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CORRELATIONS BETWEEN SOIL REDNESS AND SOIL PROPERTIES THAT AFFECT NON-NATIVE ANNUAL PLANT DISTRIBUTION IN CHAPARRAL AND CALIFORNIA SAGE SCRUB

Madeline Blua

CORRELATIONS BETWEEN SOIL REDNESS AND SOIL PROPERTIES THAT AFFECT NON-NATIVE ANNUAL PLANT DISTRIBUTION IN CHAPARRAL AND CALIFORNIA SAGE SCRUB

A Thesis

Presented to the

Faculty of

California State University,

San Bernardino

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

in

Earth and Environmental Sciences

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by

Madeline Blua

June 2020

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ABSTRACT

Non-native annual plant species have degraded California Sage Scrub and chaparral and present obstacles to shrubland restoration. Red soil patches in chaparral and California Sage Scrub of San Bernardino and Riverside counties appear to support fewer non-native annual plants than non-red soils. The purpose of this study was to confirm differences in vegetation cover between red and non-red soils in shrublands and to use soil analyses to determine possible causes. During vegetation surveys conducted in April of 2018, it was confirmed that red soil sites had lower cover of non-native plants and higher cover of native plant species than the non-red soils. Greenhouse experiments with one non-native annual, *Bromus rubens*, indicated that this grass grew poorly on red soils when compared to growth on non-red soils. An initial soil analysis of several critical plant nutrients did not explain the difference in plant growth. However, an analysis of the supply rate of nutrients over a period of five months suggested that phosphate availability was more limited on red soils. Additionally, the red soils had a lower percentage of sand when compared to non-red soils. It is possible that further research may lead to potential management options that can restore native shrublands by impeding the success of non-native annual species.

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CHAPTER ONE

INTRODUCTION

Literature Review

The displacement of California Sage Scrub (CSS), an ecosystem marked by drought-deciduous shrubs, and hard chaparral, an ecosystem dominated by evergreen shrubs, by non-native annual species has been a growing issue in Southern California (Cox et al. 2014; Allen et al. 2018). The dwindling of the native habitat not only decreases the diversity of the plant communities, but also further stresses endangered animal species such as the Stephens' Kangaroo Rat and California Gnatcatcher (Minnich and Dezzani 1998). Attempts to restore these shrublands on degraded sites have led to the conclusion that the presence of non-native annual plants (e.g., non-native grasses and mustard species) presents a major obstacle to shrubland restoration (Cox and Allen 2008; Engel 2014). Casual observations that red soil patches in local shrublands appear to support fewer non-native annual plants suggest that some edaphic factor in these red soils may suppress non-native annual plant growth and assist in the persistence or recovery of shrublands (Pamela Padgett, USDA Forest Service, and Kimberlyn Williams, CSUSB, personal observations).

Chaparral and California Sage Scrub

Both chaparral and CSS are found in Mediterranean-type climate with mild, wet winters and hot, dry summers. Chaparral ecosystems can be found along low-elevation mountains (300-1,500 m) from Baja California to as far north

as Washington state (Keeley and Davis 2007). Chaparral is characterized by dense evergreen shrubs and subshrubs such as *Adenostoma fasciculatum* Hook and Arn. and species of *Ceanothus* (Keeley and Davis 2007). CSS is a plant community that thrives in the semiarid interior and along the coast of California (Rundel 2007). Most species in CSS are drought-deciduous, but evergreen species and succulents are found within it as well (Rundel 2007). *Salvia* species are common in CSS as well as *Artemisia californica* Less. and *Encelia farinosa* A. Gray ex Torr.

California's shrublands are critical, rich, and diverse habitats. Of the over four thousand native plant species in California, 24% are found in chaparral and 44% of those are considered rare species (Halsey and Keeley 2016). California has the highest mammal diversity of any state in the United States, is fourth in bird diversity, and fifth in reptile diversity; many of these animal species are inhabitants of shrublands (Halsey and Keeley 2016). Two bird species, the wrentit (*Chamaea fasciata*) and the California thrasher (*Toxostoma redivivum*) are found exclusively in chaparral and CSS (Halsey and Keeley 2016). The loss of CSS has led to listing 11 mammals, 26 birds, and 10 reptiles as either threatened or endangered (Rundel 2007).

In addition to being important habitat, these shrublands perform many important ecosystem functions. Removal of native shrublands has been shown to increase erosion on hillsides and mountain slopes (Mooney and Parsons 1973). The typical slopes of the San Gabriel mountains have rates of erosion less than

8,000 kg per hectare during pre-fire years, while the first year after a fire can have erosion rates up to 230,000 kg per hectare (Mooney and Parsons 1973).

Non-native Plants

Non-native species have been present in California for hundreds of years. Pollen records indicate that *Erodium cicutarium* (L.) Aiton, a plant native to Eurasia, was brought to California as early as the mid-17th century (Mensing and Byrne 1998). Many more European exotics were brought in the 18th century during Franciscan mission times (Minnich and Dezzani 1998). Since then, more non-native plants have arrived in multiple waves as new human populations immigrated to California (Minnich and Dezzani 1998).

Non-native annual species such as *Hirschfeldia incana* (L.) Lagr.-Fossat, *Bromus diandrus* Roth, and *Centaurea melitensis* L., among many others, have flourished and outcompeted native vegetation in a widespread manner. CSS declined by 36% between 1929 and 1998 in the Riverside-Perris basin area and most recent estimates of CSS loss is as high as 85% (Minnich and Dezzani 1998; Cox and Allen 2008). Much of this lost CSS has been replaced by non-native annuals. Current human activities such as land grading and increasing nitrogenous compounds through burning fossil fuels are further allowing the spread of these non-native plants into shrubland communities.

There are two main factors that allow for the establishment of these non-native annuals: changes in soil nutrients and a physical disturbance. Increased nutrients in the soil, especially nitrogen (N), give non-native annuals a

competitive edge (Allen 2014). N deposition from anthropogenic pollution, such as burning fossil fuels, alters the soil microorganisms and encourages the displacement of native species by non-native species that are more successful in high-N soils (Allen 2014). Although N changes are a critical factor in vegetation type conversion, displacement of shrublands by non-native species is not likely to occur rapidly without a physical disturbance such as fire (Vourlitis 2017).

Fire

Many disturbances upset the native plant community enough to allow for the invasion of non-native annual species including prolonged drought, livestock grazing, and housing development (Barbour et al. 1993; Vourlitis 2017). The most concerning change, however, are the increasing number of fires, partially due to an overall increase in the wildland-urban interface. Shorter fire intervals decrease shrublands and lead to domination by non-native plants (Syphard et al. 2019).

Infrequent fire is part of the natural disturbance regime in California's shrublands. Fires would have occurred every 30-150 years depending on the location (Keeley 2012; Halsey and Keeley 2016). These shrublands are an ignition-limited ecosystem meaning that they typically carry enough fuel for fires to burn and spread but are limited by the lack of an ignition source (Keeley 2012). Before the twentieth century, fires were most commonly started by lightning strikes and by Native Americans as a management tool (Rundel 2007; Keeley 2012). Natural fires are typically high-intensity crown fires due to very little

fuel on the soil's surface and the extent of fire is determined by wind strength (Keeley and Davis 2007; Halsey 2016).

Shrubland plants have several methods to reestablish themselves after fire. Some species resprout from unburned root crowns while native annual species which grow from the seed bank, produce an abundance of seeds the year following a fire (Hanes 1971; Rundel 2007). Many shrubland species even have seeds that require fire for germination (Hanes 1971). Most chaparral species are not long-distance seed dispersers so new vegetation that sprouts after a fire is typically from the seed bank in the soil, or from adjacent undisturbed plants (Keeley and Davis 2007). Many species in CSS have seeds that are easily dispersed by wind. The first growing season after a fire, resprouting species produce an abundance of flowers and seeds that tend to establish the second year after a fire (Malanson and Westman 1985; Rundel 2007).

As a result of the increased human population, people are now the main ignition source and fires are more frequent than would naturally occur (Keeley 2012). The short fire intervals do not allow the shrublands to regenerate and produce seeds in between burns, which allows the non-native annuals to dominate (Mooney and Parsons 1973). If fires do increase but remain near the lower limit of the natural fire-return intervals, chaparral may remain (Halsey and Keeley 2016). However, the removal of shrubs that do not resprout, such as some species of *Ceanothus*, cause the decline of a chaparral community because stands become less diverse and more susceptible to invasion by non-

native annual plants (Halsey and Keeley 2016). Non-resprouting species are also put at a disadvantage from increased fires because seed banks are depleted (Keeley and Davis 2007; Halsey and Keeley 2016). Frequent fires promote the growth of non-native annual plants that ignite more readily than shrubland species which can create a positive feedback loop (Rundel 2007). In some cases non-native species were even spread intentionally to seed burned areas as a misguided attempt to prevent erosion (Mooney and Parsons 1973; Keeley and Davis 2007).

Fires not only change vegetation, but can also lead to changes in the soil as well. As organic matter is burned off during a fire, the bulk density of the surface soil horizon may increase as the soil structure collapses (Neary et al. 2005). The depth at which these changes occur are shallow as the temperature of the soil is minimally effected at depths beyond 5 to 10 cm (Neary et al. 2005). Fire also increases soil hydrophobicity by causing the volatilization and condensation of organics which results in a decrease of water infiltration and an increase in erosion (Hubbert et al. 2006). Fires can lead to decreased cation exchange capacity and changes in plant-available nutrients; these changes are variable and depend on the temperature thresholds and soil-type. (Neary et al. 2005).

Soil Effects on Vegetation

Soil properties have many implications on vegetation distribution and growth. Physical properties such as soil texture and structure are major factors in

plant root growth and microorganism distribution. Pore space is also important to the distribution of gases in a soil; substantial pore spaces are required to supply enough oxygen to roots and microorganisms (Hausenbuiller 1985). Bulk density, the dry weight of soil within a volume, is an indicator for soil porosity and can restrict root growth at bulk densities over 1.65 g/cm^3 (Natural Resources Conservation Services 2008). The physical properties can also control the availability and movement of plant nutrients (Bronick 2004). The chemical properties also influence vegetation distribution. Plant-limiting nutrients such as nitrogen and phosphorus have varying availabilities depending on the soil. Some soils contain elements in high amounts that are toxic to many plant species (Hausenbuiller 1985). As a result of these properties and others, plant species are frequently limited by soil type.

Mafic and ultramafic soils exhibit pronounced effect on shrubland vegetation distribution. These soils have a low calcium to magnesium ratio and have high concentrations of heavy metals that are toxic to many plants when compared to soils produced from more felsic rock types. Serpentine soil is one of the most commonly cited example of an ultramafic soil. Serpentine soils contain nickel concentrations that are typically high enough to prove toxic to non-adapted plant species and are frequently inhabited by endemic species such as *Arctostaphylos viscida* ssp. *pulchella* (Howell) P.V. Wells and *Garrya congdonii* Eastw. (Motomura 2006). *Adenostoma fasciculatum* is typically sparse on the ultramafic serpentine soils but can dominate where calcium levels are higher and

on gabbro soils (Motomura 2006). Other shrubland species are known to reside on ultramafic soils although they tend to be dwarfed, less productive, and different in species composition (O'Green et al. 2007). Gabbro soils are mafic soils that also have a low calcium to magnesium ratio and high levels of heavy metals, but are less extreme than serpentine soils. Wilson et al. (2009) found during vegetation distribution studies on Pine Hill in El Dorado County, California that there were many shrubland species found only on gabbro soils: *Ceanothus roderick*i W. Knight, *Galium californicum* ssp. *sierrae* Dempster & Stebbins, *Fremontodendron decumbens* R.M. Lloyd, and *Wyethia reticulata* Greene.

Although both chaparral and CSS can be adapted to inhabit soils such as the ones described above, there are general soil characteristics that they prefer. In California, shrublands are frequently found on Mollisols, Inceptisols, and Entisols (Soil Science Division Staff 2017). Chaparral species tend to establish on rocky, shallow soils but are also found in deep, eolian sands in coastal regions (Keeley and Davis 2007). These soils vary in substrate (granitic rocks, sandstones, weathered volcanic rocks etc.) but tend to be low in nutrients and moisture, and are susceptible to erosion (Keeley and Davis 2007). Because chaparral plants are evergreen and are frequently found on shallow soils, their roots are able to grow into narrow rock fissures to ensure a consistent water supply. This makes the C and/or R horizons hydrologically important to chaparral species (Hibbert et al. 1982).

CSS is found on a wide range of soils, typically limited only by salinity, with many of the species effective at dominating disturbed sites (Rundel 2007). CSS is commonly found on granitic, sandstone, diatomaceous earth, serpentinite, and volcanic substrates (Rundel 2007). Soil type also plays a role in the likelihood that a CSS community is invaded by non-native species. A study in the Riverside-Perris Plain showed that resistance of CSS to non-native plant encroachment depended on the substrate type: between 1929 and 1998 shrub cover declined by 50% on granitoid rocks, Pauba Formation sandstone, and other Pleistocene sandstones; 30-60% on the Jurassic Bedford Canyon Formation and Santiago Peak volcanics; and only 20% on gabbro basalts (Minnich and Dezzani 1998). Because plant communities show preference for different soil types, it may be that soil color can be an indicator for soil characteristics that can hinder or help the growth of certain plant species and communities.

Soil Color

One of the first noticeable attributes of a soil is its color-- it has been used in ancient civilizations to characterize soil. Writings from 2nd century Rome indicate that color was considered an important attribute, especially as it related to agriculture (Warkentin 2006). Current soil scientists still use color to describe and characterize a soil because it is indicative of a soil's chemistry, mineralogy, and pedogenesis. Some soil orders, such as Mollisols, cannot be determined without evaluating color. Soil color can be an indicator of the texture, aeration,

soil drainage, and the location and movement of the water table (Richardson and Daniels 1993). For example, as soils become more leached they can become rubified (reddened) as a result of hematite and other iron oxide formation (Sauer 2010).

Although many factors are involved in producing soil color including organic matter (dark), salts (light/white), quartz-dominated silicates (light), reduced metals (green/gray), and oxidized metals (many various colors), this study focuses on the rubified soil in oxidized, semi-arid ecosystems of Southern California (Natural Resources Conservation Service 2000). In these environments, iron oxides are the dominant soil color factor. The most common iron oxide goethite (FeO(OH)) imparts yellowish-brown hues on a soil. Hematite (Fe_2O_3), another common iron oxide gives soil a reddish color and is likely the cause of red soils at the sites in this study (Graham and O'Green 2010). Even small amounts of hematite can have a substantial impact on color because these fine-grained minerals coat the larger grains of other minerals (Richardson and Daniels 1993). However, even the color from iron oxides can be masked by dark humic matter or manganese oxides, and these caveats need to be considered if using soil color as a proxy for mineral identification (Schwertmann 1993).

While goethite is widespread across all climatic zones, hematite typically occurs in the tropic and subtropic regions (Sposito 1989). Both are formed in aerobic conditions and are non-soluble in water. Hematite is favored over goethite in conditions with neutral pH, rapid turnover of biomass, and most

importantly higher temperatures (Schwertmann 1993). Soils of varying colors can be found adjacent to one another due to minor changes in topographic slope and position, hydrology, vegetation, and parent lithology. Soil colors tend to be brighter in well-drained sites (Richardson and Daniels 1993). For example, in Southern California redder horizons tend to occur at the top edge of hillsides while duller colored soils are found in the flat divide on top of hills and in depressions (Richardson and Daniels 1993). This is likely because weathering is more intense on lower slope positions from the additional water running from uphill; weathered sediments are transported downhill with the runoff in addition to alluvial fan activity (Graham and O'Green 2010). It is also suggested that microbes preferentially break down hematite over goethite to Fe^{2+} minerals. This process requires outside energy in the form of carbon and as a result soil organic carbon influences the distribution of iron oxides (Richardson and Daniels 1993).

Not only do iron oxides impact the color of the soil, but they also play a role in the chemical properties of a soil as well. Although to a lesser degree than soil organic matter and clays, iron oxides react effectively with other ions and influence the supply of nutrients and toxic ions to plants (Barrow 1996). The surfaces of iron oxide crystals are covered with OH functional groups that contribute substantially to the adsorption of phosphate, silicate, arsenate, and other compounds (Sposito 1989). They also frequently mask the properties of other soil particles by coating them and affecting the behavior of substances in the soil by forming aggregates (Essington 2004). Additionally, iron oxides

increase the carbon stabilization in a soil because of the substantial surface areas (50-300 m^2/g) they provide to form complexes through co-precipitation and chelation (Sposito 1989; Huang 2016).

Because iron oxides influence both soil chemistry and soil color an objective method of determining soil color and minerology is crucial. The Munsell color classification system allows the user to describe soil color in a standardized format using three properties: hue, value, and chroma. Hue is the component that is used to determine the base color of the soil (i.e. red, yellow, green, blue, purple). A soil's hue is defined by a number (from 2.5 to 10) followed by the color initial (R=red, YR= yellow-red, GY= green-yellow, etc.). The value is the lightness of the color and ranges from 2 (blacker) to 8 (whiter). Chroma is the saturation of the particular hue; the scale ranges from 2 (neutral) to 8 (saturated). All three of these numbers, in addition to the color designation, are required to define the soil's color. For example, the Munsell number 7.5 YR 4/6 means that the soil has a hue of 7.5, is yellow-red, has a lightness value of 4, and a chroma of 6. As a result of the variable parent material and climates, Southern California soils commonly have hues varying from 2.5 yellow to 10 red with an even wider variety of hues being less common (Munsell 2016). Spectrometers are another method used to identify soil color. Both portable and laboratory equipment, such as the Nix Pro Color Sensor and Konica Minolta CR-400, are capable of analyzing soil color with high accuracy (Stiglitz et al. 2016).

Soil color has been suggested as a promising approach for proxy assessment of iron oxide content, ideally conducted alongside complementary analyses of soil minerology or elemental geochemistry (Baumann 2016). Using the Munsell system, it is possible to estimate the content of hematite; Torrent et al. (1983) used the Munsell system to assign one number to a soil, called the Redness Rating, which was found to have a linear relationship with the hematite content. This method was found to be accurate across a wide range of soils found in Europe and Brazil (Torrent et al. 1983). The Redness Rating is calculated by the following equation: (10-Hue)*Chroma/Value; where hue, value, and chroma are obtained using the Munsell classification. Although it is not a direct measure of hematite content, the Redness Rating is a low-tech method that offers and initial proxy for hematite content estimates. More direct methods such as x-ray diffraction, x-ray fluorescence, scanning electron microscope, are widely used and can be improved when used in a differential method. Mössbauer spectroscopy, a form of γ-ray absorption spectroscopy proves to be a useful and non-destructive method for analyzing iron oxides (Sposito 1989).

