Title

Climate and plant resource controls on coastal sage scrub ecohydrology and succession

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Climate and plant resource controls on coastal sage scrub ecohydrology and succession

DISSERTATION

submitted in partial satisfaction of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

in Earth System Science

by

Scot Parker

Dissertation Committee:
Professor Michael Goulden, Chair
Professor James Randerson
Professor Steven Allison

2019

DEDICATION

To

Karen Parker

For your unending patience, support, and love

“I know of no pleasure deeper than that which comes from contemplating the natural world and trying to understand it.”
- Sir David Attenborough

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I thank my committee members, Dr. Steven Allison and Dr. James Randerson, for your comments, insight, advice, and course corrections along the way. Several times I would have found myself pushing down dead ends without your guidance and wisdom. Your feedback throughout my Ph.D. and on my dissertation at the end was invaluable and helped elevate this work to defendable quality. At every committee meeting, I felt humbled and honored to have the opportunity to benefit from your intelligence, insight, knowledge, and experience, and I am enormously grateful for your willingness to serve on my committee. Thank you as well for your kindness and support through some difficult times over the years.

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proofreading, for listening to endless rehearsals, and of course for the many years of our friendship to date. Thank you to my family for forgiving me whenever I couldn’t make it to a family event, for putting up with my frequent lack of communication, and for supporting me throughout the years. In particular I want to thank Brian and Shelly Gragg for being the most supportive set of parents-in-law that I could hope for, Dr. Don Gragg for your prescient words as I embarked on this journey, my parents Merle and Vicki for encouraging my love of nature as a child, and my brother Nathan for not giving me too much of a hard time for not visiting you in Portland throughout this process. Thank you to my dive buddies, Scott Dreslinski, Dr. Roy Hobbs, Mike Faust, Ludek Subrt, Cliff Simon, Chris Kirkman, Dan Brown, Mitch Pingrey, Amanda Pingrey, Dr. Katie Schaefer, Lillian Jaeger, and many more for putting up with all the dives I have had to miss. Thank you to my SCUBA students for your patience as I finished my Ph.D. Thank you to all the rest of my friends – Sarah Barr, Kaitlyn Smith, Erin Delman, Alexandria McEnroe, Matt McKnett, Lauren Gragg, Alan Newton, Adam Bradshaw, Mike Masukawa, Lisa Masukawa, Dr. Aggie Fielder Szymanska, Dan Fielder, Tina Geller, Jessica Wang, Dr. Elliot Sherman, Dr. Aimee Sherman, Dr. Wenshan Wang, Dr. Lu An, Dr. Cheng Dang, Dr. Robert Wood, Dr. Kathleen Johnson, and so many more for all the support over the years.

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ABSTRACT OF THE DISSERTATION

Climate and plant resource controls on coastal sage scrub ecohydrology and succession

By

Scot Parker

Doctor of Philosophy in Earth System Science

University of California, Irvine, 2019

Professor Michael Goulden, Chair

The ability of ecosystems to recover from disturbance likely has limits, and shifting disturbance regimes or altered recovery conditions may cause ecosystem degradation and increase vulnerability to species invasion and type conversion. Human activities affect disturbance-prone ecosystems in many ways, including fire frequency, introduction of invasive species, and shifts in water, nutrients, and other plant resources. This dissertation investigates the effects of altered precipitation and nitrogen input on adjacent coastal sage scrub (CSS) and grassland communities in the Santa Ana Mountain foothills during post-fire recovery.

Chapter two examines the ecohydrology of CSS and grassland to determine their respective water use strategies and investigate how they coexist and differ under similar climates. Deeper roots and access to stable deep-water stores allow CSS to employ a conservative growth and water use strategy, whereas grassland follows a “live fast, die young” strategy with rapid,

intense water withdrawal over a shallower depth range and ~~a~~ shorter growing season. While a mature CSS community tolerates the presence of invasive annuals, a disturbance pattern that kills CSS individuals completely and prevents post-fire resprouting may increase vulnerability to invasion.

Chapter three examines the impact of altered resources on CSS successional patterns. Altered water input is an important controller of successional rate for drought-adapted ecosystems, with reduced water decelerating and increased water accelerating succession. The combination of restricted water and added nitrogen may produce a fundamental shift in CSS succession away from a shrub-dominated community, leading to increased vulnerability of CSS to invasion by Eurasian grassland.

Chapter four investigates the transient maximum ecosystem productivity hypothesis. A transient productivity maximum occurs in the CSS independent of nitrogen or water inputs, indicating this phenomenon is likely driven by light availability and dominance by plant species that have been selected to rapidly capture space. Increased nitrogen and reduced water availability both shift the vegetation type responsible for the transient maximum from the native nitrogen-fixing subshrub *Acmispon glaber* to Eurasian grasses. Increases in drought and nitrogen deposition may reduce the importance of *A. glaber* during CSS fire recovery, with cascading effects on ecosystem function.

CHAPTER 1

Introduction

Human activities such as urbanization, grazing, land use change, introduction of invasive species, climate change, habitat degradation, and nutrient deposition are reducing biodiversity and negatively impacting ecosystems worldwide (*Aerts and Berendse*, 1988; *Wilson*, 1992; *Ehrlich and Daily*, 1993; *Butchart et al.*, 2010; *Cardinale et al.*, 2012) and will likely continue to do so in the future. Conservation areas protect ecosystems from the direct effects of urbanization, grazing, and land use change, but other consequences of human activities such as climate change and nutrient deposition can cause habitat degradation even within these conservation areas. These impacts may be local (e.g., urbanization, grazing, and land use change), regional (e.g., nutrient deposition and invasive species introduction), or global (e.g., climate change).

The California Floristic Province, noted for its high biodiversity and endemism (*Stein et al.*, 2000), is suffering massive habitat loss and threat of extinction due to human activities (*Myers*, 1990; *Schoenherr*, 1992; *Myers et al.*, 2000; *Brooks et al.*, 2002; *Barbour et al.*, 2007) and has been identified as a biodiversity hotspot and recommended as a priority for global conservation efforts (*Myers et al.*, 2000). Among the threatened communities is southern California's coastal sage scrub (CSS), whose habitat has decreased considerably because of the expansion of urban areas and changing land use, and indirectly through ecosystem type conversions: by 2005, nearly half of southern California's coastal sage had been converted to Eurasian grasslands (*Wieslander et al.*, 1933; *Thorne et al.*, 2006; *Talluto and Suding*, 2008), with several endemic plant and animal species threatened with extinction due to habitat loss. This situation will worsen, with southern California among the regions projected to experience the greatest change in climate in the continental United States by the end of the century (*Bell et al.*, 2004; *Hayhoe et al.*, 2004; *Loarie et al.*, 2008; *AghaKouchak et al.*, 2014; *Romero-Lankao, et al.*, 2014; *Berg and Hall*, 2015; *Diffenbaugh et al.*, 2015; *Hall et al.*, 2018; *Swain et al.*, 2018). Coastal sage is now considered to be an endangered ecosystem and the threat of vegetation type conversions in the remaining areas of coastal sage is of critical concern for conservation (*Kirkpatrick and Hutchinson*, 1980; *Wilson*, 1999; *Myers et al.*, 2000; *Padilla et al.*, 2009; *Cox and Allen*, 2011).

Disturbance-adapted ecosystems such as CSS tend to follow characteristic recovery patterns and are necessarily well-adapted to their historic disturbance regimes; however, their adaptations likely have limits, and changes in disturbance regimes or recovery conditions from the historical norm may affect an ecosystem's ability to recover (*Tilman*, 1985; *Davis and Shaw*, 2001; *Syphard et al.*, 2007; *Hoffmann and Sgrò*, 2011; *Silva et al.*, 2013). By its nature, disturbance reduces the competitive dominance of established species and opens the possibility that the subsequent recovery trajectory will lead to species shifts relative to the pre-disturbance community; therefore, the post-disturbance recovery period may represent a window of increased vulnerability to invasion and ecosystem type conversion (*D'Antonio and Vitousek*, 1992; *Mack and D'Antonio*, 1998; *Pyšek et al.*, 2010; *Seastedt and Pyšek*, 2011; *Keeley and Brennan*, 2012; *Kimball et al.*, 2014). Different species within an ecosystem may not be equally susceptible to chemical or physical conditions such as drought or nitrogen deposition, with some species displaying greater responses than others (*Baer, et al.*, 2003). Disturbance recovery patterns influence the climate by controlling the duration and magnitude of disturbance-related climate forcings, such as carbon emissions and storage, changes in surface albedo, and changes in nutrient cycling; therefore, understanding how human impacts affect ecosystem recovery from disturbance is an important question from both an ecological and earth system science perspective.

Human impacts on the biosphere have altered the CSS disturbance regime and recovery conditions through the introduction of invasive species, increases in fire frequency and nitrogen deposition, and climate change, including increased drought and precipitation variability (*Whisenant*, 1990; *D'Antonio and Vitousek*, 1992; *Chapin et al.*, 2000; *Dale et al.*, 2001; *Keeley and Davis*, 2007; *Fenn et al.*, 2010; *Turner*, 2010; *Enright et al.*, 2011; *AghaKouchak et al.*, 2014; *Berg and Hall*, 2015; *Diffenbaugh et al.*, 2015; *Hall et al.*, 2018). These changes have altered the competitive relationships that drive CSS succession and have decreased the ability of CSS to return to pre-disturbance conditions in many areas, leading to habitat degradation and loss. The main factors controlling the conversion of coastal sage to Eurasian grassland are drought severity, nitrogen deposition, and fire frequency (*Keeley et al.*, 1981; *Allen et al.*, 1998; *Allen et al.*, 2005; *Keeley et al.*, 2005b; *Keeley et al.*, 2006; *Wood et al.*, 2006; *Talluto and Suding*, 2008; *Rao and Allen*, 2010; *Keeley and Brennan*, 2012). These factors will become increasingly problematic for native coastal sage ecosystems in the future as Earth's climate changes and urban areas expand.

In the cismontane region of southern California that contains the majority of coastal sage scrub ecosystem, future climate change is projected to manifest as an increase in precipitation variability, a decrease in total number of rain days per year, a decrease in total annual rain, and an increase in rainfall during extreme precipitation events (*Bell et al.*, 2004; *Hayhoe et al.*, 2004; *Seager et al.*, 2007; *Loarie et al.*, 2008; *AghaKouchak et al.*, 2014; *Romero-Lankao, et al.*, 2014;

Berg and Hall, 2015; *Diffenbaugh et al.*, 2015; *Hall et al.*, 2018; *Swain et al.*, 2018). Models indicate that changes in precipitation patterns will lead to increased aridity and that future droughts will tend to become more severe. Nitrogen deposition, particularly surrounding large population centers in southern California, greatly exceeds baseline levels and is expected to increase as urban areas expand (*Allen et al.*, 2005; *Fenn et al.*, 2010). Increased nitrogen deposition due to urban air pollution is thought to favor ecosystem type conversions to exotic grasslands (*Allen et al.*, 1998; *Wood et al.*, 2006; *Rao and Allen*, 2010; *Kimball et al.*, 2014). Fire frequency is expected to increase concurrently with the projected increase in drought frequency and severity and with population growth and urban expansion, which led to an increase in human-driven ignitions (*Keeley and Davis*, 2007; *Syphard et al.*, 2007).

Four main questions motivated this dissertation: 1) How do CSS and Eurasian annual grassland differ in water access and use under similar climate regimes? 2) How does altered water and nitrogen availability affect CSS fire recovery? 3) Is there a transient productivity maximum during CSS succession, and if so, how do altered water and nitrogen affect it? 4) What are the implications of projected changes in resource availability for the CSS ecosystem? Chapters two through four of this dissertation address questions one through three respectively, while question four is investigated throughout the dissertation.

To address these questions, this research used a long-term water- and nitrogen-manipulation experiment constructed in adjacent CSS and grassland communities at Loma Ridge in the foothills of the Santa Ana mountains immediately following the Santiago wildfire that occurred in October, 2007. Data collection began in the 2008-2009 growing season, and included measurements of the physical environment and ecosystem structure and function made on scales from minutes to years to capture processes that occur both within and between growing seasons during fire recovery. Aspects of the physical environment that were monitored include both surface and deep soil moisture, soil matric potential, soil and air temperature, relative humidity, fuel moisture, leaf wetness, soil texture, and precipitation. Ecosystem structure and function was monitored through plot- and community-scale measurements of EVI and NDVI and measurements of productivity and community composition within the treatment plots.

Chapter two seeks to explain why CSS and Eurasian grassland appear to be alternative stable states under similar environmental conditions in southern California. The two communities were determined to have different water-use strategies that enabled them to in a stable mosaic over long periods of time. The differing water-use strategies and phenological patterns of the two ecosystems indicate that, while recovering and mature CSS communities are tolerant of invasive annual presence, CSS establishment in a Eurasian grassland is highly unlikely to occur. Physiological properties of CSS confer resilience and resistance to invasion by Eurasian grasses during the fire recovery period. However, this chapter suggests that substantial alterations in the disturbance regime may impact CSS fire recovery enough to favor ecosystem type conversion to Eurasian grassland.

Chapter three investigates patterns of CSS succession under altered resource conditions using a conceptual framework that includes three non-mutually-exclusive patterns through which altered resources may impact succession. Altered resource availability may amplify or diminish changes in ecosystem properties during succession, such as total cover, NPP, or individual species abundance. Altered resource availability may accelerate or decelerate succession, leading to a more rapid or slower return to pre-disturbance conditions. In extreme cases, altered resource availability during recovery may alter the successional trajectory in such a way that potentially irreversible changes to ecosystem structure and function may result, such as ecosystem type conversion. All three of these patterns occurred in various combinations under different water and nitrogen inputs. This indicates that these resources are strong controllers on CSS successional patterns and suggests that alterations in these resources may have long-lasting impacts on CSS survival.

Chapter four investigates the ecological concept of the mid-succession transient productivity maximum within the context of CSS fire recovery. This chapter demonstrates the existence of this phenomenon during CSS fire recovery, and shows that it occurs across a range of water and nitrogen inputs. This suggests that another factor controls this response, likely the combination of increased light availability and the abundance of species that have evolved to rapidly capture unoccupied above and belowground growing space in the post-disturbance environment. While altered resources did not affect the existence of a transient productivity maximum, they did shift the vegetation type responsible for this maximum from a highly productive native subshrub to invasive herbaceous annuals. This suggests that species-level effects of altered resource availability may play an important role in successful CSS fire recovery in the future.

Chapter five synthesizes the previous chapters and summarizes their findings within the context of the motivating research questions. This chapter describes some practical lessons learned throughout this thesis, which may be used to improve future study design and research practices. Finally, this chapter discusses some important avenues for future research regarding CSS fire recovery and long-term survival.

