dry habitats, samples qualitatively classed as "moist" when collected had the highest active bacterial biomass estimates (Table 5).

Bissett and Parkinson (1980) reported active bacterial biomass in burned and unburned subalpine coniferous forest soils of 33 and 32 $\mu\text{g g}^{-1}$ dry soil respectively from the A horizon, and 217 to 634 $\mu\text{g g}^{-1}$ dry soil from the LFH horizon in July. The central seep habitat most closely resembled forest soils reported by Ingham et al. (1989) and Bissett and Parkinson (1980). Active bacterial biomass in agricultural soils reported by Sakamota and Oba (1994) ranged from 82 to 263 $\mu\text{g g}^{-1}$ dry soil. Ingham et al. (1989) reported 1 $\mu\text{g g}^{-1}$ dry soil for prairie and meadow soils, and 10 $\mu\text{g g}^{-1}$ dry soil in forest soils. Subalpine coniferous forest soils had 1.29 and 1.78 $\mu\text{g g}^{-1}$ dry soil in July samples of burned and unburned LHF horizon samples, respectively (Bissett and Parkinson 1980). The A horizon active bacterial biomass was 0.12 $\mu\text{g g}^{-1}$ dry soil in both burned and unburned soils in July (Bissett and Parkinson 1980). The east and west dry habitats at Knowles Canyon resembled the A horizon of Bissett and

Parkinson (1980). The backwall and central seep habitats had more bacteria than prairie and meadow soils (Ingham et al. 1989), or subalpine coniferous forest soils (Bissett and Parkinson 1980), but lower than the lodgepole pine forest soils examined by Ingham et al. (1989), or agricultural soils studied by Sakamota and Oba (1994).

Active fungal:active bacterial biomass ratios

There is a positive relationship between active fungal biomass and active bacterial biomass across the hanging garden (Figure 8a). Within each habitat, however, regression was significant only in the east dry study area (Figure 8b). The ratios of active fungal biomass:active bacterial biomass were positively related to soil moisture when all data were considered together (Figure 9a), and within each habitat (Figure 9b). This is expected since both fungal and bacterial biomasses were related to soil moisture. The relation is much weaker for the ratio than for each component.

The backwall area had smaller active fungal:bacterial biomass ratios than meadow, prairie or forest soils reported by Ingham et al. (1989), but differences between meadow (1.2), prairie (0.8), and the backwall average (0.36) were relatively small. Three of four backwall soil samples were dominated by bacteria; fungus and bacteria in the fourth sample were similar (Table 5). In contrast, central seep soils were heavily dominated by fungi (Tables 5 and 6), and thus resembled pine forest soils studied by Ingham et al. (1989). This is surprising since central seep vegetation is comprised primarily of grasses, ferns, and sedges (94% of vegetative cover, Table 3). Burned and unburned subalpine coniferous soils were also heavily dominated by fungi, with active fungal:bacterial biomass ratios of 168 to 450 (Bissett and Parkinson 1980).

Soil community characteristics of the dry habitats were extremely variable. Non-zero values for fungal or bacterial biomass may represent relictual patches of pre-fire conditions. Samples showing essentially no microbial activity probably came from areas that burned more intensely. Only one soil sample that looked very dry when collected had any active fungi, and active bacterial biomass in these dry samples was also zero or very low (Table 5). Non-zero fungal/bacterial biomass ratios were generally dominated by fungi, and thus resembled the forest soils more than meadow or prairie soils studied by Ingham et al. (1989). This is interesting since there were no conifers in the garden prior to the fire, and no conifers have colonized since the fire.

The ratio of active fungal to active bacterial biomass has been shown to vary depending on plant community (Ingham et al. 1989, Coleman et al. 1990). Meadow, and to some extent prairie soils were dominated by bacterial biomass, while the coniferous forest soil studied was dominated by fungal biomass. If this is a general characteristic of soil communities, healthy hanging garden soil communities would be predicted to be dominated by bacterial biomass, since they most closely resemble meadows in their plant growth forms and taxa (e.g., dominated by graminoids and herbaceous dicots).