Overview of Study

The purpose of this study was to test for associations between soil color (specifically redness) and dominance of a site by native vs non-native species, as well as to determine whether color is correlative with plant-limiting soil chemical and physical properties. Due to previous observations, it was expected that there was a relationship between soil redness and non-native species' ability

to be successful in chaparral and CSS in Riverside and San Bernardino Counties. Chapter Two focuses on the relationship between soil color and vegetation cover. The vegetation cover for both native and non-native species was measured and compared between paired red and non-red sites. Each soil color was also given a “Redness Rating” which was correlated with the vegetation cover percentage. Chapter Three focuses on germination, emergence, and growth of *Bromus rubens* (L.) Husn. *(*synonym *Bromus madritensis ssp. rubens)*, a non-native grass species that was found within most of the study sites and common throughout Southern California. Chapter Four examines the differences in physical soil characteristics analyzed between red and non-red soils. Organic matter, soil texture, and water infiltration, all of which have the potential to affect the distribution of plant species, were compared between the red and non-red soils. Chapter Five discusses various chemical soil characteristics and plant nutrients. Chapter Six concludes with a summary of all the research and possible future research.

CHAPTER TWO

RELATIONSHIPS BETWEEN VEGETATION COVER AND SOIL COLOR

Introduction

Chaparral and CSS are at risk of becoming replaced by non-native plants; however, some locations seem to be more resistant to type conversion than others. The first part of this study was designed to test the hypothesis that there are true differences in vegetation cover between red and non-red soils as had been casually observed. This chapter focuses on verifying an association between soil color and vegetation cover by answering two questions: Is there lower cover of non-native species on red soils than on non-red soils? Is there higher cover of native species on red soils than on non-red soils? To ensure that other non-soil factors did not affect results, a paired-site method was used. Each red soil site was paired with a non-red soil site of similar topographical position and location so that differences in climate, slope, aspect and potential species composition would not affect detection of vegetation differences between red and non-red soils. Further analysis of these data examined potential linear relationships between Torrent's soil Redness Rating (Torrent 1983) and cover of native and non-native species.

Methods

Site Descriptions

All study sites (Figure 1) were located in a chaparral or CSS plant community in the northern portion of Riverside County and southern portion of San Bernardino County. The city of Loma Linda, which is centrally located to all the study sites, has an average annual precipitation of 15.5 inches and an average temperature of 65.2°F from 1981 to 2010 (U.S. Climate Data).

Paired sites were chosen to compare red and non-red soils. During the summer of 2017, satellite imagery was used to find possible locations with prominently red soil. When ground truthing revealed that soils were not red, a nearby site with red soil in the same topographic position (e.g., on the same ridge) was selected, or if such a site was not available, a replacement site was selected from satellite imagery. A paired non-red site, with comparable slope and aspect, was also chosen by satellite imagery near each red site. There were two site pairs located in San Timoteo Canyon in Riverside County, and six pairs in San Bernardino County: three pairs on Badger Hill located behind California State University, San Bernardino and three pairs located off of Cloudland Truck Trail. Figure 1 shows the locations of Badger Hill, Cloudland Truck Trail, and San Timoteo Canyon.

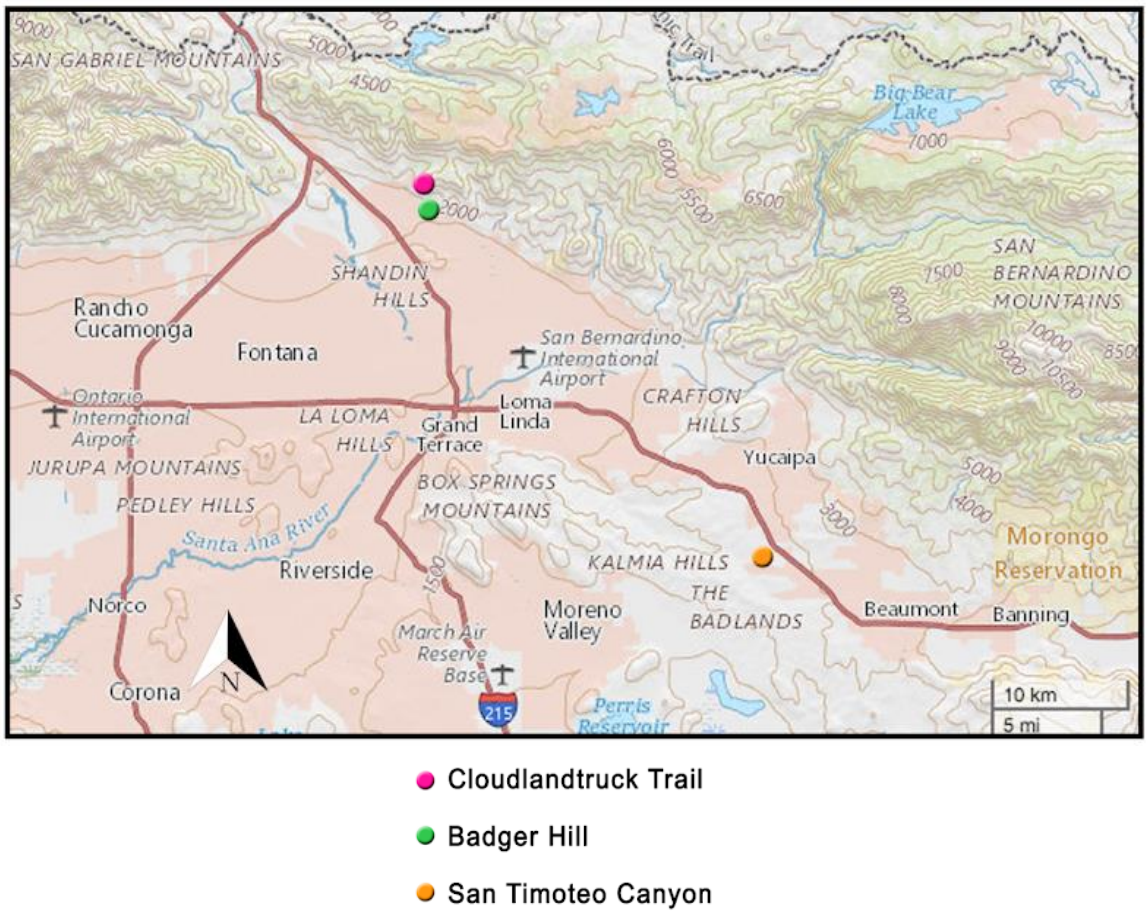


Figure 1. Map of the three locations of the study sites.

In addition to these pairs of sites, two additional sites were identified as possible examples of extremes and exceptions. When establishing the sites in San Timoteo Canyon, it was discovered that there was a location near one of the pairs that had red soil and seemed to have an abundance of non-native plants. This site was grouped in with a pair close by and is called the “Weedy Red” site. Another pair on Cloudland Truck Trail also included a third site. About ten meters above the red site was a red “bald” site that had very little vegetation and extremely red soil. This site was grouped with the nearby set and is called “Red

Bald.” Both these additional sites were the extremes for vegetation cover on red soils—one had very little vegetation growing and the other was dominated by non-native annual species. All individual site locations are shown in Figure 2.

The three study site pairs on Badger Hill were located in the San Bernardino North quadrangle. The underlying bedrock consists of Pelona Schist and the overlying soil is the Friant soil series (National Cooperative Soil Survey 2001; Dibblee and Minch 2004). The Friant series is a shallow, well-drained Mollisol formed from weathered schist or gneiss. (National Cooperative Soil Survey 2001). This soil is found on slopes between 9-75 percent with soil profiles 14 to 18 inches thick. These soils are typically 10YR 3/3 on the Munsell scale (National Cooperative Soil Survey 2001).

The sites on Cloudland Truck Trail are located within the San Bernardino North quadrangle. The underlying bedrock is composed of gneiss and marble (Dibblee and Minch 2004). The soils are classified as “Trigo family-Lithic Xerorthents” and are composed of weathered granodiorite (Soil Science Division Staff 2017). Soils in this map unit are typically 10YR 4/3 at the surface with values that increase with depth (National Cooperative Soil Survey 2001). The sites of Set 7 are located on top of a Pleistocene landslide (Qvols) that formed during the uplift of the San Bernardino Mountains.

The sites in San Timoteo Canyon were located on “badland” soil, which shows little profile development due to severely eroded, steeply sloping unconsolidated sedimentary substrates (Knecht 1971; Soil Science Division Staff

2017). The underlying bedrock consists of consolidated alluvial sediments and is located in the El Casco quadrangle (Dibblee and Minch 2003). The soil color has not been assessed by the NCSS.

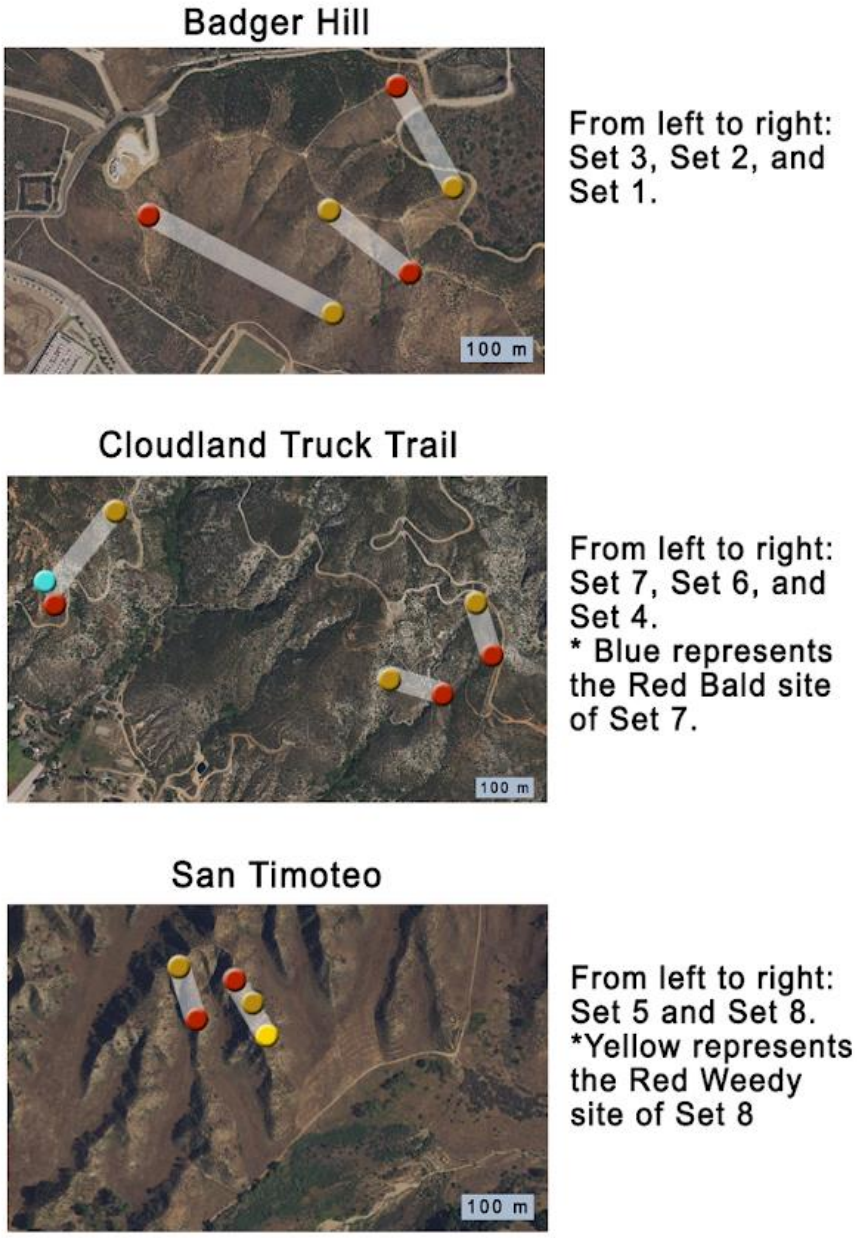


Figure 2. Map of sites at each of the three locations.

Paired sites were located over a range of topographic positions. Set 1 sites were located on southeast facing slopes and had elevations of 538 m (red) and 515 m (non-red). Set 2 sites were on southwest facing slopes and had elevations of 540 m (red) and 563 m (non-red). Set 3 sites were on east facing slopes and had elevations of 474 m (red) and 485 m (non-red). Set 4 sites were located on west facing slopes and had elevations of 738 m (red) and 771 m (non-red). Set 5 sites were on located on top of a ridge and had elevations of 671 m (red) and 684 m (non-red). Set 6 sites were on south facing slopes and had elevations of 709 m (red) and 714 m (non-red). Set 7 sites were on south facing slopes and had elevations of 654 m (red), 710 m (non-red), and 659 m (Red Bald). Set 8 sites were on northeast facing slopes and had elevations of 671 m (red), 677 m (non-red), and 680 m (Weedy Red). The GPS coordinates of each site can be found in Appendix A, Table A-1. At each site, a 5 x 5 m plot was established in the center of what was determined to be the best vegetative representation of the site, avoiding obvious anthropogenic disturbances, such as trails or old berms.

Color Characterization of Soils

After pairs were chosen, the soil color was measured using a Munsell Soil Chart to ensure that the red and non-red soils objectively differed in color. All samples were moistened and were measured outdoors using natural daylight in accordance to the Soil Survey Manual (Soil Science Division Staff 2017). Once soil samples were classified using the Munsell system, these numbers were used

to give the soil a Redness Rating number described by Torrent et al. (1983) using the equation RR=(10-H)*C/V where H is the hue, C is the chroma, and V is the value.

Preliminary Vegetation Survey

A vegetation survey was conducted early in the growing season in February of 2018 to determine whether herbaceous vegetation cover differed between red and non-red soils and whether a more thorough vegetation survey was warranted. At the time of this survey, many of the herbaceous plants were small and unidentifiable, some having only produced cotyledons, so there was no differentiation between native and non-native species. The vertical point frame sampling method was used to determine herbaceous cover (Levy and Madden 1933, Bonham 1989). The point frame was one meter long, constructed from PVC pipe with ten long pins inserted perpendicularly through holes at 10-cm intervals. Within each plot two transects were laid out oriented magnetic North/South and located one meter from the plot edge. Sampling was done by placing the pin frame perpendicular to the transects at preset random intervals and located to either the east or west of the transect in a preset random pattern. The sampling method is illustrated by Figure 3. The pin frame was set perpendicular to the ground and each pin drop was recorded as either green herbaceous vegetation or no herbaceous vegetation. Each plot contained 100 points of data.

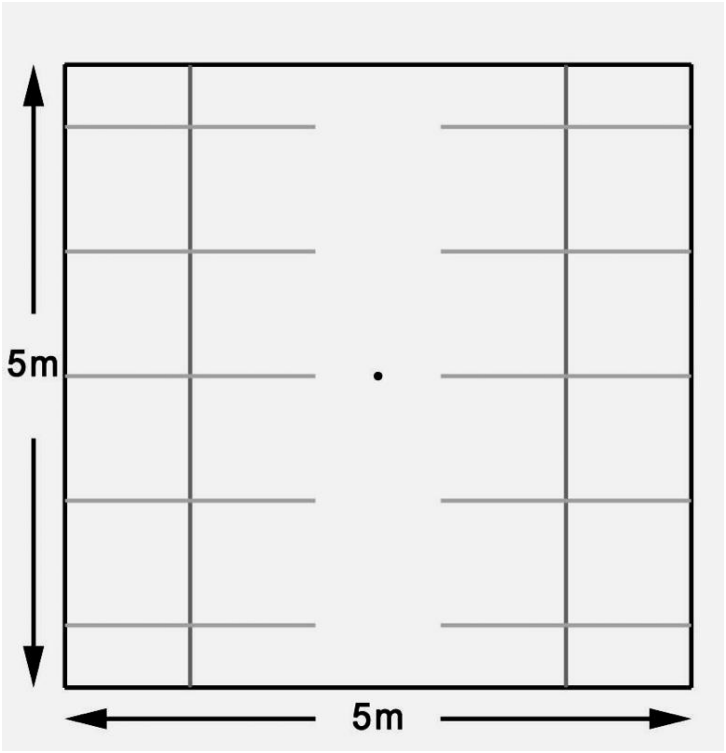


Figure 3. Sampling method used during initial vegetation survey.

To determine whether the differences in vegetation cover between each pair was consistent across all eight pairs, a sign test was used. This test was chosen because other tests give more weight to comparisons with large differences; because vegetation was sampled on different days, the differences between sets could be more variable than if all had been surveyed the same day. The Red Bald and Weedy Red were not included in the statistical analysis because this statistical test only compares paired data.

Species Identification and Percent Cover

A second vegetation survey was completed in late April 2018. Because herbaceous vegetation was more fully developed, it was possible to identify the

plant species. To capture shrub cover as well as herbaceous cover, a coarser point-intercept method with a longer pin was used. Five evenly spaced transects were established in each plot, and a pole (1.21 m long and 8 mm in diameter) was dropped through a sleeve attached to a bubble level every 25 cm along the five transects (Figure 4). Each species the pole made contact with was recorded separately for each point at all 100 points for each plot. Percent non-native cover was calculated as the number of points hitting non-native species; percent native cover was calculated similarly. A comprehensive list of species within the plot was made as well.

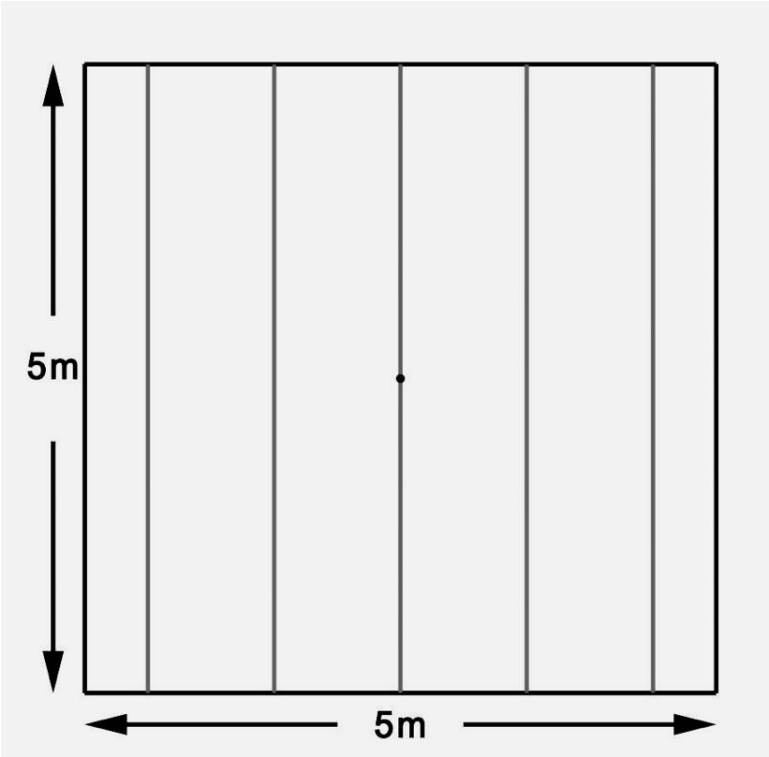


Figure 4. Sampling method used during the species identification survey.