CHAPTER 2

Impact of altered precipitation on the ecohydrology of a seasonally dry deciduous shrubland

2.1 Abstract

Coastal sage scrub (CSS) and grassland have historically formed a stable mosaic under a relatively uniform physical template in southern California; this suggests that these two communities may represent alternative stable states under a similar climate regime. However, invasive Eurasian grasses have displaced much of California’s native grassland and, to a lesser extent, CSS over the past two hundred years, causing uncertainty regarding the future of CSS. We manipulated water inputs at a site in the foothills of the Santa Ana Mountains in southern California to 1) determine the spatial and temporal patterns of water storage and withdrawal to determine differences in access to water between the two communities, 2) examine the effects of manipulated water input on each community, and 3) compare aboveground phenology with water use strategy for each community to infer the controls on observed patterns of belowground water. We observed much more extreme surface drying in the grassland than in shrubland. This pattern was reversed at depths below 75 cm, where the grassland soil was consistently wetter than the corresponding layer of shrubland soil, indicating significantly deeper rooting depth in shrubland than in grassland. The seasonal withdrawal intensity was greater in the grassland than in the shrubland in the top 50 cm, but seasonality was apparent in the shrubland over a greater depth range and longer period, indicating a more conservative growth pattern and water use

strategy in the shrubland and an aggressive, “live fast, die young” strategy in the grassland. The restricted-water treatment in the shrubland resulted in an unexpected increase in moisture at 50 to 125 cm depth that may be partly explained by shifting vegetation dominance from deeply rooted shrubs to shallowly rooted herbaceous species. These contrasting water-use strategies may create a competitive advantage to one community over the other in the future, given that southern California is projected to experience an increase in drought and precipitation variability with climate change.

2.2 Introduction

Plants have evolved several strategies to cope with dry environments (*Lambers et al.*, 2008). Many succulents and cacti adapted to regions with low and unpredictable precipitation rely on CAM photosynthesis to increase water use efficiency (*Szarek et al.*, 1973; *Luttge*, 1987; *Winter et al.*, 2005) and shallow rooting to maximize water uptake during brief wet periods (*Jordan and Nobel*, 1984; *Hunt and Nobel*, 1987; *Graham and Nobel*, 1999; *North and Nobel*, 1998). Annual grasses and forbs in seasonally dry regions germinate rapidly following the first rain of the wet season; these plants are characterized by shallow root systems and rapid growth (**Figure 2.1**) (*Hesla et al.*, 1985; *Schenk and Jackson*, 2002). Annuals flower and senesce once soil water becomes depleted, following a “live fast, die young” strategy (*Dyer and Rice*, 1999; *Clary et al.*, 2004). Perennial herbs and shrubs tend to be more deeply rooted, withdraw water more slowly than shallowly rooted annuals, and use various strategies to reduce water loss during the dry season (*Hesla et al.*, 1983; *Jackson et al.*, 1999; *Jackson et al.*, 2000; *Schenk and Jackson*, 2002; *Hinojo-Hinojo et al.*, 2019). Many semi-arid shrubs are drought-deciduous and drop their leaves during the dry season and regrow them early in the wet season (*Mooney and Dunn*, 1970; *Mooney and Kummerow*, 1971). Evergreen shrubs reduce water loss through tight stomatal closure during the dry season and thick, waxy cuticles (*Abril and Hanano*, 1998). Shrubs often grow substantially more slowly than annuals, but live for years. Large evergreen shrubs and trees may largely avoid drought through deep rooting (*Mooney and Dunn*, 1970; *Mooney and Kummerow*, 1971; *Keeley and Davis*, 2007).

The foothill regions of Southern California are characterized by a mosaic of Coastal sage scrub (CSS) and annual grasslands and a Mediterranean climate, with a characteristic wet season from November through April and a summer drought from May through October (*Barbour et al.*, 2007). Coastal sage scrub is a diverse community comprised of subshrubs, woody drought-deciduous shrubs, and evergreen shrubs and that is found from just above sea level to 600 m elevation. Southern California's annual grasslands are dominated by invasive Eurasian species, with native grasses and forbs making up a minority of the community (*Dyer and Rice*, 1999; *Germino et al.*, 2016). Invasive grasses have displaced much of California's native grassland and, to a lesser extent, coastal sage scrub over the past two hundred years (*Jackson*, 1985; *Dyer and Rice*, 1997; *Wood et al.*, 2006). The future of the coastal sage scrub ecosystem is uncertain, with displacement by invasive grasses representing a significant threat (*D'Antonio and Vitousek*, 1992; *Minnich and Dezzani*, 1998).

Southern California's annual grasslands germinate following the first significant precipitation of the wet season, grow rapidly, then flower and senesce within a few weeks of the last rain (*Murphy*, 1970; *Slade et al.*, 1975; *Mooney et al.*, 1986; *Chiarello*, 1989; *Keeley et al.*, 2005a; *Lambers et al.*, 2008). The coastal sage scrub community uses several strategies to minimize water loss during the dry season; drought-deciduous species drop their leaves by mid-summer and regrow them following the first significant rain of the wet season (*Mooney and Dunn*, 1970; *Mooney and Kummerow*, 1971), while evergreen species tend to have thick, waxy leaf cuticles and tightly close their stomata during the dry season, reaching leaf water potentials as low as -10 MPa (*Pivovaroff et al.*, 2014). CSS species tend to have deep and/or broad root systems, allowing them to access deeper soil water throughout the year, in contrast to the more shallowly-rooted grassland species (**Figure 2.1**) (*Clary and Save*, 2004). Coastal sage scrub is a fire-adapted ecosystem with a fire return interval of roughly forty years (*Keeley et al.*, 2005b); crown fires are common, and required to trigger germination of seeds for some species of shrub (*Keeley and Keeley*, 1984). Most coastal sage scrub species survive a fire with their root systems intact, and resprout from the root crown during the subsequent growing season (*Keeley and Keeley,* 1984; *Malanson and Westman,* 1985; *Keeley et al.,* 2005b; *Keeley et al.,* 2006). With intact root systems, these individuals remain relatively unaffected by competition from invasive grasses for surface water. Differences in the two communities' water use strategies may contribute to the stability of the ecosystem types where they currently co-occur (*Caylor, et al.,* 2009; *Parolari et al.,* 2015). Moreover, contrasting water-use strategies may create a competitive advantage to one community over the other in the future, given that southern California is projected to experience an increase in drought and precipitation variability with climate change (*Hayhoe et al.,* 2004; *Wood et al.,* 2006; *Seager et al.,* 2007; *Loarie et al.,* 2008; *AghaKouchak et al.,* 2014; *Romero-Lankao, et al.,* 2014; *Berg and Hall*, 2015; *Hall et al.,* 2018).

We manipulated precipitation and nitrogen inputs at a site in the foothills of the Santa Ana Mountains in southern California to investigate the hypothesis that coastal sage scrub and invasive grassland represent alternative stable states (*May*, 1977; *Law and Morton*, 1993; *Beisner et al.*, 2003) for southern California's Mediterranean climate and to study the impacts of climate change and urbanization on these ecosystems. This site provides an excellent opportunity to study the ecohydrology of coastal sage scrub and grassland communities and seek to understand their individual adaptations to the seasonality of shallow water availability in low-elevation southern California in a post-disturbance context. The two communities are adjacent and the boundary between the two has been immobile over the past eighty years (**Figure 2.2**), suggesting long-term stability of the two communities. The entire site burned in a wildfire in 2007, and the experimental treatments have been ongoing since 2006 in the grassland and 2008 in the shrubland. The plots have been well-monitored during this time, allowing us to study the ecohydrology of these two ecosystems during the post-fire recovery period and through the progression to mature ecosystems.

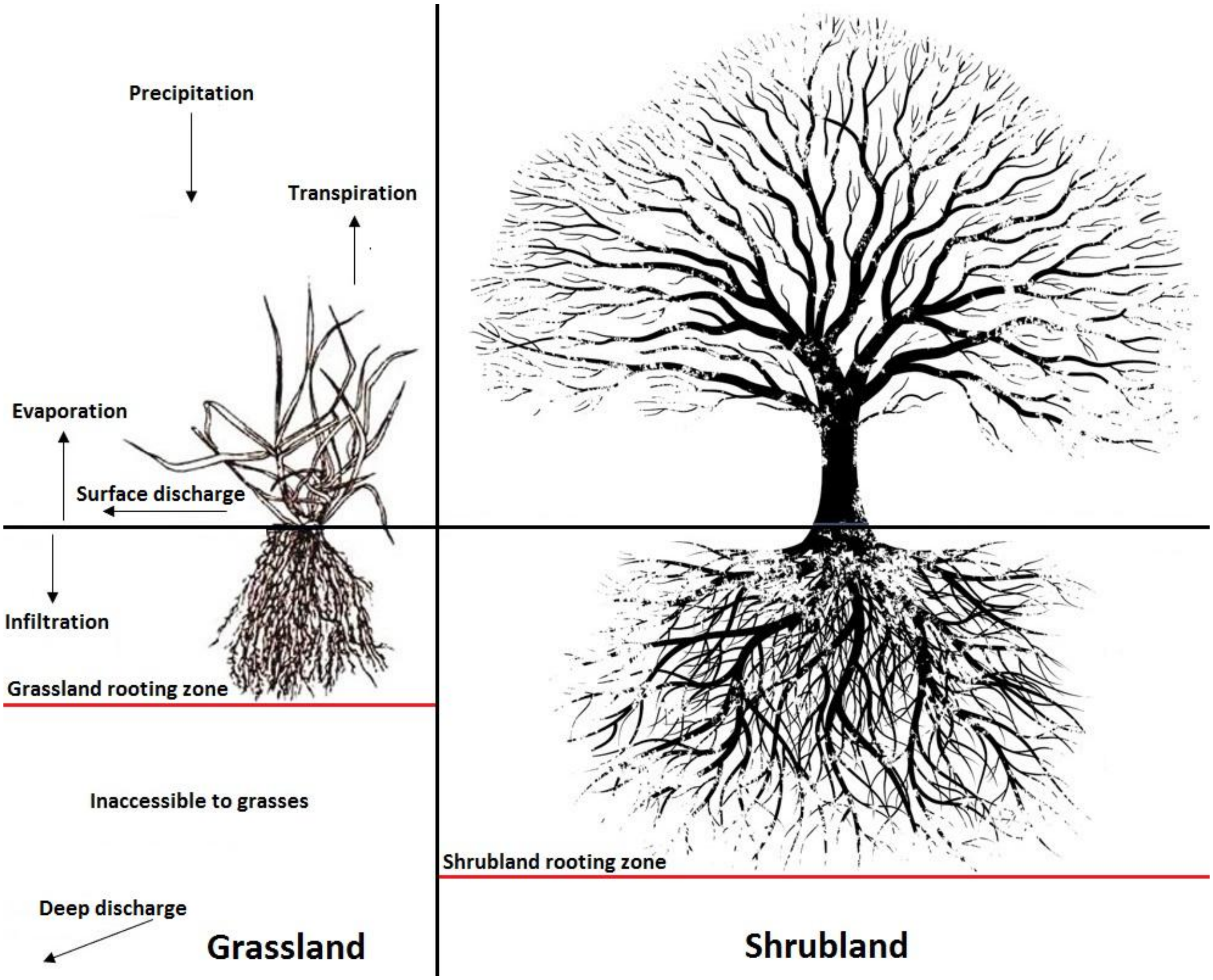

Figure 2.1: Ecohydrology characteristic of grassland and shrubland. Grassland and shrubland rooting depths are relative, and illustrate the shrubland's access to deeper soil moisture inaccessible to herbaceous vegetation. Arrows indicate water fluxes.

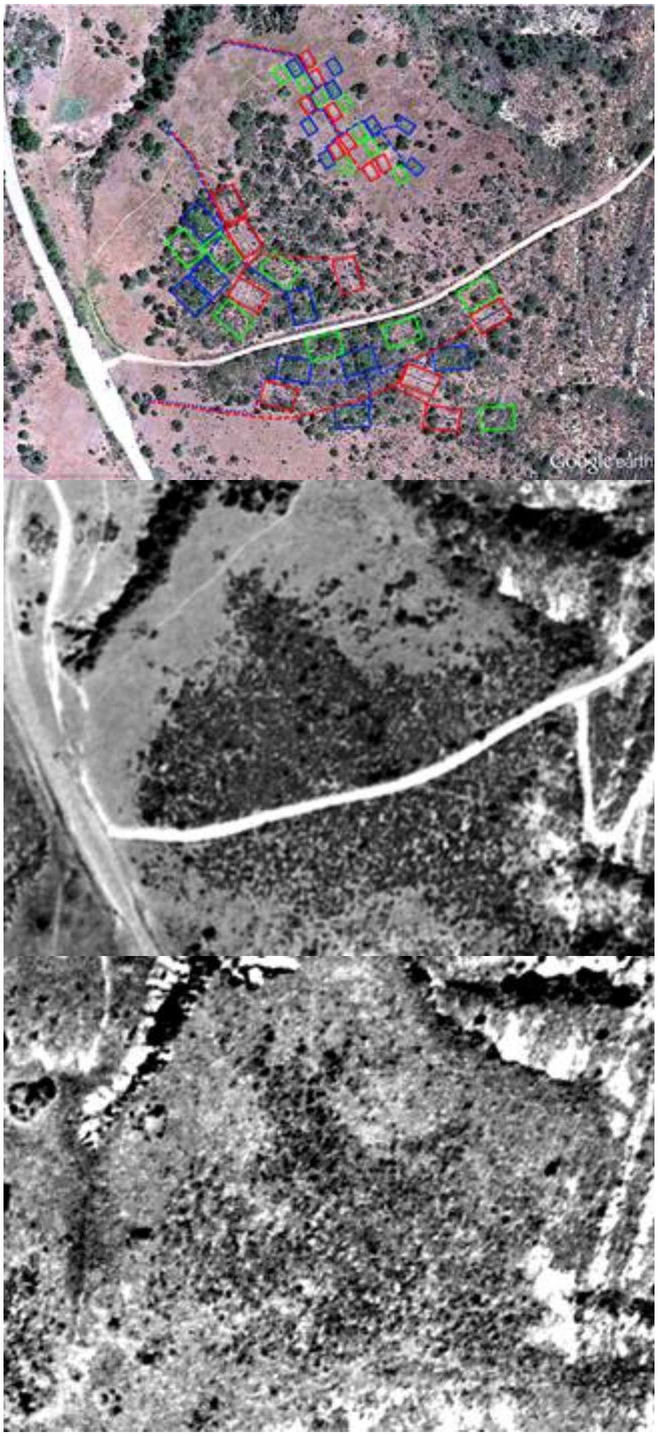

Figure 2.2: (Top) Satellite image of the Loma Ridge experimental site (*Google Earth*, 2012, http://earth.google.com/web/). Coastal sage scrub plots are to the south, grassland plots are to the north. Plots are color-coded by water treatment, with red indicating restricted, blue indicating added, and green indicating ambient water input. Dashed lines indicate drainage and irrigation systems. (Middle) 1977 historical aerial photograph of Loma Ridge (University of California, Santa Barbara Library, Aerial Flight TG-7700, http://mil.library.ucsb.edu/apcatalog). (Bottom) 1939 historical aerial photograph of Loma Ridge (University of California, Santa Barbara Library, Aerial Flight C-5925, http://mil.library.ucsb.edu/apcatalog).

Because of the physiological differences between these plant communities and the stable existence of both under similar geographic and climate regimes, we hypothesize that they employ different strategies to maximize growth during periods of water availability and to respond to the summer drought (*Laio et al.*, 2001; *Caylor et al.*, 2009). Coastal sage scrub has been shown to be a more deeply rooted community than annual grasslands and thus can access deeper soil water (*Rundel*, 2007). Coastal sage scrub can therefore enjoy a longer growing season, as these deeper water stores are less accessible and less subject to surface drying by competitors (*Clary et al.*, 2004). Annual grasses have much shallower root systems and are characterized by shorter growing seasons than Coastal sage scrub communities (*Bartolome et al.*, 2007); consequently, we hypothesize that grasslands are capable of rapid withdrawal of shallow water to support their rapid growth during the wet season, but are subject to rapid senescence as surface soil moisture dries following the end of the wet season. When shrub and grass species co-occur, this leads to competition for water resources. We hypothesize that these invasive grasses are much more efficient at withdrawing shallow soil water than native shrubs, and can outcompete shrubs in this depth range. Once shrubs have extended roots below the rooting zone of these grasses, they can begin to access this water without competition and water stress diminishes.