The fungal:bacterial biomass ratio is related to total respiration of the soil community, which determines rates of decomposition and nutrient mineralization (Sakamoto and Oba 1994). With high bacterial and fungal numbers, there is a large turnover of plant detritus into bacterial and fungal biomass. If predators of these organisms are present, the result should be high availability of nutrients for plants in the spring (E. R. Ingham, pers. comm.). Low bacterial and fungal biomass may indicate the system has low fertility, or there is rapid turnover (low standing crop) of bacterial and fungal biomass, in which case fertility may be high.

There is some evidence that high fungal:bacterial biomass ratios occur in late successional seral stages, while early seral stages are characterized by small ratios (Insam and Domsch 1988, Insam and Haselwandter 1989, Sakamoto and Oba 1994). The most successional advanced habitat, the central seep area, did have the largest fungal:bacterial ratios, which supports this theory. Dry habitat soil samples either had large ratios, or no detectable fungal or bacterial activity (Table 5). The dry habitats are in the earliest successional stage, but their ratios may reflect pre-fire plant community composition more than current conditions. The kind of vegetation community that might be expected to become established, or to persist at a site can be predicted from the fungal to bacterial biomass ratios of soil samples (Ingham et al. 1989, Coleman et al. 1990). Most work has been done in agricultural systems; there is a need for more work in natural ecosystems.

The Knowles Cañon hanging garden soil community does not follow patterns of fungal:bacterial biomass ratios predicted by Ingham et al. (1989) or Coleman et al. (1990). We need to continue sampling the soil communities of the burned garden to determine changes in community structure as succession proceeds. Soil samples should be collected from nearby, undisturbed hanging gardens to characterize hanging garden soil communities for comparison. It is expected that soil communities will be more similar between gardens than the

plant communities since soil organisms disperse more widely (E. R. Ingham, pers. comm.), but soil depth and development, moisture, and aspect will all affect composition as well.

Soil nematodes

Estimated total nematode numbers ranged from 0 to 5.1 g⁻¹ of dry soil (Table 5). All four habitats had samples with no nematodes present. The maximum found in each habitat ranged from two in DW to 126.3 in the central seep. Both the backwall and central seep areas had relatively high numbers. Regression of total nematode numbers on soil moisture was not significant (Figure 10a) using data pooled across habitats. Within each habitat, the relationship between total nematode numbers and soil moisture varied (Figure 10b). However, in the two dry habitats, only samples from moist soil had nematodes (Table 5).

The kinds of nematodes present in the different habitats also showed an interesting pattern (Table 5). Both the central seep and backwall habitats had high fungal biomass, yet only the backwall soil contained many fungal-feeding nematodes. More bacteria-feeding nematodes than any other type were found in backwall and dry habitats. The central seep habitat was dominated by root-feeding nematodes. Colonization after the fire has been most rapid and extensive in the central seep area (photos from March 1990, nine months after the fire, show grasses in this area). Plant cover was 70.1% as opposed to 42.1% along the backwall, and 0.2-5.8% in the dry habitats. Not surprisingly, no root-feeders were found in the dry habitats. Even if root-feeding nematodes survived the fire in these areas, they would have faced four years without any plants on which to feed.

Conclusions

Plants growing in the different habitats of the Knowles Cañon hanging garden reflect differences in the existing environments. Species found in the central seep and backwall habitats are typical hanging garden species, with a few exotics that regularly invade moist habitats (e.g., *T. ramosissima*, *P. monspeliensis*). The dry habitats remain largely unvegetated because they are still dry. Even native and introduced annuals (e.g., *M. albicaulis*, *B. rubens*, *B. tectorum*, *Salsola iberica*) have not become established on the dry sites. Revegetation in these areas has been limited primarily to vegetative re-growth from surviving rootstocks or rhizomes.

Soil samples revealed moisture is present 10-15cm below the surface in some areas of the dry habitats. The *P. australis* patch appears to be exploiting this water source. Plants might become established first in the dry habitats in the areas where soil moisture is near the surface, but wetting of the surface soil may be necessary for germination. Because the burned garden is in an alcove, it receives almost no direct precipitation. Saturation of the surface soil is probably a rare event; seedling establishment in these areas is expected to be rare as well. Restoration of disturbed hanging gardens may require transplanting rooted plants that can tap sub-surface water as opposed to seeding the area.

