The Impact of Hydromulch on Native and Non-native Species in a Post-Fire Recovery Period within Los Angeles' Griffith Park

> by Bailey Blosser and Joelle Jahng

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Joelle Jahng University of California, Los Angeles 708 Skyview Terrace Ventura, CA 93003 JoJahng@gmail.com (805) 479-7003 **Abstract** Non-native plant growth after a fire is often a common characteristic associated with a fireadapted plant community. The relationship between native and non-native plant growth after a fire and the application of erosion-control measures such as hydromulch is not well understood. In this paper, we explore the relationship between diversity, richness, and abundant growth rates in an urban wilderness park setting of native and non-native California chaparral. In the spring of 2008, we studied Los Angeles' largest urban park, Griffith Park, that experienced an 800-acre fire in May of 2007 and an application of hydromulch to 500 acres of the park. We used the Shannon diversity index and the Student *t* test to find diversity levels and to measure variation among samples in order to determine if there is a relationship between native and non-native species diversity, richness, and growth rates and the application of hydromulch. We found that plots with no or partial application of hydromulch had slightly higher indices of diversity and richness than plots without hydromulch. No relationship was apparent between hydromulch application and non-native growth dominating over native growth, however there was an overall higher frequency of non-native plant counts, specifically *Brassica nigra* (Black Mustard) and *Daucus carota* (Queen Anne's Lace) over native species plant counts regardless of hydromulch coverage.

Keywords Urban – Native & Non-native species – Hydromulch – Species richness – Species dominance – Species diversity

Introduction

Griffith Park encompasses over 4,210 acres within the eastern Santa Monica Mountain range and is situated in the densely populated region of downtown Los Angeles, making it the "largest municipal park with urban wilderness area in the United States."(Mukri 2007) Due to its arid climate, Griffith Park is characterized by a variety of natural California chaparral, oaks, mixed scrub, and walnuts. Specifically, the most abundant native and non-native species within the Parks boundary are provided in Table 1.

NATIVE	NONNATIVE
COAST LIVE OAK	PERUVIAN PEPPER TREE
Quercus agrifolia	Shinus molle
POISON OAK	GIANT REED
Toxicodendron diversilobum	Arundo donax
MULE FAT	COCKLEBUR
Baccharis salicifolia	Xanthium strumarim
CALIFORNIA BLACK WALNUT	TREE TOBACCO
Juglans californica	Nicotiana glauca
LEMONADEBERRY	EUCALYPTUS
Rhus integrifolia	Eucalpytus globulus
CALIFORNIA BLACKBERRY	PALMS
Rubus ursinus	Palmaceae
TOYON	CASTOR BEAN
Heteromeles arbutifolia	Ricinus communis
LAURAL SUMAC	BLACK MUSTARD
Rhus laurina	Brassica nigra
BIGPOD CEANOTHUS	FENNEL
Ceanothus L.	Foeniculum vulgare
CALIFORNIA SUNFLOWER	PAMPAS GRASS
Eucilia californica	Cortaderia selloana
CALIFORNIA SAGEBRUSH	PINES
Artemisia californica	Pinus californica
BLACK SAGE	AGAVE
Salvia mellifera	Agave americana
DEERWEED	ERODIUM
Lotus scoparius	Erodium gruinum
CHAMISE	QUEEN ANNE'S LACE
Adenostoma fasciculatum	Daucus carota
RATTLESNAKE WEED	MILKTHISTLE
Euphorbia albomargniata	Silibum marianum
WILD CUCUMBER	WHITE HOREHOUND
Marah fabaceus	Marrubium vulgare

Table 1 The mostcommon native and non-native plant species inGriffith Park.

Griffith Park is adapted to a Mediterranean-type climate, characteristic of Southern California in general, and has an ecosystem of mostly chaparral shrubland. In early May 2007, a fire destroyed nearly 800 acres throughout Griffith Park. Wildfires are a natural occurrence in this habitat, but this particular ecosystem "is not adapted to fire in the general sense, but rather particular fire patterns. This means that too much fire, or fire at the wrong time of the year, can completely destroy the system, allowing it to be replaced by weedy, non-native grasses." (Halsey 11:6). The primary factors driving large fires are high temperatures, low humidity, and Santa Ana winds, all of which are classified as extreme weather. Vegetation cannot withstand wildfires under these conditions, as such fires are nearly impossible to stop. The persistence of global climate change coupled with population growth has increased fire frequency, and because this directly affects our region, our ecosystem is at risk of "reaching record low vegetation moisture levels and great amounts of dead vegetation due to desiccation". (Halsey 11:6-7) Restoring habitats to their natural state post-fire is extremely important in maintaining biodiversity and a healthy ecosystem, thus in post-fire recovery planning it is important to note that "after habitat loss, invasive species have been identified as the second greatest threat to the preservation of biodiversity worldwide." (Krapp 11:12)