To test these hypotheses, we analyzed the plant-soil water relations of these two communities in four main ways. First, we measure the patterns of water storage and withdrawal to examine whether the coastal sage scrub community is able to access deeper soil water than the grassland community. Second, we examine the soil moisture dynamics in the two communities to test whether the grassland is able to withdraw more water from a given depth range than the shrubland. Third, we investigate the effects of the water manipulations on the spatial and temporal patterns and magnitude of water withdrawal. Fourth, we compare aboveground phenology with water use strategy for each community to determine the interactions between water use strategy and growth patterns in an effort to infer the controls on observed patterns of belowground water.

2.3 Methods

Study location

We constructed a precipitation and nitrogen manipulation experiment during 2006 through 2008 that included adjacent coastal sage scrub and grassland communities. The site is on a gentle northwest-facing slope near the crest of Loma Ridge in the foothills of the Santa Ana Mountains (117.704^{o} W, 33.742^{o} N). The climate in the area is Mediterranean, with an annual average high of 24.1^{o} C and an annual average low of 9.7^{o} C. Long-term temperature records along with the presence of *Malosma laurina*, a frost-intolerant species, indicate that the temperature rarely drops below 0^{o} C. Temperatures during the wet season range from an average high of 21.0^{o} C to an average low of 6.2^{o} C while temperatures during the dry season range from an average high of 27.3^{o} C to a low of 13.1^{o} C (Tustin Irvine Ranch weather, 1902-2003, http://www.wrcc.dri.edu). The site receives an annual mean precipitation of 327 mm, which mainly falls during the November to April wet season (Orange County Public Works, 1897-2014, http://www.ocwatersheds.com).

The site is currently managed by the Irvine Ranch Conservancy, with an emphasis on conservation, recreation, and education. The site was part of the Irvine Ranch throughout the 20th century, and the main land use was grazing, which ended in the early 2000s. The experimental site burned in 2007, 1998, 1967, 1948, and 1914 (CAL FIRE Fire and Resource

Assessment program, http://frap.cdf.ca.gov/). We conducted a controlled burn on half of the experimental area in February, 2007; the site subsequently burned in the Santiago wildfire in October, 2007. In our analysis, we combined the plots subjected to the controlled burn and the plots that burned only in the wildfire.

Physical template

The site is a mosaic of annual grassland dominated by invasive species and deciduous shrubland with some evergreen chaparral species. The border between the two communities is well-defined and has remained largely immobile over the past 80 years, as shown by historic aerial photographs (**Figure 2.2**).

We performed a soil texture analysis using samples taken from each experimental plot at depths of 0, 15, 30, 45, 100, and 200 cm. Samples were dried at 105^{o} C, and then pulverized and sieved to pass a 10-mesh sieve. 150 mL of a 17 g/L sodium hexametaphosphate solution was added to the soil, and samples were agitated on a horizontal shaker for 60 minutes. Samples were brought to a constant volume of 1 L with deionized water in a graduated cylinder, mixed, and the density of the suspension was measured with a hydrometer after 40 seconds to determine the silt plus clay fraction and after 2 hours to determine the clay fraction. This method has a 2% detection limit and is reproducible to within 8%.

The soil texture was remarkably consistent with depth and also between the grassland and shrubland patches (**Figure 2.3**). Given the grassland to shrubland similarities in both soil and climate, the physical environment is assumed to be similar in the two plant communities; therefore, the stability of each ecosystem and the border between the two presumably has a biological component.

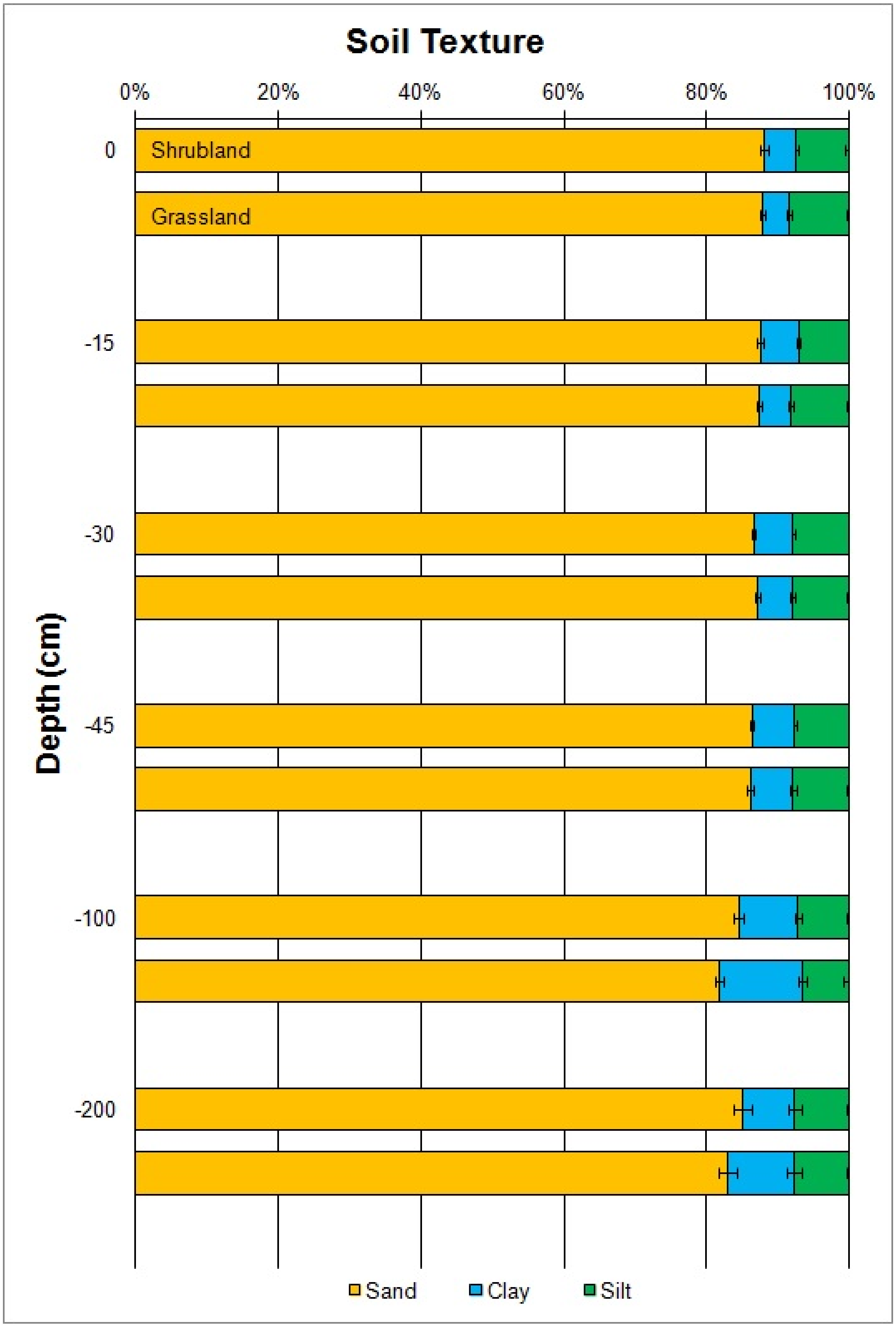

Figure 2.3: Soil texture of the grassland and coastal sage scrub sites across a 200 cm depth profile. Values are mean fraction ± standard error.

Experimental design and water treatments

The manipulations consist of twenty-four 18.29 x 12.19 m plots in the coastal sage scrub and twenty-four 9.14 x 6.10 m plots in the grassland. Eight plots in both the grassland and shrubland were randomly selected to receive 40% additional water input while another eight were randomly selected to receive 40% restricted water. The plots were split lengthwise, with one side of each plot randomly selected to receive added nitrogen. Each half plot was further split into three subplots, 2 x 2 m in the grassland and 4 x 4 m in the shrubland. The uphill subplot of each plot were subject to possible artifacts due to wind and lateral water flow, and data collection was focused in the lower two subplots in each plot.

The water restriction was achieved through the construction of frames with clear retractable polyethylene roofs. These roofs remained open for roughly 95% of the year to reduce potential temperature and humidity variation. Additionally, air temperature and relative humidity sensors installed in representative plots from the three water treatment types showed no difference in air temperature and relative humidity between the restricted-water plots and the other two water treatment types when the shelters were opened. These roofs were closed for a subset of storms to remove and store precipitation from the restricted-water plots; these closures were biased towards larger storms in an attempt to reduce both precipitation frequency and intensity. Water collected from the restricted-water plots was stored in polyethylene tanks and later pumped through irrigation manifolds installed on the added-water plots. The water was applied to each added-water plot using a dense web of drip tubing, and the amount of water added was measured using Hersey positive-displacement water meters. The tanks have a water storage capacity of 5.1 cm; this was exceeded in 2010 and 2011 due to large storms. Some water was lost from the storage tanks during these events, so our actual water manipulations ended up off target: the restricted-water treatments represented a 51% reduction in water input and the added-water treatments received an additional 33% water input as compared to the ambient plots.

The high nitrogen deposition levels observed in southern California, particularly around the Los Angeles basin, were simulated through the addition of 6 gN m^{-2} yr^{-1} to the added-nitrogen plots. Loma Ridge currently receives approximately 1.5 gN m^{-2} yr^{-1} (*Fenn et al.*, 2010), and this addition pushed these treatments well above the critical load of nitrogen for coastal sage scrub. The nitrogen was applied in two stages. 2 gN m^{-2} yr^{-1} fast-release fertilizer (15.5-0-0 calcium nitrate, 15.5% N, 0% P, 0% K, 19% Ca) was applied immediately prior to the first storm of the wet season to simulate the nitrogen flush that accompanies the first rain. The remainder of the nitrogen addition was applied approximately one month later as controlled release (4 month) fertilizer (14-0-0 calcium nitrate, 14% N, 0% P, 0% K, 19% Ca).

Field observations

Automated instrumentation arrays were installed in two plots from each water treatment in each community. These instruments were sampled every 30 minutes year-round. Each array consisted of eight Campbell Scientific CS616 soil moisture sensors, four in-house fabricated soil temperature sensors, two in-house fabricated NDVI sensors, two Campbell Scientific 506-L fuel moisture sensors, two Campbell Scientific LWS leaf wetness sensors, and an array of Campbell Scientific 229-L matric potential sensors installed at depths of 5, 10, 25, 50, and 100 cm, with an additional sensor at 200 cm in the shrubland plots only. Precipitation was measured at the site every 10 minutes with a single tipping-bucket rain gauge installed on level ground above the surrounding canopy with an unobstructed field of view above the sensor. Additional manual measurements were conducted throughout the year, including surface soil moisture, soil moisture depth profiles, and spectral reflectance (300-1200 nm) every two to three weeks during the growing season and every four to six weeks during the drying season. Surface soil moisture was further measured using permanent vertical TDR wave guides in four locations in each half-plot that were sampled with a handheld Campbell Hydrosense probe. Deeper moisture was measured by through the installation of 2 m access tubes in each plot, which were sampled with a CPN Hydroprobe 503DR neutron probe at 25 cm intervals. Spectral reflectance was measured using a handheld spectrometer around the center subplot in each half plot. Twenty measurements were collected around each grassland subplot and thirty-six measurements were collected around each CSS subplot.

An in-situ calibration of the neutron probe was conducted by excavating access holes during the late summer when the soil was driest, taking neutron probe readings through a PVC access tube identical to those installed in each experimental plot, and directly measuring the volumetric water content of the soil collected during the excavation. The volumetric and neutron probe measurements were conducted at a depth of 50 cm to avoid surface artifacts. This calibration resulted in strong agreement between the neutron probe 25 cm measurement and the 20 cm TDR measurements (**Supplementary Figure 1**).

Precipitation record

Six nearby precipitation datasets were analyzed to determine the best precipitation record for Loma Ridge. Two nearby eddy covariance towers equipped with tipping-bucket rain gauges (Ameriflux sites US-SCg, 33.737^{o} N 117.695^{o} W and US-SCs, 33.734^{o} N 117.696^{o} W, http://ess.uci.edu/~california) provided records #1 and #2, which began in 2006. Record #3 was obtained from a third tipping-bucket rain gauge that was installed in a flat area with a low plant canopy and wide sky view adjacent to the manipulations site. Record #4 was obtained from a rain gauge installed in 2013 within the manipulations area. Records #5 and #6 were obtained from two Orange County Water District stations near the site, station 247 (33.745^o N 117.704^o W, http://www.ocpublicworks.com) and station 61 (33.720^o N 117.723^o W). The first three rain gauges were merged into a single complete record to fill gaps and periods with malfunctioning gauges, giving priority to record #3, followed by #2, then by #1. This composite record was compared with the two OCWD records (#5 and #6) and the final record from within the manipulations (#4), looking for continuity, duration, reliability of data, and proximity to the manipulations. The OCWD record from station 61 (record #6) was determined to be the longest, most homogeneous record, and subsequent analyses were conducted based on this dataset. Water input for the restricted-water treatment was calculated by subtracting the precipitation during storms when the treatment roofs were closed, and input for the added-water treatment by adding the amount of water applied (**Figure 2.4**).

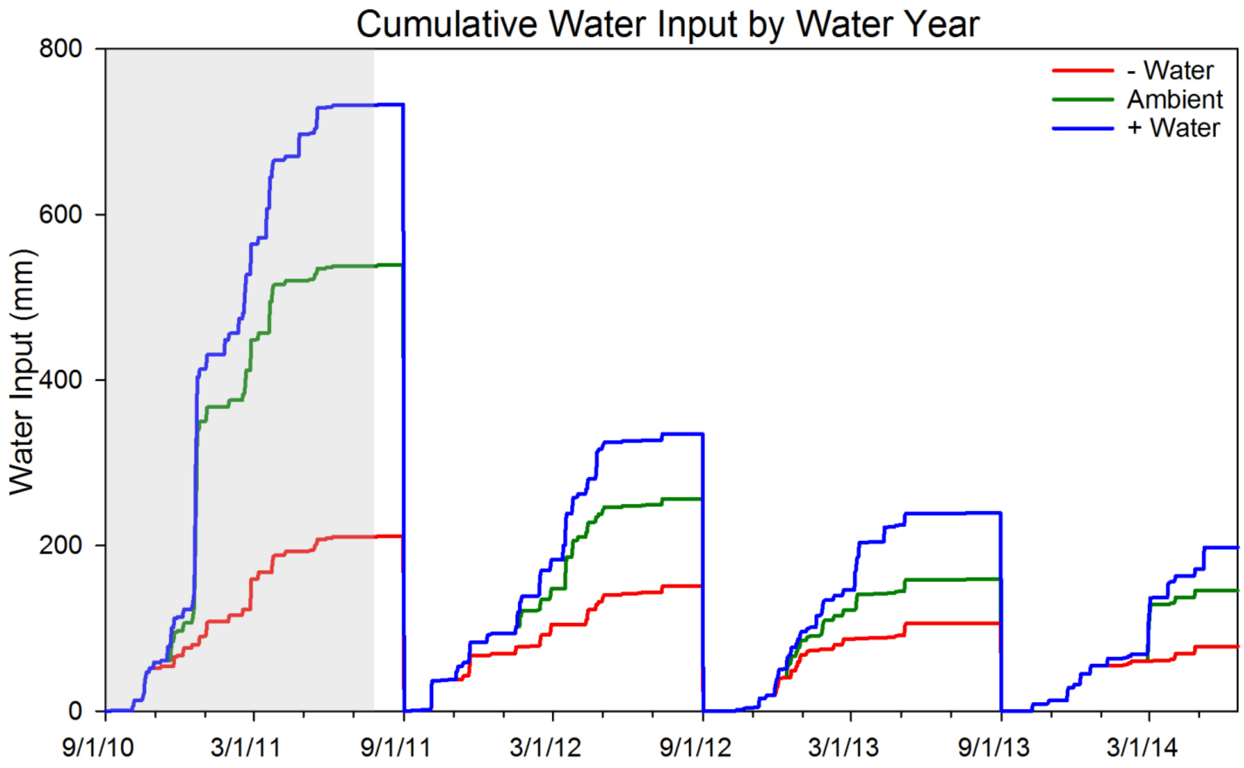

Figure 2.4: Cumulative water input for the three water treatments from 1 September 2010 through the conclusion of the study period, 17 June 2014. Gray shading indicates the period prior to the beginning of the Hydroprobe measurements of vertical soil moisture profiles in August 2011.

