The Knowles Cañon Hanging Garden, Glen Canyon National Recreation Area, Five Years after Burning: Vegetation and Soil Biota Patterns

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Abstract. Hanging garden plant communities form at seeps on cliffs. A given community may include common riparian species, disjunct populations, and species endemic to hanging gardens. What structures hanging garden communities, and how they respond to disturbance are poorly understood. In 1989, fireworks ignited a hanging garden in Knowles Cañon, destroying aboveground vegetation. Permanent plots were established in July 1993 to monitor changes in vegetation and soil biota. Revegetation of the garden has been limited to grasses, forbs, and ferns where water was present at the soil surface, and shrubs and trees sprouting from surviving rootstocks. Water drips from the overhanging cliff in the central area, where plant cover is almost 100%. Both moisture and vegetation were patchy along the backwall. The soil was dry in most of the alcove and remained unvegetated 5 years after the fire. Central area soils had more fungus than bacteria and contained mostly root-feeding nematodes. Backwall soils contained more bacteria than fungi, and mostly bacteriovore nematodes. The dry areas had little active bacteria or fungi and few nematodes.

Key words: Colorado Plateau, fire, Glen Canyon NRA, hanging garden, soil bacteria, soil fungi, soil nematodes, succession.

Hanging gardens are mesic plant communities growing on cañon walls on the Colorado Plateau that occur where groundwater seeps laterally out to the cliff surface from perched aquifers (May et al. 1995). Plant communities in hanging gardens range from small monospecific patches of vegetation on vertical cliffs to complex assemblages in large alcoves and can include common riparian species, disjunct populations, Colorado Plateau endemics, and species restricted to the hanging garden environment (Welsh and Toft 1981, Welsh 1989, Fowler et al. 1995).

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Natural disturbance of hanging garden communities is limited primarily to rock falls, sloughing of vegetation and colluvium, and herbivory. The crushed or sloughed vegetation is probably replaced by the same suite of species following disturbance (Welsh and Toft 1981). Hanging gardens are often trampled by humans resulting in significant losses of vegetation and soil, and are occasionally burned. Opportunities to study how hanging gardens respond to disturbance can provide guidance to managers in restoration efforts of hanging garden ecosystems.

The Knowles Cañon hanging garden is off the main stem of Knowles Cañon, at an elevation of 1,160 m, in Navajo Sandstone. The garden is two-tiered; the upper terrace consisting of a wide, steeply sloping ledge in a shallow alcove, and the lower section consisting of vegetation on the cliff and around the plunge basin in the cañon floor (Fig. 1).

On 4 July 1989, the Knowles Cañon garden burned from fireworks ignited by visitors. The aboveground vegetation on the upper terrace was completely destroyed, although rootstocks of some species survived. Portions of the lower garden also burned. The fire was very hot, causing rock slabs to spall off the alcove roof. Most of the organic material in the soil of the garden was burned. A few patches of dense litter, mostly leaves and seed pods of *Cercis occidentalis*, or packrat midden material remained.

Species composition of the Knowles Cañon hanging garden was recorded in 1983 (Welsh 1984). This list (see Appendix A) represents the extent of pre-fire knowledge of the hanging garden. Photo points were established and photos taken of the garden in March 1990 by GLCA Resource Management staff. In April 1992 photos were again taken from these photo points.

Post-fire vegetation patterns of the Knowles Cañon garden in 1992 appeared to be driven by two factors: surviving rootstocks and soil moisture. Vegetation was limited to herbaceous species growing in the wettest areas, and sprouting rootstocks of trees and shrubs (primarily *C. occidentalis*, *Quercus gambelii*), and the graminoids, *Phragmites australis* and *Juncus balticus*. There were some desert annuals around the periphery of the garden (e.g., *Eriogonum cernuum*, *Bromus rubens*, and *B. tectorum*). Trees and shrubs showed vigorous regrowth, some were over 2 m tall. Herbaceous species covered approximately 10% of the alcove, but plant cover was 100% in some patches. The rest of the alcove was covered by dry, rocky soil and ash.