A sign test was used to determine whether the differences in percent native and non-native cover between each pair was consistent across all eight pairs. A sign test was also used to compare native and non-native species richness across all eight pairs. The Red Bald and Weedy Red were not included in the statistical analysis.

Soil Color and Vegetation Cover

Two linear regression analyses comparing the Redness Rating and native cover and the Redness Rating and non-native cover were completed. Because they represented two “extreme” conditions, the Red Bald and Weedy Red were not included in the linear regression analyses, but were instead tested to see if they fell within the calculated 95% prediction intervals for the regressions.

Results

Soil Color

All of the red soils in the sites had hues of 5 and 7.5 yellow-red, and the less-red soils had hues of 10 yellow-red with varying values and chroma (see Figure 5). The Redness Rating for the red soils varied between 2.5 and 10 while the non-red soils all had Redness Ratings of 0.

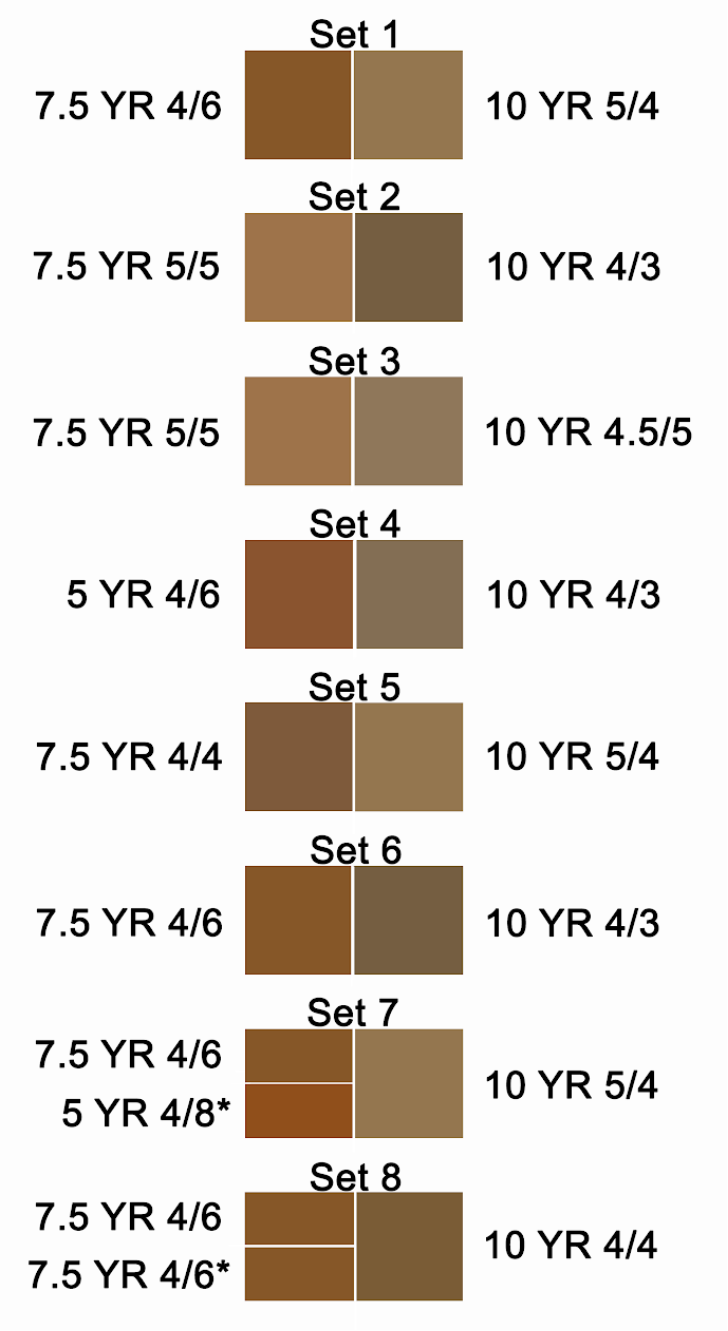


Figure 5. Soil colors at each site compared to it's pair with the Munsell color classification. Sites classified as "Red" are shown to the left, and sites classified as "Not Red" are shown to the right in each set of paired sites. The Red Bald* of Set 7 and Weedy Red* of Set 8 are also included. Colors may deviate due to variation in computer screen display and printing.

Initial Vegetation Survey

The red soil sites (not including the Red Bald and Weedy Red) had a median of 5.5% herbaceous cover during the preliminary vegetation survey in February and ranged from 0-31%. The non-red soil sites had a median of 30.0% herbaceous cover and ranged from 2-46%. The Red Bald had low herbaceous cover (1%) and the Weedy Red site had an herbaceous cover percentage in between its red and non-red site pairs (39%). Herbaceous cover percentages are shown in Figure 6.

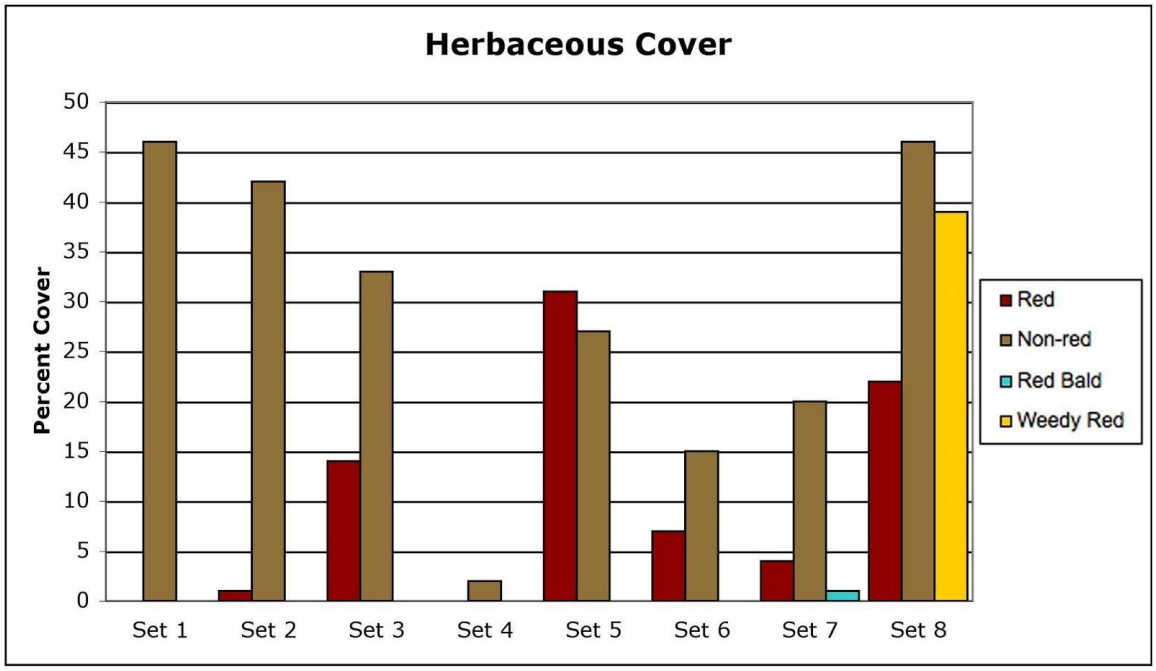


Figure 6. Percentage of herbaceous cover by paired sites.

A sign test indicated that there was lower herbaceous cover on red than on non-red soils, Z= 2.12, *p*= 0.034. Z is the test statistic and measures the

degree of agreement of the data with the null hypothesis. The p value is the level of significance.

Species Identification and Percent Cover in Spring

Overall, more native species than non-native species were found in the plots in April (Tables 1, 2, and 3). Between two and seven native species were found in each plot (Table 1).

Table 1. Number of native and non-native species identified for the red and non-red sites.

	Median	**Range**
Native Species on Red	3.5	3-7
Native Species on Non-red	3.5	2-7
Non-native Species on Red	4.5	0-8
Non-native Species on Non-red	5.5	3-9

A sign test indicated that there was no difference in native species richness between red and non-red sites, Z= 0.378, p=0.705. Another sign test indicated that there was no difference in non-native species richness between red and non-red sites, Z= 1.13, p=0.257. Tables 2 and 3 show which species were found at each site.

Table 2. Native species found at each site. R=red soil site, N=non-red soil site, W= Weedy Red site, and B=Red Bald Site.

Species	Set 1	Set 2	Set 3	Set 4	Set 5	Set 6	Set 7	Set 8
Acmispon glaber	N						R N B	
Acmispon strigosus								N
Adenostoma fasciculatum	R N	R N	R N	R	R N	R N	R B	R N
Amsincki menzesii		N			N			W
Artemesia californica	N							
Calochortus plummerae	R		R					
Ceanothus crassifolius				R		R N	R	
Croton californicus							B	
Cryptantha sp.		N	R N		R N			R N W
Cuscuta californica			R					
Eriogonum fasciculatum	R		N	R N	R N	N	R N	
Gutierrezia californica	R							
Hazardia squarrosa	R	R						
Helianthus annuus			N					
Hesperoyucca whipplei							B	
Logfia filaginoides							N	
Mirabilis californica			N					
Phacelia minor		N	N					
Rhus ovata	R							R W
Salvia apiana		N						
Salvia columburae			N					
Salvia mellifera	R	R	R	R N		R	R N	
Red Total	7	3	5	4	3	3	5	3
Non-Red Total	3	5	7	2	4	3	4	2
Red Bald							4	
Weedy Red								3

Table 3. Non-native species found at each site. R=red soil site, N=non-red soil site, W= Weedy Red site, and B=Red Bald Site.

Species	Set 1	Set 2	Set 3	Set 4	Set 5	Set 6	Set 7	Set 8
Avena barbata	N	N	N		N		N	N
Bromus diandrus	N	N	N		R N			R N W
Bromus hordeaceous								W
Bromus madritensis	R N	R N	R N	N	R	R N	R N B	R N W
Bromus tectorum	N				R			W
Centaurea melitensis	R N	R N	R		R	R	B	R W
Erodium cicutarium	R N	R N	R N		R N	R N	R B	R N W
Festuca myuros	N		R		R N		N	R N
Hirschfeldia incana	R N	R N	R N		R N	R N	R B	N W
Hypochaeris glabra	N	N	R					
Lamarckia aurea					N			
Oncosiphon piluliferum					N			
Salsola sp.					N			N W
Schismus barbatus				N				
Sisymbrium altissium		N						
Stipa coronata				N		R		
Red Total	4	4	6	0	7	5	3	5
Non-Red Total	9	7	5	3	8	3	3	6
Red Bald							4	
Weedy Red								8

A sign test indicated that non-native cover on the non-red soil was significantly higher than non-native cover on the red soils, Z= 2.82, p=0.005 (see Figure 7). A sign test indicated that the percent native cover on the red soil plots was significantly higher than the percent native cover on the less-red soils Z= 2.83, p=0.002 (Figure 8).

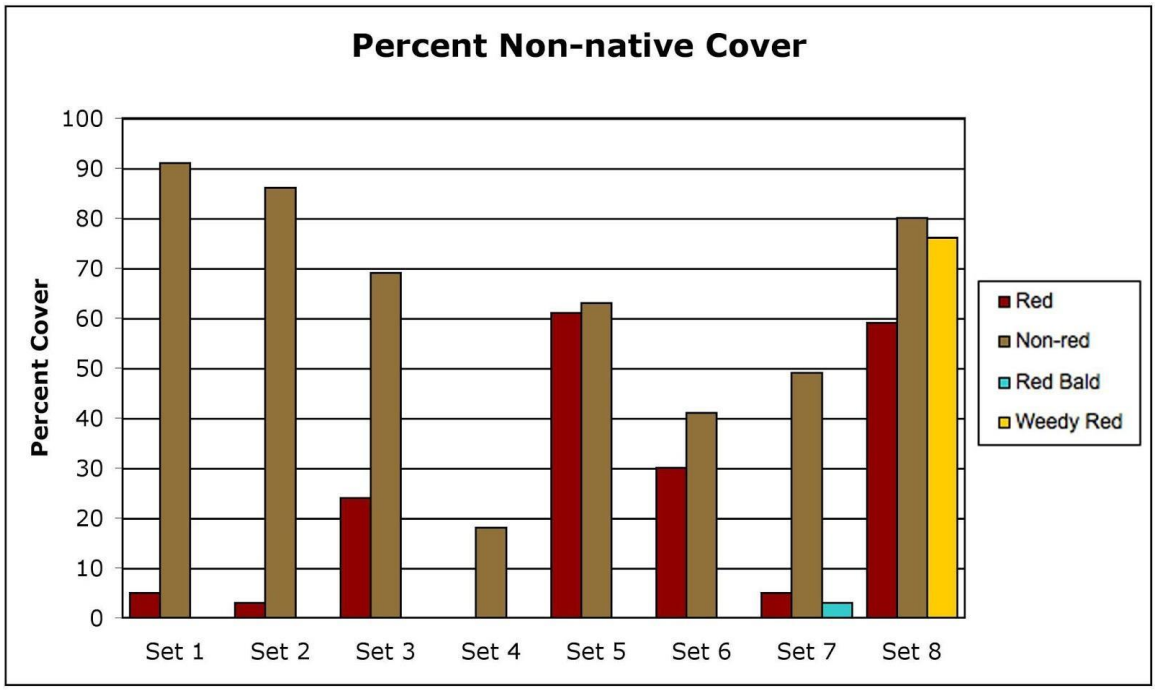


Figure 7. Percent non-native cover by paired site.

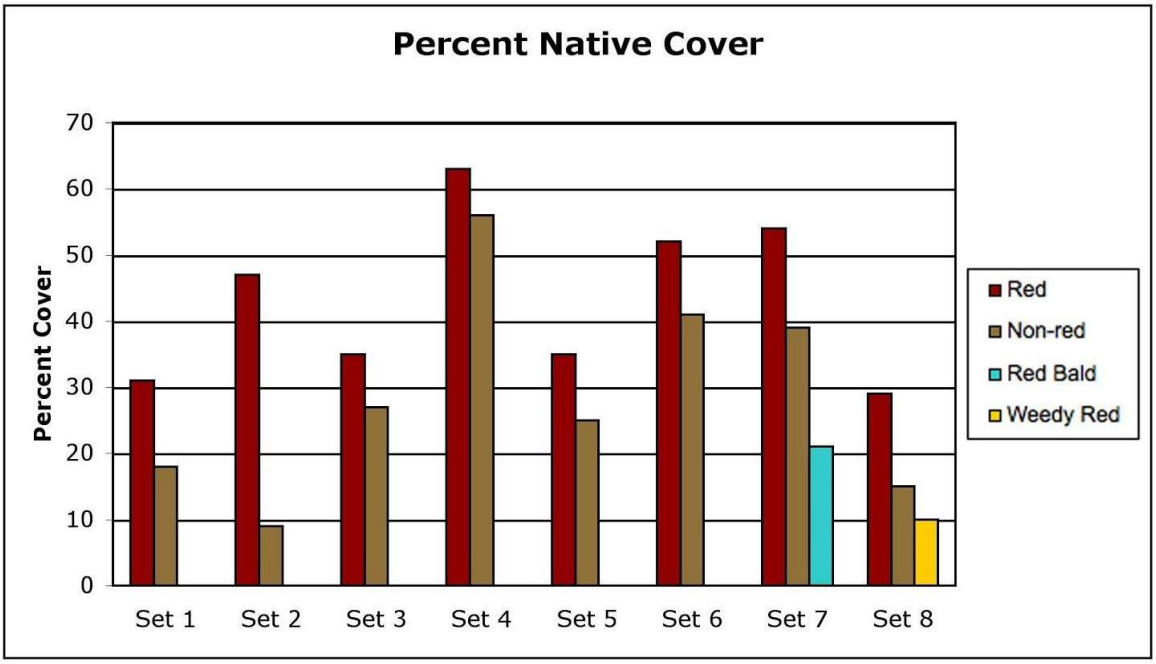


Figure 8. Percent native cover by paired site.

Soil Color and Vegetation Cover

Results of the regression analysis indicated that there was a negative relationship between the Redness Rating and non-native cover. The regression equation was *percent non-native cover = 60.0 - 9.21 * Redness Rating*, R^2 = 0.433, F(1,14) = 10.7, *p* =0.006 (Figure 9). The Red Bald and Weedy Red sites, which were not included in the regression, both fell within the 95% prediction interval. A second linear regression showed a positive correlation between the Redness Rating and native cover. The regression equation was *percent native cover = 28.3 + 4.10 * Redness Rating*, R^2 = 0.347, F(1,14) = 7.43, *p* =0.016

(Figure 10).The Red Bald and Weedy Red sites, which were not included in the regression, did not fall within the 95% prediction interval.

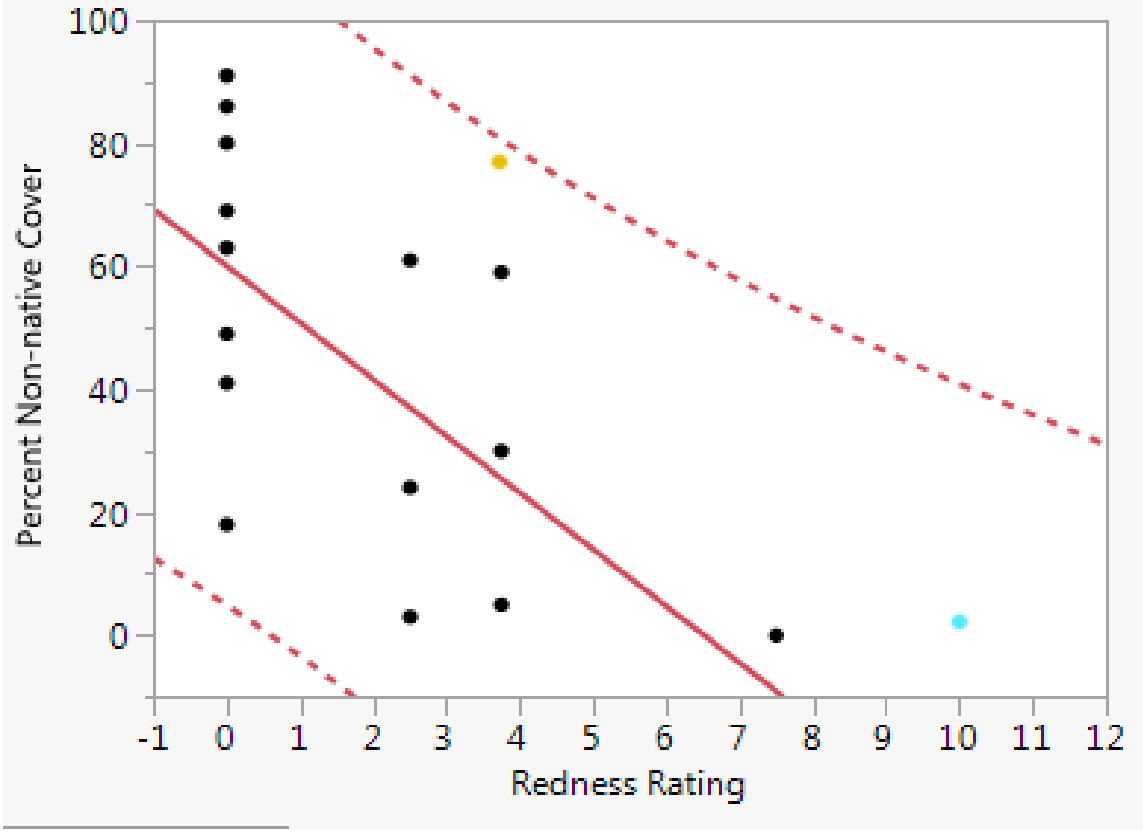


Figure 9. Linear regression of non-native cover and the Redness Rating. The Weedy Red is represented by the yellow point and the Red Bald is represented by the blue point.