2.4 Results

Patterns of soil moisture

Most precipitation fell during October through May, with considerable year-to-year variability (**Figure 2.4**). Our study period (water years 2011-2012 through 2013-2014) was drier than usual, and the final year (2013-2014) was particularly dry. The water year before the main observations began (2010-2011) was wetter than usual, and the study period may be thought of as a multi-year drying cycle starting from comparatively wet conditions. The soil moisture observations showed differences with vegetation type and water treatment that were superimposed on year-to-year precipitation variability (**Figure 2.5**).

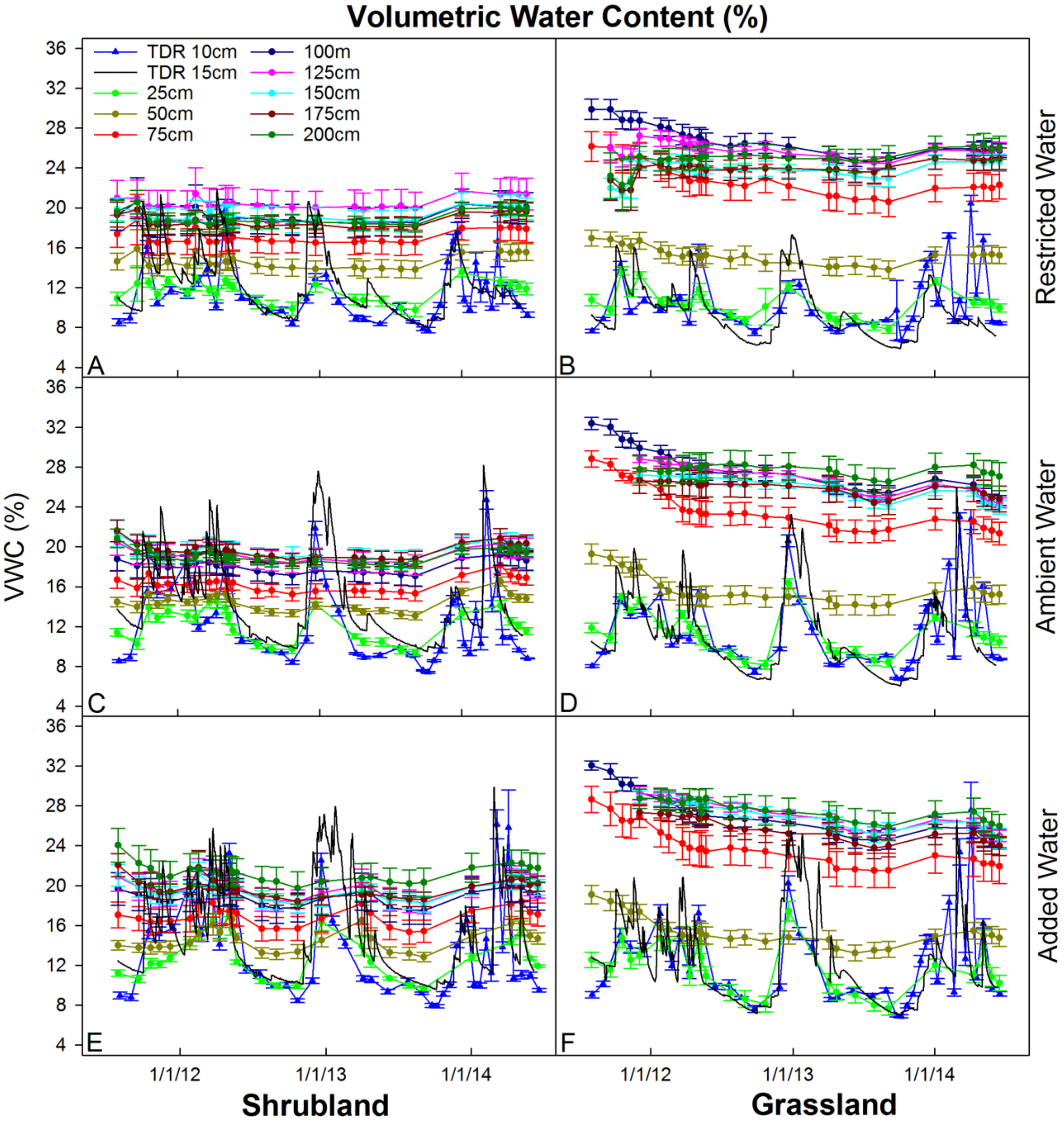

Figure 2.5: Volumetric water content (cm m^{-1}) from August 2011 to June 2014 in the shrubland (left) and grassland (right), grouped by water treatment. VWC at 10 cm was determined using a Campbell Hydrosense manual sensor to measure time-domain reflectometry (TDR) at four permanent 20 cm vertical wave guides in each plot. VWC at 15 cm was measured every 30 minutes at four permanent locations in two plots per treatment per community using Campbell CS-616 TDR sensors with 30 cm vertical wave guides. VWC from 25 to 200 cm was measured using a CPN Hydroprobe 503DR neutron probe along permanent access tubes in each plot.

There was a sharp vertical gradient in grassland soil volumetric water content (VWC) at 50 to 75 cm depth, with shallow dry soil and moist deep soil; the depth of this gradient did not vary with treatment (**Figure 2.6)**. There was considerable seasonal variation in shallow grassland moisture, and all of the treatments showed severe summer drying, which varied little with water input. The most apparent difference between grassland treatments occurred at shallow depths during the wet season, with comparatively moist soil for a comparatively long period of time in the ambient- and added-water treatments. There was remarkably little seasonal variation in deep grassland moisture content, despite large seasonal fluctuations in water input. There was modest long-term drying in the grassland at depth, especially in the ambient- and added-water treatments.

The shrubland VWC showed a modest vertical gradient, with a general tendency toward drier shallow and wetter deep soil, and a broad gradient at 50 to 100 cm depth. All CSS treatments showed severe shallow drying during the summer, which varied little between treatments. The added water treatment in the coastal sage scrub showed a large seasonal trend at all depths, with an increase in soil moisture during the wet season extending to 150 to 200 cm depth.

Differences in soil moisture between grassland and shrubland

The soil water profiles differed markedly between the grassland and shrubland. **Figure 2.7** shows the difference in volumetric water content between the grassland and shrubland over time. Surface drying was much more extreme in the grassland than in shrubland**,** and the upper 50 cm of grassland soil were 4 to 6% VWC drier than the corresponding layer of shrubland soil. The shallow grassland soil was always drier than the shallow coastal sage scrub soil, with little seasonal or treatment variation. The vegetation type difference was flipped at depths below 75 cm, where the grassland soil was consistently 6 to 10% wetter than the corresponding layer of shrubland soil. The effect of vegetation type on deep moisture showed modest variation with treatment and time. For example, the deep soil moisture excess in the grassland relative to shrubland in the restricted-water treatment was greatest in the early part of the study and at 75 to 125 cm depth.

Differences in soil moisture with treatment

The restricted-water grassland treatment was drier than the ambient- and added-water treatments at shallow depths during the wet season, presumably as a direct effect of the relative rates of water input (**Figure 2.8)**. Likewise, the restricted-water grassland treatment was drier than the ambient- and added-water treatments beneath 125 cm, especially during the first two years of observations, presumably as a consequence of reduced deep infiltration in the restricted-water treatment during 2010-2011. The shrubland showed a comparatively larger treatment difference than did the grassland. The shrubland ambient-water treatment was wetter than the restricted-water treatment above 50 cm during the wet season, and the added-water treatment was wetter than the ambient-water treatment overall. The shrubland wet season increase in soil moisture extended deeper in the added-water treatment than in the ambient-water treatment. The shrubland restricted-water treatment was unexpectedly wetter than the shrubland ambient-water treatment at a depth of 75 to 150 cm.

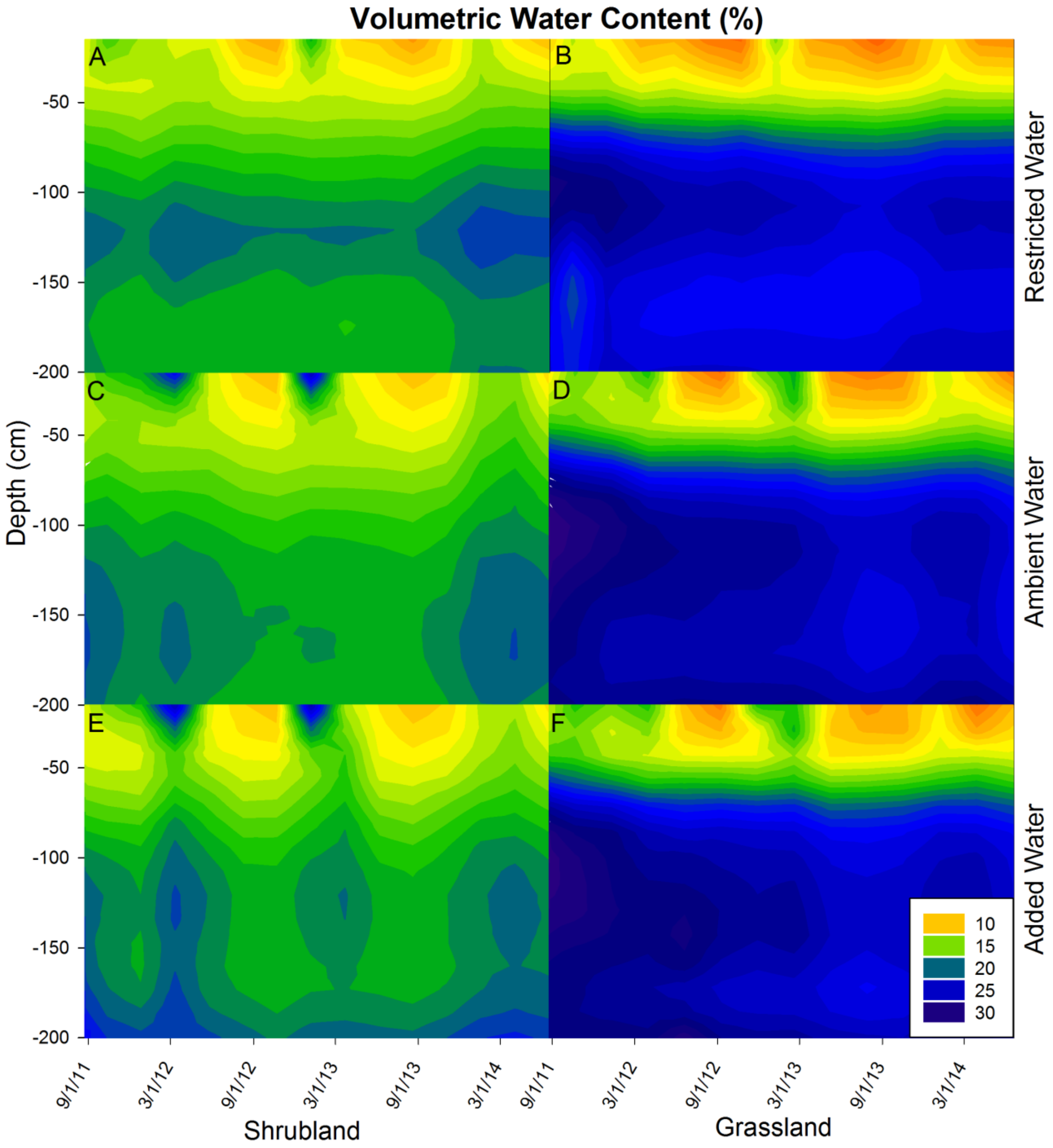

Figure 2.6: Kriging contour plots of volumetric water content (cm m^{-1}) across 200 cm depth profiles from August 2011 to June 2014 in the shrubland (left) and grassland (right), grouped by water treatment. Data from 50 to 200 cm were collected using a CPN Hydroprobe 503DR neutron probe. Surface data down to 50 cm was collected using Campbell CS-616 TDR sensors sampled electronically then averaged daily.

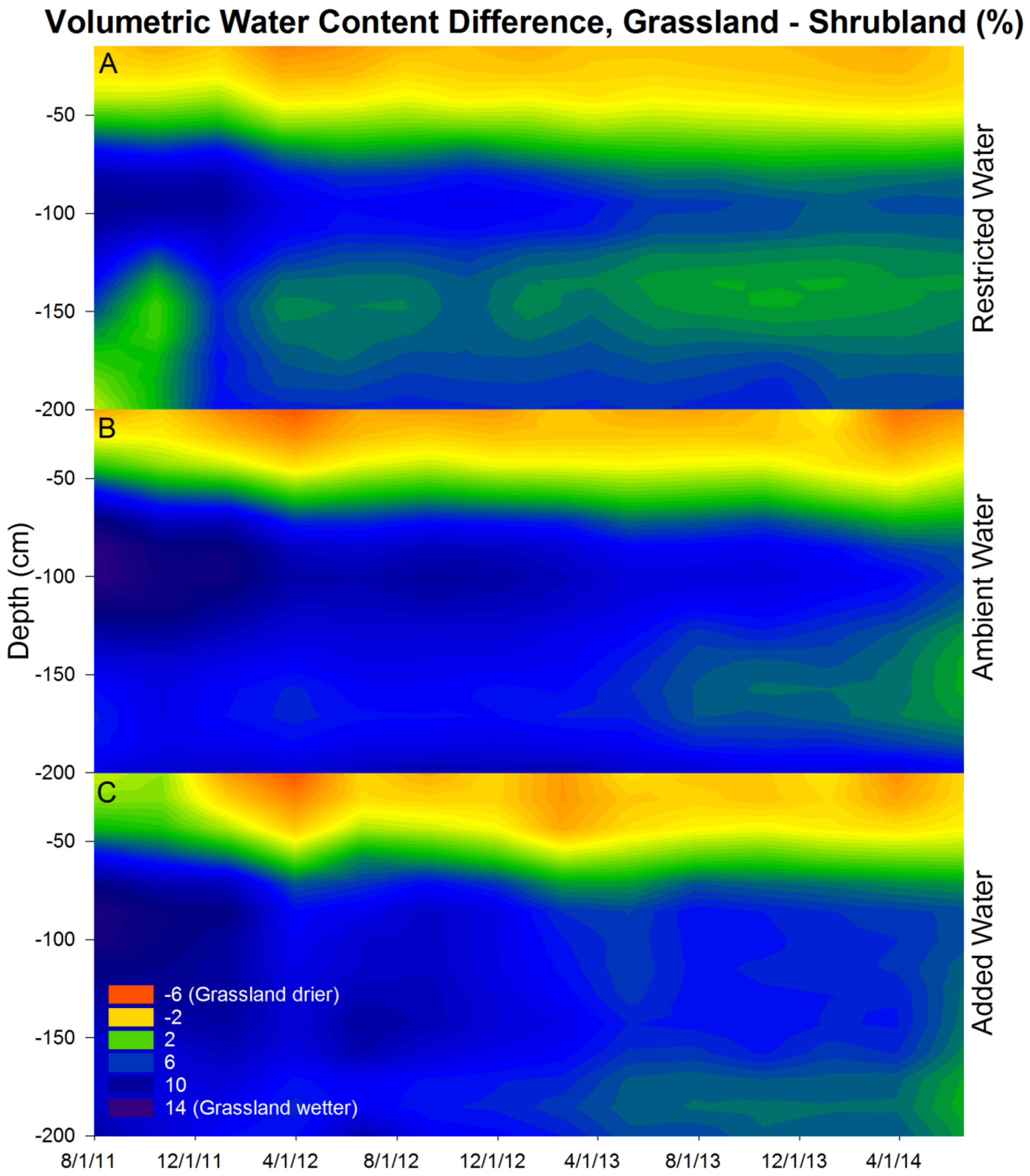

Figure 2.7: Kriging contour plots of volumetric water content difference (cm m^{-1}) between the grassland and shrubland across 200 cm depth profiles from August 2011 to June 2014, grouped by water treatment. Data from 50 to 200 cm were collected using a CPN Hydroprobe 503DR neutron probe. Surface data down to 50 cm was collected using Campbell CS-616 TDR sensors sampled electronically then averaged daily.