Nothing is known about soil communities in hanging gardens, including how changes in soil community structure may affect hanging garden plant succession. Fire generally lowers microbial biomass and respiration, the degree of reduction depends on heat and duration of the fire (Raison and McGarity 1980, Pietikainen and Fritze 1993, Fritze et al. 1993, 1994). Recovery rates also depend on how hot the fire was, amount of ash deposited, and degree of vaporization of soil carbon (Raison 1979, Fritze et al. 1994). Monitoring the soil community in the burned garden over time will provide data on soil community changes. Shifts in plant and soil communities can be

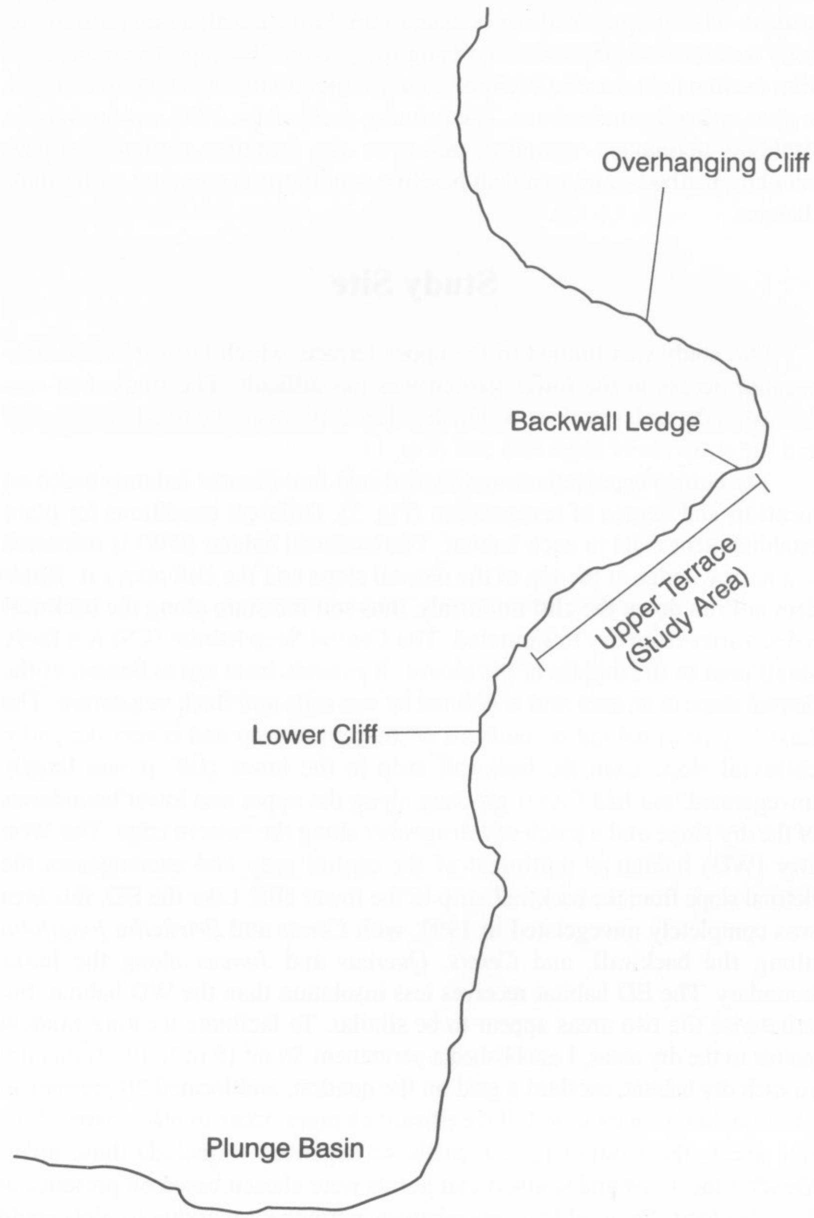

Fig. 1. Schematic drawing of the Knowles Cañon hanging garden, showing a cross-section through the cliff at the alcove and a plan view of the upper terrace.

examined for correlated patterns. Strong correlations may provide guidance for resource managers in more effective protection and restoration of hanging gardens. The fire provided the National Park Service with an opportunity to study successional processes in a hanging garden. This report presents data from the first field season (1993) of a long-term monitoring study of changes in plant and soil communities. The primary goals of the 1993 season were to establish permanent sampling points in the hanging garden, evaluate sampling methods, and establish baseline conditions to compare with future changes.

Study Site

The study was limited to the upper terrace, which burned completely, because access to the lower garden was too difficult. The study area was defined as the colluvial slope within the alcove, between the overhanging cliff and the steep lower slope and cliff (Fig. 1).

