

UNIVERSITY OF CALIFORNIA SAN DIEGO

Tracking Potential Carbon Gain of Post-Fire Coastal Sage Scrub Ecosystems; The Roles of
Invasion and Drought

A Thesis submitted in partial satisfaction of the requirements
for the degree Master of Science

in

Biology

by

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University of California San Diego

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ABSTRACT OF THE THESIS

Tracking Potential Carbon Gain of Post-Fire Coastal Sage Scrub Ecosystems; The Roles of
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by

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Professor Elsa Cleland, Chair

Coastal sage scrub (CSS) ecosystems are invaluable biodiversity hotspots and carbon sinks, characterized by a Mediterranean-type climate and native plants adapted to drought. With climate change causing increased droughts and wildfires in Southern California, CSS systems are experiencing large-scale disturbances that allow fast-growing invasive species to dominate slower growing natives. In this experiment we used a handheld crop scanner to

quantify the normalized difference vegetation index (NDVI) as a proxy for ecosystem-level plant productivity in a partially burned CSS preserve in San Marcos over a two-year period. Part of the preserve recovered with primarily invasive species while another remained native-dominated, producing three experimental areas: burned invaded, burned native, and unburned. We also observed how imposing drought affected each burn treatment area. We found that during the first experimental year, burn treatment affected maximum NDVI value, day of maximum NDVI, and day of green-up. Burned invaded and unburned treatments had the earliest days of maximum NDVI and green-up, as well as the highest maximum NDVI values. The burned native treatment lagged in all three values. Drought treatment only affected day of maximum NDVI, causing a delay across all treatments. In the second year, no significant differences in NDVI were found among burn or drought treatment types, likely owing to the increased recovery of burned areas that approached NDVI levels of the unburned reference area. Our results showed that in the early stages of wildfire recovery, invaded areas can be more productive than native-dominated areas during the wet season, but in as little as two years native vegetation can recover to have similar levels of productivity as invasive-dominated areas. Hence, efforts to remove invasive species and promote native shrub recovery have the potential to enhance long-term CSS carbon storage following wildfire.

Introduction

Plant phenology, the timing of developmental and life stages, plays a vital role in determining where plant species can grow and, by extension, the plant communities that climates can support (Piao et al. 2019). Phenology controls the life histories and carbon storage capabilities of plants on an individual level and drives carbon storage on an ecosystem level (Keenan et al. 2014). Phenological traits such as green-up, senescence, and flowering dates are typically genetic and vary from species to species but also exhibit plasticity under changing weather conditions, such as variations in temperature or precipitation, particularly as a result of climate change (Cleland et al. 2007). Phenology is highly coupled to a plant's environment and has allowed populations of species to adapt to droughts and high temperatures over time (Keller et al. 2011). With the rise of global climate change, ecosystems around the world are experiencing shifts in yearly temperature fluctuations and precipitation events, to the point that seasons are beginning to change time frames (Kutta & Hubbart 2016). This discrepancy has the capability of reducing ecosystem productivity and carbon storage as climate change is projected to increase drought frequencies beyond what native species are adapted to handle (Cook et al. 2018).

In coastal sage scrub (CSS) ecosystems, native species are generally well adapted for drought conditions (Kirkpatrick & Hutchinson 1980). CSS is primarily characterized by a Mediterranean climate, consisting of a hot, dry season throughout the Summer and Fall, followed by a cooler, wet season during Winter and Spring (Cleland et al. 2016). Large dry spells between precipitation events lead to native plant species specializing in drought tolerance and drought avoidance traits, including physical adaptations such as deep rooting depth and high-water use efficiency, as well as phenological adaptations such as being drought-deciduous and senescing

leaves during the dry season (Rundel 2007). The CSS ecosystem in Southern California is dominated by shrubs, including both drought-deciduous (e.g. *Salvia mellifera*) and evergreen (e.g. *Malosma laurina*) functional types (Cleland et al. 2016). The species that dominate CSS display an array of drought tolerance adaptations, therefore native CSS systems are resistant to seasonal drought and can maintain some level of primary productivity year-round even during the dry season (Gillespie et al. 2018).

CSS is also heavily influenced by the presence and frequency of wildfires (Westman 1981). Due to the prolonged dry season, CSS systems often experience fires in the summer and fall when most plant biomass is dry and easily burnable (Fleming et al. 2009). Fires open space in CSS for shrub seedlings, and a variety of native herbaceous species only grow in CSS clearings formed by fires, as they would otherwise be shaded and out competed for resources by older, deeply rooted shrubs (Conlisk et al. 2016). Some CSS shrub species can also resprout following wildfire (Keeley & Keeley 1984). Fire can thus be beneficial for the growth, biomass turnover, and maintenance of species diversity in CSS; but with climate change increasing rates of drought, fires are increasing in severity and frequency (Goss et al. 2020). This increase in wildfires risks depleting native seed banks and decreases the ability of native shrubs to resprout, causing altered or limited ecosystem recovery (Giessow & Zedler 1996, Westman 1981).

When fires occur in CSS, they open space for native herbaceous species, as well as opportunistic invasive species, to grow (Reilly et al. 2020). Invasive species in Southern California, namely mustards (*Brassicaceae*) and brome grasses (*Bromus*), are highly flammable compared to the woody and dense native shrubs (Giessow & Zedler 1996). They also have a drought escape life strategy, which is characterized by rapid initial growth and early flowering, followed by senescence and death at the first sign of drought (Blumenthal et al. 2020). They lack

the drought avoidance and tolerance strategies that native species have acquired to survive seasonal drought conditions, such as deep roots or thick leaves. However, due to their lack of investment in leaf longevity and water use efficiency traits, these invasives create high nitrogen, high photosynthetic capacity leaves that allow them to grow rapidly when rain is present in the wet season (Funk et al. 2016). This tradeoff leads to a large buildup of biomass after precipitation events, that then dries out at the start of Southern California's dry season when fires are most prevalent. The added fuel leads to larger, more intense fires that raze native vegetation and make more space for invaders (Balch et al. 2013). Since they have a fast growth rate, mustards and other invasive grasses can quickly overtake a burned area before native seedlings establish, effectively converting native CSS space into invaded grasslands (Prater et al. 2006). The result is a positive feedback loop where fires allow invasive species to grow, which then go on to fuel more fires.