On May 18, 2007, the General Manager from the Department of Recreation and Parks released the following statement, "We have critical damage to the ecosystem and to allow nature to repair and heal burned areas, we need to protect and stabilize the soil." Furthermore, John Knapp, a member of the Catalina Island Conservancy, wrote the following statement in a publication titled 'Managing Invasive Plants Before and After a Fire': "Establishment of invasive plant species in wildlands can often reinforce a positive invasive plant/fire feedback loop, a cyclical cycle of one factor reinforcing another, leading to alterations in fire frequency and intensity, vegetation community diversity, structure and function, and loss of native species." Additionally, "establishment of 'fire-loving' invasive plant species, those species that benefit from fire, can exasperate the risks to native species survival and to ecosystem health." (Knapp 11:12-13) Griffith Park is in its early stages of post-fire recovery, so not only planning but also preventing the potential introduction of invasive species into the ecosystem should be a priority. After a deliberation period, a team of scientists and various fire ecology specialists determined that the application of hydromulch across the burnt hillsides would be the most suitable method for temporarily stabilizing hillsides near surrounding residential areas, eliminating the threat of land and mudslides and further topsoil erosion. This hydromulch consists of wood or other vegetative fibers mixed with a natural organic guar gum tachifier and water, and does not contain any seeds (Griffith Park Blog 2007). Because hydromulch is a relatively new post-fire recovery technique, both short-term and long-term effects of hydromulch are still unknown, making the vegetative restoration process ambiguous up to this point.

Our research is centered on hydromulch and nonnative plants because nonnative plant invasion is one of the most important issues facing land managers today. Nonnative plants can permanently alter ecosystem structure and function. Fire disturbance is considered one of the primary factors promoting nonnative invasion (Bell, 2008). When natural fire regime is altered, even highly fire-adapted plant communities can become vulnerable to competition from non natives. California has become host to about 1,000 non-native plant species, with about 100 as pest or invasive plants. These create problems within California's landscape that include: increasing the intensity, frequency, and size of wildfires, altering soil chemistry and nutrient levels, lowering water tables, displacing or out competing native plant species, degrading habitat for native animals and organisms, providing habitat for undesirable non-native animals and organisms, etc (Bell, 2008).

While this hydromulch has served its purpose to prevent further soil erosion and land/mudslides, it is a possibility that this heavy topcoat of hydromulch has averted the ability for vegetation to resprout, regrow, and ultimately restore the hillsides to their natural state. Research on this controversial and relatively unknown process of hydromulching serves to analyze whether hydromulch encourages the growth of nonnative species while inhibiting growth of native California chaparral in a post-fire recovery environment. As of early March 2008, vegetation growth was slow, making it difficult to identify the dominant vegetation types in the area, however the goal of this study is to assess whether hydromulch encourages the growth of nonnative species in the post-fire setting, and if so, how it will disturb the natural landscape, biodiversity, and ecosystem functioning within Griffith Parks 4,200 acres.

Methods

Study Site

The area of study was carried out in Los Angeles, California (34°08'S, 118°37'E); the arid Mediterranean climate combined with fire-dependent characteristics of natural chaparral and underbrush pose significant risks for brushfires. Chaparral, coastal sage scrub, and valley grassland habitats within Griffith Park and the greater southern California region are well adapted to fires and return to their natural state within a few years of a fire under normal conditions. We looked to study the return of native vegetation under abnormal conditions- which includes the application of hydromulch. The climate is Mediterranean and characterized by warm summers (average summer maximum 79.° F), mild winters (average winter minimum 67°F), and average rainfall of 17.46 inches per year, as measured from 1971-2000 (NOAA National Weather Service). The study site was on a south-facing slope located on the southeast end of Griffith Park in the Cadman Watershed, as marked in Figure 1. This area of study was chosen for its application of hydromulch as a post-fire erosion-control method due to its moderate to heavy risk of landslides, its proximity to surrounding neighborhoods, and its south-facing slope characteristics of a low abundance of vegetation. Because the study was initiated almost ten months after the fire had occurred, this site was chosen for its minimal amount of vegetation growth at the initial start of data collecting, as opposed to other (northfacing) slopes that already contained some mature plant growth. These conditions better suit the nature of this study since its purpose is to analyze the rate of *new* vegetation growth of native versus non-native plants after the application of hydromulch.