The burned upper terrace was divided into four distinct habitats based on location and degree of revegetation (Fig. 2). Different conditions for plant establishment exist in each habitat. The backwall habitat (BW) is restricted to a narrow ledge at the top of the detrital slope and the cliff above it. Water does not run down the cliff uniformly, thus soil moisture along the backwall ledge varies from dry to saturated. The Central Seep habitat (CS) is a fairly small area in the middle of the alcove. It extends from top to bottom of the detrital slope in an area and is defined by wet soils and thick vegetation. The East Dry (ED) habitat is southeast of the central seep and covers the entire colluvial slope from the backwall strip to the lower cliff. It was largely unvegetated, but had *Cercis* growing along the upper and lower boundaries of the dry slope and a patch of *Phragmites* along the eastern edge. The West Dry (WD) habitat is northwest of the central seep and encompasses the detrital slope from the backwall strip to the lower cliff. Like the ED, this area was completely unvegetated in 1993, with *Cercis* and *Brickellia longifolia* along the backwall, and *Cercis*, *Quercus* and *Juncus* along the lower boundary. The ED habitat receives less insolation than the WD habitat, but otherwise the two areas appear to be similar. To facilitate locating random points in the dry areas, I established a permanent 50 m^2 (5 m X 10 m) quadrat in each dry habitat, overlaid a grid on the quadrat, and located 20 permanent plots randomly on each grid. If significant changes occur in other parts of the dry areas, the monitoring can easily be expanded to include those areas. Quadrat locations and transect end points were chosen based on presence of large boulders that would provide relatively permanent markers so plots could be relocated even if the stakes were lost.

Only the narrow ledge of the backwall was sampled because of the difficulties of sampling an overhanging cliff. Plots were located from random numbers along a 30 m transect in the middle of the backwall. All plots are

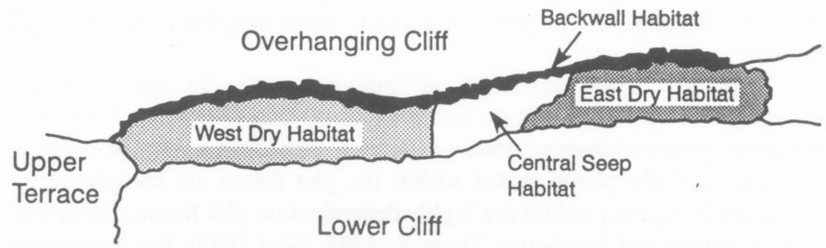

Fig. 2. The upper terrace is shaded to show locations and approximate shapes of the four habitats delineated for this study. the upper terrace shown in plan view corresponds to the upper slope delineated in the cross-section and comprises the entire study area.

permanently marked. Only herbaceous plants were recorded along the backwall: Canopy cover of trees and shrubs was not recorded because of the difficulty in trying to estimate cover above the plots in the confined space of the backwall ledge.

The CS is an irregularly shaped area in the center of the garden with mostly saturated soils, and thick grass or fern cover over most of it. Plots were established along four transects across the garden (two running downslope from the backwall and two traversing the garden roughly along contours). Only the ends of the transects are permanently marked. Plot were located from random numbers along a tape measure stretched between the transect end points.

Methods

A list of all plant species seen in and around the burned hanging garden was made in 1993 as part of a general survey of hanging garden plant community composition in GLCA by John Spence (GLCA unpublished data). Species found on the upper terrace within the defined study area were used as an estimate of the maximum number of species that might occur within each habitat for evaluating the effectiveness of the sampling protocol. Species on the cliff below the terrace, on the overhanging cliff, or found outside the alcove on the terrace were excluded.

Nested frequency (Hironaka 1985, Smith et al. 1987) and percent cover (modified from Daubenmire 1959, see below) for rock, bare ground, litter, and each plant species were estimated in 20 permanent plots in each habitat. Different sized plots were sampled in the four habitats because plant density and total area were different. The dry habitats were sampled with 0.25 m^2 plots (a total of 5 m^2). The central area was sampled with 0.1 m^2 plots (a total of 2 m^2). Twenty 0.05 m^2 plots (1 m^2 total) 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), and indicates presence/absence within each plot, providing a relative index of abundance. Only plants rooted within the plot frame are considered for frequency. 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 recommended (Hironaka 1985). Frequency values are calculated by summing the nested frequency scores across the plots for each species then dividing by the number of plots (20), and multiplying by 100. Frequency values using this method range from 0–400.