This fire mediated shift in plant community structure also affects the overall primary productivity and carbon storage of CSS ecosystems. Semi-arid regions such as CSS are among the largest contributors to interannual gross primary productivity (GPP) variation, and are valuable land carbon sinks (Ahlström et al. 2015). Invasive grasslands and areas invaded by forbs store less overall carbon on average when compared to native dominated CSS systems (Caspi et al. 2019, Wheeler et al. 2016). The rapid growth and mass senescence of invaded systems due to the wet and dry seasons of CSS leads to an overall less stable and productive ecosystem (Caspi et al. 2019). In contrast, native species maintain biomass year-round with milder fluctuations in productivity, and shrubs create long term carbon sinks in their woody structures (Gray 1982). Invasive species degrade the carbon storage of the systems they invade: a

service of particular importance as climate change and atmospheric carbon increases (Bradley et al. 2006).

As a result of climate change, fire frequency and intensity have been increasing in Southern California. Global climate change has contributed to increases in annual temperatures as well as more frequent and severe drought events (Goss et al. 2020). Increased drought can cause widespread mortality of smaller shrubs, contributing of the regime shift away from hardy shrubs towards drought escaping herbaceous vegetation, including invasive species (Jacobsen & Pratt 2018). Climate change is acting to fuel the positive feedback of wildfires and invasive herbaceous species in CSS, an act which in turn degrades the ecosystem's capability to store carbon (Talluto & Suding 2008). It is vital to determine how far invasive species diminish the annual productivity of CSS following wildfires, and how the difference in productivity is impacted by extreme drought conditions.

In this study we sought to observe the effects of fire and invasive plant species on the primary productivity, and therefore carbon storage capability, of CSS ecosystems. We conducted this study at the Palomar San Marcos Campus Preserve. The preserve consists of a large area of predominantly native CSS vegetation. In 2021, the area experienced a 6.4-acre fire, resulting in unburned and burned sections. As the burned area recovered, a portion of it grew primarily invasive herbaceous species, while the other portion was made up of native herbaceous and shrub species. The extent of invasion was determined by a species composition survey conducted in the year following the fire, which found that 70% of the invaded area was occupied by *Hirschfeldia incana*, an invasive mustard. Utilizing these two areas with distinct recovery patterns, we constructed an experiment comparing the effects of invasion, wildfire, and drought on plant productivity through the use of the normalized difference vegetation index (NDVI). The

NDVI provides a reliable indicator of overall plant productivity and has been used to extrapolate phenological data, such as green-up and senescence dates, in previous studies (Esch et al. 2019, Pettorelli et al. 2005, Gamon et al. 1995). It has also been shown to be highly correlated with aboveground biomass carbon storage (Wani et al. 2021). NDVI is a more flexible measure than others in that it can measure the biomass and productivity of an area at an ecosystem level, rather than an individual one, particularly with respect to percent vegetative cover and responses to water stress (Wang et al. 2016). NDVI is also sensitive to changes in plant productivity in response to seasons and precipitation differences (Wang et al. 2003).

In this experiment, we hypothesized that burned invaded areas would display a rapid increase in NDVI value during the wet season, given the ability of invasive vegetation to capitalize on resources quickly, and a sharp decline in NDVI value in the dry season due to the drought escape strategy of invasives. The burned native area was predicted to have lower NDVI values compared to the burned invaded area during the wet season due to the slow growth of native shrubs, but exhibit higher NDVI values in the dry season. We also expected that unburned areas of natural CSS vegetation would have the highest and most consistent NDVI values due to the robustness of mature native shrubs. In addition, we hypothesized that drought would lead to decreases in NDVI values across all experimental groups, particularly in the dry season when water is scarce. The effect of drought was also predicted to have a disproportionately large effect on the burned areas since seedlings and invaders are less adapted to drought conditions and less likely to withstand them (Esch et al. 2019). When considering phenological timing, we predicted that the burned invaded area would have sooner green-up and senescence dates when compared to both native areas due to their drought escape traits. Additionally, it was hypothesized that

drought would exacerbate this differential, and that the unburned native vegetation would have the latest senescence date due to the high presence of mature evergreen shrubs.

Methods

Data was gathered from the Palomar San Marcos Campus Preserve in areas of native, unburned CSS and areas burned by the 2021 wildfire. Across the 1.8 km² preserve, three sites were formed to act as burn treatment types: a burned area regrowing primarily invasive species, a burned area regrowing primarily native species, and an unburned area of CSS to act as a control. These treatment types were referred to as burned invaded, burned native, and unburned. In each burn treatment, twelve 4 x 4 m plots were established for a total of 36 plots across the experiment. Half of the plots in each burn treatment had a drought shelter erected over them to limit precipitation and form a drought treatment group. The shelters acted as rainout shelters that passively blocked 66% of ambient precipitation from entering the plots and were constructed in accordance with Drought-Net International Drought Experiment protocol without the addition of rain gutters and trenches. Although NDVI measurements began on May 20, 2022, drought shelters were installed on October 21, 2022. The other half of the plots were left undisturbed and acted as an ambient water treatment. Plots with and without shelters were alternated in placement to control for localized differences in abiotic factors such as slope incline or soil make-up. The experimental set up resulted in six drought plots and six ambient plots for each burn treatment group. Disruption of the plots was avoided as much as possible so as not to interfere with vegetation growth, although occasionally small amounts of understory biomass were extracted for other experiments in areas of the plots which would not affect NDVI measurements.

After plots and drought shelters were erected in 2022, NDVI measurements were taken for a total of two years until May 2024. Measurements were taken roughly every ten days throughout the experiment, except in the summer months where measurements were taken monthly. This was due to the high temperatures and lack of precipitation, which resulted in

minimal variation in NDVI during the summer months. At the first rain event of the fall, NDVI measurements returned to being taken every ten days to track the green-up timing of plots. NDVI values were collected utilizing a RapidSCAN CS-45 Handheld Crop Sensor. The sensor was held at a consistent height of 1.5m off the ground when scanning, resulting in a 1.24m x 0.26m scanned area. Scan height only varied in the case of some drought treatment plots which, due to the slope of the ground, had shelters hanging lower than 1.5m above the ground. In these instances, the sensor was held directly beneath the drought shelter roof to ensure the roofing material would not interfere with the NDVI values. NDVI measurements were taken from the four corners of each plot and then averaged to create a single NDVI measurement per plot, per day. NDVI measurements were only taken on days without precipitation. The RapidSCAN sensor is advertised as being able to collect consistent NDVI values regardless of ambient light level; however, two anomalous NDVI recordings on January 16, 2023 and April 12, 2023 were removed from the study due to unusually low values, likely because they were collected in the late afternoon when ambient light levels were low.

Volumetric water content (VWC) was collected in each plot utilizing three Tomst TMS-4 sensors, which rely on time domain reflectometry to estimate the water content of soil. The sensors tracked VWC at depths of 0-12.5 cm, 12.5-25 cm, and 37.5-50 cm. Each sensor was placed at a consistent depth, although in some plots the deepest sensor could not reach 50 cm due to large rock deposits. In these instances, the sensor was placed as deeply as possible. The sensors were installed March 20, 2022, and recorded VWC every 15 minutes until May 2023.