Microbial biomass is reduced immediately after burning (Meiklejohn 1955, Ahlgren and Ahlgren 1965, Miller et al. 1955). Fire intensity influences the depth to which soil biota are affected (Ahlgren 1974), and recovery is more rapid if the soil is moist (Bissett and Parkinson 1980). In a number of studies, microbial communities reached pre-burn levels in 2-3 years, either by a dramatic increase to levels above pre-burn with a gradual decline to pre-burn levels (Ahlgren and Ahlgren 1965, Ahlgren 1974), or a gradual increase to pre-burn levels from low immediately post-burn levels (Wright and Bollen 1961, Meiklejohn 1965). Bissett and Parkinson (1980) found significant differences between soil bacterial and fungal biomasses from burned areas and adjacent unburned soil six years after the fire. Differences were related to plant community differences (forest vs. grassland in unburned vs. burned areas), and shifted seasonally as moisture availability changed. Changes in the soil community were expected to continue as successional shifts in vegetation cause changes in litter characteristics and soil temperature regimes (Bissett and Parkinson 1980).

Fritze et al. (1994) found that total microbial biomass was reduced 50% by burning, but it increased over time; the microbial carbon:organic carbon ratio increased steadily for 11 years following fire before stabilizing (Fritze et al. 1993). Soil drying by the fire accounted at least part of the microbial biomass reduction (Fritze et al. 1993, 1994). Recovery of the community depended on moisture of the humus layer (Fritze et al. 1993, 1994).

The relationship between soil moisture and soil community biomass is evident in the Knowles Cañon samples, especially the bacterial component. Average active bacterial biomass in the backwall and central habitats was 3.6 and 4.3 $\mu\text{g g}^{-1}$ dry soil respectively, while the dry habitat active bacterial biomass averaged only 0.13 (west) to 0.5 (east) $\mu\text{g g}^{-1}$ dry soil. Fungal comparisons are not as distinct, backwall and east dry averages were essentially

equal. However in the east dry habitat where active fungal biomass ranged from 0 to $14.61 \mu\text{g g}^{-1}$ dry soil, the two high biomass values came from sites with moist soil (Table 5).

Soil bacteria and fungi are nutrient sinks (Blair et al. 1990, Coleman et al. 1990, Setälä et al. 1991). Burning mineralizes these nutrients along with those held in plant litter before the fire. Plants respond with vigorous growth after fire in response to this flush of available nutrients (Oberle 1969, Christensen and Muller 1975, Raison 1979, Odum 1989), and thus may not need the soil community to recycle nutrients from plant biomass at this time. Plants need sufficient soil moisture to acquire nutrients from the soil (Larcher 1980). The ability of plants to capitalize on fire-released nutrients depends on soil moisture. Re-colonization of backwall and central seep habitats has been fairly rapid because both nutrients and water are available. Very few plants have become established in the dry habitats, even though available nutrient levels are probably high, because there is no water at the surface.

Decomposer community composition has been shown to affect soil nutrient dynamics (Blair et al. 1990, Ineson et al. 1982, Clarholm 1981, Ingham et al. 1985). How dynamics shift with changes in community structure varies among ecosystems. For example, decomposition and nitrogen concentration both decreased in prairie litter following removal of microbial grazers, but both increased in forest litter, and decomposition increased without a change in nitrogen concentrations in meadow litter (Ingham et al. 1989, Coleman et al. 1990). These patterns can be explained based on trophic interactions between decomposers and their predators (Coleman et al. 1990). More ecosystems need to be studied to determine if there are general patterns in responses.

Soil moisture appears to be the primary controlling factor for both plant and soil communities in the Knowles Cañon hanging garden at present. Biotic interactions are expected to become more important in the wetter habitats as succession proceeds. Changes in the central seep plant community will probably be driven by plant-plant interactions (e.g., competition), and perhaps soil community-plant interactions (e.g. nutrient flux) in the future, since almost all available space has been colonized. The backwall habitat still has large bare areas, and soil moisture levels are somewhat variable. Plant distribution may reflect the patchy nature of soil moisture, variation in the soil community, differential survival and/or dispersal of propagules in this habitat, or some combination of these factors. Soil moisture availability dominates both plant and soil communities in the dry habitats. The re-establishment of hanging garden plants in these dry areas will depend on changes in the current distribution of soil moisture.