Plant cover was estimated as the percent of the entire plot frame covered by a species and recorded as a cover class: 1 = <1%, 2 = 1–5%, 3 = 5–25%, 4 = 25–50%, 5 = 50–75%, 6 = 75–95%, 7 = 95–100%. Cover was 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 (e.g., rock, bare ground, etc.) were also estimated using these cover classes.

Percent absolute cover for a species was estimated by multiplying the mid-point of each cover class by the number of plots assigned to that cover class, summing over all cover classes and dividing by the number of plots. Percent cover and frequency were calculated for each species, and for rock, litter, and bare ground in each area. Percent cover for all species was summed to obtain a total plant cover value for each area.

Species-area curves were constructed by plotting the cumulative number of species detected vs. the cumulative area sampled. This was used to evaluate the effectiveness of the sampling design in detecting species present in each habitat (Smith 1974). The number of species that occurred in plots in a habitat was divided by the total number of species observed during plot sampling and the general survey as another measure of sampling effectiveness.

The longest canopy diameter (d_1), and longest diameter (d_2) perpendicular to d_1 were measured for individual *Cercis* to estimate canopy cover of these trees. Trees with overlapping canopies were not measured because of the difficulties of determining canopy boundaries. Canopy cover (CC) was estimated for each tree as: $CC = \pi*[(d_1+d_2)/4]^2$. Canopy cover was summed and average canopy cover per tree calculated.

Twenty soil samples were collected at random points, four each from backwall and central seep habitats, and six from each dry habitat. Each soil sample was a 5 cm diameter core, 15 cm deep, except in the backwall habitat where soil depth ranged from 3 to over 15 cm. Depth of backwall samples were to bedrock, or to 15 cm. Samples were collected 13 July 1993, placed in zip lock bags, and kept on ice until shipped to the Soil Microbial Biomass

Service (SMBS), Oregon State University for analysis. Soil samples were analyzed as described in Ingham et al. (1989) and Coleman et al. (1990). Soil moisture was measured in each sample by subtracting the weight of dry soil from wet soil weight, and is reported as the weight of water that would be associated with one gram of dry soil (g H_2O g^{-1} dry soil). Active bacterial biomass and active and total fungal biomass are reported as μg microbe g^{-1} dry soil. Total nematode numbers and trophic composition of the nematode assemblage were determined, and are reported as # nematodes g^{-1} dry soil.

Results and Discussion

Vegetation

Twenty-three species, and seedlings of an unidentified dicot, were observed in the garden (Table 1). Fourteen species and the dicot seedlings occurred in or over at least one of the 80 permanent plots established (Table 2). The other nine species were uncommon and were often growing on the periphery of the study area. The species list from Welsh (1984) is reproduced in Appendix A. It is not clear from the list which species might have been present on the upper terrace before the fire. Ten of the 24 species Welsh observed in 1983 were present in the upper terrace in 1993 and are marked with an asterisk in Table 1.

The effectiveness of the sampling design varied among habitats. For the whole garden, 62.5% of species seen occurred within one or more sampling plots (15 of 24). Figure 3 shows the accumulation of species detected in sampling vs. the total area sampled (species/area curves) for each of the four habitat patches. The percent of the total number of species observed in each habitat that occurred in sample plots are indicated at the end of each curve. The number of species occurring in plots leveled off in each habitat (Fig. 3), but the curves for the central seep and backwall habitats indicate that additional species might be detected if more plots are examined. The central seep habitat was probably adequately sampled considering that most of the species not detected were rare. More of the backwall should have been sampled and the transect should be extended at both ends for future sampling. In the dry habitats, the low detection rate was a function of the plants occurring around the edges of the habitats and the random plots being located throughout the areas. Additional plots in the dry habitats would monitor a greater total area, which may improve sampling effectiveness as the dry areas begin to be revegetated.

Table 2 presents frequency and cover estimates from plots in each habitat patch. Bare ground and rock covered most of the dry areas. The CS had over 25% of the area unvegetated, and the backwall was almost 50% bare ground or rock. Litter was on the surface in almost every dry plot (frequencies of 380--WD, 395--ED), but except for patches of unburned leaf and seed pod mats,

Table 1. Species observed in the burned portion of the Knowles Cañon hanging garden, 12–13 July 1993, and the habitats in which they were growing. Species present somewhere in the garden in 1983 are marked with an asterisk (Welsh 1984).