NDVI data were analyzed in R to assess phenological traits and patterns (R Core Team, 2021). Seasonal maximum NDVI value for each plot was determined, then an ANOVA test utilizing the *car* package was run to assess the effects of burn and drought treatment on peak

NDVI value as well as the day of peak NDVI (Fox, 2019). To determine green-up and senescence dates, a smooth spline curve was applied to the NDVI data for each plot, and derivatives were taken for each observation. Green-up and senescence dates were determined by selecting an appropriate threshold for each phenological date of interest and selecting the earliest derivative value that exceeded it. Phenological dates were then assessed using an ANOVA test to look for significant effects of burn and drought treatment type on date of green-up and senescence for each year. Given the study was conducted from May 2022 until May 2024, the data set contained two periods of green up and one period of senescence, which correlated with Southern California's wet and dry seasons. May 20, 2022 was the date of the first NDVI measurement and was treated as day zero. The ggplot2 package was utilized to visualize data results (Wickham, 2016).

Results

When observing NDVI from May 2022 to May 2024, two growing periods and one senescence period were clearly visible (Figure 1). All treatments generally adhered to a pattern of increased NDVI during the wet seasons and decreased NDVI during dry seasons. At the start of the experiment, NDVI values were relatively low in both burned treatment types, with the unburned treatment having higher NDVI. At the onset of the first wet season in November 2022, all treatments experienced increases in NDVI until May 2023 when the dry season began, and plants in all treatments senesced. In August of 2023, Hurricane Hillary hit Southern California, bringing abnormally high precipitation levels, and led to an increase in NDVI across all treatments before the start of the wet season. This secondary increase declined briefly before the true commencement of the 2024 wet season, but overall caused a shorter dry season than is typical for the area. VWC data aligned with precipitation events in San Marcos and increases correlated with increased NDVI (Figure 1). Additionally, VWC only began to differ between drought treatments after shelters were erected above the drought plots. After shelters were erected, drought treatments showed significantly lower rates of water loss and water infiltration compared to ambient plots, demonstrating their efficacy in diminishing precipitation (Lipson 2023).

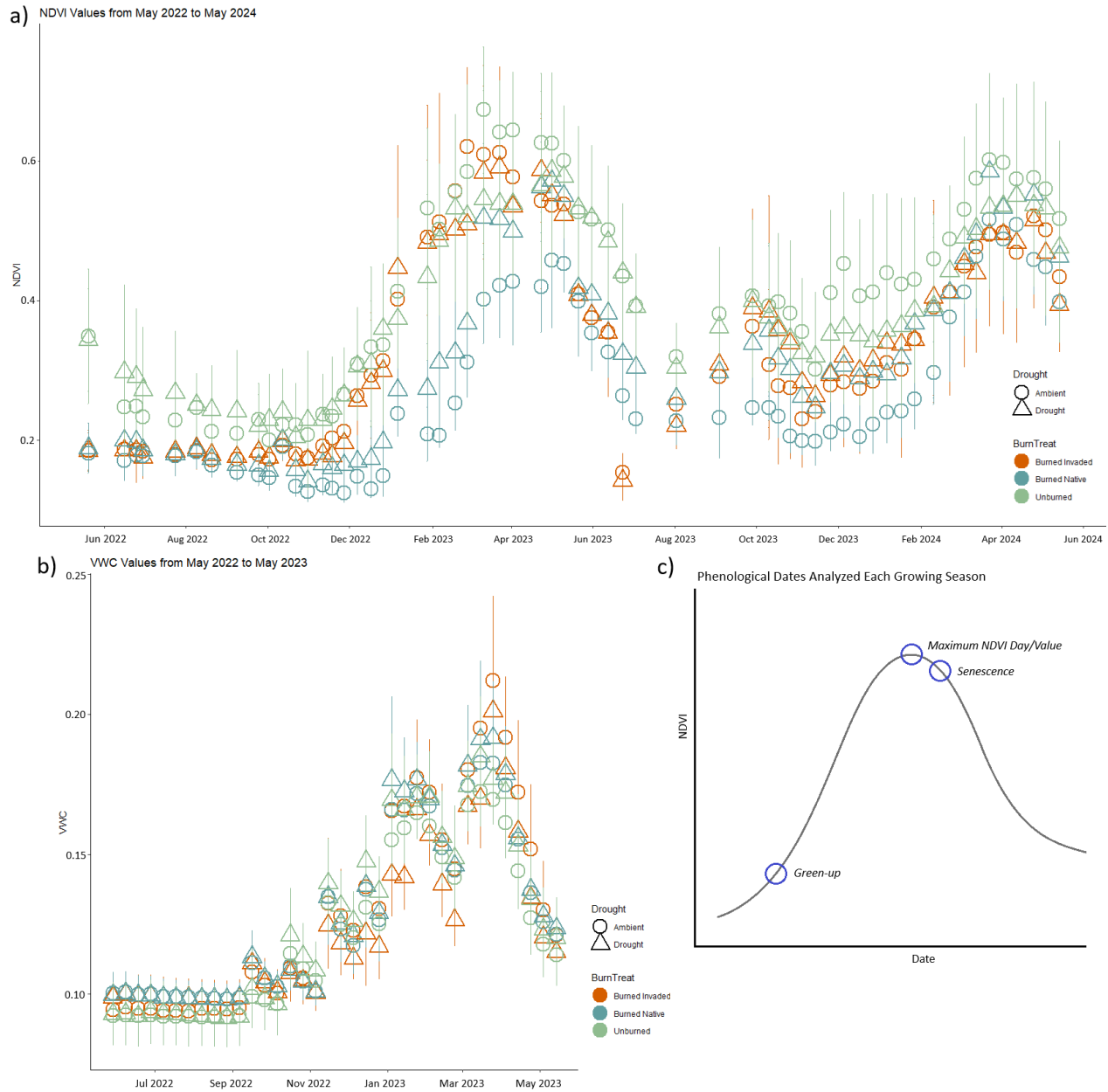


Figure 1: a) Mean NDVI and b) mean VWC value by burn and drought treatment from a) May 2022 to May 2024 and b) May 2022 to May 2023. Error bars represent ± 1 SD. High VWC correlates with NDVI during the first year. c) For NDVI, four phenological traits were accessed for each growing season: green-up, senescence, and maximum NDVI date/value.