Fig. 1 Aerial view of Griffith Park

(http://www.laparks.org/dos/parks/griffithpk/gp_info.htm)



Plant Sampling

Nine circular plots were established, each with a diameter of six meters in which data was collected and analyzed. Furthermore, the plots were separated by a horizontal and vertical distance of approximately 23 meters measured between the centers of two consecutive plots. The nine plots were situated at three different elevation heights with three plots per elevation height. The plots vary in percent cover of hydromulch, three plots with full coverage, three plots with partial coverage hydromulch, and three plots with no hydromulch. One plot of each coverage category is contained within each elevation height, so that there is a total set of each full coverage hydromulch, partial coverage hydromulch, and no coverage hydromulch per gradient level. Comparing the rate of vegetation growth over time among varying

hydromulch coverage allowed us to determine the degree to which hydromulch has affected post-fire recovery of vegetation in regards to native versus non-native species.

GIS spatial data was utilized to control for a moderate burn severity area of study and GPS latitude and longitude coordinates were taken to measure exact locations of each plot along the slope. GIS data was utilized to combine GPS coordinates, burn severity, and slope elevation onto one map. Incorporating elevation into our study is significant because moisture content in soils varies along a gradient, and thus predominant vegetation species within each plot may also vary.

Five field visits were conducted every other week over a period of three months from April to June of 2008 to monitor and collect data for plant growth. Initial observations were concentrated on tracking the progression of vegetation growth within the nine plots. The counting of plants was monitored manually and data was collected for individual species count, density of plants, and total abundance. After the collection of data, analysis was conducted to differentiate plant species and monitor growth rates of native and non-native species within plots and compare their rates of growth due to varying proportions of hydromulch.

Plant Sorting and Statistical Analyses

Plant data extracted to test our hypothesis was organized into taxonomic order, counted, and quantified to measure total plant density, species diversity, and species richness. In order to test the validity of the hypothesis proposed in this study, a variety of statistical methods were utilized derived from C. Philip Wheater (2000) and the World Agroforestry Center (2008) to test species richness, species diversity, relative abundance, frequency and species dominance.

Species richness is calculated by counting the number of individual species. Although its interpretation is straightforward, calculating species richness can be difficult because identification of separate species is not always easy in the field, especially at early growth stages (pre-flowering). A value of species richness must also indicate the sample size for which species richness has been calculated, which will be expressed as the number of individuals sampled.

Relative Abundance is measured to find the variance that will show how close or far individual species are to the average species richness value as well the relative abundance of a given species within each plot.

$$S_{avg} = \frac{\sum_{i=1}^{n} S_i}{n}$$

The Shannon diversity index (H), indicates diversity levels by calculating the proportional abundances, p(i), of each species. The Shannon diversity index is calculated from the proportional abundances p(i) of each species (abundance of the species/total abundances, noted here as p(i) = n(i) / N) as:

$$H = -\sum_{i=1}^{S} p_i \ln(p_i)$$

The higher the index H, the higher level of species diversity within the plot.

We also applied our data to a paired t-test, used with one measurement variable and two nominal variables, to calculate the p-value (0.05) and test for a significance between native and non-native species in order to reject or accept the null hypothesis. The null hypothesis is that the mean difference between paired observations is zero, which indicates that the means of the groups are equal. The difference between the observations is calculated for each pair, and the mean and standard error of these differences are calculated. Dividing the mean by the standard error of the mean yields a test statistic, ts, that is t-distributed with degrees of freedom equal to one less than the number of pairs. (Sokal and Rohlf 1995) Additionally, this is a test to measure equality of variances, frequency, and association between plot coverage type and the presence of native and non-native species.