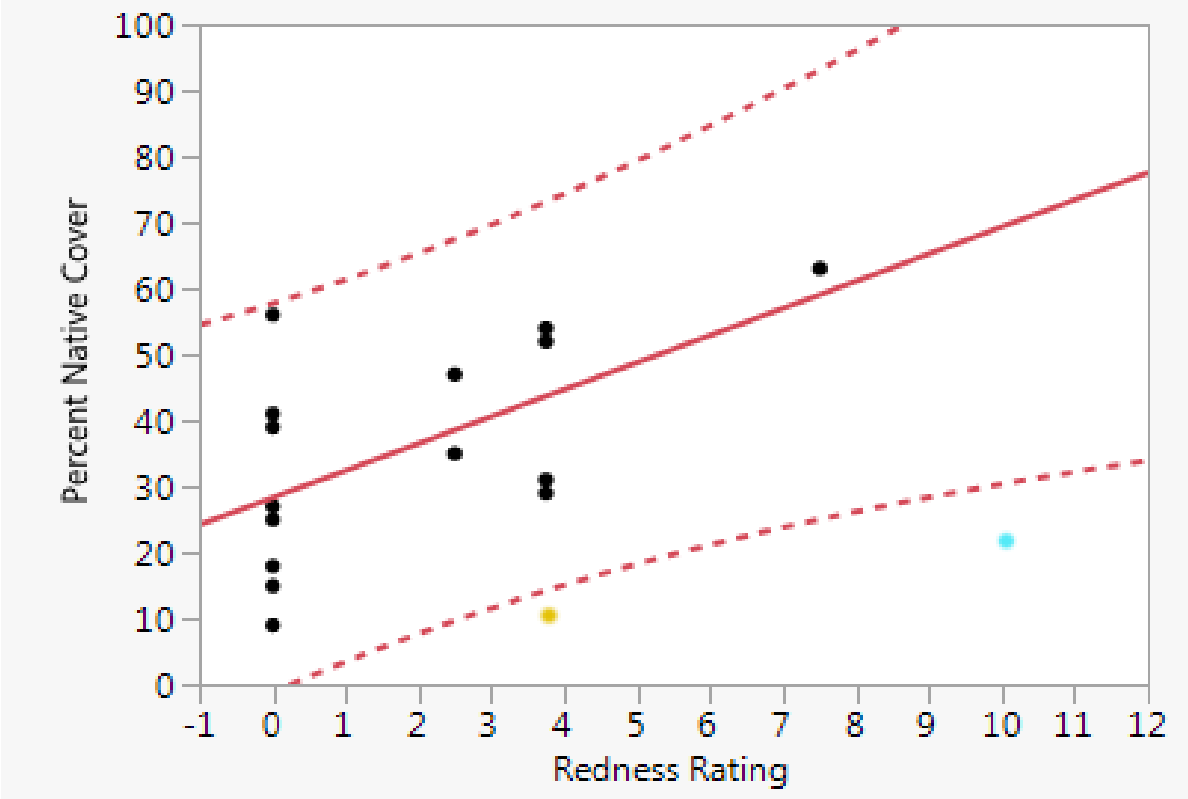


Figure 10. Linear regression of native cover and the Redness Rating. The Weedy Red is represented by the yellow point and the Red Bald is represented by the blue point.

Discussion

The original observations, that red soils appeared to support fewer non-native plants, was confirmed by the results in this study. All the sites with red soil also had a higher percent of native cover than their non-red counterparts. The Sets on Badger Hill (Set 1, 2, and 3) had the greatest differences in non-native cover between red and non-red soils. If the vegetation cover is a result of soil conditions that also affect soil color, the effect was greatest at these sites.

The sets located on Cloudland Truck Trail (Sets 4, 6, and 7) had the highest percentages of native cover of both the red and non-red sites. The non-red sites at these locations also had low percentages of non-native cover although not as low as their red pair. The Red Bald had both low native and non-native cover which indicates soil conditions that may be inhospitable to most plant species.

Both sets located in San Timoteo Canyon (Set 5 and Set 8) had only minor differences in vegetation cover between the red and non-red sites; the highest percentages of non-native cover on red soil were found at these locations. The Weedy Red site of Set 8 which had a non-native cover percentage in between its red and non-red pair, and a native cover percent lower than both its red and non-red pair.

The negative correlation between the Redness Rating of the soil and the non-native cover indicate the possibility that soil color can be an indirect measure of some edaphic factor that influences the success of non-native species in shrublands. Even the Red Bald and Weedy Red sites, which represented two extremes and apparent outliers fell within the 95% prediction intervals of the linear regression. The linear regression between native species cover and the Redness Rating showed a positive correlation. Native species cover on the Red Bald and Weedy Red sites did not fall within the 95% prediction interval for this regression analysis; they had lower cover of native vegetation than predicted from the redness of their soil. It is likely that the Red Bald was not within the 95%

prediction interval because it had very low vegetation cover all together. Although the sites in San Timoteo Canyon, including the Weedy Red site, are located within an ecological reserve, agricultural activities including livestock grazing occurred here until 2003 (Engel 2014). It may be that these activities caused a decline in native species and an increase in non-native ones resulting in the lower than expected native cover at the Weedy Red site. This historical land use may also explain the minor observed differences in non-native cover between the red and non-red soil.

Because non-native plants interfere with native plant establishment, soil color may be a useful tool for identifying areas that are less susceptible to type conversion and are easier to restore. To explore the possibility of using soil color in restoration efforts, causal relationships need to be investigated. These results point to correlations between vegetation types and soil color but do not prove that the vegetation differences are a result of soil conditions. Evidence shows that the color of a soil is based on pedogenic processes and lithological or geomorphological factors and can impact plant nutrients, but it is also feasible that the vegetation has affected the color of the soil by the addition of organic matter.

CHAPTER THREE

GERMINATION, EMERGENCE, AND GROWTH OF *BROMUS RUBENS*

Introduction

To confirm that the differences in vegetation cover were a result of varying soil conditions, this study compared germination, emergence, and growth of the non-native annual grass *Bromus rubens* (L.) Husn. *(*synonym *Bromus madritensis ssp. rubens)* on red and non-red soils. *Bromus rubens* is a winter annual grass that originates from the Mediterranean. This species was chosen because it was ubiquitous across this study's locations during the vegetation survey and is the most abundant *Bromus* species found in California's shrublands (Keeley and Davis 2007).

For a plant species to be successful, dispersed seeds must germinate; there are many methods that plants have evolved to improve germination rates. Unlike native annual species which produce dormant seeds to maintain a seed bank, *B. rubens*' seeds germinate uniformly during the cool, moist winters. As a result of this reproductive method, this species rate of germination is greatly diminished in years of drought (Salo 2004). Studies have shown that although seed germination is slightly affected by light and temperature, the substrate seeds are in contact with has a greater impact on germination, likely as a result of water availability (Zaady et al. 2003*)*.

Emergence, the plant's ability to break through the soil surface, depends on the substrate type and the depth at which the seed is buried. The relatively heavy seeds of *B. rubens* lends itself to higher rates of emergence than others such as species of *Brassica* (Abella et al. 2012). Studies have shown that *B. rubens'* emergence rate is highest when buried less than 2 cm and is not hindered by large soil particles, i.e. gravel (Abella et al. 2012). Besides large particles, emergence can be prevented by the formation of hard crusts at the soil's surface (Hadas 2004). Their large seeds not only help with emergence but also provide resources to seedlings that assist them during unfavorable conditions until they are able to become better established (DeFalco et al. 2003).

Plant growth is complex and is affected by many factors including nutrients, pH, competition, light, and water availability. Although *B. rubens* can be successful in low nutrient soils, it grows best in soils with higher contents of carbon and nitrogen (Warembourg, and Estelrich 2001; Yoshida and Allen 2004). This species is extremely competitive as it grows a large network of roots rapidly and is able to extract water at a higher rate than many other annual species (DeFalco et al. 2003).

This portion of the study considers three aspects of *B. rubens* fitness: germination, emergence, and growth. The lack of non-native annual species on the red soils could be due to unfavorable conditions during any of these three stages, so *B. rubens* fitness was analyzed at each stage. To measure differences in germination rates between red and non-red soils, *B. rubens* seeds were placed

into permeable packets and buried at the field sites. To test for differences in emergence and growth between red and non-red soils, a greenhouse study was performed using soil collected from the field.

Methods

In Situ Germination Study of *Bromus rubens*

Bromus rubens seeds were purchased from Outside Pride, an online vendor, in January of 2019. Seeds were germinated at five pairs of sites: Sets 1-3 (Badger Hill), Set 5 (San Timoteo Canyon), and Set 7 (Cloudland Truck Trail, including the Red Bald). Seeds were put into packets to prevent the loss of seeds in the field. Packets were made of a 2x3 inch pocket of nylon fabric with 25 *B. rubens* seeds placed inside. The nylon pocket was sealed and then placed inside a wire-mesh stainless steel sleeve to prevent the destruction of the fabric and to allow for easy retrieval by using a metal detector. Appendix B2 shows an image of an example packet.

During January of 2019, four packets were deployed at five pairs of sites, each one meter away from the original site marker at magnetic north, south, east, and west. After removing small vegetation and organic matter from the soil surface, each packet was buried about 2.5 cm deep to ensure that they would not easily be uncovered or disturbed by animals.

Approximately four weeks after deployment, the seed packets were retrieved. Packets were gently rinsed and opened. Seeds that had grown a root or shoot were counted as germinated and seeds lacking any signs of these were

counted as not germinated. Some seeds were missing at retrieval, so the germination rate of each packet was calculated as the germinated seeds divided by the total remaining seeds in the packet. A two-way ANOVA was used to compare germination rates.

Greenhouse Emergence and Growth Study

Soil from the same locations used in the field study was used for the greenhouse emergence and growth studies. Soil was collected from four different points at each site and homogenized in one bag. Most of the soil that was collected was within the top 5 cm but some was collected as far down as 7 cm from the surface. A number 17 screen (2.83 mm) was used to sift out rocks and other large pieces of debris. Soil was stored in plastic bags in a refrigerator for two to seven weeks until the start of the greenhouse study.

Five 10x10 cm pots were used for each site for a total of 55 pots. A 3 cm layer of sand was placed at the bottom of each pot and packed down gently. The sand was then topped with 4 cm of the collected soil and misted until field-saturation so that the soil was able to compact to a level that would be similar to field conditions; this was done over a period of a couple weeks. Thirty-five *B. rubens* seeds were placed evenly in each pot and topped with 0.5 cm of soil. Pots were watered frequently so that the soil was kept moist.

About three weeks after planting, plants were counted and the heights of each individual plant were measured to the nearest half centimeter. Plant heights

were averaged for each pot. A two-way ANOVA was used to assess differences in *B. rubens* emergence rates and height between the red and non-red soils.

About six weeks after planting, the *B. rubens* were counted and removed from the soil by emptying the pots and rinsing the soil from the roots by gently agitating them in a tub of water. The grasses were dried for five to six days at 80°C after which the dry weights were recorded. A two-way ANOVA was used to test for differences in the total biomass.

Results

In Situ Germination

Germination of *B. rubens* ranged from 28.0% to 94.4% of the seeds remaining in each packet; between 0 and 6 seeds were missing from each packet upon retrieval. Figure 11 shows the average germination of the four packets at each site.

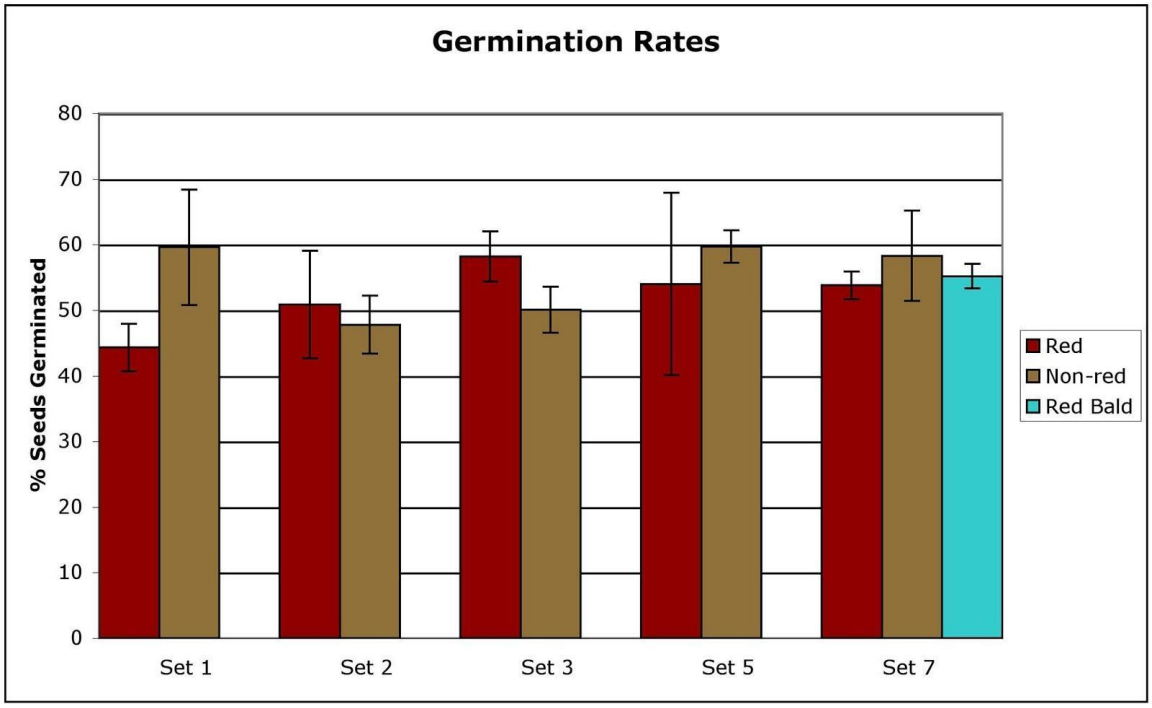


Figure 11. Average percent of germination (+/- SE, n=5) from 5 sets of field sites.

The percent of *B. rubens* germination on red soil (M=52.2, SD=14.4) was not significantly different than germination on non-red soil (M=55.1, SD=10.1). The main effect for set and the interaction of set and soil color was also not significant (Table 4).

Table 4. Statistical summary (ANOVA) of effects of soil color and site location (set) on field germination rates o*f B. rubens*.

Source	Sum of Squares	df	Mean Square	F	p-value
Set	3005	4	75.0	0.457	0.766
Soil color	82.4	1	82.4	0.502	0.484
Interaction (set*color)	638	4	159	0.972	0.437
Error	4922	30	164		
Total	5942	39			

Greenhouse Emergence

Emergence ranged from 10 to 18 plants per pot of the 35 seeds planted. Figure 12 shows the average emergence of the five pots for each site.

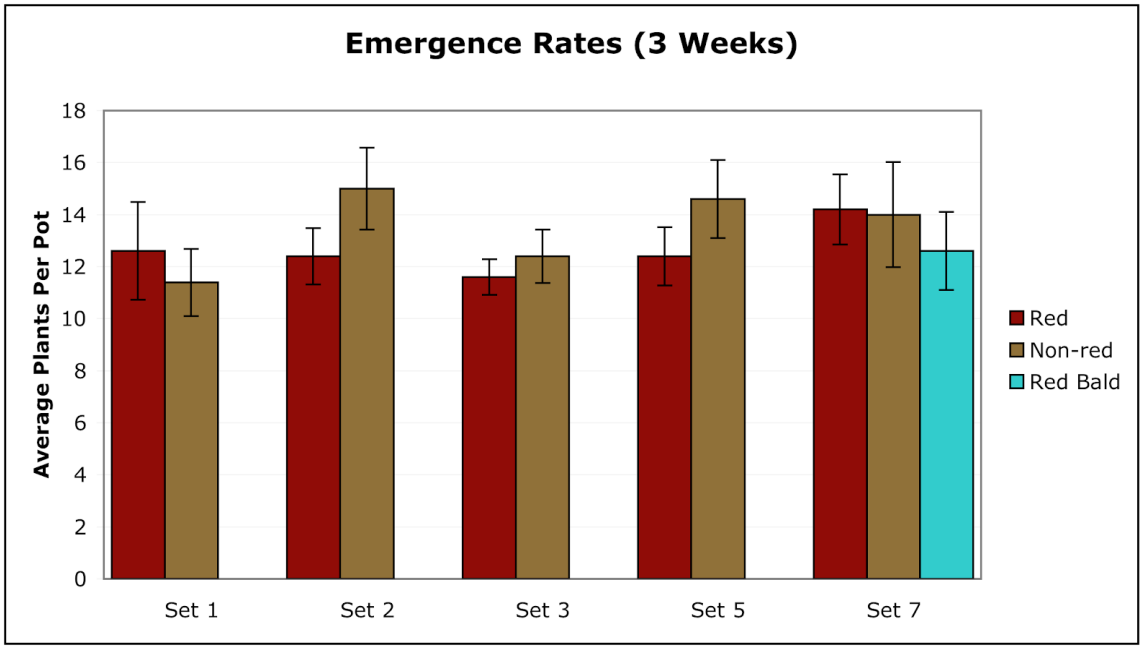


Figure 12. Average emergence (+/- SE, n=5) in pots containing red or non-red soil from 5 sets of field sites.

The percent of *B. rubens* emergence on red soil (M=12.6, SD=2.77) was not significantly different than emergence on non-red soil (M=13.5, SD=3.40). The main effect for set and the interaction of set and soil color was also not significant (Table 5).

Table 5. Statistical summary of *B. rubens* emergence at three weeks of growth in the greenhouse.

Source	Sum of Squares	df	Mean Square	F	p-value
Set	39.3	4	9.83	0.990	0.424
Soil color	8.82	1	8.82	0.888	0.351
Interaction (set*color)	25.5	4	6.37	0.642	0.636
Error	397	40	9.71		
Total	471	49			

After six weeks of growth, emergence was re-measured. Due to minor plant mortality (about 6.9%) between the three and six week measurements, the six week emergence observation was not considered in the results. This plant mortality occurred in both red and non-red soils.