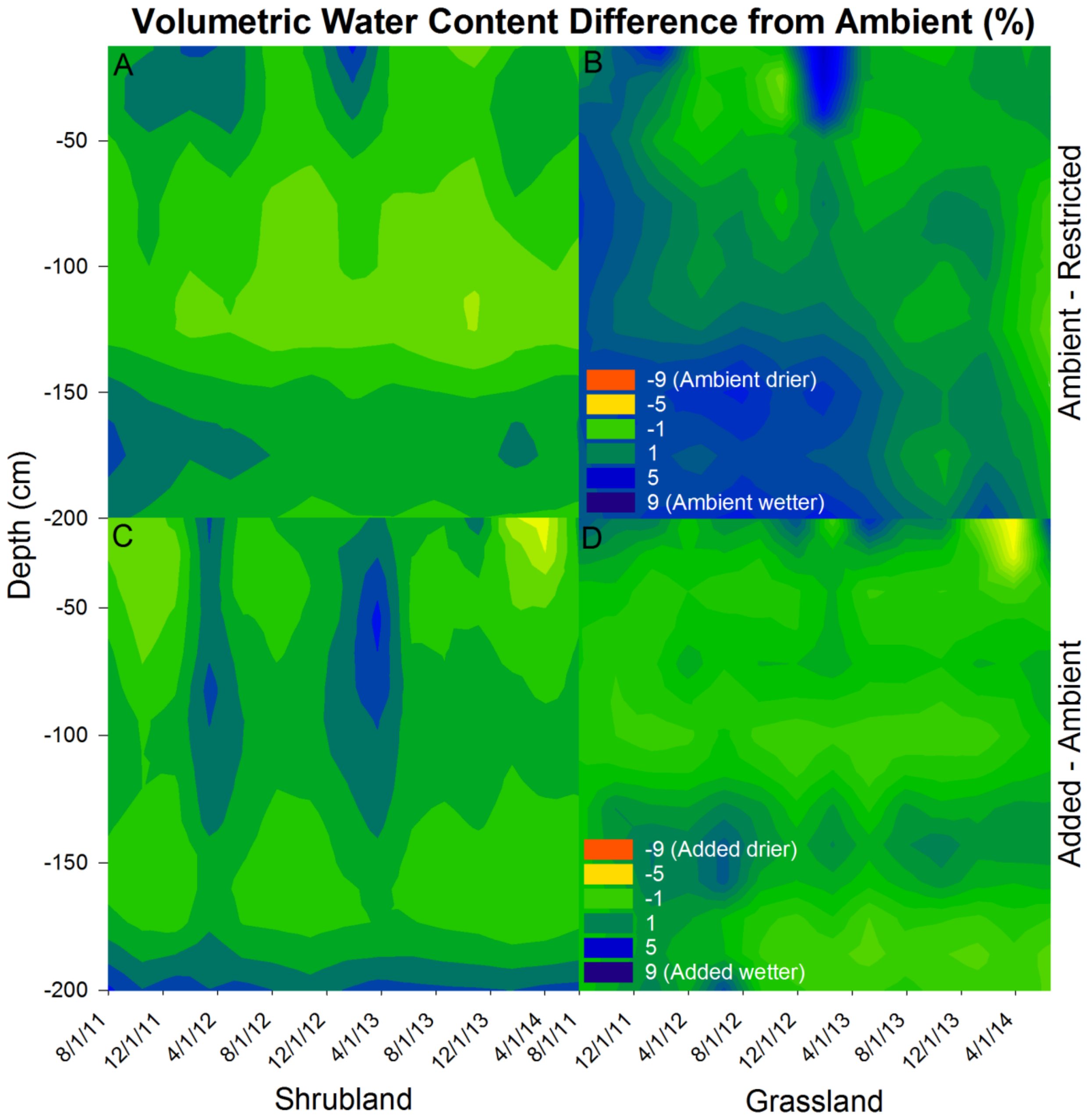

Figure 2.8: Kriging contour plots of volumetric water content difference (cm m^{-1}) between the ambient-water and restricted-water treatments (A, B) and between the added-water and ambient-water treatments (C, D) in the shrubland (left) and grassland (right) across 200 cm depth profiles from August 2011 to June 2014. Data from 50 to 200 cm were collected using a CPN Hydroprobe 503DR neutron probe. Surface data down to 50 cm was collected using Campbell CS-616 TDR sensors sampled electronically then averaged daily.

2.5 Discussion

Water use strategies in shrubland and grassland

The contrasting soil water content depth profiles (**Figures 2.5, 2.6**) are most easily explained by a large difference in rooting depth between the two communities (*Davis and Mooney*, 1986; *Sala et al.*, 1989; *Seyfried and Wilcox*, 2006; *Parolari et al.*, 2015). The soil profile in each community may be divided into two zones: a surface zone of active withdrawal and a deeper zone of more stable water content (**Figure 2.1**). The depth of the zone of active withdrawal is controlled by rooting depth. The active withdrawal zone was approximately 50 cm deep in the grassland, and 100 to 200 cm deep in the shrubland. These findings are in agreement with previously reported shrubland and grassland rooting depths (*Hellmers et al.*, 1955; *Coupland and Johnson*, 1965; *Kummerow et al.*, 1977; *Canadell and Zedler*, 1995; *Canadell et al.*, 1996; *Schenk and Jackson*, 2002). The zone of stable soil water content occurs below the rooting zone and displays relatively constant moisture without a distinct seasonal signal. This zone is largely decoupled from rapid fluctuations in moisture input and withdrawal. The sharp soil moisture discontinuity with depth in the grassland suggests that most of the grassland species have similar rooting depths and phenologies. The comparatively broad depth gradient in the shrubland is consistent with a range of rooting depths and phenologies within that community (*Hellmers et al.*, 1955). The shrubland includes shallowly rooted herbaceous species, moderately deeply rooted drought-deciduous shrubs, and deeply rooted evergreen shrubs, such as *Malosma laurina*, which are often associated with the chaparral community.

The shrubland and grassland communities differed in the amount, or intensity, of soil water withdrawal. The withdrawal intensity in the grassland was greater than in the shrubland over the zone of active withdrawal in the grassland; as a result, the grassland was significantly drier than the shrubland to a depth of 50 cm, with peak differences of 6 cm water per meter of soil. These peak differences coincided with the herbaceous growing season, particularly in the ambient- and added-water treatments. The shrubland did not display the same intensity of withdrawal at any depth, but did display evidence of withdrawal over a longer duration, indicating an extended growing season, and over a greater depth range, indicating access to deeper water stores.

Effects of water treatments on soil moisture

Soil moisture reflects the balance between precipitation, irrigation, infiltration, net lateral flow, deep discharge, evaporation and transpiration (*Rodriguez-Iturbe et al.*, 1999; *Rodriguez-Iturbe*, 2000; *Bonan*, 2015). Water input influences soil moisture both directly by controlling the immediate addition of water and moistening of soil, and indirectly by controlling the density and type of vegetation and the rate and depth of withdrawal (**Figure 2.1**) (*Hickel and Zhang*, 2006; *Ladson et al.*, 2006; *Feng et al.*, 2012). All things being equal, added water should increase soil moisture to the point of saturation. However, shifts in vegetation density and type with water availability may counteract this tendency, thereby reducing the effect of added water on soil moisture (*Zhang et al.*, 2001).

The direct effects of water input on soil moisture were most apparent during the wet season and near the surface in both the grassland and shrubland (**Figure 2.8**). The ambient-water treatment in the grassland was moister than the restricted-water treatment near the surface during the wet season. This is the zone of most rapid soil moisture uptake in the grassland, and the greater input of water at the surface would be expected to translate into an increase in soil water content. The effect of added water on the grassland soil moisture declined with depth, with little or no treatment effect at a depth of 50 to 125 cm. This zone shows consistently high soil moisture and is apparently below the main rooting depth; this zone is probably near saturation year-round and additional water is largely lost to deep discharge. Finally, the effect of reduced water on soil drying increased again below 150 cm. This zone may reflect the maximum depth of infiltration in the restricted-water treatment and the lack of recharge below 150 cm.

Added wet season water in both the grassland and shrubland had little effect on the soil moisture content during the subsequent dry season. This likely reflected a plant-mediated feedback on soil moisture through growth and accelerated moisture uptake. Hence, added moisture promoted herbaceous growth and extended the herbaceous growing season, therefore increasing shallow moisture withdrawal in both the grassland and shrubland, which quantitatively offset the moisture addition and resulted in similar levels of shallow moisture during the dry season regardless of water input during the preceding wet season.

The restricted-water treatment in the shrubland resulted in an unexpected increase in moisture at 50 to 125 cm depth that may be partly explained by an indirect effect mediated by shifts in vegetation type (*Zhang et al.*, 2001). The bottom of this anomalous wetting zone may be explained by the lack of deep infiltration in the restricted-water treatment in the shrubland, as was also inferred in the grassland. The top of the anomalous wetting zone may be explained by changing vegetation dominance in the restricted-water shrubland treatment and a decrease in rooting depth associated with a shift from deeply rooted shrubs to shallowly rooted herbaceous species (*Hodnett et al.*, 1995). Hence, the restricted-water treatment in the shrubland decreased the shrub abundance relative to herbaceous species, which led to shallower rooting and decreased moisture uptake at 50 to 125 cm depth; reduced water input consequently increased soil moisture.

Grassland and shrubland as alternative stable states

Grasslands and shrublands co-exist throughout southern California, often forming a mosaic similar to that seen at Loma Ridge (**Figure 2.2**) (*Freudenberger et al.*, 1987; *Barbour et al.*, 2007). The two ecosystems occur side by side at Loma Ridge on similar soil and in a similar climate (**Figure 2.3**). The boundary between the two vegetation types has remained stationary since at least 1939 (**Figure 2.2**). The combination of a relatively uniform physical template (soil texture, aspect and slope, climate), and a stationary boundary despite substantial interannual precipitation variation and the occurrence of four wildfires since 1948 implies a high degree of ecological inertia and is consistent with the interpretation that grassland and shrubland ecosystems are alternative stable states (*May*, 1977; *Law and Morton*, 1993; *Beisner et al.*, 2003).

Annual grasses and perennial shrubs display contrasting, mutually exclusive water use strategies that are each effective and that may maintain the local vegetation mosaic despite uniform physical conditions (*Hesla et al.*, 1985; *Dyer and Rice*, 1999; *Jackson et al.*, 1999; *Jackson et al.*, 2000; *Schenk and Jackson*, 2002; *Clary et al.*, 2004*; Hinojo-Hinojo et al.*, 2019). The annual grasses at Loma Ridge have adopted a strategy that emphasizes shallow rooting, rapid growth, a relatively short life span, preemptive soil moisture use, and a tight phenological coupling with recent water input. The perennial shrubs have adopted a strategy that emphasizes deeper rooting, slower growth, a relatively long life span, a reliance on larger soil moisture stocks, and less phenological coupling with recent water input. Annual grasses are capable of rapid and extreme moisture depletion to a rooting depth of approximately 50 cm, but lack the deep rooting of shrubs (**Figure 2.6**). Annual grasses cope with the lack of deep moisture access by germinating rapidly at the start of the wet season, using the accessible water as rapidly as possible during the wet season, and setting seed as soon as the soil dries (*Murphy*, 1970; *Slade et al.*, 1975; *Mooney et al.*, 1986; *Chiarello*, 1989; *Keeley et al.*, 2005a; *Lambers et al.*, 2008). The perennial drought-deciduous and evergreen shrubs have evolved a comparatively conservative water use strategy that relies on deeper water stores and an expanded growing season. Drought-deciduous shrubs minimize water loss during the subsequent dry season by leaf senescence, while evergreens minimize dry-season water loss through a combination of thick, waxy cuticles and the ability to tightly close their stomata (*Mooney and Dunn*, 1970; *Mooney and Kummerow*, 1971; *Abril and Hanano*, 1998).

The end result is a density-dependent positive feedback that is mediated by the vertical distribution of soil moisture and that reinforces a vegetation type's advantage. Hence, shallowly-rooted grassland preempts the establishment of shrubs as a consequence of the intensity of water withdrawal. The shallow grassland soil was always drier than the shallow shrubland soil (**Figure 2.7**) and shrubs may have difficulty establishing in dense grassland (*Harrington et al.*, 1991; *Eliason and Allen*, 1997). This establishment phase appears critical in excluding shrubs from closed-canopy grasslands; shrubs that become established in grasslands and access the moisture stocks below the grass rooting zone become quite large and persist (personal observation). Conversely, shrubs tolerate the presence of grasses within a shrubland community well (*Kimball et al.*, 2014). An established shrubland has an active withdrawal zone far deeper than that of the grasses (**Figure 2.6**), and these roots persist through fire (*Barbour et al.*, 2007); crown-resprouting shrubs can access deep water during succession, despite the transient abundance of annual grasses and forbs during this period. This positive feedback, especially within grasslands, tends to push locations to either grassland or shrubland, thereby accounting for a vegetation mosaic.

We also observed a negative feedback between water input and soil moisture, which helps explain the lack of a strong treatment effect on soil moisture and the long-term stability of vegetation distribution despite large precipitation variability. For example, the severity of summer moisture dry-down in the grassland varied little with water input, apparently as a result of compensatory growth and increased moisture losses during wet years (*Murphy*, 1970). This negative feedback would stabilize established grasslands against shrub invasion during wet periods. Similarly, reduced water inputs in the shrubland increased the availability of moisture at 50 to 125 cm above that measured under ambient-water conditions, which presumably reduces the effects of reduced water input on any remaining shrubs. Both of these negative feedbacks will stabilize the grass-shrub mosaic against large precipitation variability, and may ultimately reduce vulnerability to climate change.