$$t = \frac{\overline{X_1} - \overline{X_2}}{S_{\overline{x_1} - \overline{x_2}}}, \qquad S_{\overline{x_1} - \overline{x_2}} = \sqrt{\frac{n_1 s_1^2 + n_2 s_2^2}{n_1 + n_2 - 2}} \sqrt{\frac{n_1 + n_2}{n_1 n_2}}$$

The equality of variance, or Anova test is used to determine the existence, or absence of a statistically significant difference between the mean value of two ore more groups of data. The purpose of an Anova test is to determine the existence, or absence of a statistically significant difference amongst several group means. Anova actually uses variance to help determine if the various means are equal or not. The formula is as follows:

$$F = \frac{nS^{*2}}{S^2}$$

Lastly, a chi-squared test was used to compare observed counts of species to the expected counts. This shows if there is enough difference significantly speaking, to rule out the 50/50 hypothesis, meaning native and non-native species are equally distributed throughout the plots.

$$X^{2} = \frac{(x_{1} - E_{1})^{2}}{E_{1}} + \frac{(x_{2} - E_{2})^{2}}{E_{2}} + \dots + \frac{(x_{k} - E_{k})^{2}}{E_{k}}$$
$$= \sum_{i=1}^{k} \frac{(x_{i} - E_{i})^{2}}{E_{i}}$$

Results

Species Richness

The species richness values for each of the nine plots over 5 separate weeks, as illustrated in Table 2, shows how species richness has increased over a time of three months. The hydromulched plots indicate an overall lack of individual species richness, however this is because these values do not take into consideration the total number of species within each plot. It is clear that the non hydromulched plots, even in the beginning stages of post-fire recovery, indicated higher values of species richness than those plots which did contain hydromulch.

	Week 1	Week 2	Week 3	Week 4	Week 5	Average
Hydro 1	4	4	4	4	4	4
Hydro 2	4	4	5	4	4	4.2
Hydro 3	1	1	1	3	3	1.8
Partial 1	3	3	5	6	7	4.8
Partial 2	6	7	7	8	9	7.4
Partial 3	5	8	8	7	7	7
Non 1	4	5	5	6	6	5.2
Non 2	5	7	6	7	5	6
Non 3	7	7	7	8	7	7.2
Average	4.3333	5.1111	5.3333	5.8889	5.7778	

Table 2. Species richness values over time.

Species Diversity

The Shannon Index of Diversity (H) represents how diverse an area is based on p, the proportion of individuals for a species, and n, the number of individual species (or abundance). Diversity is measured as a value between 0 and 1, 1 representing greater diversity while a lower H value indicates lower diversity.

The total number of species counted, for both native and nonnative plants within each plot type, was summed to find the 6 abundance values. Our initial hypothesis focused on hydromulch and its impact on the growth rates of native and nonnative species in the post-fire setting, predicting a greater growth rate for nonnative species especially in the presence of hydromulch. The proportion of native to nonnative species in the hydromulch plots is closely correlated, while the proportion of species in no hydromulch is seemingly different. This is an early indicator that hydromulch has impacted the structure of the park.

		Abundance	Proportion	Shannon Index of Diversity
Full				0.6253
Hydromulch				
•	Native	136	0.56	
	Non-native	103	0.43	
Partial				0.6809
Hydromulch				
•	Native	279	0.58	
	Non-native	198	0.415	
No				0.6876
Hydromulch				
•	Native	216	0.68	
	Non-native	101	0.31	

Table 3 Shannon Index of Diversity (H) values for all three plot types (Full, Partial, No Hydromulch)
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Even though the species richness values were low for hydromulch, the diversity index clearly indicates high diversity. Based on these two charts alone, our data indicates that there is greater diversity and species richness in no and partial hydromulch plots.

Paired T-Test

The paired t-test is appropriate here because the differences between the total number of native and nonnative species across all nine plots may or may not be normally distributed. It does not matter if they are normally distributed because this test proves whether there is significance between the number of native and nonnative species.