Species	Backwall	Center seep	East dry	West dry
*Adiantum capillus-veneris**	x	x		
*Artemisia ludoviciana**			x	
*Brickellia longifolia**	x	x		x
*Bromus rubens**	x	x	x	
Carex aurea		x		
*Cercis occidentalis**	x	x	x	x
*Cirsium rydbergii**	x			
Conyza canadensis		x		
Gnaphalium chilense	x	x		
Juncus balticus	x			
Lobelia cardinalis	x	x		
Mentzelia albicaulis				x
*Mimulus eastwoodiae**	x			
Muhlenbergia andina		x		
Panicum acuminatum	x	x		x
*Phragmites australis**			x	
Polypogon monspeliensis	x	x		
Polypogon semiverticillata	x	x		
*Quercus gambelii**		x		
*Solidago sparsiflora**	x	x		
Sonchus asper		x		
Stephanomeria tenuifolia	x			
Tamarix ramosissima	x	x	x	x
Unknown dicot seedling	x	x		
Total number of species	15	17	7	9

litter was comprised of small leaf pieces. Litter covered less of the BW and CS habitats, largely because living plant material was growing over the litter.

Six species were observed on the east side and were used in species-area calculations (Table 1). *Cercis occidentalis* was rooted along the upper and lower edges of the east dry within the study area and was included in calculating species-area sampling efficiency (Fig. 3), because some trees had

Table 2. 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 frequency	Central cover	Central frequency	East dry cover	East dry frequency	West dry cover	West dry frequency
Rock	29.08	230	6.95	125	58.25	385	40.02	395
Bare ground	18.93	205	21.45	175	33.58	310	42.58	385
Litter	13.43	290	10.80	270	21.38	395	28.70	380
Adiantum capillus-veneris	41.28	255	29.63	150				
Artemisia ludoviciana					0.75	20		
Brickellia longifolia			3.88	5				
Bromus rubens			1.50	30				
Carex aurea			3.55	80				
Cercis occidentalis			0.02	15				
Conyza canadensis			0.48	40				
Gnaphalium chilense			0.18	35				
Lobelia cardinalis	0.33	55	0.15	0				
Mentzelia albicaulis					0.15	0		
Muhlenbergia andina			0.15	15				
Panicum acuminatum	0.15	20	2.02	25			0.15	0
Polypogon semiverticillata	0.35	45	28.20	280				
Tamarix ramosissima					4.88	0		
Unknown dicot seedling	0.05	10						
Total vegetation cover	42.16		70.08		5.78		0.15	

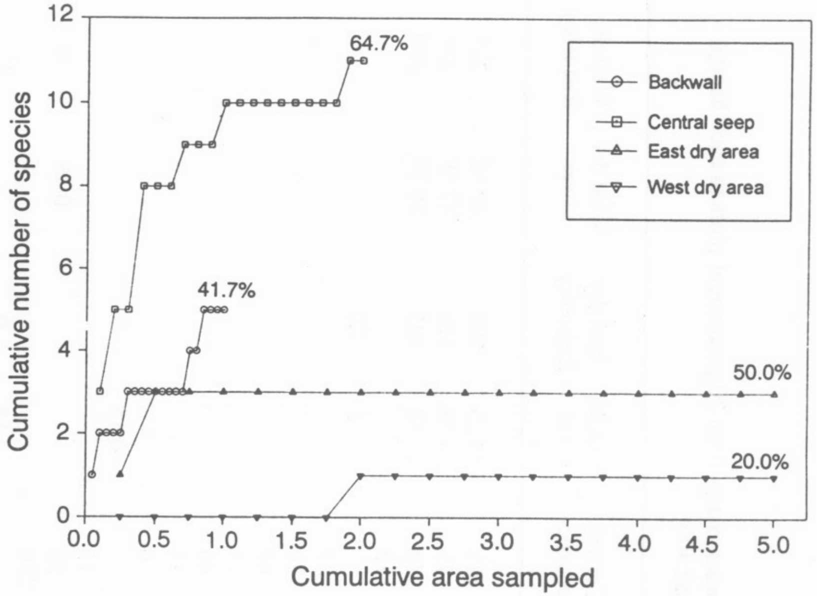

Fig. 3. Species-area curves for each habitat, showing the cumulative number of species with increasing area sampled (= # of plots). Percent of total number of species observed in each habitat that were recorded in sample plots are indicated for each curve.

canopies hanging over the dry area. Three of six possible species occurred in at least one vegetation plot. Total vegetation cover in the east dry area was estimated at 5.8% (Table 2).