Phenological dates were extracted from the larger dataset by fitting a smoothed spline to average NDVI values for each plot, and then searching for derivatives that exceeded a specified threshold. Thresholds varied for each phenological date due to differently behaving curves at the time points of interest and were chosen based on visual suitability to the data. Thresholds were

consistent for each phenological date across all plots except for plot 6 in the 2023-2024 green-up period, which required a more sensitive threshold to detect an accurate NDVI increase. Plots were then grouped by burn and drought treatment type and average phenological dates were compared.

Table 1: F and p values for green-up day (2022-2023 and 2023-2024), date of maximum NDVI (2022-2023 and 2023-2024), maximum NDVI value (2022-2023 and 2023-2024), and senescence (2023) from a two-way ANOVA analysis analyzing burn and drought treatment. Significant p values are indicated by *, and degrees of freedom are indicated in F values.

	Burn Treatment		Drought Treatment		Burn:Drought	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Green-up 2022-2023	7.0437 _{2,30}	0.003105*	0.231 _{1,30}	0.6342	0.2379 _{2,30}	0.7898
2023-2024	2.384 _{2,30}	0.1094	0.7446 _{1,30}	0.395	0.4271 _{2,30}	0.6563
Date of Max NDVI 2022-2023	24.7787 _{2,30}	<.001*	6.5394 _{1,30}	0.01585*	2.7997 _{2,30}	0.0768
2023-2024	0.1669 _{2,30}	0.8471	0.1951 _{1,30}	0.6619	0.6564 _{2,30}	0.526
Max NDVI Value 2022-2023	6.7142 _{2,30}	0.003892*	0.0823 _{1,30}	0.7762	2.2279 _{2,30}	0.1253
2023-2024	1.0562 _{2,30}	0.3604	0.1648 _{1,30}	0.6877	0.8378 _{2,30}	0.4425
Senescence 2023	0.4512 _{2,30}	0.6411	0.2629 _{1,30}	0.6119	2.427 _{2,30}	0.1054

Table 2: Mean and ± 1 standard deviation for green-up day (2022-2023 and 2023-2024), date of maximum NDVI (2022-2023 and 2023-2024), maximum NDVI value (2022-2023 and 2023-2024), and senescence (2023) across all burn and drought treatment types.

	Burned Invaded				Burned Native				Unburned			
	Ambient		Drought		Ambient		Drought		Ambient		Drought	
	<i>Mean</i>	<i>SD</i>	<i>Mean</i>	<i>SD</i>	<i>Mean</i>	<i>SD</i>	<i>Mean</i>	<i>SD</i>	<i>Mean</i>	<i>SD</i>	<i>Mean</i>	<i>SD</i>
Green-up 2022-2023	181.2	18	192.7	31.3	215.3	37	219.8	26.8	181.2	22.9	177.8	15.8
2023-2024	503.8	77.1	497.2	90.8	580.7	54.8	526.5	85.1	493.8	69.6	490	66.5
Date of Max NDVI 2022-2023	289.5	11.8	295.2	18.5	342.5	17.9	347.7	6.5	303	25.9	339.2	22.6
2023-2024	637.7	134	667	78.5	628.5	128.8	626.8	128	667.8	72.2	586	167.1
Max NDVI Value 2022-2023	0.6483	0.0973	0.6435	0.0715	0.5006	0.0651	0.5879	0.0674	0.6908	0.0739	0.6329	0.1217
2023-2024	0.5585	0.1228	0.5442	0.0874	0.5333	0.073	0.612	0.0872	0.6239	0.1004	0.6024	0.1465
Senescence 2023	325	24.6	325.3	22.4	342.8	35.5	324.2	28.6	319.3	28.4	352.7	33.8

The experiment captured two growing seasons and therefore two green-up time periods were analyzed: May 2022-2023 and May 2023-2024. In the May 2022-2023 time frame, burn treatment had a significant effect on green-up day ($F_{2,30} = 7.0437$, $p = 0.003105$), and drought

treatment was insignificant (Table 1). The unburned treatment had the earliest mean green-up day of 180 (11/16/2022), and the burned invaded treatment had a comparable mean of day 187 (11/23/2022) (Figure 2). However, the burned native treatment had a significantly later mean green-up day of 218 (12/24/2022), a difference of 31 days when compared to the invaded treatment (Table 2). In the May 2023-2024 growing period, neither burn treatment nor drought treatment had a significant effect on day of green-up (Table 1). Green-up was between day 490 and 581 for all plots, which falls between 9/22/2023 and 12/22/2023 (Table 2).