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Table 1. Cover classes with corresponding percent cover ranges and mid-points for each cover class, modified from Daubenmire (1959).

Cover Class	% cover range	Mid-point of class
1	< 1%	0.5
2	1-5%	3.0
3	5-25%	15.0
4	25-50%	37.5
5	50-75%	62.5
6	75-95%	85
7	95-100%	97.5

Table 2. Species observed in the burned portion of the Knowles Cañon hanging garden, 12-13 July 1993, and the habitats in which they were growing.

	Back <u>wall</u>	Central <u>seep</u>	East <u>Dry</u>	West <u>Dry</u>
<i>Adiantum capillus-veneris</i>	x	x		
<i>Artemisia ludoviciana</i>			x	
<i>Astragalus cf. zionis</i>				x ²
<i>Brickellia longifolia</i>	x ¹	x		x ³
<i>Bromus rubens</i>	x	x	x	x ²
<i>Carex aurea</i>		x		
<i>Cercis occidentalis</i>	x ¹	x	x ³	x ³
<i>Cirsium rydbergii</i>		x		
<i>Conyza canadensis</i>		x		
<i>Eriogonum cernuum</i>				x ²
<i>Gnaphalium chilense</i>	x	x		
<i>Juncus balticus</i>				x
<i>Lobelia cardinalis</i>	x	x		
<i>Mentzelia albicaulis</i>			x	
<i>Mimulus eastwoodiae</i>	x			
<i>Muhlenbergia andina</i>		x		
<i>Panicum acuminatum</i>	x	x		x
<i>Phragmites australis</i>			x	
<i>Polypogon monspeliensis</i>	x	x		
<i>Polypogon semiverticillata</i>	x	x		
<i>Quercus gambelii</i>		x	x ²	x ²
<i>Solidago sparsiflora</i>	x	x		
<i>Sonchus asper</i>		x		
<i>Stephanomeria tenuifolia</i>	x			
<i>Tamarix ramosissima</i>	x ¹	x	x	x
<u>Unknown dicot seedling</u>	x	x		
Total number of species	14	18	7	9

¹Shrub species not sampled in backwall transect, nor included in calculations of the completeness of sampling effort in the backwall habitat.

²Species located along the lower edge of the area, encroaching from dry slopes, which were not considered to be part of the plant community of the dry study areas.

³Shrub species found along interface of the dry habitats and backwall habitat. Included in species/area curve analyses because they overhang dry habitats (*C. occidentalis* also occurs along the lower edge of dry habitats).

Table 3. Percent cover and frequency estimates of plants, and ground characteristics from 20 permanent plots in each habitat (see text for plot sizes in each habitat). Frequency can range between 0 and 400.

Species	backwall cover	backwall freq	central cover	central freq	east dry cover	east dry freq	west dry cover	west dry freq
Rock	29.08	230	6.95	125	58.25	385	40.02	395
Litter	13.43	290	10.80	270	21.38	395	28.70	380
Bare ground	18.93	205	21.45	175	33.58	310	42.58	385
<i>Adiantum capillus-veneris</i>	41.28	255	29.63	150				
<i>Artemisia ludoviciana</i>					0.75	20		
<i>Brickellia longifolia</i>			3.88	5				
<i>Bromus rubens</i>			1.50	30				
<i>Carex aurea</i>			3.55	80				
<i>Cercis occidentalis</i>			0.02	15				
<i>Conyza canadensis</i>			0.48	40				
<i>Gnaphalium chilense</i>			0.18	35				
<i>Juncus arcticus</i> *								
<i>Lobelia cardinalis</i>	0.33	55	0.15	0				
<i>Mentzelia albicaulis</i>					0.15	0		
<i>Muhlenbergia andina</i>			0.15	15				
<i>Panicum acuminatum</i>	0.15	20	2.02	25			0.15	0
<i>Polypogon semiverticillata</i>	0.35	45	28.20	280				
<i>Tamarix ramosissima</i>					4.88	0		
Unknown dicot seedling	0.05	10						
Total vegetation cover	42.16		70.08		5.78		0.15	

**Juncus arcticus* was present in the west dry area, but did not occur in any study plots.

Table 4. Canopy diameters, and estimated canopy cover of *Cercis occidentalis* measured 13 July 1993 at the burned Knowles Canyon hanging garden.