Five species were found on the west side and all were located around the edges of the dry area. *Brickellia longifolia*, *Tamarix ramosissima*, and *Panicum acuminatum* occurred along the upper edge of the west study area with at least some canopy hanging over the dry area. *Juncus balticus* was found at the lower edge of the study area. *Cercis occidentalis* was present at both upper and lower edges of the west dry study area. Only one species (*P. acuminatum*) occurring within the defined west dry study area was detected in one of the 20 plots sampled (Fig. 3), and it was rooted outside the plot. Vegetation cover in the 50 m^2 sampling plot was only 0.15% (Table 2).

Sampling along the backwall was designed to monitor only herbaceous vegetation. Tree and shrub species (e.g., *Cercis*, *Brickellia*, and others) were not included in calculating the species-area relationship. Twelve herbaceous species were found along the backwall (Table 1), only five of which occurred in one or more sample plots (Fig. 3). Plants covered only 42.2% of the

backwall ledge, and 18.9% of the ledge was bare soil 4 years after the fire (Table 2), even though most of the backwall was moist. Vegetation was dominated by *Adiantum capillus-veneris* (estimated cover 41.3%, 97.9% relative plant cover), and a frequency of 255 (Table 2). The backwall habitat was very heterogenous, as indicated by high species richness and patchy vegetation cover.

The central seep was the most heavily vegetated habitat; total plant cover was estimated to be 70.1%. Much of the area had 100% vegetation and/or litter cover. Seventeen plant species were present (Table 1), 11 of which occurred in plots (Fig. 3). *Adiantum capillus-veneris* (cover 29.6%, frequency 150) and *Polypogon semiverticillata* (cover 28.2%, frequency 280) dominated central seep vegetation (Table 2).

Nine *C. occidentalis* in the west dry area, and eight in the east dry area were measured (about half the trees in each area). Total cover for the 17 trees was 84.5 m^2, average cover per tree was 4.97 $\pm$ 3.67 m^2. The total number of trees was similar in the two areas (19 trees in the west area, 17 trees in the east area), but canopy cover in the WD (61.2 m^2) was much greater than in the ED (23.2 m^2). Average canopy cover was also significantly greater in the west dry area: Mean CC_{WD} = 6.8 $\pm$ 3.71 m^2, Mean CC_{ED} = 2.9 $\pm$ 2.45 m^2 ($t_{d.f.13}$ = 2.58, P = 0.023).

Soil Community

Extremely variable soil conditions exist within and between habitats. Table 3 shows soil moisture, active and total fungal biomass, active bacterial biomass, and nematode numbers determined for each soil sample. Variability in soil parameters across the garden make it impossible to generalize about conditions beyond the immediate sample sites.

Soil Moisture

Central seep samples had more moisture than soil from the other three habitats (Table 3). In the BW, the samples above the CS were drier than samples on either side of the central area. Three ED samples and two WD samples were contaminated by water during transit. Soil moisture was not determined for these samples. The contamination of samples with water in transit did not affect estimates of soil biota, only the soil moisture measurements were erroneous (E. Ingham, Director, SMBS, personal communication).

Table 3. Results of soil community analysis for each soil sample in all habitats. Soil moisture is reported as g H_2O g^{-1} dry soil, fungal and bacterial biomass estimates are reported as µg g^{-1} dry soil, and nematodes are reported as number g^{-1} dry soil.

Site	Sample number	Field moisture[a]	Soil H_2O	Active fungal biomass	Total fungal biomass	Active bacterial biomass	Fungal algal biomass ratio	Total number nematodes	Nematode fungivores	Nematode bactivores	Nematode root feeders
Backwall	1	moist	0.24	0.67	37.67	6.42	0.104	0.90	0.33	0.39	0.17
	2	dry	0.06	0.25	46.54	1.94	0.129	0.81	0.05	0.75	0
	3	moist	0.08	0	24.42	1.84	0	0	0	0	0
	4	moist	0.15	4.96	17.86	4.10	1.21	0.28	0.14	0.14	0
Central seep	1	moist	0.56	12.32	74.29	2.32	5.31	5.1	0.14	0.14	1.17
	2	moist	0.61	18.30	132.41	1.91	9.58	0	0	0	0
	3	moist	0.48	31.14	295.74	6.29	4.95	0.18	0.06	0	0.06
	4	moist	1.02	64.86	1591.99	6.52	9.95	0.24	0	0	0.12
East dry	1	dry	b	0.32	1.21	0.06	5.33	0	0	0	0
	2	moist	0.10	0	1.91	0.13	0	0.31	0	0.28	0
	3	dry	b	0	0.59	0	c	0	0	0	0
	4	moist	0.03	4.30	112.20	0.31	13.87	0.16	0.12	0.04	0
	5	dry	b	0	0	0.05	0	0	0	0	0
	6	moist	0.16	14.61	66.59	2.47	5.92	0.05	0	0.04	0
West dry	1	dry	0.01	0	0	0.04	0	0	0	0	0
	2	moist	b	0.76	3.30	0.32	2.38	0	0	0	0
	3	moist	b	0.14	1.33	0.39	0.359	0.08	0	0.08	0
	4	dry	0.01	0	2.63	0.04	0	0	0	0	0
	5	dry	0	0	.46	0	c	0	0	0	0
	6	dry	0.01	0	1.63	0	c	0	0	0	0