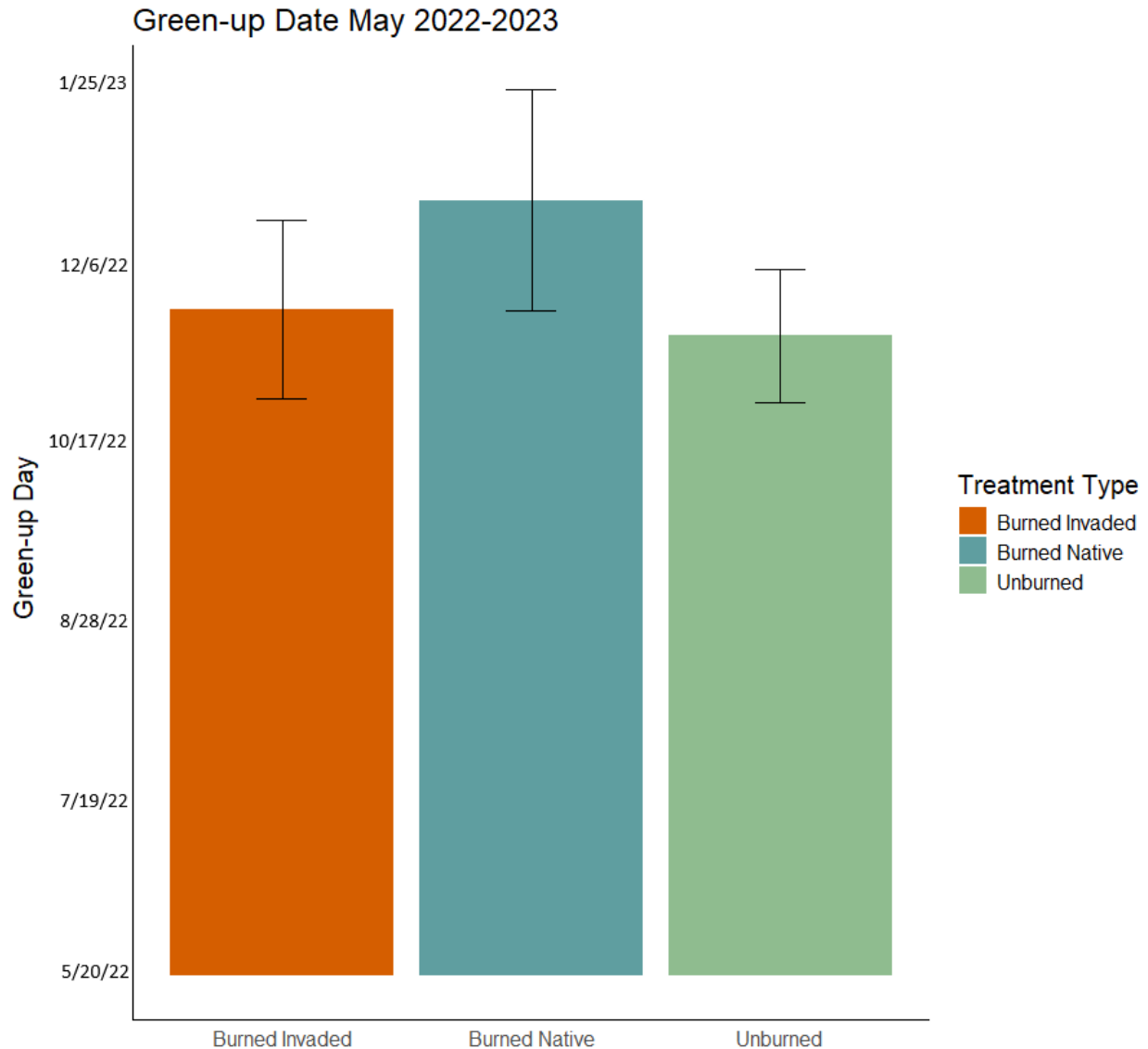


Figure 2: Mean green-up day during the May 2022- May 2023 growing period by burn treatment type. Error bars represent ± 1 SD. The unburned treatment had the earliest green-up day (11/16/2022), and the burned native treatment had the latest (12/24/2022).

We also found the maximum, or peak, NDVI values for each treatment type within each growing season. From May 2022-2023, both burn treatment and drought treatment type were found to have a significant effect on maximum NDVI day ($F_{2,30} = 24.7787$, $p < 0.001$, $F_{1,30} = 6.5394$, $p = 0.01585$) (Table 1). The burned invaded ambient treatment had the earliest maximum NDVI day of 290 (3/6/2023), and the burned invaded drought treatment had the next earliest day

of 295 (3/11/2023). The unburned treatment maximum NDVI occurred on day 303 (3/19/2023) in the ambient treatment and day 339 (4/24/2023) in the drought, while the burned native treatment maximum NDVI occurred on day 343 (4/28/2023) in the ambient treatment and 348 (5/3/2023) in the drought (Figure 3). On average, ambient treatments reached maximum NDVI 15 days sooner than drought treatments, with the unburned treatment having the largest differential between water treatments (36 days) (Table 2). In the second growing period from May 2023-2024, neither burn treatment nor drought treatment type influenced maximum NDVI day (Table 1). Maximum NDVI day ranged from 586 to 668 for all plots, which falls between 12/27/2023 and 3/18/2024 (Table 2).

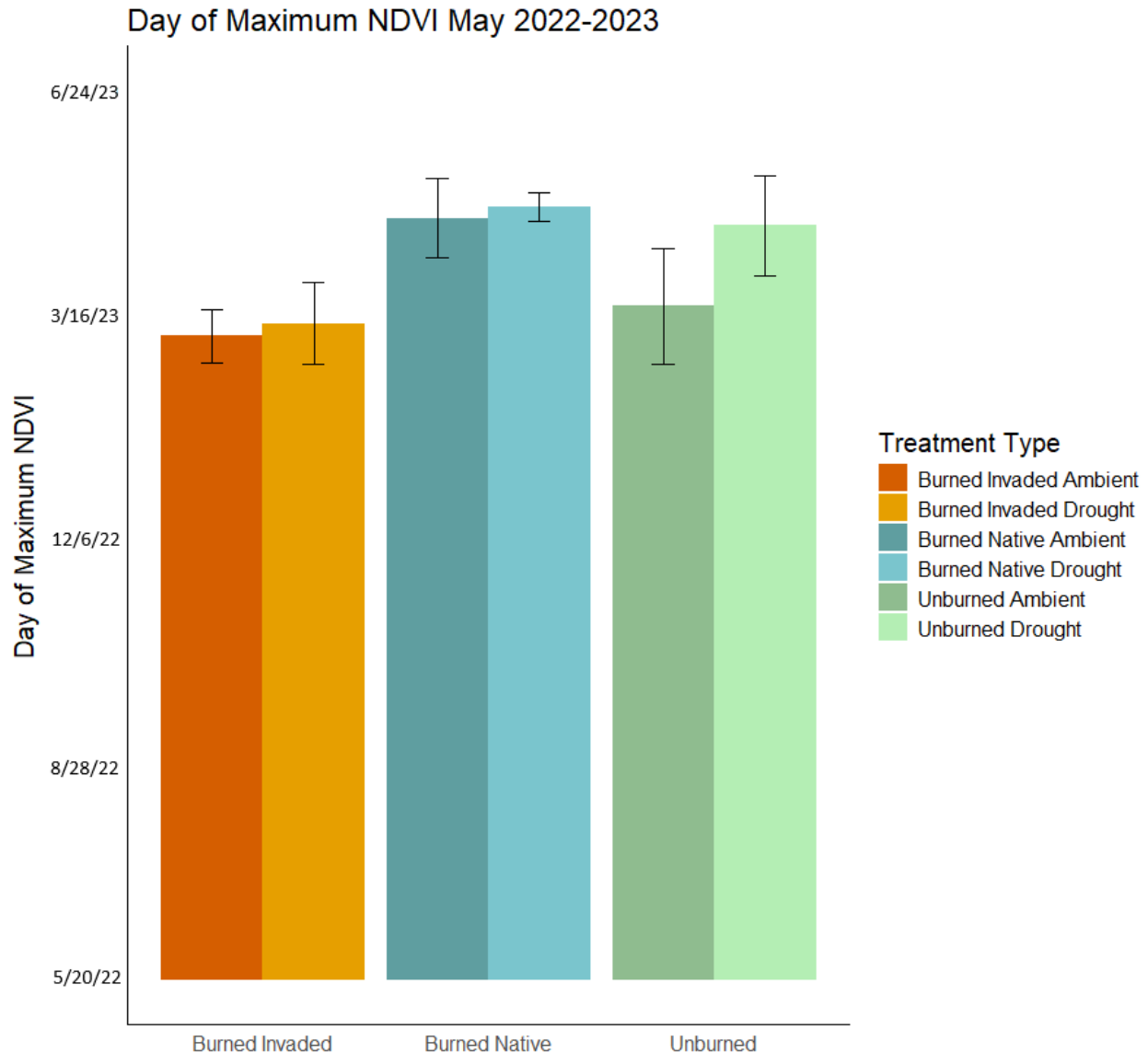


Figure 3: Mean day of maximum NDVI value during the May 2022-2023 growing period by burn and drought treatment. Error bars represent ± 1 SD. The burned invaded ambient treatment had the earliest day (3/6/2023) and the burned native ambient treatment had the latest (5/3/2023).