<u>TREE #</u>		<u>DIAM1</u>	<u>DIAM2</u>	<u>AVE D</u>	<u>COVER (m²)</u>
WD #1		4.2	3.9	4.05	12.88
WD #2		2.7	2.1	2.4	4.52
WD #3		2.9	2.0	2.45	4.71
WD #4		3.5	3.0	3.25	8.30
WD #9		3.2	2.4	2.8	6.16
WD #15		4.7	3.2	3.95	12.25
WD #17		2.0	1.2	1.6	2.01
WD #18		3.0	2.7	2.85	6.38
WD #19		2.3	2.2	2.25	3.98
ED #1		0.9	0.8	0.85	0.57
ED #2		2.6	1.8	2.2	3.80
ED #3		1.8	1.6	1.7	2.27
ED #4		1.9	1.8	1.85	2.69
ED #5		3.1	2.4	2.75	5.94
ED #6		1.0	0.8	0.9	0.64
ED #7		0.9	0.8	0.85	0.57
ED #10	4.1	1.8	2.95	6.83	
Total cover		Average cover per shrub			
West	61.2m ²	6.8 $\pm$ 3.71m ²			
East	23.2m ²	2.9 $\pm$ 2.45m ²			

Table 5. Results of soil community analysis for each soil sample in all habitats. Soil moisture is reported as g H₂O g⁻¹ dry soil, fungal and bacterial biomass estimates are reported as µg g⁻¹ dry soil, and nematodes are reported as # 25g⁻¹ dry soil.

SITE	SAMPLE	DRY WT SOIL		SAMPLE MOIST ²	ACTIVE FUNGAL		ACTIVE BACTER		TOTAL NO. NEMAT	FUNG- VORES	NEMATODE	
		1g WET ¹	H ₂ O		MASS	MASS	MASS	RATIO ³			BACTI- VORES	ROOT FEEDERS
Backwall	1	0.81	0.24	wet	0.67	37.67	6.42	0.104	22.4	8.3	9.7	4.2
	2	0.94	0.06	dry	0.25	46.54	1.94	0.129	20.2	1.2	18.8	0.0
	3	0.92	0.08	wet	0.00	24.42	1.84	0	0.0	0.0	0.0	0.0
	4	0.87	0.15	wet	4.96	17.86	4.10	1.210	6.9	3.5	3.5	0.0
Central	1	0.64	0.56	wet	12.32	74.29	2.32	5.310	126.3	3.5	3.5	29.2
	2	0.62	0.61	wet	18.30	132.41	1.91	9.581	0.0	0.0	0.0	0.0
	3	0.68	0.48	wet	31.14	295.74	6.29	4.951	4.4	1.5	0.0	1.5
	4	0.50	1.02	wet	64.86	1591.99	6.52	9.948	6.1	0.0	0.0	3.0
East dry	1	0.96	0.05 ⁴	dry ⁴	0.32	1.21	0.06	5.333	0.0	0.0	0.0	0.0
	2	0.91	0.10	wet	0.00	1.91	0.13	0	7.7	0.0	7.0	0.0
	3	0.98	0.02 ⁴	dry ⁴	0.00	0.59	0.00	⊛	0.0	0.0	0.0	0.0
	4	0.97	0.03	wet	4.30	112.20	0.31	13.871	4.1	3.0	1.0	0.0
	5	0.93	0.07 ⁴	dry ⁴	0.00	0.00	0.05	0	0.0	0.0	0.0	0.0
	6	0.86	0.16	wet	14.61	66.59	2.47	5.915	1.2	0.0	1.0	0.0
West dry	1	0.99	0.01	dry	0.00	0.00	0.04	0	0.0	0.0	0.0	0.0
	2	0.92	0.09 ⁴	wet ⁴	0.76	3.30	0.32	2.375	0.0	0.0	0.0	0.0
	3	0.98	0.03 ⁴	wet ⁴	0.14	1.33	0.39	0.359	2.0	0.0	2.0	0.0
	4	0.99	0.01	dry	0.00	2.63	0.04	0	0.0	0.0	0.0	0.0
	5	1.00	0.00	dry	0.00	0.46	0.00	⊛	0.0	0.0	0.0	0.0
	6	0.99	0.01	dry	0.00	1.63	0.00	⊛	0.0	0.0	0.0	0.0