[a]Field moisture: indicates whether soil sample was dry or moist when collected.
[b]Samples got wet in transit, soil moisture could not be determined.
[c]No bacteria detected in these samples, thus fungal to bacterial biomass ratios could not be calculated.

Soil Fungal Biomass

Total and active fungal biomass in soils showed the same general pattern of abundance, but total fungal biomass was more variable. Central seep samples had the greatest fungal biomass. Sample ED4, taken in a mat of *Cercis* seed pod and leaf litter, and ED6, taken in the middle of the *Phragmites* patch had very high fungal biomass estimates compared to the other four ED samples. Both were moist at the 10–15 cm depth. The highest fungal biomass value in the west dry area (WD2) also came from a sample taken in seed pod and leaf mat and was moist at 10-15 cm when collected. Active fungal biomass estimates in Knowles Cañon hanging garden soils were lower than levels reported for agricultural soils (91 to 377 µg g^{-1} dry soil, Sakamoto and Oba 1994), but were similar to prairie (0.8 µg g^{-1} dry soil) and meadow (1.2 µg g^{-1} dry soil) soils (Ingham et al. 1989). Ingham et al. (1989) found pine forest soils had higher active fungal biomass (80 µg g^{-1} dry soil) than any Knowles Cañon hanging garden soils.

Soil Bacterial Biomass

Active bacterial biomass was greatest in the central seep habitat, but differences between central and backwall areas were small (Table 3). In both dry habitats samples qualitatively classed as "moist" when collected had the highest active bacterial biomass estimates (Table 3). The backwall and central seep habitats had more bacteria than prairie and meadow soils (1 µg g^{-1} dry soil, Ingham et al. 1989), but less than lodgepole pine forest soils (10 µg g^{-1} dry soil, Ingham et al. 1989), subalpine coniferous forest soils (12 µg g^{-1} dry soil, Bissett and Parkinson 1980), or agricultural soils (82-263 µg g^{-1} dry soil, Sakamoto and Oba (1994).

Active Fungal: Active Bacterial Biomass Ratios

There was a positive relationship between active fungal biomass and active bacterial biomass across the hanging garden ($r^2 = 44.4\%$, $P = 0.0008$; Fig. 4). Three of four backwall soil samples were dominated by bacteria: fungus and bacteria in the fourth sample were similar (Table 3). The backwall area had smaller active fungal:bacterial biomass ratios than meadow, prairie or forest soils reported by Ingham et al. (1989), but differences were relatively small (meadow: 1.2; prairie: 0.8; and backwall: 0.36). In contrast, central seep soils were heavily dominated by fungi (Table 3), resembling pine forest soils (8) studied by Ingham et al. (1989). This is surprising since central seep vegetation was primarily grasses, ferns, and sedges (94% of vegetative cover, Table 2), floristically similar to meadows.