This study suggests that a disturbance pattern that results in increased mortality of resprouting shrubs may increase vulnerability to invasion by exotic grasses and possibly ecosystem type conversion. For example, increased fire frequency that causes repeated die-backs of aboveground shrub biomass, leading to a depletion of root carbohydrate stores and a progressively diminished resilience to disturbance, could push the community to grass dominance. Under such a disturbance regime, the shrubland recovery pattern would shift away from resprouting and would be forced to rely more and more on seedling establishment. Annual grass establishment and productivity is tightly coupled with recent water input (*Murphy*, 1970), and these grasses are capable of a much higher intensity of water withdrawal than are shrubs. Without a protective canopy of mature shrubs to reduce light penetration to the soil and thus reduce the density of herbaceous annuals in the understory, shrub seedlings would compete directly with annual grasses for shallow moisture; in such a scenario, the more conservative water-use strategy employed by shrubs would prove a hindrance and invasive annual grasses would have a significant competitive advantage (*Padilla and Pugnaire*, 2007). This is a realistic scenario for the CSS ecosystem; the fire frequency in native CSS habitat is increasing due to human ignition, and the combination of population growth and climate change-driven increases in drought frequency and duration may further increase the fire frequency in southern California in the future (*Syphard et al.*, 2007).

CHAPTER 3

Long-term water and nitrogen manipulations alter community composition and successional trajectory in a drought-deciduous shrubland

3.1 Abstract

Periodic disturbances such as fire and drought drive species evolution and community assemblage toward increased resistance and resilience to disturbance, and natural ecosystems are by necessity well adapted to the historic disturbance regime. However, this adaption likely has limits, and disturbance regimes or recovery conditions that fall outside of the historical range may increase an ecosystem's vulnerability to invasion and type conversion. In particular, shifts in resource availability have the potential to alter the competitive relationships that help drive succession, potentially altering successional patterns and leading to changes in an ecosystem's ability to return to pre-disturbance conditions. We established a precipitation and nitrogen manipulation experiment in a seasonally-dry coastal sage scrub community immediately following fire to explore the impacts of altered plant resources on succession. We were able to decrease total cover and shrub fractional cover and slow the transition from an herbaceous-dominated to a shrub-dominated community substantially through water restriction, and we saw evidence of an acceleration of succession through a faster transition to a shrub-dominated community under added-water conditions. Nitrogen addition under restricted-water conditions resulted in a substantial decline of total and shrub cover and was the only treatment in which shrub cover declined throughout the study. Our results suggest that water input is an important controller of successional rate for drought-adapted ecosystems and that the combination of

restricted water and added nitrogen may produce a fundamental shift in coastal sage scrub fire recovery patterns. Hence, increased aridity due to climate change and increased nitrogen deposition due to population growth in southern California may increase the vulnerability of coastal sage scrub to invasion by Eurasian grassland.

3.2 Introduction

The post-disturbance recovery period may represent a window of increased vulnerability to invasion and ecosystem type conversion (*Zedler et al.*, 1983; *D'Antonio and Vitousek*, 1992; *Mack and D'Antonio*, 1998; *Pyšek et al.*, 2010; *Seastedt and Pyšek*, 2011; *Keeley and Brennan*, 2012; *Kimball et al.*, 2014), and it is important to understand how forcings such as climate change, increased fire frequency, and nitrogen deposition affect natural ecosystems during this period (*Whisenant*, 1990; *Chapin et al.*, 2000; *Dale et al.*, 2001; *Turner*, 2010; *Enright et al.*, 2011). Ecosystems that experience periodic disturbance undergo characteristic successional patterns during recovery that lead back to the initial conditions (*Chapin et al.*, 2011). Periodic disturbances such as fire and drought drive species evolution and community assemblage toward increased resistance and resilience to disturbance (*Holling*, 1973; *Chapin et al.*, 2011), and natural ecosystems are by necessity well adapted to the historic disturbance regime (*Chapin et al.*, 2011; *Seidl et al.*, 2014). However, this adaption likely has limits, and disturbance regimes or recovery conditions that fall outside of the historical range may increase an ecosystem's vulnerability to invasion and type conversion (*Westman and O'Leary*, 1986; *Vitousek*, 1990; *Lloret et al.*, 2003; *Chapin et al.*, 2011; *Keeley and Brennan*, 2012). In particular, shifts in resource availability, such as water input or nitrogen deposition, have the potential to alter the competitive relationships that help drive succession, potentially leading to changes in an ecosystem's ability to return to pre-disturbance conditions (*Tilman*, 1985; *Silva et al.*, 2013; *Kimball et al.*, 2014).

Southern California's coastal sage scrub (CSS) is a fire-prone, fire-adapted shrubland with a fire return interval of approximately forty years (*Keeley et al.*, 2005b). CSS is dominated by evergreen and drought-deciduous shrubs, which recover from wildfire by either resprouting from root crowns or seed germination (*Malanson and O'Leary,* 1982; *Kimball et al.*, 2014). Crown resprouters have evolved high resilience to frequent wildfire through their ability to rapidly regrow following top-kill (*Westman and O'Leary,* 1986). Characteristic CSS fire succession can be broken into three stages (*Westman,* 1981; *Malanson and O'Leary,* 1982; *Westman,* 1982; *Keeley and Keeley*, 1984; *Malanson,* 1984; *Malanson and Westman,* 1985). The first stage begins shortly after fire and persists for one or two years, during which the community is dominated by annual grasses and forbs. Early fire-following ephemeral forbs with a short growing season (two to three months) dominate the community in the first year after fire. Longer-lived annual forbs and grasses increase in the second growing season, which expands the growing season length and ecosystem productivity. Stage two occurs from approximately three to seven years after fire, and is characterized by the gradual expansion of shrub and subshrub cover at the expense of grasses and forbs. Ecosystem productivity can be high during this stage, particularly during wet years. Stage three represents a mature shrubland that persists until the next disturbance. Grasses and forbs occur in the understory and in open patches between shrubs; the productivity of these herbaceous annuals is gradually diminished as the shrub canopy closes.

Climate change is projected to increase precipitation variability in southern California, leading to more intense or frequent droughts (*Hayhoe et al.*, 2004; *Seager et al.,* 2007; *Loarie et al.,* 2008; *AghaKouchak et al.,* 2014; *Romero-Lankao, et al.*, 2014; *Berg and Hall,* 2015; *Diffenbaugh et al.,* 2015; *Hall et al.*, 2018; *Swain et al.,* 2018). Altered drought, precipitation variability, and nutrient deposition may shift the availability of resources to plants. An alteration of resource availability may affect succession in at least three non-mutually-exclusive ways. First, altered resource availability may increase or decrease the amplitude of the changes in ecosystem or community properties during succession (*Tilman*, 1985), such as total cover, NPP, or the abundance of individual species (**Figure 3.1a**). Second, altered resource availability may accelerate (*Abrams and Scott*, 1989; *Abrams and Nowacki*, 1992) or decelerate (*Kimball et al.*, 2014) the changes in ecosystem properties during succession, such as total vegetation cover (**Figure 3.1b**) or the rate of species transition and hence species composition (**Figure 3.1c**). Third, in extreme cases, altered resource availability may have a long-lasting and irreversible effect on ecosystem properties or species composition, leading to a type conversion (*Kimball et al.*, 2014), such as the replacement of shrubland by grassland (**Figure 3.1d**). These possibilities are not mutually exclusive, and increased resources could lead to both an acceleration and amplification of recovery, while a decelerated and/or diminished recovery could ultimately lead to an irreversible type conversion.

We established a precipitation and nitrogen manipulation experiment in a coastal sage scrubland that burned in October, 2007 to explore these possibilities. We crossed three levels of water input (restricted, ambient, and added) with two levels of nitrogen input (ambient and added) to investigate the effects of increased or reduced resource availability on fire recovery. We then followed the ecosystem properties (principally cover) and plant community composition (principally the relative abundance of herbaceous annuals and perennial shrubs) over time. We hypothesized that the effects of altered plant resources on recovery and succession could be interpreted based on the patterns described in **Figure 3.1**.

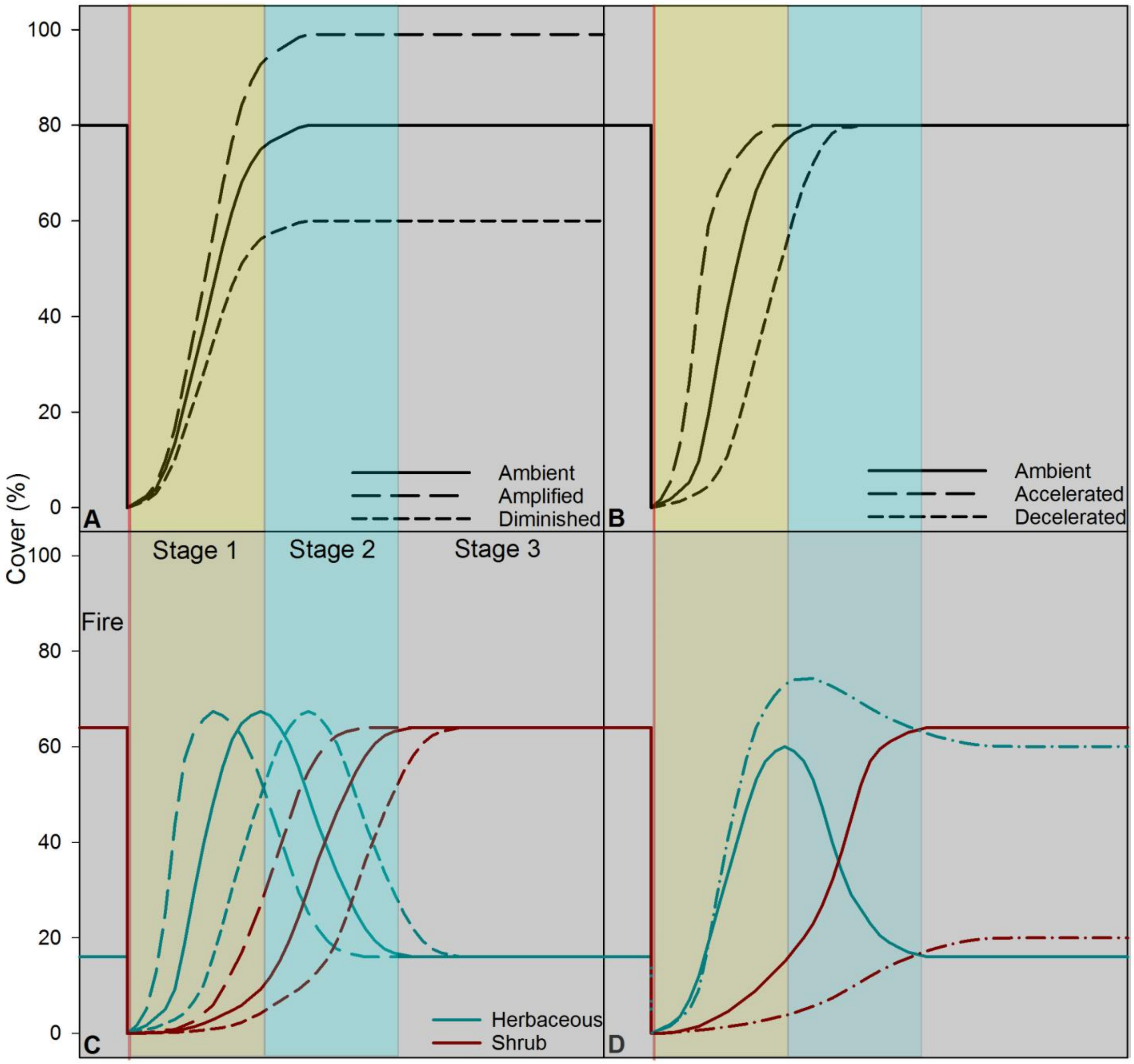

Figure 3.1: Conceptual diagram representing shifts in patterns of secondary succession in coastal sage scrub: (A) total vegetative cover successional signals indicating amplification and reduction in succession relative to ambient cover, (B) total vegetative cover successional signals indicating an acceleration and a deceleration of succession relative to ambient cover, (C) successional signals visible herbaceous and shrub fractional cover indicating an acceleration and a deceleration of succession relative to ambient cover, (D) successional signal visible in herbaceous and shrub fractional cover suggesting ecosystem type conversion from a shrub-dominated to an herbaceous annual-dominated ecosystem.

3.3 Methods

Study location

We manipulated precipitation and nitrogen input in adjacent grassland and shrubland communities in the foothills of the Santa Ana Mountains, at Loma Ridge, on land managed by the Irvine Ranch Conservancy at 117.704^{o} W, 33.742^{o} N. The site sits at 350 m of elevation on a gentle northwest-facing slope. The site is a mosaic of annual grassland and deciduous shrubland, with the borders remaining well-defined and largely immobile over the past 80 years, as seen from aerial photographs. The site experiences a Mediterranean climate, with a winter wet season and a summer dry season. Annual mean precipitation (1902-2014) is 327 mm, falling primarily between November and April. Ambient precipitation was slightly below average during the first two years of the experiment (264 and 253 mm in 2007-2008 and 2008-2009, respectively), increasing to 403 mm during the third year (2009-2010) and 595 mm during the fourth year (2010-2011). Years five through seven (2011-2014) marked the beginning of a prolonged drought, with precipitation falling from 224 mm in year five to a low of 124 mm in year seven (**Figure 3.2**) During the wet winter season, temperatures range from an average high of 21.0^{o} C to an average low of 6.2^{o} C (Tustin Irvine Ranch weather, 1902-2003, http://www.wrcc.dri.edu). During the characteristic summer (May through October) drought, the site receives negligible precipitation, and experiences temperatures ranging from a high of 27.3^{o} C to a low of 13.1^{o} C. Long-term temperature records along with the presence of *Malosma laurina*, a frost-intolerant species, indicate that the temperature rarely drops below 0^{o} C.