Greenhouse Growth

Plant height after three weeks ranged from 0.5 cm to 7 cm. Figure 13 shows the average height in cm of the five pots for each site.

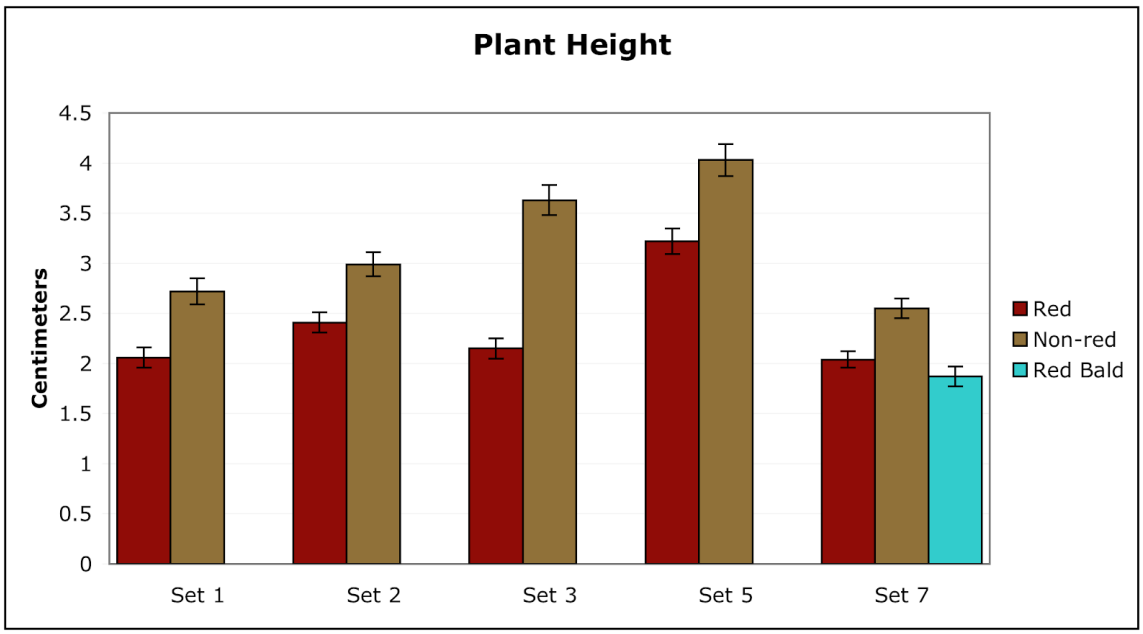


Figure 13. Average height of plants in centimeters (+/- SE, n=5) in pots containing red or non-red soil from 5 sets of field sites.

The heights of *B. rubens* on red soil (M=2.4, SD=0.6) were significantly less than the heights of *B. rubens* on non-red soil (M=3.2, SD=0.7). The main effect for set and the interaction of set and soil color was also significant (Table 6). These results indicate that the reduced plant heights on red soils from some sets are more extreme than that on red soils from other sets.

Table 6. Statistical summary of B. rubens plant height at three weeks of growth.

Source	Sum of Squares	df	Mean Square	F	p-value
Set	10.9	4	2.72	23.1	<0.0001
Soil color	8.16	1	8.16	69.2	<0.0001
Interaction (set*color)	1.66	4	0.416	3.53	0.015
Error	4.72	40	0.118		
Total	25.4	49			

After six weeks of growth, *B. rubens* biomass in each pot ranged from 0.080 g to 1.35 g. Figure 14 shows the average weight in grams per pot by site.

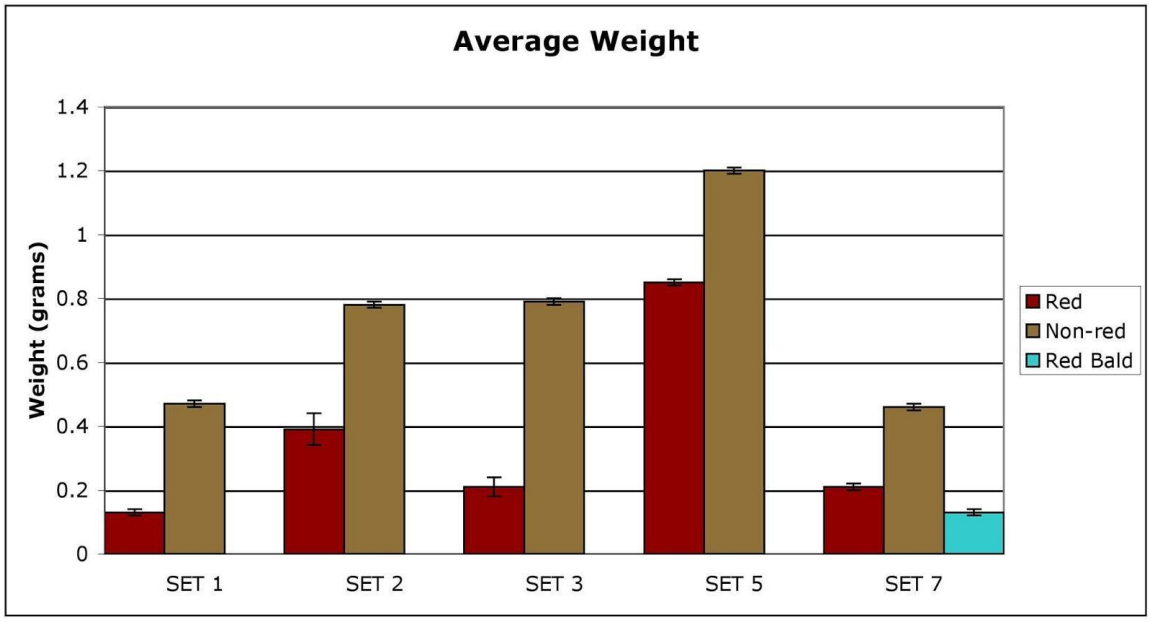


Figure 14. Average weight of plants in grams (+/- SE, n=5) in pots containing red or non-red soil from 5 sets of field sites.

Total biomass of *B. rubens* on red soil (M=0.36, SD=0.28) was significantly lower than biomass of *B. rubens* on non-red soil (M=0.74, SD=0.29). The main effect for set and the interaction of set and soil color was also

significant (Table 7). These results also reflect reduced plant mass on red soils from some sets are more extreme than that on red soils from other sets.

Table 7. Statistical summary o*f B. rubens* plant weight at six weeks of growth.

Source	Sum of Squares	df	Mean Square	F	p-value
Set	3.40	4	0.850	94.5	<0.0001
Soil color	1.84	1	1.84	204	<0.0001
Interaction (set*color)	0.154	4	0.039	4.29	0.006
Error	0.360	46	0.009		
Total	5.76	55			

Discussion

B. rubens germination did not differ among the field sites, indicating that observed differences in vegetation cover are not a result of poor germination on red soils. Because germination mainly depends upon temperature and moisture, it is unsurprising that germination rates were similar; the sites were paired so that the study would be unaffected by microclimate variation. It was expected that two sites with similar topographic position and location would be approximately the same in terms of precipitation and temperature.

Additionally, emergence rates did not differ during the greenhouse study; however, it is possible that soil disturbance during the study reduced factors that non-natives would face in the natural environment that could impede emergence.

For example, Abella et al. (2012) showed that gravel decreases the emergence rate of *B. rubens*, but during this study large grains (> 2.8 mm) were screened out. Many of the field sites seem to have formed a desert pavement (V horizon) that could hinder the emergence of plants but as a result of the methods, could not be observed in the greenhouse study. Appendix B6 is an example of the rocky surface that had formed at some of the site locations that may prevent small seedling from breaking through the soil's surface.

Another factor that could affect emergence in the field but not during our greenhouse study is the formation of a surface crust. Some soils will form a crust on the surface after periods of wetting and drying. In an attempt to recreate this effect in the greenhouse study, the pots were heavily and repeatedly watered with the soil allowed to dry in between waterings prior to planting the seeds; however, these efforts may not have been enough to form a crust.

The lower emergence rates during the greenhouse study than germination rates during the field study indicate that there are other impediments to emergence than just the formation of a desert pavement or crust. It may be that the warmer setting of the greenhouse study caused fewer seeds to germinate; *B. rubens* germinate best in cooler temperatures (Corbineau et al. 1992).

Despite germination and emergence being similar between red and non-red soils, *B. rubens* grown on non-red soil were taller at three weeks, and had more mass at six weeks than seedlings grown on red soil. As a result, the greenhouse study supports the vegetation survey findings that there was less

non-native cover on red soils than non-red soils. These findings suggest that the distribution of the non-native species is not a result of chance or the inability of non-native seeds to access the red soil sites, but rather some edaphic factor that is unfavorable to the non-native plants. Under ideal conditions (planted at a preferred soil depth, no competition with other species, plenty of sunlight, and frequent watering) the *B. rubens* planted on the red soils were still not as successful as the *B. rubens* planted on the non-red soils. It was also observed that the *B. rubens* planted on the red soils were beginning to turn brown at the tips of the leaves by the end of the growth study. Many soil factors could cause growth differences, thus, a thorough comparative soil analysis was warranted.

CHAPTER FOUR

PHYSICAL CHARACTERISTICS OF SOIL

Background

Soil is a complex system that includes both biotic and abiotic components. A soil's physical properties encompass the size and arrangement of solid particles and how those particles affect the movement or storage of gases and water. Soil includes solid, aqueous, and gaseous components. The solid phase of a soil is composed of minerals and organic matter. Minerals make up the largest fraction of a soil and are derived from parent material, weathered parent material, and soil solution precipitates. Organic matter accumulates in soil through the decay of plant debris and other organisms, and from the excrement of soil organisms. Water in varying, dynamic amounts is found absorbed to mineral surfaces and OM as well as bound to crystal lattice structures; any space not occupied by water is filled with N_2, O_2, and CO_2 gases. These components vary across landscapes, the soil profiles, and through time.

Soil Components and Formation

Pedogenic minerals form from the physical, chemical, and biological weathering of precursor parent materials. Which minerals form depends on many factors including the parent material, topography, climate, and the type and distribution of organisms (Coleman et al. 2004). Minerals are defined based on their chemical composition and structural characteristics. The elemental makeup

is highly variable but is predominantly oxygen, silicon, phosphorous, sulfur, aluminum, and alkaline earth metals (Coleman et al. 2004). The proportions and crystallographic arrangement of these elements give the mineral specific properties such as hardness, color, crystal shape, and cleavage (Hausenbuiller 1985). Oxides, phyllosilicates (sheet silicates), and amorphous silica are common secondary (pedogenic or authigenic) minerals in the arid soils of Southern California.

Soil organic matter (SOM) comes from many sources: plant litter, microorganisms, and macrofauna. Organisms break down the detritus into humic and nonhumic substances. Nonhumic substances are the biological molecules such as peptides, carbohydrates, lipids, and nucleic acids that are used as substrates by microorganisms (Essington 2004). Humic substances are recalcitrant materials with a broad range of highly complex compositions and do not fall into a particular biochemical category (Essington 2004). SOM plays an important role in the chemical and physical properties of soil. It acts as a reservoir for microorganism and plant nutrients, changes soil aggregate stability, and increases a soil's water retention capabilities (Essington 2004).

Soil water performs many critical functions within soil systems. It is required in great amounts by plants to make up for transpirational losses and is required by plants and soil organisms for cell maintenance and turgidity (Hausenbuiller 1985). It regulates chemical reactions including hydration-hydrolysis, acid-base, and oxidation-reduction reactions among many others

(Essington 2004). Soil water also controls the movement of ions and other substances as it moves vertically and laterally through the soil (Hausenbuiller 1985; Essington 2004).

Soil gases depend on depth, texture, climate, and hydrology, and fluctuate daily as well as seasonally. Oxygen within the soil can range from percentages similar ot atmospheric content to below 1% and CO_2 can range from atmospheric levels to nearly 20% (Hausenbuiller 1985). The percentages of O_2 and CO_2 are mostly influenced by microbial respiration but can also differ depending on the activities of plants and other soil organisms (Hausenbuiller 1985). Gases enter and exit a soil through two processes: mass flow and diffusion. Mass flow is the movement of gas due to changes in barometric pressure. Diffusion is the movement of individual gases within a mixture depending on the concentration (partial pressure) of that gas in the soil and atmosphere (Hausenbuiller 1985).

All of these soil components vary through the different layers of the soil profile. The soil profile is the stratified layers (horizons) that are visible with a vertical cut through the soil. A profile is divided into several master horizon types. The O horizon is the surface horizon made up of decomposing plant materials but can be thin or absent in locations with little vegetation. The V horizon may form in arid regions and tends to form via dust accumulation below a layer of crust or rock fragments. It is characterized by a platy, prismatic, or columnar structure and vesicular pores (Soil Science Division Staff 2017). More commonly, and especially outside of dusty or arid regions, an A horizon is usually the first

mineral horizon, usually but not always present below the O horizon. A horizons also contains some accumulated organic matter making the horizon a darker color than the horizons below. Organic matter also leads to leaching (eluviation) of ions and some particulate matter from the A horizon. An E horizon, when present, reflects eluvial loss of iron, clays, and aluminum. It has less organic matter than the A horizon and tends to have a coarser texture than the horizon below (Soil Science Division Staff 2017). B horizons are called the zone of accumulation because they accumulates the leached materials from the A and E horizons. C horizons are the slightly weathered, unconsolidated (typically sedimentary) parent material. Profiles formed directly on bedrock may lack a C horizon and instead exhibit an “R” horizon designation (indurated bedrock) or Cr horizon (consolidated but soft sedimentary rock). There are few pedogenic additions, losses, or transformations within C and R horizons and they represent the lowest reach of the soil profile (Fuller 1975)(Soil Science Division Staff 2017).

Soil Texture

Soil texture, an important physical property, is the ratio of sand, silt, and clay present in a soil. In the USDA system (CITE), sand ranges in mean diameter from 2.00-0.05 mm and can be further subdivided into very coarse (2.00-1.00 mm) to very fine (0.10-0.05 mm) sand classes. Silt ranges between 0.05-0.002 mm in size and clay is anything less than 0.002 mm (Hausenbuiller 1985). To put these sizes in perspective, sand particles can be seen by the unaided eye and

individual grains can be felt. Individual silt particles can be seen using an ordinary light microscope, while clay particles are often too small to see using a light microscope, but depending on the sample, some grains can be differentiated at 50-100x magnification (Hausenbuiller 1985). Clays are especially important parts of a soil because of their high surface area and their generally greater chemical reactivity relative to other sized particles. One gram of clay can have a surface area of several hundred square meters (Coleman et al. 2004). Clays play a critical role in adsorbing and desorbing organic and inorganic constituents in soil (Coleman et al. 2004).

The texture of a soil can also be correlated with the soil mineralogy. McFadden and Weldon (1987) found that the silt content of soil was closely related to the iron oxide content of a Holocene soil in the Cajon Creek, California. These increased iron oxide and silt contents may reflect eolian additions to the soil.

Soil Structure

Soil structure is the arrangement of the various soil particles into geometric patterns – aggregates-- that can be classified by shape, size, and stability (Bronick 2004, Osman 2015). Aggregation is the most fundamental result of pedogenesis: without aggregates, soil would not exist as we know it. Soil texture, clays, organic matter, and organisms all have an effect on soil structure.

Soil texture can impact the soil structure: larger soil particles such as sand typically do not form aggregates on their own while swelling clays tend to create

well-formed, dense aggregates (Hausenbuiller 1985). These clays also shrink as they dry and cause cracks to form in the soil as the volume decreases. Organic matter also directly influences the stabilization of aggregates and pores resulting in changes in bulk density and aggregate stability. Ultimately, organic matter and soil structure profoundly affect the infiltration capacity (Fischer 2015).

Clays and organic matter play a secondary role in soil aggregation through their surface charges. Cations tend to form bridges between particles or stimulate the precipitation of compounds that act as bonding agents; clays and organic matter are especially susceptible to bonding (Bronick 2004). Some cations such as Si^{4+}, Fe^{3+}, Al^{3+} and Ca^{2+} promote the precipitation of certain compounds that bond soil particles and others such as Na+ destroy the flocculation (Bronick 2004)**.**

Organisms and climatic factors also play a role in soil structure formation. Roots, fungal hyphae, and soil fauna deform and compress soil aggregates as well as fracture rock and bind soil together. The freezing-thawing or wetting-drying processes cause changes in soil structure as well (Coleman et al. 2004).

Soil Water

The availability of water in soil is a particularly important soil property that can vary dramatically with location and time. Soil water is critical because it is essential for the weathering of minerals, the decay of organic matter, and the growth of plants and soil organisms. Water also controls the movement of nutrients and the availability of oxygen in the soil. Water is held in a soil by two

forces: adhesion and cohesion. Adhesion is the force that holds water to the surface of soil particles and cohesion is the attraction of water molecules together (Hausenbuiller 1985). As a result of these forces, water can resist the downward force of gravity in small pore spaces, e.g. finer textured soils have greater matric potential.

Many factors control soil water. Climate plays a major role in water availability through the precipitation regimes and the evaporation rate. The Mediterranean climate of the Southern Californian shrublands is characterized by high intensity rain storms of short duration (Fierer 2002). Such rainstorms have high potential for surface runoff, which can lead to soil erosion and therefore nutrient loss. While climate controls the pattern and amount of precipitation, the physical properties of a soil affect the amounts that enters the soil system and how much is retained over time. Soil texture and structure are major factors in the movement and retention of fluids through regulating density, compactness, and porosity (the open space within soil) (Hausenbuiller 1985; Bronick 2004; Osman 2015). Organic matter can cause soil to become hydrophobic, increasing the amount of water that runs off the surface, but live vegetation can increase the permeability of a soil. These combined factors vary the levels of permeability, the ease at which a fluid can flow through the soil.

Infiltration and Water Retention

The infiltration capacity determines how much precipitation is absorbed into a soil and how much is left as surface runoff. The infiltration capacity is

largely due to the physical properties near the soil's surface (Fischer 2015). Pores at the soil's surface are first to receive water and provide the pathways through which the water will flow to greater depths (Hausenbuiller 1985). More water is able to infiltrate a soil that is more permeable. Water typically moves slower through fine-textured soils, but can move rapidly if the soil particles are well-aggregated and form pathways via strong macroporosity (Hausenbuiller 1985).

Determining the infiltration capacity of soil is critical in understanding how much water may be available to plants. There are two ways in which water at the soil surface moves through a soil: downward as a result of gravity or a multitude of directions through capillary action (Clothier 2001). During a rain event, little water is able to move laterally due to that space being occupied by other water molecules.