When assessing the maximum NDVI value for the May 2022-2023 growing season, only burn treatment type was significant ($F_{2,30} = 6.7142$, $p = 0.003892$) (Table 1). The unburned treatment had the highest mean maximum NDVI of 0.6618, with the burned invaded treatment having a mean maximum NDVI of 0.6459, and the burned native treatment having the lowest mean maximum NDVI of 0.5443 (Figure 4, Table 2). In the May 2023-2024 growing season

neither burn treatment type nor drought treatment type was significant (Table 1), and average maximum NDVI across all plots was 0.5790 (Table 2).

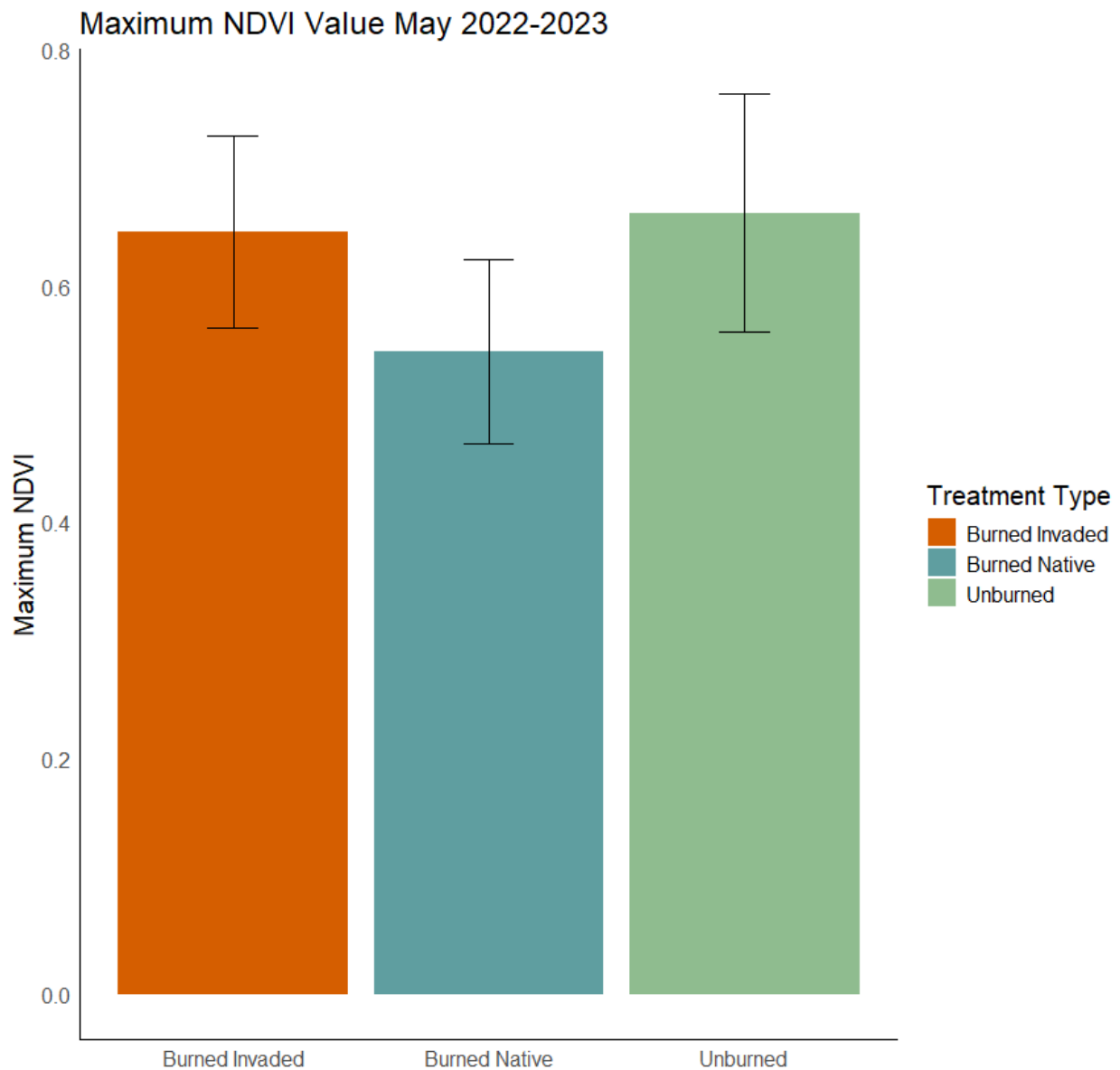


Figure 4: Mean maximum NDVI value during the May 2022-2023 growing period by burn treatment. Error bars represent ± 1 SD. The unburned treatment had the highest NDVI value (0.6618) and the burned native treatment had the lowest (0.5443).

The final point evaluated in the dataset was senescence date, which occurred between February 2023 and September 2023: the period from the end of the peak wet season through the end of the summer. Senescence was defined as the first date in which NDVI measurements

significantly decreased. Neither burn treatment type nor drought treatment type was found to have a significant effect on day of senescence (Table 1), which ranged from day 320 (4/05/2023) to day 353 (5/08/2023) (Table 2).

Discussion

Unburned CSS habitat had consistently higher NDVI values, and therefore productivity, when compared to recovering burned areas (Figure 1). The unburned areas of CSS maintained higher NDVI compared to burned areas in both drought and ambient precipitation conditions throughout all seasons, except for the burned invaded treatment during the start of the 2022-2023 wet season and the onset of Hurricane Hilary. Both cases can be explained by the ability of invasive herbaceous species to capitalize on large amounts of precipitation following prolonged dry periods faster than natives (Davis et al. 2000). But while the burned invaded treatment experienced high peaks in NDVI comparable to the unburned treatment, the same plots also faced harsh declines at the onset of the dry season, occasionally dropping lower than the burned native treatment. This pattern was consistent with the known drought escape strategy of invasive species in Southern California (Blumenthal et al. 2020). In comparison, the unburned treatment also peaked during the wet season, but maintained the highest level of NDVI during the dry season by virtue of the mature evergreen *Malosma laurina* and drought tolerant *Artemisia californica* and *Salvia mellifera* shrubs present throughout the plots (Cleland et al. 2016).