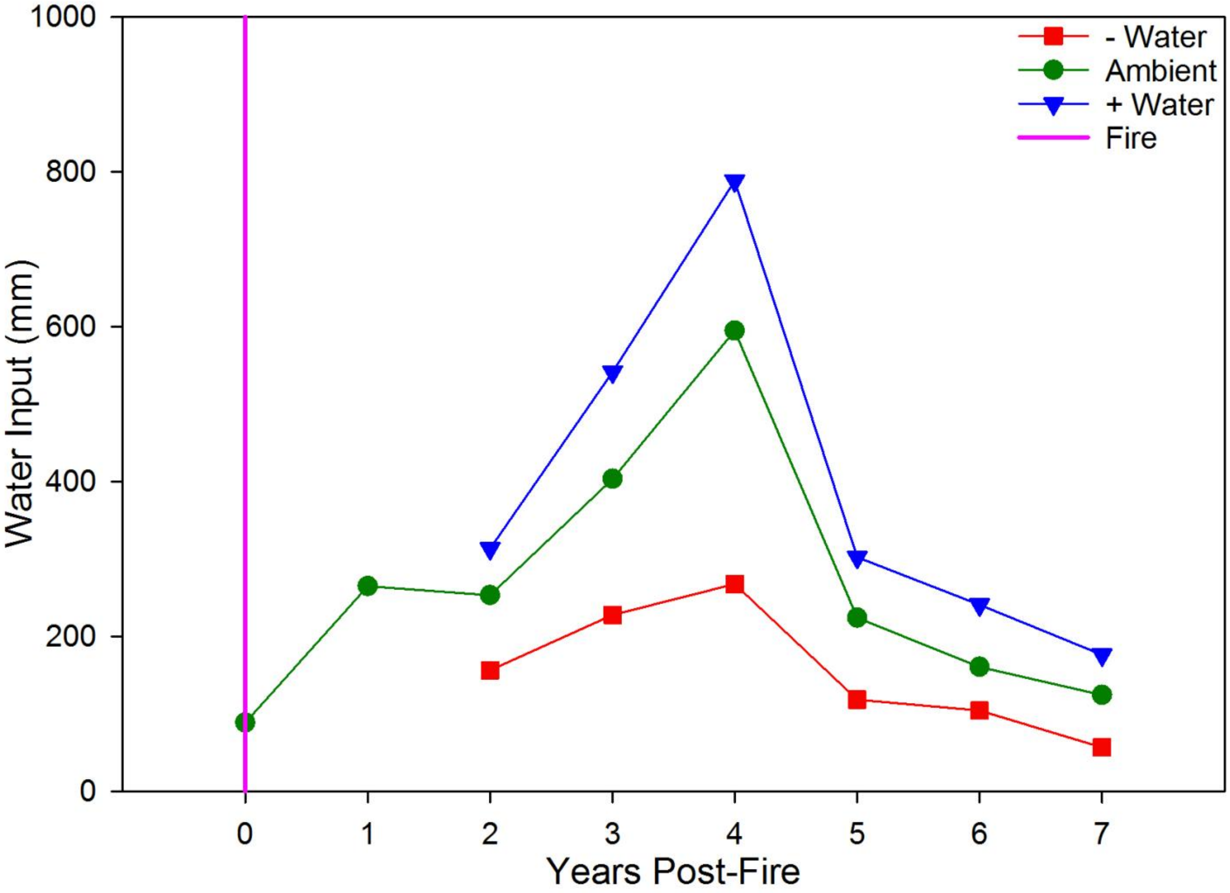

Figure 3.2: Annual ambient water input (mm) beginning in 2006-2007 (green) and water input in the added-water treatment (blue) and restricted-water treatment (red) beginning in 2008-2009, concurrent with the beginning of the water manipulations. Vertical line denotes the Santiago wildfire that occurred prior to the 2007-2008 growing season; x-axis denotes years subsequent to fire. Ambient precipitation record was obtained from Orange County Water District station 61 (33.720^o N 117.723^o W, http://www.ocpublicworks.com).

CSS is a fire-prone and fire-adapted ecosystem, with a natural fire return interval of approximately 40 years (*Keeley et al.*, 2005b); this interval has been decreasing due to human ignitions. The Loma Ridge site burned in 1914, 1948, 1967, 1998, and 2007 according to the CAL FIRE Fire and Resource Assessment Program (http://frap.cdf.ca.gov/). We applied a controlled burn to half of the experimental area in February 2007, prior to the construction of our experimental plots. The remainder of the site burned in the Santiago wildfire in October 2007.

We have not observed significant differences in the ecosystem properties and species composition between the controlled burn and Santiago wildfire plots and therefore pooled all of the plots in subsequent analyses.

Experimental Design

The manipulations consist of twenty-four 18.29 x 12.19 m plots in the coastal sage scrubland, oriented with the long axis of each plot following the slope. We applied ambient, added, and restricted-water treatments to the plots, with a target of 40% added and 40% restricted water. The plots were split lengthwise and half of each plot received added nitrogen. Each half-plot was further split into three 4 x 4 m subplots. Data collection was conducted primarily in the lowest two subplots in each plot to minimize artifacts from lateral water flow and wind on the upslope side of each plot.

The restricted-water plots were constructed with frames upon which were mounted clear retractable polyethylene roofs. These plots remained open for roughly 95% of the year, which reduced potential temperature and humidity artifacts, as verified by air temperature and relative humidity sensors installed in representative plots from each water treatment which showed no difference in air temperature and relative humidity between the restricted-water plots and the other two water treatments when the shelters were open. We closed these roofs for a subset of storms to restrict water input, focusing on larger storms to reduce both precipitation frequency and intensity. The water collected from these plots was stored in polyethylene tanks; this water was subsequently pumped through irrigation manifolds installed in the water addition plots. The water manipulation system had a storage capacity of 5.1 cm; this was exceeded in 2010 and 2011 when the site experienced intense storms. Our water manipulations therefore represented a 51% water restriction and 33% water addition to the corresponding treatments.

We added 6 gN m^{-2} yr^{-1} to one side of each plot; this input increased the annual nitrogen input over the ambient deposition of 1.5gN m^{-2} yr^{-1} (*Fenn et al.*, 2010). Our nitrogen application was conducted in two stages. First, we applied 2 gN m^{-2} yr^{-1} to each added-nitrogen plot in the form of fast-release fertilizer (15.5-0-0 calcium nitrate, 15.5% N, 0% P, 0% K, 19% Ca) shortly before the first storm of each wet season to simulate the nitrogen flush that accompanies the first rain. The remainder was applied approximately one month later as controlled (4 month) release fertilizer (14-0-0 calcium nitrate, 14% N, 0% P, 0% K, 19% Ca).

Field observations

We selected two plots from each water treatment from each ecosystem to host automated instrumentation arrays. These instruments were sampled on a 30 minute interval year-round. Each array consisted of eight Campbell Scientific CS616 soil moisture sensors, four in-house fabricated soil temperature sensors, two in-house fabricated NDVI sensors, two Campbell Scientific 506-L fuel moisture sensors, two Campbell Scientific LWS leaf wetness sensors, and an array of Campbell Scientific 229-L matric potential sensors installed at depths of 5, 10, 25, 50, and 100 cm, with an additional sensor at 200 cm in the shrubland plots only. We measured precipitation at the site every 10 minutes with a single tipping-bucket rain gauge installed on level ground with an unobstructed field of view above the sensor. We conducted additional manual measurements throughout the year. Every 2-3 weeks during the growing season, we sampled surface soil moisture, spectral reflectance from 300-1200 nm, and soil moisture depth profiles. These measurements were reduced to a 4-6 week interval during the dry season. The surface soil moisture measurements were conducted using a Campbell Hydrosense probe with fixed vertical TDR wave guides permanently installed in the soil at four locations per half-plot. Spectral reflectance was measured around the central subplot in each half plot at 20 locations per grassland subplot and 36 locations per CSS subplot. Soil moisture depth profiles were measured using a neutron probe at 25 cm intervals to a depth of 2 m. We measured species composition at the end of the growing season in the two lower subplots in each half-plot. Each subplot was divided into sixty-four 0.25 m^2 squares, with each square representing 1.6% of the total cover of that subplot. We recorded the number of squares in which a given species accounted for the majority of cover and normalized the data to account for canopy overlap.

Precipitation record

Six nearby precipitation datasets were analyzed to determine the best precipitation record for Loma Ridge. Two nearby eddy covariance towers equipped with tipping-bucket rain gauges (Ameriflux sites US-SCg, 33.737^o N 117.695^o W and US-SCs, 33.734^o N 117.696^o W, http://ess.uci.edu/~california) provided records #1 and #2, which began in 2006. Record #3 was obtained from a third tipping-bucket rain gauge that was installed in a flat area with a low plant canopy and wide sky view adjacent to the manipulations site. Record #4 was obtained from a rain gauge installed in 2013 within the manipulations area. Records #5 and #6 were obtained from two Orange County Water District stations near the site, station 247 (33.745^o N 117.704^o W, http://www.ocpublicworks.com) and station 61 (33.720^o N 117.723^o W). The first three rain gauges were merged into a single complete record to fill gaps and periods with malfunctioning gauges, giving priority to record #3, followed by #2, then by #1. This composite record was compared with the two OCWD records (#5 and #6) and the final record from within the manipulations (#4), looking for continuity, duration, reliability of data, and proximity to the manipulations. The OCWD record from station 61 (record #6) was determined to be the longest, most homogeneous record, and subsequent analyses were conducted based on this dataset. Water input for the restricted-water treatment was calculated by subtracting the precipitation during storms when the treatment roofs were closed, and input for the added-water treatment by adding the amount of water applied (**Figure 3.2**).

Integrated EVI

We established an annual metric based on the hand-held EVI observations. We determined a baseline EVI for each growing season by averaging measured EVI from the beginning and the end of each water year (September and August). We calculated the cumulative growing season EVI by linear interpolation above the non-growing-season baseline.

3.4 Results

Coastal sage scrub ambient wildfire recovery

Most field observations began during the second year after the fire (2008-2009). The coastal sage shrubland rapidly reestablished vegetative cover following the fire, with total cover reaching 96% under ambient conditions by the second growing season after the fire (**Figure 3.3**). Community composition was initially dominated by herbaceous grasses and forbs (79%), with invasive annual grasses accounting for 48% cover and native forbs making up 31%. Perennial shrubs accounted for 17% of cover. Perennial shrubs had replaced herbaceous annuals as the dominant plant type by year four (2010-2011), accounting for 54% of total living cover compared to 45% herbaceous annuals. Total living cover dropped to 77%, shrub cover decreased to 48%, and herbaceous cover decreased to 28% by the seventh growing season (2013-2014), coincident with a series of dry years (**Figure 3.2**).

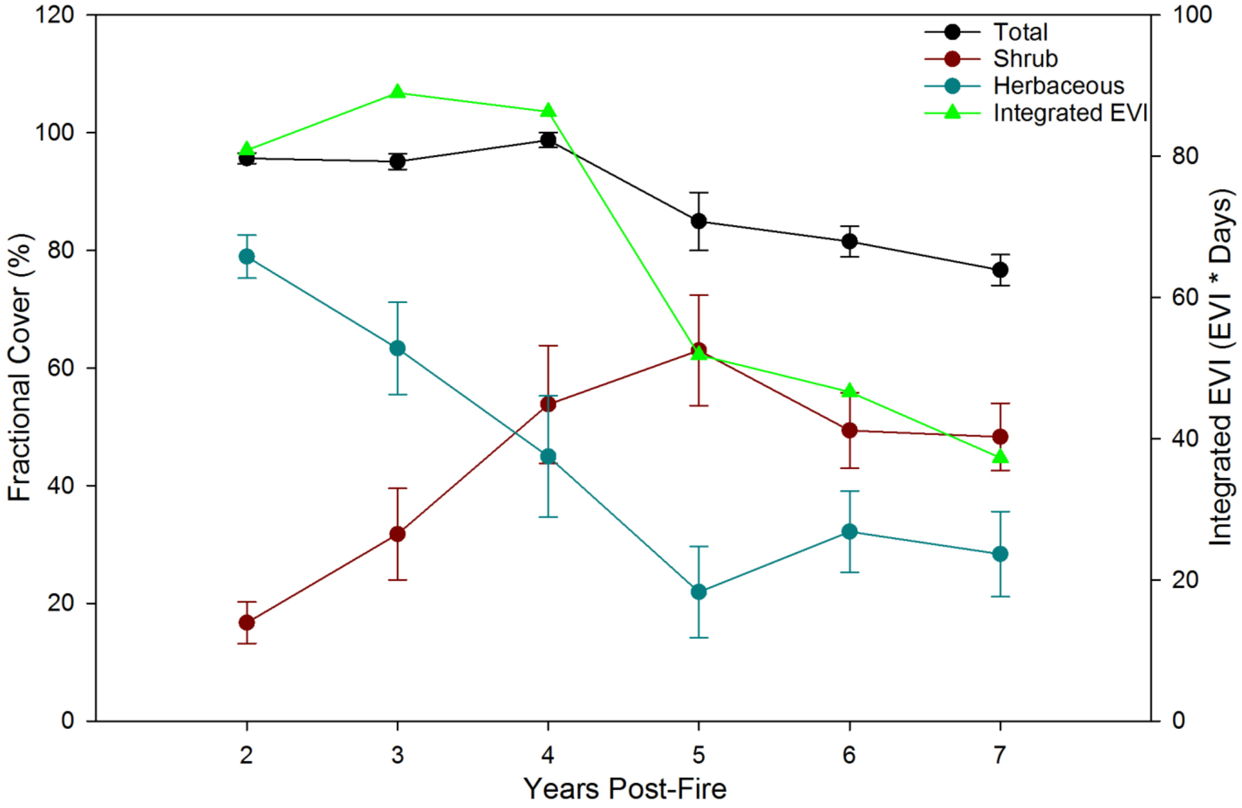

Figure 3.3: Fractional cover (%) of shrubs (dark red) and herbaceous annuals (cyan), total vegetative cover (%, black), and Integrated EVI (EVI * Days, green) in the ambient-water treatment throughout the study period, years two through seven post-fire; points represent mean ± standard error.

Integrated EVI was consistent from the second through fourth years after the fire, beginning at 80.9 EVI*Days in year two (2008-2009) and peaking at 89.0 EVI*days the following year. EVI dropped in the fifth year (2011-2012) and continued to decrease through the end of the experimental period, reaching a minimum of 37.3 EVI*Days in the seventh year (2013-2014). Integrated EVI reflects the combined effects of leaf density and longevity, and plant type, increasing with dense, longer-lasting cover and an increasing proportion of deciduous leaves, and decreasing with sparse, ephemeral cover and an increasing proportion of evergreen leaves.

Anecdotal observations during the first growing season after the fire indicate cover was dominated by short-lived ephemeral forbs, with shrub seedlings and small resprouts covering a small fraction of the area.

Treatment effects on total live cover, vegetation composition, and EVI

Total live cover did not differ significantly between the added- and ambient-water treatments during the first three years of data collection (**Figure 3.4a**). Total cover in the added-water treatment remained high (92% and 93%) in the fifth and sixth water years (2011-2012 and 2012-2013), before dropping in the seventh year post-fire (2013-2014), to 82%. Total cover in the restricted-water treatment was consistently lower than in the other two water treatments, ranging from a high of 95% in the fourth year (2010-2011) to a low of 37% in the seventh year post-fire (2013-2014). Total cover in the ambient-water treatment was generally similar to that in the added-water treatment, except for a more rapid drop-off in the sixth and seventh years after the fire. These trends tracked the variability in water input with the treatments and year-to-year shifts in precipitation (**Figure 3.2**).