Just as important as water's ability to enter a soil is its capacity to stay in the soil. Field capacity describes the point in time at which a soil holds drops just below saturation and the downward movement of water slows as matric potential equals and exceeds gravitational potential (Hausenbuiller 1985). The amount of water held at field capacity is determined by soil texture; coarse sand will readily accept water, but the water will quickly percolate away from plant roots through the relatively large and well-connected macropores. Clays, on the other hand, contain more pore microporosity in which to store water (Fuller 1975). Due to water's cohesive and adhesive properties, water first drains or evaporates from

larger pore spaces and then progressively from the smaller ones that hold the water more tightly (Hausenbuiller 1985). Fine-textured soils have a greater ability to retain water as a result of the greater total pore space and the higher proportion of small pores (greater matric potential) (Hausenbuiller 1985).

Purpose of Study

Because correlations between soil color and vegetation cover have been established in the previous chapters, this part of the study examined the physical differences between red and non-red soils to illuminate possible mechanisms for the observed differences in vegetation. This research was centered on three variables: organic matter content, soil texture, and water infiltration.

This study considered differences in organic matter content because it is possible that a high percentage of organic matter can mask the redness of a soil and also change the amount of plant nutrients within the soil. If the organic matter content does not vary between the red and non-red soils, it can be assumed that it does not play an important role in the color of the non-red soils. Organic matter also plays vital roles in a soil's nutrient content and availability, water storage and availability, and aggregate stability and bulk density. Another variable, soil texture, could affect vegetation growth by influencing root growth, nutrient availability, and water availability. Finally, because plants differ in their water requirements, it is possible that differences in water infiltration between red and non-red soils were the cause of vegetation differences.

Methods

For analyses of the soil organic matter content and texture, about 700 g of soil was collected from three points on each plot in January of 2019 and combined into a plastic bag. After removing large sticks, leaves, and rocks from the top of the soil, soil was collected from 0-5 cm below the surface. Large rocks were removed from the samples by hand. Soils were sieved through a 2 mm screen and oven-dried at 105°C for 16 hours as standard practice described in the Soil Survey Laboratory Methods Manual (2004).

Soil Organic Matter

Approximately 10 grams of oven-dried soil samples were weighed, and then placed in a muffle furnace at 400°C for 6.5 hours to remove organic matter (loss on ignition, LOI) after which samples were weighed again. The mass lost in the muffle furnace is assumed to be the soils total organic matter content (Soil Survey Staff 2014). The percent of organic matter was calculated. A Wilcoxon signed-rank test was used to compare differences in organic matter content between the red and non-red soils.

Soil Texture

Soil texture was determined using the hydrometer method (Gee and Bauder 1986). Approximately 65 grams of each dried soil sample was soaked in a 1 M solution of sodium hexametaphosphate for 18 hours and then disaggregated in a blender for 5 minutes. Each sample was placed in a 1 L graduated cylinder and mixed into the full water column with a plunger. A

hydrometer was used to measure fluid density at 45 seconds and 9 hours during settling (Gee and Bauder, 1986). A Wilcoxon signed-rank test was used to compare the percentage of sand between red and non-red soils. Another Wilcoxon signed-rank test was used to compare the clay content of red and non-red soils.

Infiltration Rates

Accurate infiltration rate measurements must eliminate the lateral water movement due to capillarity. The double ring infiltrometer serves this need for measuring infiltration rate. The buffered rings, one ring inside another, are both filled with water. The water in the outer ring minimizes the lateral movement of water from the inner ring Clothier 2001).

The infiltrometer used in this study was a Turf-Tec double ring infiltrometer (Turf-Tec International, Tallahassee, Florida, USA). Infiltration rates were taken during the summer of 2018 to avoid the possibility of high moisture levels in the soil and were measured three times for each site. Each of the three measurements were taken within the previously established plots. The infiltrometer was worked into the soil until the lip of the outer ring was flush with the ground's surface. The outer and inner rings were quickly filled with water so that the inner ring had 4 inches of water and a timer was started. The timer was stopped when there was only 1 inch of water remaining in the inner ring. Because the infiltration rates were highly variable within each site, the median value was taken as the likely best estimate of infiltration across that site. A

Wilcoxon signed-rank test was then used to compare infiltration estimates on the paired red and non-red sites.

Results

Soil Organic Matter

A Wilcoxon signed-rank test showed that there was not a significant difference in the organic matter content for red (Median=4.56, range=2.68-6.32) and non-red (Median=4.35, range=2.51-5.46) soils; W= 7, p> 0.05 (Figure 15).

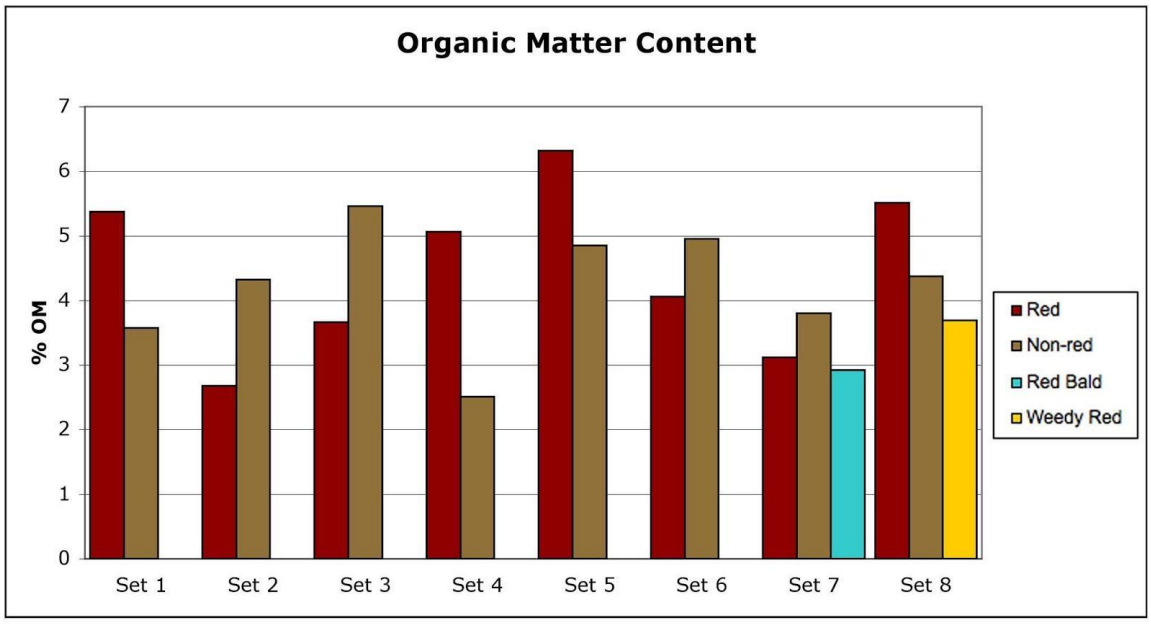


Figure 15. Percent of organic matter in soils.

Soil Texture

The Wilcoxon signed-rank test indicated that there was a significant difference in the sand content for red (Median=51.5, range= 36.3-54.8) and non-red (Median= 63.9, range= 49.7-68.6) soils, with non-red soils having higher sand content (W= 34, p= .02). However, there was no significant difference in the clay content for red (Median=12.4, range=3.6-20.7) and non-red (Median= 7.12, range= 5.3-14.6) soils; W= 24, p> 0.05 (Figure 16). It remains possible that the hydrometer method did not disaggregate the cemented iron oxides and that the clay fraction is higher than was represented by this analysis. Table 8 shows the soil texture classification from each site.

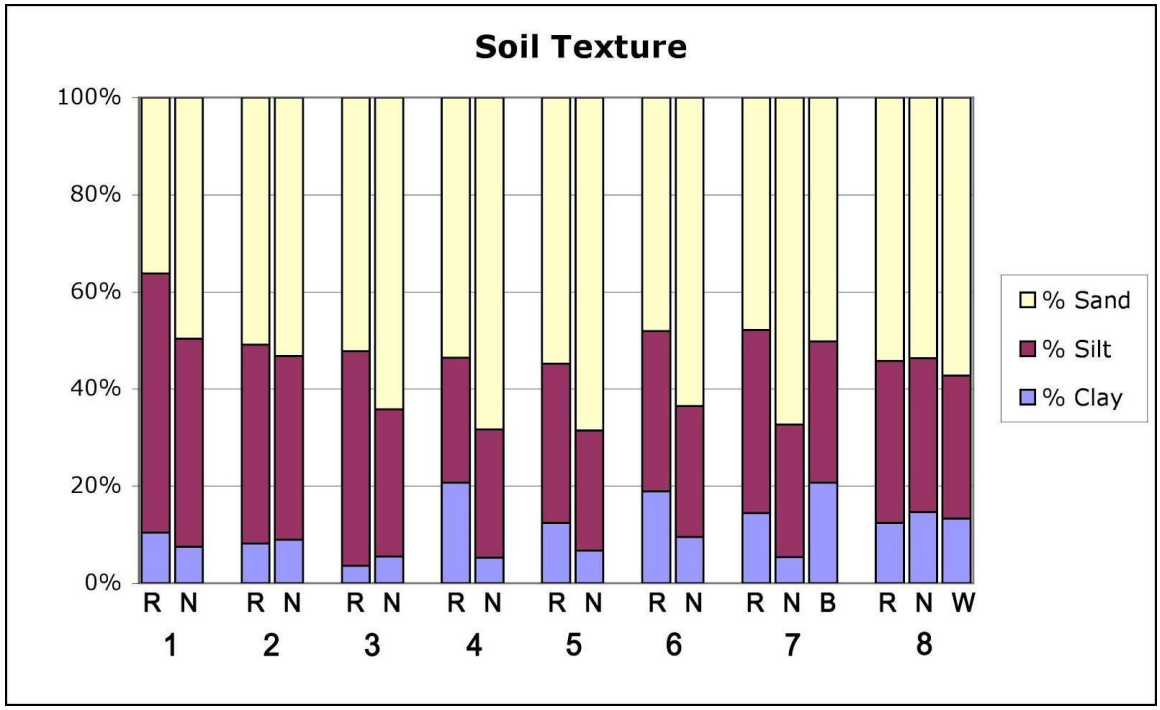


Figure 16. Soil texture for each site. Numbers on the x-axis represent set number and letters represent soil (R= red, N= non-red, B= Red Bald, W= Weedy Red).

Table 8. Soil texture classification of each site.

Set 1	
Red	silt loam
Non-red	loam
Set 2	
Red	loam
Non-red	sandy loam
Set 3	
Red	sandy loam
Non-red	sandy loam
Set 4	
Red	sandy clay loam
Non-red	sandy loam
Set 5	
Red	sandy loam
Non-red	sandy loam
Set 6	
Red	loam
Non-red	sandy clay loam
Set 7	
Red	loam
Non-red	sandy loam
Red Bald	loam
Set 8	
Red	sandy loam
Non-red	sandy loam
Weedy Red	sandy loam

Infiltration Rates

A Wilcoxon signed-rank test, indicated that the infiltration rate of the non-red soils (median=6.8 range= 1.3-9.7) was not statistically significantly different than the median infiltration rate on the red soils (median=3.9 range= 2.3-6.9); W=9, p> 0.05 (Figure 17).

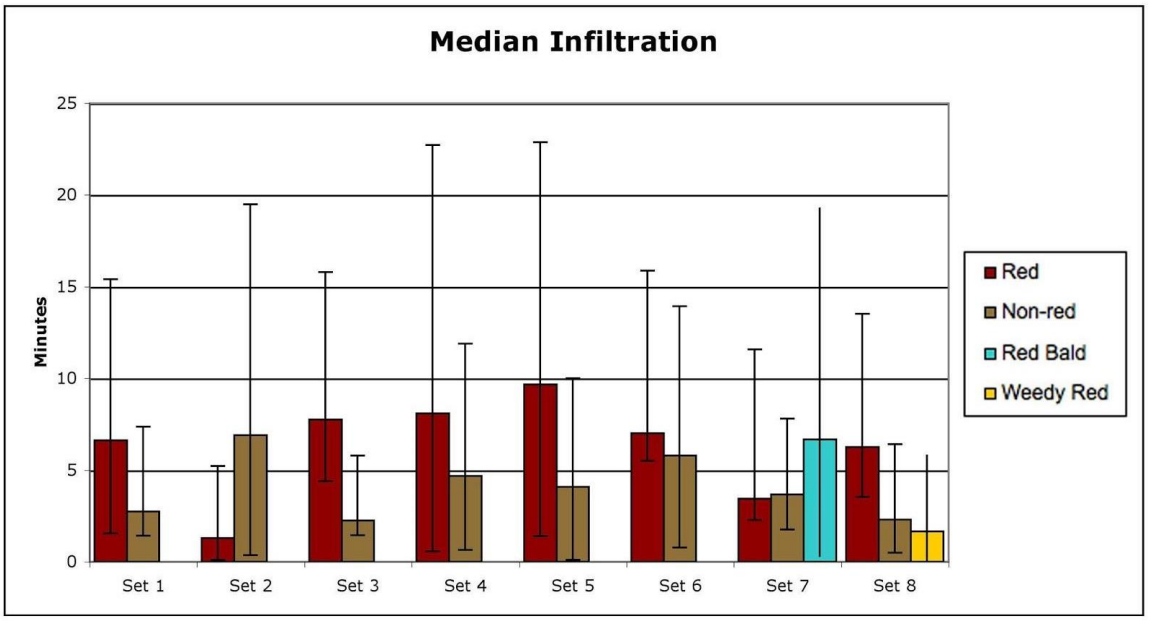


Figure 17. Median infiltration rates at each site. The error bars represent the shortest and longest infiltration rates measured at each site. Only the median values were used in the statistical analysis.

Discussion

The percentage of organic matter (OM) did not differ consistently between red and non-red soils. Although OM within a soil varies depending on the type of vegetation, Caspi et al. (2019) also found that OM did not vary between CSS and non-native habitat types. OM is important for storing nutrients; plant nutrients will be addressed in the next chapter.

It was expected that the clay content would be higher in the red soils because the small particle size of secondary oxides make them part of the clay fraction. But no measured differences in the clay content between red and non-red soils was consistent across all the sets; however, this may be due to the cementation of clay-sized particles into larger particles that were not completely disaggregated during the soil texture analysis. Although there were no measured differences in the clay content, the non-red soils had a higher sand content than the red soils. The soil texture can have implications when it comes to soil chemistry. Soils with higher sand content are typically more porous and as a result are less likely to store nutrients and water for plant use. The red soils had on average 11.5% less sand than the non-red pair; whether this is a significant enough difference to cause the observed variation in plant growth is unknown.

Even though there were measured differences in the sand content, infiltration rates did not vary between red and non-red sites. However, infiltration rates were highly variable, even within the same plot. For example, infiltration measurements taken where there was an abundance of vegetation typically

resulted in a higher infiltration rate whether or not the measurement was taken on a red or non-red site. The observed differences in infiltration rates within a site is likely due to the presence of macropores along roots.

Other than differences in the sand content, none of the physical soil characteristics that were measured were significantly different. The differences observed in the sand content can have implications for water and nutrient retention within the soil. Measuring the soils' ability to retain water and comparing soil structure should be considered for future research. The next chapter addresses plant nutrient differences within the soils. Based on the results of the textural analysis, it was expected that the nutrients would be lower in the red soils due to their higher sand content.

CHAPTER FIVE

VARIATION OF SOIL CHEMISTRY AND PLANT NUTRIENTS BETWEEN RED AND NON-RED SOILS

Introduction

Plants are known to require at least sixteen elements in varying proportion to grow properly (Fuller 1975). Of the sixteen, carbon, hydrogen, and oxygen, are taken up by plants through air or water. Nitrogen, phosphorus, calcium, magnesium, sulfur, and potassium are taken up by plants from the soil in large amounts and are considered macronutrients. The other elements, iron, manganese, molybdenum, boron, copper, zinc, and chlorine, are typically not limiting nutrients because they are required in small amounts, and some can even prove toxic in high concentrations. The presence of these sixteen elements in a soil is not enough for plants-- they need to be in the form of soluble or exchangeable ions for plant uptake (Hausenbuiller 1985). Soluble ions are nutrients that are free within the soil solution. Exchangeable ions are attached to the ion exchange complexes of organic matter, phyllosilicate minerals, oxides, and other soil components. To be released, exchangeable ions need to be displaced by another ion, typically H_3O+, which is excreted by plant roots or by plant symbionts.

These ions can be either positively charged cations, or negatively charged anions. Because soil particles are negatively charged, cations are adsorbed onto

the exchange complex of soils where they can persist for long periods of time. Anions, however, are usually available in their soluble form and are readily leached from soil because soil particles typically have a smaller anion exchange capacity. Cation exchange capacity is largely pH dependent.

In addition to influencing the cation exchange capacity, the soil pH influences the solubility of plant nutrients and determines their accessibility to plants and microorganisms (Penn and Camberato 2019). Soil pH also impacts the formation of secondary minerals such as goethite and hematite (Veroney and Heck 2015). The pH can also indicate the potential microbial and enzyme activity in the soil (Veroney and Heck 2015).

Phosphorus

Phosphorus (P) is an essential macronutrient for all life forms that is used for processes including the production of ATP and DNA (Lehninger et al. 2000). All plants require P to conserve and transfer energy in cells, but higher concentrations are critical for young plants because their root systems are not as extensive and their requirements for P are higher than for mature plants (Fuller, 1975). The P content and form of P is largely determined by the pH: peak solubility of phosphate is at pH 6.5 (Parton 2005). P content is also determined by the minerology of the parent material, topography, the extent of weathering and leaching, iron and aluminum oxides, and the amount of SOM present (Hausenbuiller 1985; Parton 2005; Eger 2018). Torrent (1987) showed that Fe oxides impact the rapid and long-term sorption of phosphate within a soil. Apatite

minerals are the main source of soil P and are gradually released from the minerals through pedogenic processes and the colonization of microorganisms and plants (Izquierdo 2013). From there P can be incorporated into iron and aluminum phosphates, sorbed onto sesquioxides, immobilized by microbes, and incorporated into organic or inorganic compounds (Izquierdo 2013). Plant roots are only known to take up P in the form of phosphate anions (Richardson et al. 2005). Plant-available P is frequently deficient in soils because of the low supply rate and its tendency to rapidly form insoluble compounds; soils commonly contain 200-3000 mg P kg/soil but less than 1% is available to plants as phosphate ion (Richardson et al. 2005; Eger 2018).