No. of sp		No. of species		d^2
Plot	native nonnative		Native minus non	native
1	88	70	18	324
2	14	15	-1	1
3	46	14	32	1024
4	89	44	45	2025
5	60	54	6	36
6	130	100	30	900
7	97	19	78	6084
8	60	15	45	2025
9	59	67	-8	64
			$\Sigma d = 245$	Σd^2

Table 4 Paired t test for numbers of native and nonnative species across all plots. Plots 1-3: Hydromulch,plots 4-6: Partial Hydromulch, plots 7-9: No Hydromulch

t = 3.03

	<i>t</i>	
df	P = 0.05	P = 0.01
8	2.306	3.355

At df = 8 and P = 0.05, the t table value is 2.306. Since the calculated t-value is 3.03, which is larger than the table value, this shows that there are significantly more native species than nonnative species. Independent of plot type, this test shows that there are significantly fewer nonnative species compared to the native species present, ultimately rejected our initial hypothesis. Testing for equality of variances

The test for equality of variances served to show if the number of species present in each of the three plots were significant or not. The sample size (n = 15) is constant for all plot types because the 15 samples are representative of the relative abundance of both native and nonnative plant species measured in all 9 plots, 3 hydromulched, 3 partially covered, and 3 with no hydromulch, over 5 data collections. The largest variance calculated was hydromulch at a value of $S_H = 169.99$ was then divided by the smallest variance, no hydromulch at a value of $S_N = 40.68$, and was done so because if the largest and smallest variance are not significantly different from each other then the others cannot be. The calculated F_{MAX} value equated to 4.17, and when compared to the F_{MAX} table using k = 3, the number of samples we are comparing, df = 14, the degrees of freedom (n-1) of the samples, and P = 0.05, the table value only equated to 3.54. Since the calculated value was higher than the table value at P = 0.05, the variances are significantly different and again, we must accept our null hypothesis – hydromulch does not encourage faster growth rates for nonnative species in the post-fire setting.

Hydromulch, $X_{\rm H}$	Partial Hydromulch, $X_{\rm P}$	No Hydromulch, X _N
(n = 15)	(n = 15)	(n = 15)
29	31	21
33	28	21
32	19	19
35	24	25
29	31	30
7	21	16
5 5	22	16
	23	12
6	27	17
6	44	14
3 4	50	20
	42	22
5	42	23
19	52	31
29	21	34
$\Sigma X_{ m H} = 247$	$\Sigma X_{ m P} = 477$	$\Sigma X_{\rm N} = 321$
$\Sigma X_{\rm H}^{2} = 6443$	$\Sigma X_{\rm P}^2 = 16935$	$\Sigma X_{\rm N}^{2} = 7439$
X = 16.46	X = 31.8	X = 21.4
S = 13.02	S = 11.23	S = 6.37
$S^2 = 169.69$	$S^2 = 126.17$	$S^2 = 40.68$
F _{max} = Largest variance/Smallest		
variance		
$F_{max} = 169.99/40.68$	df = 14, k = 3, and P = 0.05:	
= 4.17	$F_{\text{max}} = 3.54$	

Table 5 Equality of variances test in plots with different hydromulch coverage: calculating F_{max} the test:

Because F_{max} was higher than the table value we must accept our null hypothesis and conclude that hydromulch does not encourage the growth of non-native species.

Frequency

Table 6 Test for association between plot coverage type and presence of native and nonnative species

	Native species present	Nonnative species	Row totals
		present	
Hydromulch	136	103	239
Partial Hydromulch	279	198	477
No Hydromulch	216	101	317
Columns Total	631	402	1033

Expected value (E) = Row total x Column total / Grand total Probability Value (0-1):

(239/1033) x (631/1033) = .141 E-Value

(239/1033) x (631/1033) x 1033 = 145.99

Frequency distribution charts illustrating the relative percentages of individual species over the course of 5 samples have been illustrated in Figure 2, which can be found in the index. These frequency distribution charts clearly show trends that other statistical methods have rejected. As is illustrated in the above table the most frequent species in all five pie charts are non-native species including *Brassica nigra* (Black Mustard) and *Daucus carota* (Queen Anne's lace). An interesting relationship shows that *Brassica nigra* is the dominant species in the first three weeks but gradually decreases in frequency in the last two weeks, while *Daucus carota* gradually increases in frequency in Weeks 1 and 2 to take over *Brassica nigra's* position as the highest species frequency in the last two weeks of data collecting. The non-native dominant distribution of total plant counts over native plant counts is clearly observed here.

Table 7 Test for association between plot coverage type and presence of native and nonnative species: table of expected values (E) and (O) values. The formula for calculating E is (row total x column type)/grand total.