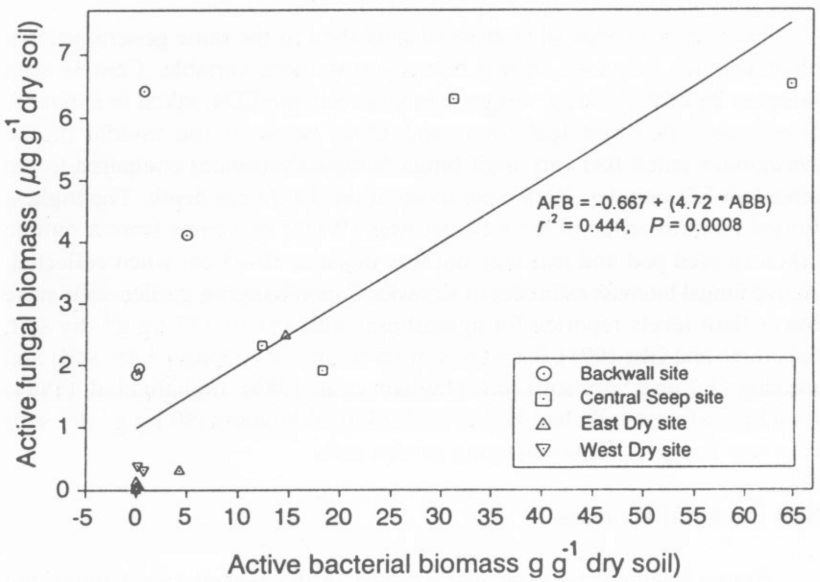

Fig. 4. Active fungal biomass (AFB) plotted against active bacterial biomass (ABB) for 20 soil samples from four study sites within the Knowles Cañon hanging garden. Linear regression line is shown.

Soil Nematodes

Estimated total nematode numbers ranged from 0 to 5.1 g^{-1} of dry soil (Table 3). All four habitats had samples with no nematodes present. The maximum found in each habitat ranged from 0.08 in WD to 5.1 g^{-1} in the central seep. Both the backwall and central seep areas had relatively high numbers. In the two dry habitats, only samples from moist soil had nematodes (Table 3). 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.

Conclusions

Plants growing in different parts of the Knowles Cañon hanging garden reflect differences in the environment of each area. Species such as *A. capillus-veneris*, *Cirsium rydbergii* and *Lobelia cardinalis*, found in the

central seep and backwall habitats, are typical hanging garden species. A few exotics that regularly invade moist habitats (e.g., *T. ramosissima*, *Polypogon semiverticillata*) were also present. The dry habitats remained largely unvegetated. Even native and introduced annuals (e.g., *Mentzelia albicaulis*, *B. rubens*, *B. tectorum*, *Salsola iberica*) have not become established on the dry sites. Revegetation in these areas has been limited to vegetative regrowth from surviving rootstocks or rhizomes along the upper and lower edges of the dry slope.

Biotic interactions are expected to become more important in the wetter habitats as succession proceeds. The backwall habitat still has large bare areas and plant distribution may reflect the patchiness of soil characteristics such as moisture or soil community composition, differential dispersal or survival of propagules, or some combination of these factors.

Moisture was present 10–15 cm below the surface in parts of the dry habitats. Both *P. australis* and *J. balticus* appear to be exploiting the subsurface water, allowing expansion into the dry habitats. The subsurface water may be capable of supporting plants, but seeds will not germinate until the surface receives water. The burned garden is in an alcove and probably receives little or no direct precipitation. Germination and seedling establishment under these conditions is probably rare. Restoration of disturbed hanging gardens may require transplanting rooted plants that can tap subsurface water as opposed to seeding the area.

There apparently was a trend towards greater microbial biomass with increasing soil moisture in the Knowles Cañon samples, but more intensive sampling is needed to determine whether soil moisture is a critical factor. Other than the abundance of root-feeding nematodes in the central seep, there was little evidence that the soil microbial community was coupled with the overlying plant community in 1993. Patterns in fungal and bacterial biomass and nematode numbers could reflect pre-fire conditions, or represent a reassortment of species following the fire. It is not clear at this time whether there is any relationship between vegetation and soil community successional processes.

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Appendix A. Plant species in the Knowles Cañon hanging garden in 1983 (Welsh 1984).

Plunge Basin

Artemisia ludoviciana
Astragalus lentiginosus
Cercis occidentalis
Baccharis salicina
Rhus trilobata
Brickellia longifolia
Sporobolus reflexa
Bromus tectorum
Cirsium rydbergii
Stephanomeria pauciflora
Bromus rubens
Erigeron bellidiastrum

Face

Epipactis giganteus
Adiantum capillus-veneris

Face (con't)

Mimulus eastwoodiae
Cirsium rydbergii
Solidago sparsiflora
Petrophytum caespitosum
Castilleja linarifolia
Primula specuicola
Lactuca sp.

Detrital Slope

Cercis occidentalis
Phragmites australis
Quercus gambelii
Calamagrostis scopulorum