Nitrogen

Nitrogen (N) is often the most limiting plant nutrient and is required for protein synthesis and plant growth (McRae 1998). The majority of N enters the soil through two main processes: N fixation and the cycling of organic matter. N fixation is the process by which microorganisms and natural processes such as lightning convert N_2 gas into ammonia and other inorganic forms of N (Follett 1995). Plants cannot directly use N_2, but some plant species form a symbiotic relationship with microorganisms that can. Other microorganisms convert organic N to inorganic forms that are available for plant use in a process called mineralization (Coleman 2004). In this process the microorganisms decompose organic matter and make N available to plants in the form of ammonium and nitrate. Nitrification is a biological process by which ammonia is oxidized first to

nitrite and then to nitrate. Denitrification is the process by which nitrate is converted to NO_x. Nitrate is easily taken up by plants, but is also readily leached from the soil because it is an anion and cannot sorb to the negatively charged sites on soil particles (McRae 1988; Follett 1995). Ammonium, however, is a positively charged ion that can easily be fixed onto clay and other soil complexes where it is easily used by plants or volatilized (Follett 1995). The changes of one form of N to another depends on the aeration and moisture state of the soil.

Microorganisms have always been the primary drivers of the nitrogen cycle, but human sources of N have exceeded natural sources since 1980 (Vourlitis 2017). Air pollution is the source of up to 95% of the available N in a soil (McRae 1988; Padgett et al. 1999). N deposition in Southern California can be as high as 20-45 kg/ha/yr and falls onto soil as either nitrate/nitric acid or ammonia/ammonium (Padgett et al. 1999; Allen et al. 2016).

Changes in Plant Communities

Current research suggests that the eutrophication of ecosystems by N deposition results in changes in species composition and native ecosystems (Padgett et al. 1999; Vourlitis 2017). Chronic N inputs have been associated with a decrease in plant diversity and an increase of non-native species across many terrestrial ecosystems (Vourlitis 2017). The magnitude of species loss depends on the individual species, soil texture, pH, and disturbance regime (Vourlitis, 2017). Because plants in California's shrublands have adapted to soils with low levels of N, anthropogenic additions to ecosystems have led to native species'

decline and an increase in non-native grasses such as *B. rubens* (Allen et al. 2016). These non-native species are able to take advantage of the excess N and become more dominant by changing microbial composition and nutrient availability (Bozzollo 2013).

Purpose of Study

The nutrient requirements of plants can vary widely by species. Nutrient additions to soil systems has allowed non-native plants to out-compete native species so it is possible that the difference in vegetation cover observed in this study is also due to differences in soil chemistry or nutrients. To address that possibility, we conducted analyses to determine whether plant nutrients were less abundant in red than non-red soils. First, we measured a range of plant nutrients, the cation exchange capacity of the soil, and salinity. This analysis offered a “snapshot” view of soil nutrients, but did not show the long-term supply rates of plants’ most limiting nutrients. To accomplish an understanding of the differences in plant-available nutrients over time, a soil resin bag study analysis was conducted.

Even with low concentrations of macronutrients, soils can be quite fertile as long as these nutrients are recycled rapidly. Because many nutrients, especially N, are soluble and mobile, a long-term sampling method is best to accurately characterize nutrient availability.

Methods

Preliminary Soil Analysis

During the summer of 2017, 500 g of soil was collected from each plot and analyzed for several soil parameters. At the time of this analysis, not all of the paired sites had been identified yet; Set 4 and Set 6 were added at a later date. Of the sets used, soil was collected from three points on each plot from 0-5 cm below the surface after removing the O horizon from the top of the soil. Large rocks were removed from the samples by hand. The samples collected from the three points from each plot were combined and sent to Fruit Growers Laboratory Inc. (FGL) in Santa Paula, California to be tested for the following:

> Nitrate, phosphorus, potassium, calcium, magnesium, sodium, sulphate, zinc, manganese, iron, copper, boron, chlorine, the cation exchange capacity, pH, salinity, and amino-N.

The laboratory methods used are shown in Table 9. The nitrate analysis was done by extracting nitrates from the soil using potassium chloride. The method of phosphorus analysis which extracts calcium, iron, and aluminum phosphates from the soil was done with hydrochloric acid and ammonium fluoride. The phosphorus analysis procedures in the FGL analysis include Soil Science Society of America (1986) methods 24-5.1 for soils with a pH less than 6 and 24-5.4 for soils with a pH of 6 and above. These methods extract acid-soluble forms of P including calcium, iron, and aluminum phosphates in acidic soils and forms of phosphorus that are soluble in sodium bicarbonate in alkaline

and neutral soils. Potassium, calcium, magnesium, and sodium include analyses for both soluble and exchangeable forms and their cation exchange capacities. The analysis showed the sulfate extractable by barium chloride. Values shown for zinc, manganese, iron, copper, and boron represent what was extractable by ammonium acetate. Additional analyses included are chloride measured by titration and salinity measured with a conductance probe. Amino-N, which was tested for in addition to nitrate, is the pool of nitrogen in humus form that has potential to become plant-available.

Table 9. Analytical methods used by FGL.

Item Description	FGL Testing Method
Nitrate-Nitrogen	Methods of Soil Analysis 33-8.1 (1982)
Phosphorus	Methods of Soil Analysis 24-5.1 (1982)
Potassium	Methods of Soil Analysis 13-3.5 (1982)
Sulfate	Methods of Soil Analysis 10-3.7 (1982)
Iron	Methods of Soil Analysis 17-3.1 (1982)
pH	Methods of Soil Analysis 10.3.1 (1982)
Calcium	Methods of Soil Analysis 14-2.1 and 14-2.2 (1982)
Magnesium	Methods of Soil Analysis 14-2.1 and 14-2.2 (1982)
Sodium	Methods of Soil Analysis 13-4 (1982)
Zinc	Methods of Soil Analysis 13-4 (1982)
Copper	Methods of Soil Analysis 13-4 (1982)
Salinity	U.C. Method S: 5.0, California Analytical Methods Manual
Sodium Adsorption Ratio (SAR)	Calculation
Boron	Methods of Soil Analysis 13-4 (1982)
Chloride	Standard Method 407c, American Water Works Association (1985)
Manganese	Methods of Soil Analysis 18-3.2 (1982)
Cation Exchange Capacity	Calculation: Summation of Cations
Amino-N	Woods End Laboratories, Inc., Mount Vernon, ME, USA

A Wilcoxon signed-rank test was used to compare each parameter between red and non-red soils.

Long-term Supply Rate of Nitrate, Ammonium, and Phosphate

While chemical extraction from a soil sample offers a static view of soil nutrients, the ion-exchange resin bag method represents the bioavailable nutrients through the entire incubation period (Sherrod 2003). The ion-exchange resin within the bags holds onto positively and negatively charged ions that are replaced by ions in the soil as they move through the bag with percolating rainwater. This is a preferred method to measure soil N because it captures plant-available ions and allows for an understanding of their supply rate (Jones 2011). Nitrate lands on a soil's surface as dry deposition where it will remain until precipitation solubilizes and percolates it (Padgett et al. 1999). With this method, differences in the supply rates of nitrates, phosphates, and ammonium between red and non-red soils were determined.

Resin bags were made with 2-inch square nylon packets containing approximately 10 grams of Amberlite IRN-150 ion-exchange resin (Göransson et al. 2016). The resin bags were soaked in nano-pure water prior to distribution. Ten resin bags were not deployed and kept in air-tight bags as method blanks. A total of six resin bags were deployed in each plot during February of 2018. Each plot was divided into four quadrants. Two bags were buried in the NW and SE quadrants, and one bag was buried in both the SW and NE quadrants at a depth of 5 cm. To ensure that the resin bags were retrievable, flagging tape was buried with one end in the soil about one inch below the resin bag and the other end of the tape left exposed.

In July of 2018, resin bags were recovered and carefully placed in plastic bags. Deployed bags and method blanks were taken back to the lab and analyzed for nitrate, ammonium, and phosphate. Each resin bag was placed inside an Erlenmeyer flask. 100 ml of nano-pure water was added to the flask and the samples were shaken on an orbital shaker for 30 minutes. After shaking, the water was drained. This process was repeated twice for each sample. After rinsing the resin bags, 75 ml of a 2 molar potassium chloride solution was added to each flask. After 20 minutes of soaking the flasks were put on an orbital shaker for 30 minutes. The solution was poured into vials. This process was completed twice for each sample. After extraction, the solution was analyzed on a Lachat QuikChem 8500 flow injector with reagent blanks.

pH

Soil pH was also measured because it influences the availability of important plant nutrients. Although pH was one of the parameters measured during the preliminary soil analysis, additional sites were added to the study after the preliminary soil analysis. To ensure that the differences in methods or time of soil collection was not contributing to differences in pH, all soil samples were remeasured for the analysis.

During February of 2019, soil pH was tested in the lab using soil that was collected in January of 2019. Using a Oakton Ecotester pH2+, the saturated paste method as described in the Kellog Soil Survey Laboratory Method manual

5.0 was followed (Burt 2014). Soil pH was compared between red and non-red soils using a Wilcoxon signed-rank test.

Results

Preliminary Soil Analysis

None of the parameters tested in the FGL analysis were significantly different between red and non-red soils. Tables 10 and 11 show the results of these analyses.

Table 10. Soil analysis results for Sets 1-3 comparing red (R) and non-red (N) soils.

	Set 1		Set 2		Set 3	
Analysis	**R**	**N**	**R**	**N**	**R**	**N**
Nitrate-N	34.4	17.2	21.2	16	10.4	26.4
P-P2O5	110	27	64	137	174	82
K-K2O (Exch)	618	298	885	308	404	607
K-K2O (Sol)	42.5	14.2	131	23.4	52.4	119
K exch/sol	14.54	20.99	6.76	13.16	7.71	5.1
Ca (Exch)	4410	9300	5450	4570	2000	4970
Ca (Sol)	107	150	225	109	89	347
Ca exch/sol	41.21	62	24.22	41.93	22.47	14.32
Mg (Exch)	1120	1250	569	972	262	642
Mg (Sol)	45.4	35.6	50.1	33.9	21.1	89
Mg exch/sol	14.54	20.99	6.76	13.16	7.71	5.1
Ca/Mg Sol	2.36	4.21	4.49	3.22	4.22	3.9
Ca/Mg Exch	3.94	7.44	9.58	4.7	7.63	7.74
Na (Exch)	90	100	<80	<80	<80	<80
Na (Sol)	34	31	30	28	19	24
SO4	104	74	144	102	76	207
Zn	5	3	20	9	8	15
Mn	96	43	81	72	54	66
Fe	56	47	112	95	45	62
Cu	4	3	4	3	2	2
B	0.52	0.24	0.48	0.44	0.32	0.88
Cl-	42.5	39.7	210	8.5	35.5	119
CEC	9.33	14.4	8.44	9.26	4.45	7.84
CEC-Ca	58.9	80.6	80.6	61.6	56.2	79.1
CEC-Mg	24.7	17.8	13.9	21.6	12.1	16.8
CEC-K	3.52	1.1	5.57	1.77	4.81	4.11
CEC-Na	1.08	0.75	0	0	0	0
CEC-H	11.8	<1.00	<1.00	15.1	27	<1.00
pH	5.72	6.63	6.03	5.47	5.71	6.74
Salinity	0.3	0.26	0.44	0.22	0.2	0.57
SAR	0.3	0.3	0.2	0.3	0.2	0.1
Amino-N	87.5	77.5	177.5	97.5	77.5	117.5

Table 11. Soil analysis for Sets 5, 7, and 8 comparing red (R) and non-red (N) soils.

	Set 5		Set 7			Set 8		
Analysis	**R**	**N**	**R**	**N**	**RB**	**R**	**N**	**RW**
Nitrate-N	26	22.8	18	15.2	196	17.2	18.4	19.2
P-P2O5	18	37	18	64	37	55	46	46
K-K2O (Exch	591	179	320	196	330	351	318	430
K-K2O (Sol)	23.7	11.7	7.6	8.2	17.2	16	10.5	19
K exch/sol	30.29	22.63	23.9	21.94	19.19	15.3	24.94	42.11
Ca (Exch)	9940	6010	1130	8100	6730	7610	9060	8900
Ca (Sol)	163	148	134	172	498	160	160	175
Ca exch/sol	60.98	40.61	84.33	47.09	13.51	47.56	56.63	50.86
Mg (Exch)	1760	1150	1960	1180	2100	1780	3950	2030
Mg (Sol)	42	46.8	36.8	45	238	55.9	90.4	58.3
Mg exch/sol	24.94	15.3	42.11	23.9	19.19	21.94	30.29	22.63
Ca/Mg Sol	3.88	3.16	3.64	3.82	2.09	2.86	1.77	3
Ca/Mg Exch	5.65	5.23	5.77	6.86	3.2	4.28	2.29	4.38
Na (Exch)	<80	<80	90	<80	90	90	130	100
Na (Sol)	27	21	26	18	94	43	61	41
SO4	91	73	83	108	90	206	202	137
Zn	3	6	3	5	1	9	4	12
Mn	75	32	69	37	73	101	88	106
Fe	36	62	45	50	27	105	73	116
Cu	3	2	4	2	3	5	5	6
B	0.32	0.28	0.24	0.2	0.28	0.36	0.36	0.4
Cl-	7.1	4.3	12.8	22.7	169	4.3	58.1	63.8
CEC	16.3	9.96	18.4	12.6	14.1	13.5	19.7	15.6
CEC-Ca	76.1	75.3	76.6	80.2	59.6	70.4	57.4	71.2
CEC-Mg	22.2	23.7	21.9	19.3	30.6	27.2	41.3	26.8
CEC-K	1.93	0.95	0.92	0.83	1.24	1.38	0.86	1.46
CEC-Na	0	0	0.51	0	0.73	0.75	0.73	0.7
CEC-H	<1.00	<1.00	<1.00	<1.00	7.8	<1.00	<1.00	<1.00
pH	6.92	6.53	6.72	6.99	5.78	6.18	6.42	6.14
Salinity	0.33	0.26	0.26	0.29	1.33	0.3	0.38	0.32
SAR	0.2	0.2	0.3	0.2	0.4	0.4	0.5	0.3
Amino-N	57.5	67.5	57.5	65	37.5	105	82.5	120

Resin Bag Analysis

Upon retrieval, it became apparent that many of the resin bags had been lost or damaged while in the field. At some sites all resin bags were found, but at most sites there was one or more missing. Table 12 shows the number of retrieved and intact resin bags at each site. It was originally planned that a nested ANOVA would be used for the statistical analysis of the data, but because of the low numbers of resin bags that were retrieved, a Wilcoxon signed-rank test was used. Resin bag data were averaged by site and each site's average phosphate, nitrate, and ammonium concentrations were compared between red and non-red soils with three Wilcoxon-signed ranks tests.

The resin bag analysis revealed significant differences in key plant nutrients between red and non-red soils. Phosphate was significantly lower for red soils (Median= 0.665, range= 0.23-12.42) than non-red soils (Median= 6.86, range= 2.63-40.23) soils; Z= 13, p= 0.039 (Figure 18). Nitrate for red soils (Median= 198, range= 98.3-1170) was significantly higher than nitrate in non-red soils (Median= 121, range= 37.6-1126); Z= -14, *p*= 0.027 (Figure 19). There was no significant difference in the ammonium for red (Median= 12.64, range= 1.98-19.8) and non-red (Median= 3.33, range= 1.76-30.7) soils; Z= -4, *p*= 0.320 (Figure 20).

Table 12. The number of intact resin bags that were retrieved after field deployment.

	Red	Non-red	Red Bald/Weedy Red
Set 1	6	3	
Set 2	4	3	
Set 3	6	1	
Set 4	5	6	
Set 5	3	4	
Set 6	6	6	
Set 7	6	5	6
Set 8	2	5	4

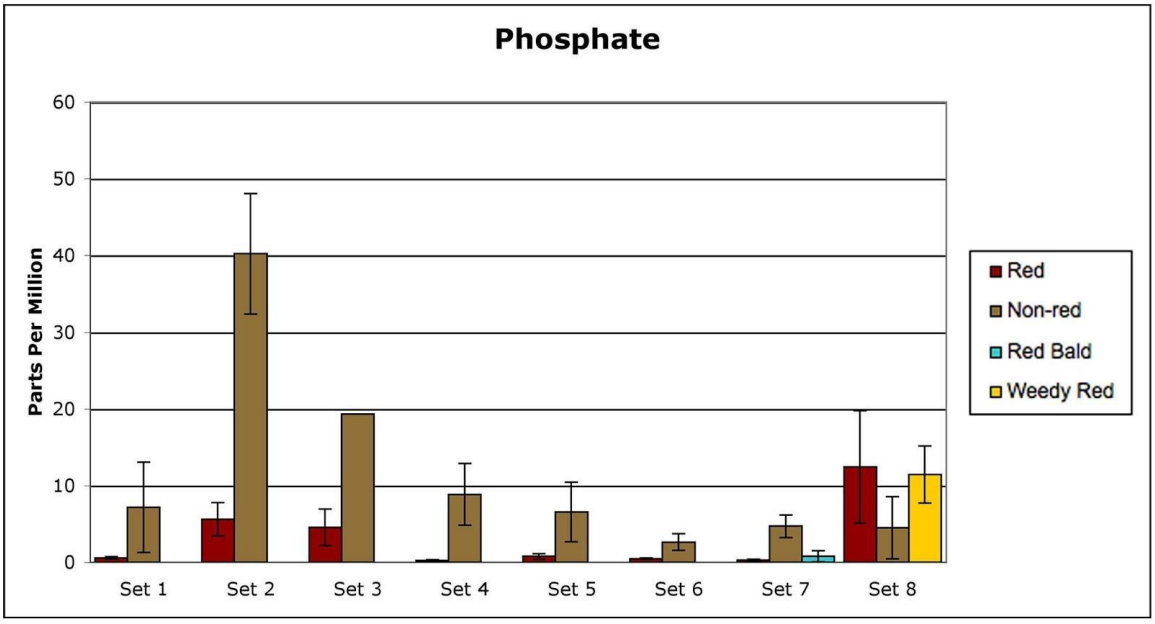


Figure 18. Phosphate concentration of extracted solution from soil resin bags in parts per million.

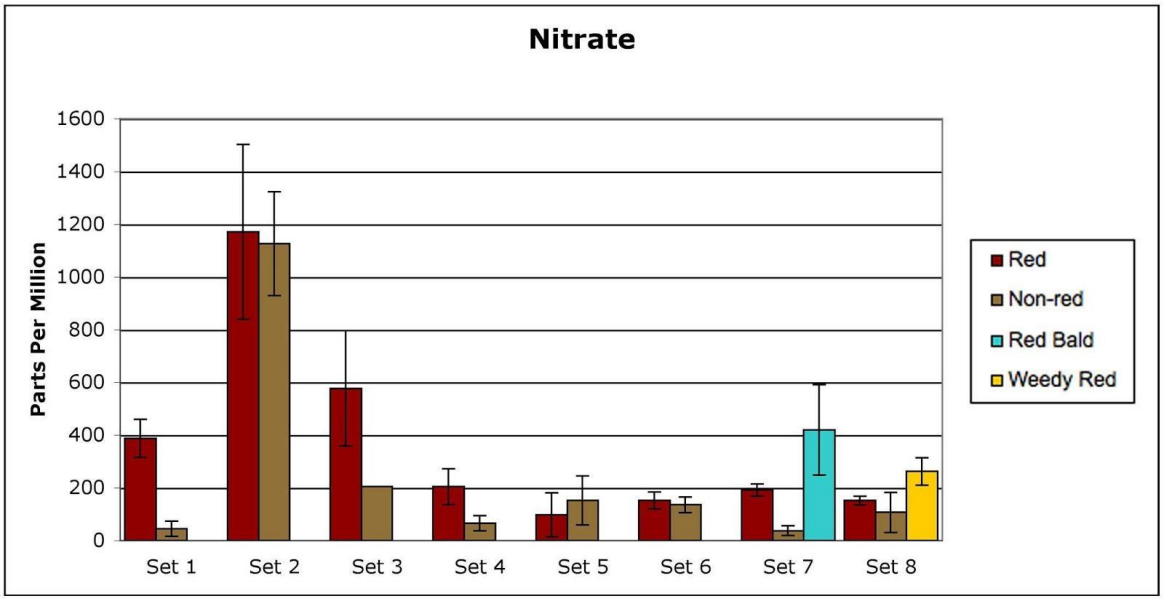


Figure 19. Nitrate concentration of extracted solution from soil resin bags in parts per million.