The burned native treatment, in contrast, had low NDVI when compared to other treatments. At the start of the experiment soon after the fire, the burned native treatment had NDVI values on par with the burned invaded treatment. Both were low due to being predominantly composed of seedlings and young resprouts during a dry season. However, at the start of the wet season, when the unburned and burned invaded plots experienced sharp NDVI increases, the burned native plots saw milder increases. This pattern was likely due to the slow growth rate of native CSS shrubs, which cannot capitalize on precipitation events and resources as quickly as herbaceous species, particularly as seedlings when they have shallow taproots

(Prater et al. 2006). However, during the 2023 dry season when the burned invaded treatment experienced massive NDVI declines, the burned native treatment approached and occasionally surpassed the burned invaded treatment. Following the 2023 dry season, the burned native treatment continued to match the NDVI of the burned invaded treatment, even with the onset of the 2023-2024 wet season. This displayed how native CSS can be outcompeted in biomass by invasive species following wildfire, but that this dominance is heavily coupled to the presence of precipitation. This fluctuation related to rainfall also matches the conclusions Esch et al.(2019) reached in their study assessing the carbon storage of native CSS and invasive herbaceous vegetation. The comparable NDVI values among the burned treatment types in the 2023-2024 year shows how, given time to mature and recover, native CSS vegetation produces NDVI values similar to invasive vegetation. Given the high NDVI of the unburned treatment type regardless of season, in future years the burned native treatment may grow to have consistently higher NDVI than the burned invaded treatment as the CSS vegetation matures to pre-fire levels.

Drought treatment tended to have a varied effect on NDVI. Across most statistical analysis drought treatment had an insignificant effect on NDVI. When observing Figure 1, ambient water treatments in the burned invaded and unburned treatments generally had higher NDVI values than the drought treatment. The differential was highest at the start and peaks of the wet season and diminished greatly at the onset of the dry seasons. However, in the burned native treatment the drought treatment type had higher NDVI than the ambient treatment, breaking the trend seen in the other experimental groups and in Wang et al. (2016). Following a similar pattern to the other burn treatment types, the difference between drought and ambient NDVI values in the burned native treatment also reached its most extreme during the wet seasons and diminished in the dry season. Based on the soil moisture data from November 2022 to May

2023, drought shelter plots had significantly lower stored soil moisture, indicating that drought shelters were receiving less water as intended (Lipson 2023). In addition, when soil content was analyzed across all plots, drought treatment plots consistently had higher nitrogen values across all burn treatment types, likely due to an increased temperature effect (Lipson 2023). This increase in nitrogen may have allowed water efficient native species to grow better in drought plots than ambient despite the lack of water and, due to their high-water use efficiency, were impacted far less by reduced precipitation levels compared to the invasive vegetation (Davis & Mooney 1985). The unburned treatment also didn't experience an increase in productivity when in drought conditions, likely because, while the mature shrubs are highly water use efficient, the increase in nitrogen was not enough to influence their growth due to their large size and slow growth rate as seen in other CSS-based studies (Lawrence 2015).

When looking at phenological dates, results were mixed across the experiment, particularly during later time points. In the first 2022-2023 wet season, some clear patterns arose among green-up date, maximum NDVI day, and maximum NDVI value. Burn treatment type had a significant effect on all three factors. In both green-up date and maximum NDVI day, the burned invaded and unburned treatments had the earliest dates, with green-up occurring well before maximum NDVI day. The opportunistic invasive species and mature CSS took quick advantage of the precipitation at the onset of the wet season and peaked in biomass relatively quickly. Of the two, the mature CSS vegetation greened-up earlier, which aligns with the findings of Esch et al. (2019). The two treatment types also had similar maximum NDVI values in the 2022-2023 wet season, with the unburned treatment exceeding the burned invaded treatment. For all three traits, the burned native treatment lagged. It had the latest green-up and maximum NDVI dates, and the lowest NDVI peak. This can be attributed to the slow growing

nature of native CSS shrubs as seedlings. Of the three data points assessed in the 2022-2023 year, drought treatment type was only significant for maximum NDVI day. Across all burn treatments, the ambient treatment achieved maximum NDVI sooner than the drought treatment. This is expected since lower precipitation levels should limit the speed at which vegetation can grow, which also echoes the findings of Esch et al. (2019).

In the 2023-2024 year, the NDVI data was more inconsistent. Across the four data points analyzed during the time period (senescence date, green-up date, maximum NDVI day, and maximum NDVI value), neither burn nor drought treatment type had a significant effect. In particular, the dates for senescence, green-up, and maximum NDVI were highly variable. There were two key reasons behind this variance: frequency of summer NDVI measures and the presence of Hurricane Hilary. The frequency of NDVI measurements in the summer mainly affected our ability to discern senescence date. During the summer months, NDVI measurements were taken once a month as opposed to every 10 days. This was originally done due to the assumption that plant growth would be minimal during the dry season. While NDVI did stay relatively stagnant throughout the summer months, the lack of measurements diminished our ability to assess senescence and minimum NDVI dates with any amount of statistical significance. The senescence dates that we ascertained were done by analyzing the first point of decrease in NDVI following the peak growing season, which was highly variable between plots and is likely less reliable than a minimum NDVI date would have been. The second factor affecting phenological dates in the 2023-2024 year was Hurricane Hilary, which hit Southern California in August of 2023 and brought uncharacteristically large amounts of precipitation during the dry season. This caused a premature growth spike across all plots. The secondary bump in NDVI before the start of the wet season is clearly visible across all treatment types in

Figure 1. This sudden increase in precipitation likely led to staggered green-up and maximum NDVI dates for all plots. Another point to consider given the insignificance of burn and drought treatments in the 2023-2024 year is the recovery time afforded to each burn treatment. During the second wet season, the burned invaded and burned native treatments had statistically equivalent NDVI values with each other and the unburned treatment, indicating that the burned treatments were substantially recovered when compared to the start of the experiment. This is also indicated by the lack of significant factors in the maximum NDVI value in the 2023-2024 year. It is likely that, given the time to grow and recover, there is no longer much difference in NDVI, and therefore productivity, among the burned and unburned plots (Keeley & Keeley 1984). It is also possible that, given the unusually large amount of precipitation the year experienced, the drought shelters did not significantly hamper vegetative growth and therefore didn't impact NDVI.