¹DRY WT 1g WET: the dry weight of 1 g of wet soil.

²SAMPLE MOIST: indicates whether soil sample was dry or moist when collected.

³FUNG/BACT RATIO: Ratio of active fungal biomass to active bacterial biomass

⁴Samples got wet in transit, soil water shown does not represent field moisture content.

⊛ No bacteria detected in these samples, thus fungal to bacterial biomass ratios could not be calculated.

Table 6. Summary of soil community parameters in each habitat, units are the same as in Table 5.

	Backwall	Backwall	Central Seep	Central Seep	East Dry	East Dry	West Dry	West Dry
	Mean $\pm$ s.d.	Range	Mean $\pm$ s.d.	Range	Mean $\pm$ s.d.	Range	Mean $\pm$ s.d.	Range
Soil moisture (g g ⁻¹ dry soil)	0.13 $\pm$ 0.08	0.06 to 0.24	0.67 $\pm$ 0.24	0.48 to 1.02	0.097 $\pm$ 0.065 [*]	0.03 to 0.10 [*]	0.008 $\pm$ 0.005 ^b	0 to 0.01 ^b
Active fungal biomass	1.5 $\pm$ 2.34	0 to 4.96	31.76 $\pm$ 23.49	12.3 to 64.9	3.2 $\pm$ 5.84	0 to 14.6	0.15 $\pm$ 0.304	0 to 0.76
Total fungal biomass	31.6 $\pm$ 12.92	17.9 to 46.54	523.6 $\pm$ 718.40	74.29 to 1592	30.4 $\pm$ 47.91	0 to 112.2	1.6 $\pm$ 1.26	0 to 3.3
Active bacterial biomass	3.6 $\pm$ 2.16	1.84 to 6.42	4.3 $\pm$ 2.48	0.91 to 6.52	0.50 $\pm$ 0.97	0 to 2.47	0.13 $\pm$ 0.18	0 to 0.39
Fungal/Bacterial biomass	0.36 $\pm$ 0.569	0 to 1.21	7.45 $\pm$ 2.684	4.95 to 9.95	5.02 $\pm$ 5.693	0 to 13.87 [⊛]	0.68 $\pm$ 1.14	0 to 2.38 [⊛]
Total nematode numbers	12.4 $\pm$ 10.72	0 to 22.2	34.2 $\pm$ 61.45	0 to 126.3	2.17 $\pm$ 3.14	0 to 7.7	0.33 $\pm$ 0.82	0 to 2.0

⊛ One east dry sample, and two west dry samples had no bacteria in them, thus fungal:bacterial biomass ratios could not be calculated.

*Mean calculated from three uncontaminated samples, all were moist when collected. Three samples that were dry when collected got wet during transport, these samples were not used in soil moisture calculations.

^bMean calculated from four uncontaminated samples, all were dry when collected. Two samples that were moist when collected got wet during transport, these samples were not used in soil moisture calculations.

Figure 1. Schematic drawing of the Knowles Cañon hanging garden, showing approximate positions of vegetation, photo points, patches of vegetation, trees, and large boulders. Ceoc = *Cercis occidentalis*, Quga = *Quercus gambelii*, Agse = *Agrostis semiverticellata*, Adca = *Adiantum capillare-veneris*, Arlu = *Artemisia ludoviciana* Ciry = *Cirsium rydbergii*, Juar = *Juncus arcticus*, Brlo = *Brickellia longifolia*, Tara = *Tamarix ramosissima*, Phau = *Phragmites australis*.