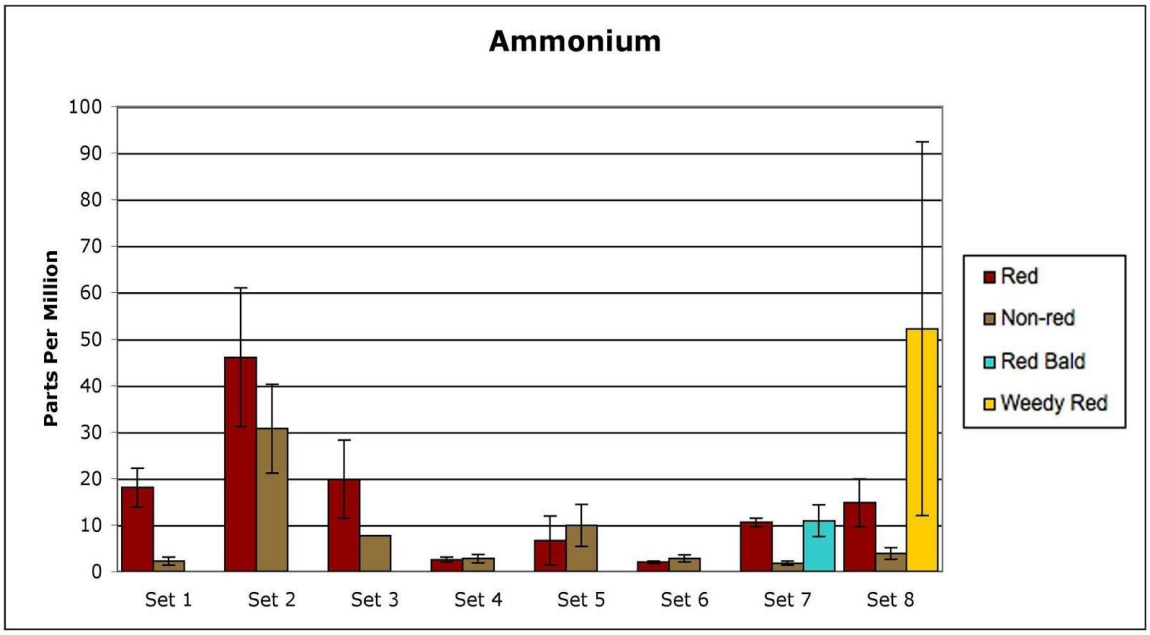


Figure 20. Ammonium concentration of extracted solution from soil resin bags in parts per million.

pH

There was no significant difference in the pH for red (Median=5.95, range=1.1) and non-red (Median=6.25, range=1.3) soils; Z=9.5, p=.894 (Figure 21).

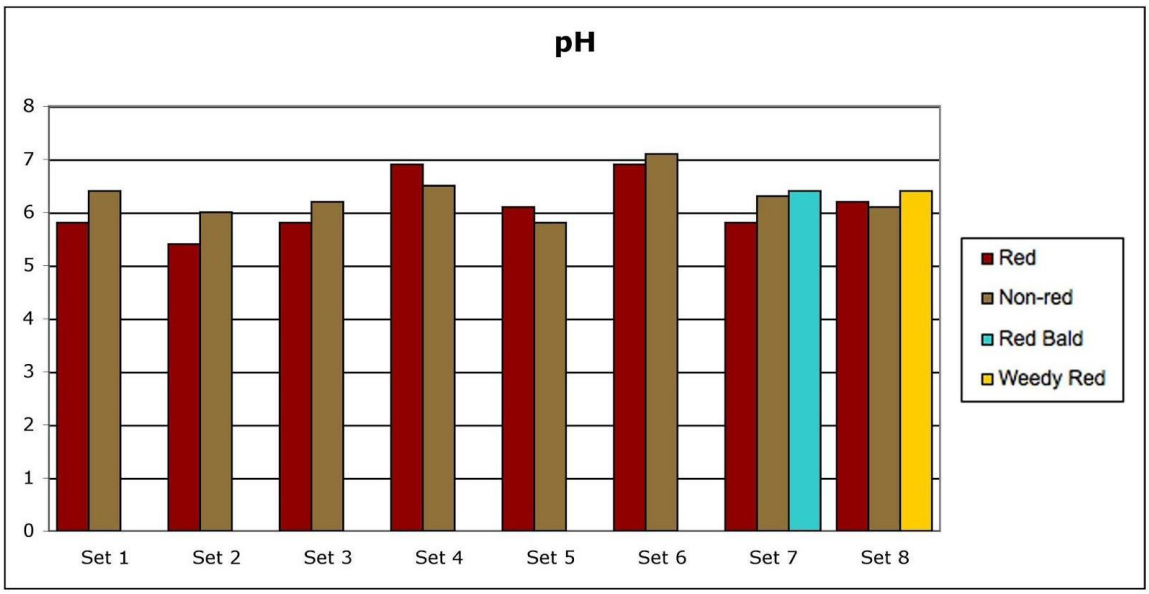


Figure 21. Soil pH.

Discussion

The FGL analysis found that neither the nitrate nor phosphorus content was significantly different between red and non-red soils as the resin bag analysis had found. Both the FGL and resin bag analyses used KCl to extract nitrates meaning the inconsistencies in nitrate between the two analyses are a reflection of the short-term versus the long-term nitrate availability. The inconsistent findings between the FGL and resin bag analyses were not unexpected because the different methods answer different questions. While the resin bag method focused on measuring N and P over an extended period of time and is likely to be more telling when it comes to how these nutrients affect

plants, the results of the FGL analysis only measured the N and P in the soil at the time the sample was taken. Because of this, the FGL analysis is better suited for comparing nutrients or other parameters that remain more stable in the soil through time (e.g. copper, iron, salinity, etc.); however, not even these measurements could explain the differences in vegetation cover or growth of *B. rubens*.

Previous research suggests that additional nitrate allows non-native annuals to increase, but the growth of non-native annuals on the non-red soils were not explained by higher nitrate levels in this study (Bozzollo 2013; Allen et al. 2016; Vourlitis 2017). Because of the close proximity of the red soil sites to their non-red pair, the higher nitrate levels observed on red soil could not be explained by variation in nitrate deposition. Nitrate does not as readily sorb to soil particle surfaces due to its negative charge and as a result moves easily with the soil water. Typically, sandier soils with high rates of water infiltration cause nitrate to leach more rapidly from soil. Although it would be expected to see lower levels of nitrate on the sandier, non-red soils, the lower nitrate levels on the non-red soils could indicate a higher rate of uptake by plants.

Ammonium was not statistically different between resin bags buried in red and non-red soils. Because of its charge, ammonium easily binds to soil particles instead of being leached by water. Because the FGL analysis reported similar cation exchange capacities (a measurement of a soil's ability to hold onto

cations) between red and non-red soils, the supply rate of ammonium would be the main factor controlling the ammonium content of the soils.

The lower amounts of phosphate observed in the red soils could be what limited the growth of non-native annual plants. Although there are other forms of organic P that plants can use by exuding enzymes or organic acids, the resin bag results reflect the availability of phosphate, the form of P that is most easily acquirable by plants (Richardson et al. 2005). Greater amounts of phosphate are typically associated with weathering rock and organic matter decomposition but are also affected by pH and soil minerals. Soils in this study had a pH between 5.4 and 7.1, so it is possible that the pH played a role in the P availability if the soil minerals varied between red and non-red soils. Soil pH influences the precipitation of Al, Fe, and Ca phosphates. Generally P is most available to plants at a near-neutral pH; in acidic soils Fe and Al phosphates form, while Ca phosphates form in high pH soils (Penn and Camberato 2019). How this affects plant-available forms of P also depends on soil minerals; for example, soils with higher concentrations of soluble Al and Fe oxides will result in less soluble Al and Fe phosphates to maintain the equilibrium constant of the reaction (Penn and Camberato 2019). Torrent (1987) showed that total phosphate sorption within a soil can be greatly influenced by the iron oxide content within a soil. The red soils may have had a higher iron oxide or differing iron oxides that allowed for greater phosphate adsorption and decreased phosphate in the soil solution.

CHAPTER SIX

CONCLUSIONS

Summary

The findings from the vegetation survey and *B. rubens* studies suggest that the low non-native cover on red soils is a result of an edaphic factor affecting plant growth. The presence of non-native annual species in shrublands is frequently associated with an opening created by land disturbance (Vourlitis 2017), but in this study *B. rubens* still failed to be as successful on red soils in greenhouse conditions. *Bromus rubens* growing in the red soils not only had lower growth, but were also observed to have leaves that were turning brown at the tips. Although there are many factors that could contribute to the absence of non-native vegetation in the field and lower growth rates of *B. rubens* in the greenhouse, this research found that nitrate, phosphate, and sand content varied between red and non-red soils.

Resin bags buried in red soils had higher nitrate content than those buried in non-red soils. This is an unexpected result because many previous studies show that additional nitrates in soil are favorable to non-native plant growth (Allen et al. 2016; Vourlitis 2017). The phosphate content of resin bags buried in non-red soils was significantly higher than those buried in red soils. It may be that the lack of phosphate hindered growth of non-native annual species in red soil field

sites and of *B. rubens* in the greenhouse study. A common sign of P deficiency in plants is decreased growth, which was observed in *B. rubens* in this study (Plaxton and Lambers 2015).

Future Research

Differences in phosphate and nitrate between red and non-red soils is a likely cause for the observed vegetation differences. To strengthen the case for the variation in nutrients resulting in differences in native and non-native cover, an additional greenhouse study should be done. Phosphate and nitrate fertilizers could be added to soil samples collected from the field sites to see if that affects plant growth. Additionally, native species grown in these various greenhouse conditions could also be studied.

An analysis of the soil microorganisms would be useful in future research because they can influence the vegetation as well. For example, mycorrhizal fungi have the potential to affect the distribution of plant species; some plants require a symbiotic relationship with fungi to grow successfully (Plenchette et al. 1983). It is possible that the microorganisms in the red soils differed from the microorganisms found in the non-red soils which resulted in different vegetation cover.

In addition to the biological analysis, there are several physical soil characteristics that should also be considered during future research. Although the soil texture analysis done during this study provided some context of how water, nutrients, and roots move through the soil, soil structure analysis would

provide a more in-depth understanding of these factors. Poor soil structure can often be an inhibitor to plant growth because it can curtail root growth through the soil and also limit the pools of nutrients and water that are accessible to plants (Angers and Caron 1998).

Another physical soil parameter that should be considered is the formation of desert pavement. Desert pavement is the formation of a clastic surface that hinders water infiltration and as a result these soils tend to build up salts and nitrates (Cooke et al. 1993; Graham et al. 2008). There were no differences in salinity between red and non-red soils but there were higher levels of nitrates on red soils. However, it is expected that surface clasts would lead to differences in infiltration rates which was not the case. A more detailed analysis of water infiltration would be warranted. It also may be that the surface clasts are providing a physical barrier that prevents seeds from taking root and hinders seedling emergence.

Lastly, although the FGL analysis included some elemental analysis a detailed mineralogy investigation would be important for future research. The mineralogy would allow the present iron oxides to be determined and would also identify other minerals that could affect the soil conditions. The National Cooperative Soil Survey identified the soil types at each of the sites as matching its paired site, but there could be small scale variation that is not captured at the resolution the soil survey was conducted. The possibility of varying mineralogy cannot be dismissed even though the sites were closely located to one another.

As discussed in Chapter One, the mineral make-up of soil can impact vegetation communities. Although the presence of mafic and ultramafic soils are unlikely because the FGL analysis did not find high amounts of heavy metals or a low calcium to magnesium ratio, other mineralogy conditions can impact plant growth.

Conclusions

This study offered a unique perspective on the distribution of native and non-native plant species in California sage scrub and chaparral ecosystems. With these plant communities at risk of becoming displaced by non-native annual plant species, restoration ecologists need to be strategic in their efforts to preserve these critical shrublands. Soil color may be a useful tool in identifying communities that are more resistant to non-native plant invasion. Additionally, more research may be able to explain the mechanism behind the observed difference in plant communities found on red soils and may possibly be applied to native shrubland communities to impede the growth of non-native species. The continued research of the distribution of non-native species in CSS and chaparral is imperative to the preservation of these diverse habitats.

APPENDIX A

TABLES

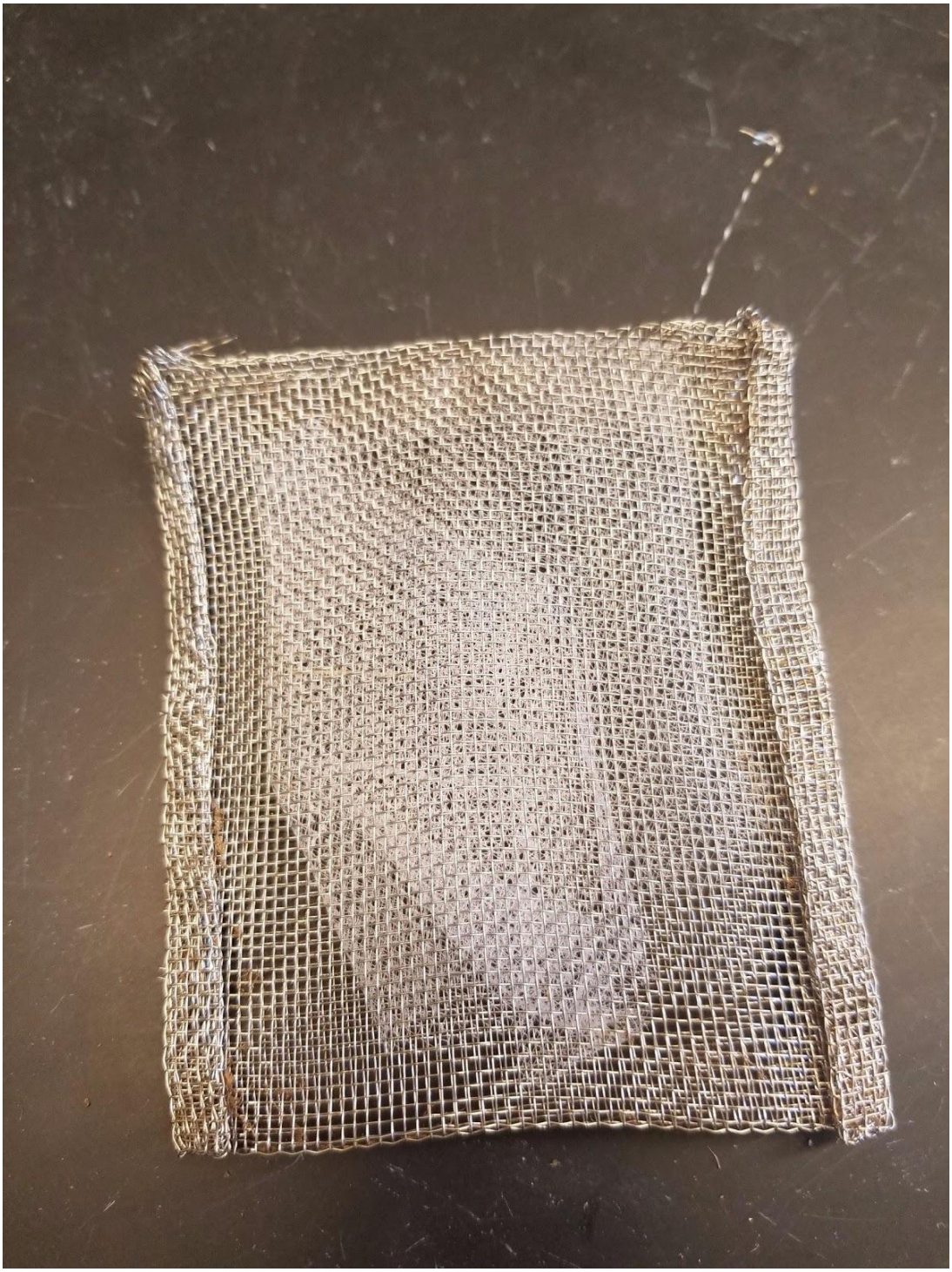
Table A1. Site GPS coordinates and location.

Set Number/Color	Latitude	Longitude	Location
1 Red	34.188433	-117.31363	Badger Hill
1 Non-red	34.186833	-117.3126	Badger Hill
2 Red	34.185401	-117.31303	Badger Hill
2 Non-red	34.186383	-117.31467	Badger Hill
3 Red	34.185983	-117.31837	Badger Hill
3 Non-red	34.184767	-117.31485	Badger Hill
4 Red	34.19885	-117.31442	Cloudland
4 Non-red	34.199933	-117.31462	Cloudland
5 Red	33.97277	-117.06705	San Timoteo
5 Non-red	33.97323	-117.06715	San Timoteo
6 Red	34.198333	-117.31556	Cloudland
6 Non-red	34.198611	-117.31639	Cloudland
7 Red Bald	34.199867	-117.32522	Cloudland
7 Red	34.199717	-117.32523	Cloudland
7 Non-red	34.20185	-117.3238	Cloudland
8 Weedy Red	33.972167	-117.06573	San Timoteo
8 Red	33.972633	-117.06595	San Timoteo
8 Non-red	33.972401	-117.06592	San Timoteo

APPENDIX B

FIGURES

Appendix B1. The point-intercept method was used during the vegetation survey. Transects were laid out and a pole was dropped vertically; any vegetation in contact with the pole were recorded.



Appendix B2. A 2X3 inch seed germination packet made from nylon fabric within a stainless steel sleeve.

Appendix B3. Using a metal detector to find the germination seed packets at the non-red site of Set 3.

Appendix B4. Greenhouse emergence and growth study.

Appendix B5. *B. rubens* growth at four weeks.

Appendix B6. The rocky surface at the red site of Set 3.

Appendix B7. An ion-exchange resin bag ready to be buried at the red site of Set 1.

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