	Native species present	Nonnative species present	Row totals
	O Calculating E E	O Calculating E E	
Hydromulch	$136 (239 \times 631)/1033 =$	103 $(239 \times 402)/1033 = 93.008$	239
·	145.99		
Partial Hydromulch	279 (477 x 631)/1033 =	198 $(477 \times 402)/1033 = 185.62$	477
•	291.37		
Non Hydromulch	216 (317 x 631)/1033 =	101 $(317 \times 402)/1033 = 123.36$	317
•	193.63	· · · ·	
Column Totals	631	402	1033

	Native species		Nonnative species	
	present		present	
	Calculating cell X ² values	Cell X ²	Calculating cell X ² values	Cell X ²
Hydromulch	$(136-145.99)^2$.6836	$(103-93.008)^2$	1.07
Tryaromaten	/145.99	.0050	/93.008	1.07
Partial	$(279-291.37)^2$.525	$(198-185.62)^2$.825
Hydromulch	/291.37		/185.62	
No Hydromulch	$(216-193.63)^2$	2.58	$(101-123.36)^{2}/$	4.05
	/193.63		123.36	
	Total $\Sigma X^2 = .6836$ -	+ .525 + 2.58 + 1.07	+.825 + 4.05 = 9.7336	
df = (r-1)(c-1) = (3)	3-1) (2-1) = 2			
n - # of no				

Table 8 Test for association between plot coverage type and presence of native and nonnative species: calculating the test statistics (X²). Formula for X² is $(O - E)^2 / E$

r = # of rows

c = # of columns

The X² table values for P = 0.05 and P = 0.01 are 5.991 and 9.210 respectively. Because our calculated X² value is higher than the table values, accepts our null hypothesis, clearly indicating the more dominant species are native to the Griffith Park landscape.

Discussion

After a three month period of data collections and analyzing species characteristics, we found that our initial hypothesis was rejected- that hydromulch did not have a significant impact on the rate of non-native species growth over native species growth. The hydromulched plots overall had a lower individual species richness, a close correlation in proportion of native to non-native species, and a lower diversity index than partial and no hydromulch plots. The paired t-test and equality of variances test showed in fact significantly fewer non-native species compared to the native species present within sample sites, which forces us to accept our null hypothesis- hydromulch does not encourage faster growth rates for non-native species in a post-fire setting. While multiple statistical methods showed an overall inability to accept our hypothesis, there are still many significant implications to be taken from the study. Hydromulch did impact the overall species richness in comparison to non hydromulched plots- there was a lower species richness in plots with hydromulch vs. plots with no hydromulch, which could imply hydromulch affecting certain species growth over others. The frequency distribution of natives vs. non-natives over three months time showed an overall higher total frequency of non-native plants like Brassica nigra (Black mustard), and Daucus carota (Queen Anne's lace), within all plots, regardless of hydromulch proportions. An interesting relationship was found among non-natives as Brassica nigra actually decreased in frequency over the three month period as initially holding highest species frequency in Weeks 1 and 2 while *Daucus carota s* increased in frequency to replace *Brassica nigra* as having the highest species frequency by Week 5. This further shows a relation and vulnerability of natural fire regimes to competition from non-natives following a fire.

The subject of non-native plant invasion in a post-fire environment is one of the most important issues facing land managers and urban policy planners today. As shown from our study, non-native plants have the ability to alter ecosystem structure and function. The risk is thus raised for increases in intensity, frequency, and size of wildfires, the alteration of soil chemistry and nutrient levels, the displacement or competition with native plant species, the degradation of habitat for native animals and organisms, and an overall threat to biodiversity (Bell, 2008). This poses new questions for future policy implications in regards to post-fire recovery methods in an urban setting. The impacts to post-fire plant recovery due to applied hydromulch is not well understood or researched for southern California so it is difficult to quantify the effects of it on an urban wilderness region. As southern California is an arid region characteristic of particular fire patterns undergoing at present a continued drought, it is critical to develop a further understanding of the implications and consequences of various methods chosen for the recovery of wilderness ecosystems within an urban landscape. Clearly there remains a strong need for information on

hydromulch as an erosion control method on wilderness ecosystems in this region and its effects on the natural recovery process to a post-fire regime.

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Figure 2 Frequency distribution charts illustrating the relative percentages of individual species over the course of five samples.