We originally hypothesized that the burned invaded treatment would have the earliest NDVI increase in the wet season, given that invasive species can quickly capitalize on resources. In large part this was confirmed: the burned invaded treatment had earlier green-up and maximum NDVI dates in the 2022-2023 growing season compared to the burned native treatment. We also assumed that the burned invaded area would experience an earlier senescence date due to drought escape phenology, which wasn't conclusive given there was no significant effect of burn treatment on senescence date. We predicted that the burned native treatment would have higher NDVI values than the burned invaded treatment during the dry season, due to the drought tolerance traits of native CSS vegetation. The results showed that the two burned treatments had comparable NDVI values during the dry season, but the gap between invaded and native treatments that originally existed during the wet season disappeared during that time. As

predicted, the unburned control treatment consistently had the highest NDVI, which makes sense given that it is dominated by mature, drought tolerant or drought avoidant shrubs. Drought treatment did not have an effect on NDVI and was only relevant for day of maximum NDVI in 2022-2023. It did not disproportionately affect burned areas and did not have a significant effect on most phenological dates. This stands in contrast to other studies in CSS systems that found a heavy correlation between rainfall and productivity, particularly among invasive herbaceous species (Bartolome 1979).

Overall, this study confirmed that herbaceous species invasive to CSS systems following wildfire have higher growth rates in the wet season when compared to recovering native vegetation. This difference diminished in the dry season, and two years after the fire we observed that recovering invaded and native areas had comparable NDVI values. This implies that, while invasive species initially have the advantage after wildfire, given enough time native species can catch up in productivity. These results are somewhat obfuscated due to the takeover of the native herbaceous species *Malacothamnus fasciculatus* in both burned treatment types which occurred late into the 2022-2023 wet season. *M. fasciculatus* is fast growing and by the end of the wet season had successfully filled nearly all empty space in the burned invaded and burned native treatments. Given that *M. fasciculatus* is a species that only germinates in post-fire environments, this pattern of takeover has previously been observed, and there was likely a large amount of seeds present in the soil seed bank prior to the fire (Morse 2023). *M. fasciculatus* likely heavily influenced the NDVI values of both treatments for the rest of the experiment due to its tall stature and high leaf coverage, therefore blurring the line between our invaded and native distinction. However, the takeover by *M. fasciculatus* in both areas also indicates the capability of native CSS species to recover after wildfire, even when areas are initially invaded. The heavy

presence of *M. fasciculatus* makes it difficult to come to clear conclusions about what invasive species mean for long term carbon storage in CSS systems. Despite this, conclusions can still be drawn from the earlier seasons of the experiment that indicate that invaded areas have higher short-term carbon storage at the start of fire recovery, but that this storage diminishes at the onset of the dry season. In addition, the constant dominance in productivity of unburned native vegetation indicates that fully mature native areas are the preferable outcome for fire recovery, and that the burned native areas, once given enough time to fully grow, would likely outcompete invaded areas which distinctly lack woody, native shrub species. This matches the findings of the Prater et al. (2006) study, which concluded that native CSS vegetation served as a more stable long term carbon sink than areas populated by annual invasives.

Throughout the experiment, NDVI values were also influenced by some hard to account for factors. NDVI is known to be largely influenced by color due to the nature of the measurement. NDVI tracks leaf greenness, and can consequently be influenced by plant species with differently colored foliage (Wang et al. 2016). *Eriodictyon crassifolium*, a common native species on the experimental site, has lighter, blue-green vegetation, when compared to the bright green *Malosma laurina* shrubs. It is possible that the dominant species in a given plot played a larger role in NDVI value than vegetation productivity. Since the same plots were measured across the experiment at the same locations, values fluctuated relative to productivity changes within plots. But when comparing plots with different species compositions, it is possible that there may have been differences that didn't accurately convey productivity levels. Additionally, NDVI values have been shown to be influenced by blooming dates, as the color of flowers at high density can influence NDVI values (Wang et al. 2016). However, the timing of bloom up in our experiment did not seem to correlate with any NDVI decreases, despite the large amount of

flowering *M. fasciculatus* dominating most of the burned treatment plots. In other experiments NDVI has been known to be heavily influenced by cloud cover and soil reflectance, but due to the small scale and ground-level approach in our experiment, these issues were negligible (Pettorelli et al. 2005).

Other experiments utilizing NDVI as a proxy for productivity and carbon storage primarily used satellite imaging (Del Grosso et al. 2018, Zhou et al. 2001, Pettorelli et al. 2005, Wang et al. 2003, Gillespie et al. 2018). This experiment afforded a more sensitive and localized measure on productivity to assess the effects of plant community composition on productivity. With the rise in wildfire frequency and intensity in Southern California it is vital to assess methods of CSS recovery and how it is impacted by the presence of invasive species. CSS systems are diminishing in size due to human development and are degrading in the face of higher invasion rates, which are further propelled by both increased human presence and increased fire occurrence (Bell et al. 2016). CSS systems provide valuable services in the form of habitats for many endemic plant and animal species, erosion protection, recreation, and carbon sinks (Bowler 2000). In the face of rising atmospheric CO₂ levels, a direct driver of increased drought and fires, it has never been more important to understand what mechanisms drive the carbon storage capabilities of ecosystems. The results of this study highlight how important it is to limit the establishment of invasive species in the post-fire recovery of CSS systems to allow native shrub species to establish, and later contribute to a more robust carbon sink.

Conclusion

Native CSS shrubs are primarily responsible for the long-term carbon storage in CSS systems, which is supported by the unburned treatment's consistently high productivity throughout our experiment. Our study showed that invaded CSS systems can produce high levels of productivity, but generally for a shorter growing season when compared to native-dominated areas. Our results show that, in the long term, it is preferable for native CSS species to repopulate burned areas as they will lead to overall greater and longer-term carbon sinks as they mature. This emphasizes the importance of monitoring CSS recovery following wildfire and the control of invasive species encroaching on native CSS systems. Drought treatment type had no effect on productivity in our experiment, potentially due to the relatively high rainfall experienced during the two growing seasons of the study. Future studies should further assess the impact of invasive and native vegetation on NDVI on a longer timescale to track the full maturation of both vegetation types to determine the scale of carbon storage that each provides. Future directions could also include species-specific NDVI analysis to determine the individual species' effects upon NDVI and productivity. Our study uniquely showed the NDVI values of recovering native and invasive vegetation in a CSS system during the first two years following wildfire, and serves as an example of the productivity patterns of varying vegetation types through the wet and dry season.

This study was in collaboration with Karagan Smith, and was a subsection of her dissertation, "Assessing the Impacts of Drought, Invasion, and Herbivory on Postfire Coastal Sage Recovery and Ecosystem Function: A Multiscale Investigation", which is currently in progress.

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