Figure 2. Schematic drawing of Knowles Canyon hanging garden showing locations of vegetation sampling plots in the dry habitats and along the backwall. The lower left corner of plots within quadrats indicated by "x." Vegetation plots in the central seep area were placed along the four transect lines shown in the figure. Soil sample locations are indicated by "3s" in the figure.

Figure 3. Schematic of plot frame used to estimate cover and record nested frequency data.

Figure 4. Cumulative number of species present in 20 sample plots in each area. East and West areas were sampled with a 0.25m² plot frame for a total of 5m² (2.5% of each dry area). The central seep habitat was sampled with 0.1m² plots (2m², 5% of area). The backwall habitat was sampled with a 0.05m² plot frame (1m², 5% of the area sampled). Percent of total number of species rooted in each habitat that were recorded in sample plots are indicated for each curve. No plants were rooted in the West dry habitat, so no percent could be calculated. One plot had one species hanging over it, and is shown in the curve for this habitat.

Figure 5a and 5b. Active fungal biomass plotted against soil moisture for samples collected from each of the four habitats. The regression line is for all data pooled across habitats, but does not include the data from samples that got wet in transit.

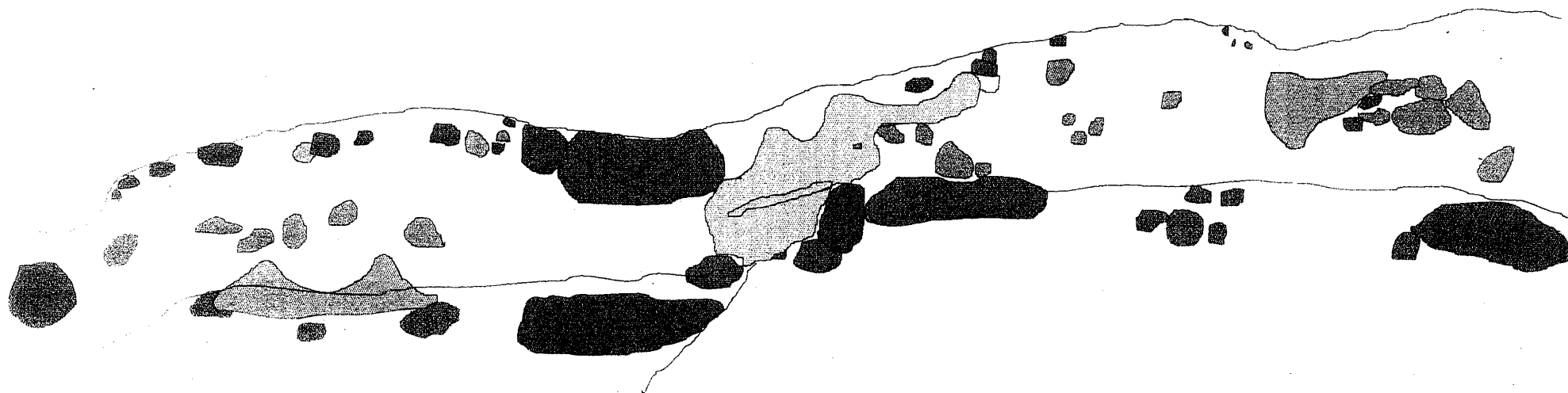
Figure 6a and 6b. Total fungal biomass plotted against soil moisture for samples from all habitats. All data were pooled for regression analysis except data from accidentally wetted samples.

Figure 7a and 7b. Bacterial biomass from soil samples in all habitats plotted against soil moisture. Regression was done with all data pooled across habitats, but contaminated samples were excluded.

Figure 8a and 8b. Fungal biomass vs. bacterial biomass

Figure 9a and 9b. Active fungal biomass/active bacterial biomass ratios vs. soil moisture.

Figure 10a and 10b. Total nematode numbers in soil samples, plotted against soil moisture, for all four habitats. Regression analysis was not significant for data pooled across habitats.



Sandstone
boulders

Cercis

Phragmites

Brickellia

Artemisia

Adiantum
and Polypogon

Quercus

Juncus

Tamarix

Drip line
trench