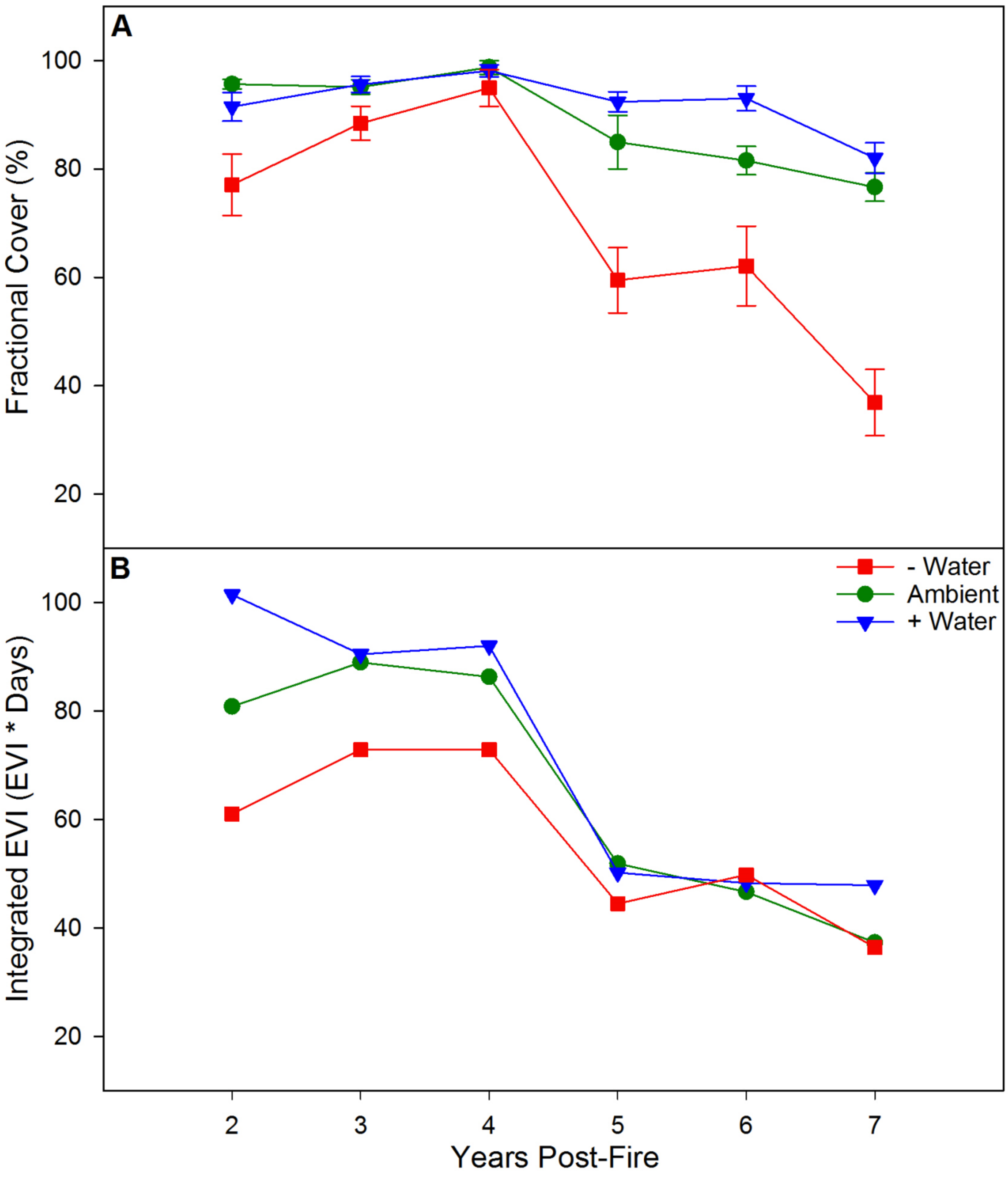

Figure 3.4: (A) Total vegetative cover in the restricted-water (red squares), ambient-water (green circles), and added-water treatments (blue triangles) throughout the study period; points represent mean ± standard error. (B) Mean Integrated EVI (EVI * Days) in the restricted-water (red squares), ambient-water (green circles), and added-water treatments (blue triangles) throughout the study period, years two through seven post-fire.

Integrated EVI differed between the water treatments during the second year after the fire (2008-2009), 61.1, 80.9, and 101.5 EVI*Days in the restricted-, ambient-, and added-water treatments, respectively (**Figure 3.4b**). Integrated EVI in the ambient- and added-water treatments converged in the third year (2009-2010), but remained substantially lower in the restricted-water treatments. Integrated EVI fell dramatically in all three treatments in the fifth year (2011-2012), to 44.4, 51.9, and 50.2 EVI*Days in the restricted-, ambient-, and added-water treatments, respectively, coincident with reduced precipitation. Integrated EVI continued to fall to 36.4 and 37.3 EVI*Days in the restricted- and ambient-water treatments by the seventh year (2013-2014), but remained fairly stable in the added-water treatments, dropping to 47.8 EVI*days. The relatively low reduced-water integrated EVI in the second year (2008-2009) relative to the ambient integrated EVI is consistent with less cover and a reduced growing-season length. The relatively high added-water EVI in this same year relative to the ambient integrated EVI is consistent with an extended growing season. The similar reduced-water integrated EVI in the sixth year (2012-2013) relative to the wetter treatments despite lower cover is consistent with shifts in leaf type.

Shrub cover differed markedly between the three water treatments, especially beginning in the fifth year (2011-2012) (**Figure 3.5a**). Shrub cover measured 17%, 17%, and 26% in the restricted-, ambient-, and added-water treatments in 2008-2009. Shrub cover increased to a peak of 63% and 80% in the ambient- and added-water treatments in 2011-2012 and 40% in the restricted-water treatments the following year. Cover gradually decreased following these peaks, dropping to 34%, 48%, and 65% in the restricted-, ambient-, and added-water treatments in the seventh year (2013-2014), coincident with a series of drier years.

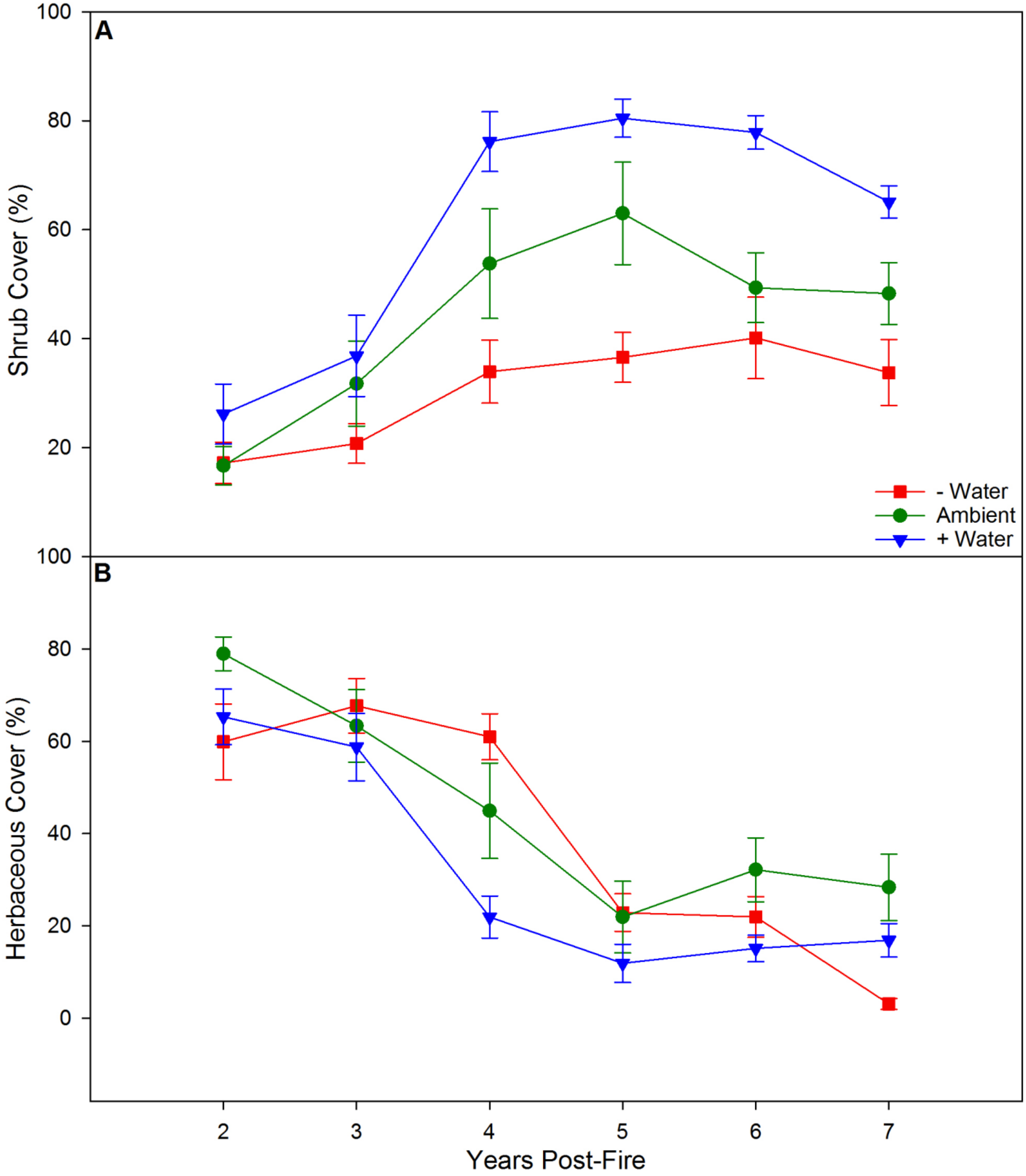

Figure 3.5: Fractional cover (%) of shrubs (A) and herbaceous annuals (B) throughout the study period (two to seven years post-fire) in the restricted (red), ambient (green), and added (blue) water treatments; points represent mean ± standard error.

Herbaceous cover was highest in 2008-2009 for the ambient- and added-water treatments, at 79% and 65% respectively (**Figure 3.5b**). Restricted-water herbaceous cover was 60% in 2008-2009 and peaked the following year at 68%. Herbaceous cover in the ambient- and added-water treatments dropped in the fifth year (2011-2012) to 22% and 12% respectively, then remained fairly stable; we measured a subsequent high of 32% herbaceous cover in the ambient-water treatment in 2012-2013 and a high of 17% herbaceous cover in the added-water treatments in 2013-2014. Herbaceous cover in the restricted-water treatments plateaued in 2011-2012 and 2012-2013 at 23% and 22% respectively then fell to a low of 3% in 2013-2014.

Nitrogen addition resulted in consistent but generally insignificant increases in herbaceous cover, and reductions in perennial shrub cover, relative to ambient nitrogen conditions (**Figure 3.6**). The largest nitrogen effect occurred for shrubs under restricted-water conditions (**Figure 3.6a**), where cover was consistently reduced by added nitrogen. In all water treatments, herbaceous cover followed a similar trend under both nitrogen treatments, but with a marginally higher magnitude under added-nitrogen conditions in most treatments during most years. Shrub cover followed a similar trend under both nitrogen treatments in the ambient-water (**Figure 3.6b**) and added-water (**Figure 3.6c**) treatments, but with a marginally higher magnitude under ambient-nitrogen conditions in most treatments during most years.

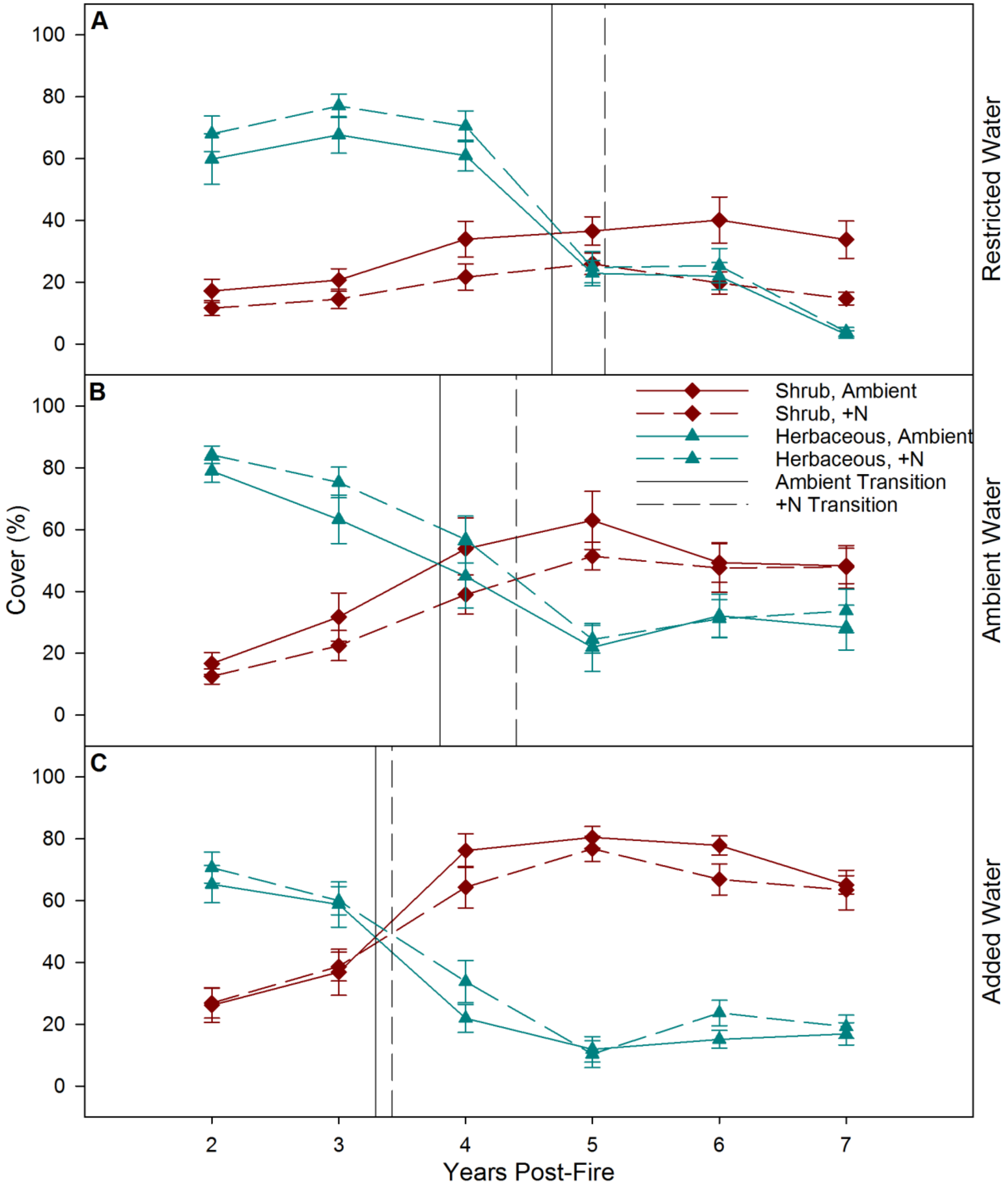

Figure 3.6: Fractional cover (%) of shrubs (dark red) and herbaceous annuals (cyan) throughout the study period (two to seven years post-fire) under ambient (solid lines) and added (dashed lines) nitrogen treatments in the restricted (A), ambient (B), and added (C) water treatments.

Relationship between water input, cover, and EVI

Total cover was well correlated with water input across all years and treatments (**Figure 3.7a**), displaying a saturating relationship: $cover\ (\%) = 98.786(1 - e^{(-0.010*\ water\ input\ (mm))})$ ($R^2 = 0.95$; 56 mm - 789 mm annual water input). Residuals were normalized to the cover predicted at a water input of 600 mm, and then analyzed by year (**Figure 3.8a**) and water treatment (**Figure 3.8b**). The residuals showed no significant trends in total cover based on year post-disturbance or water treatment, and the magnitude was small, not exceeding 0.042 when analyzed by year post-disturbance or 0.019 when analyzed by water treatment.

Integrated EVI was related to water input through the relationship $Integrated\ EVI\ (EVI * Days) = 94.046(1 - e^{(-0.005*\ water\ input\ (mm))})$ ($R^2 = 0.67$) (**Figure 3.7b**). These residuals were also normalized to the predicted integrated EVI value at water input of 600 mm and analyzed by year (**Figure 3.8c**) and water treatment (**Figure 3.8d**). EVI residuals were decreasingly positive for the first two years of the measurement, years two and three following the fire, with the highest residual calculated at 0.174 for the second year (2008-2009). The residual for the fourth year (2010-2011) was negligible, but the subsequent three years' residuals were decreasingly negative, -0.132 in the fifth year (2011-2012) increasing to -0.013 in the seventh year (2013-2014). The residuals calculated based on water treatments were 0.080, -0.021, and -0.045 for restricted-, ambient-, and added-water treatments, respectively.

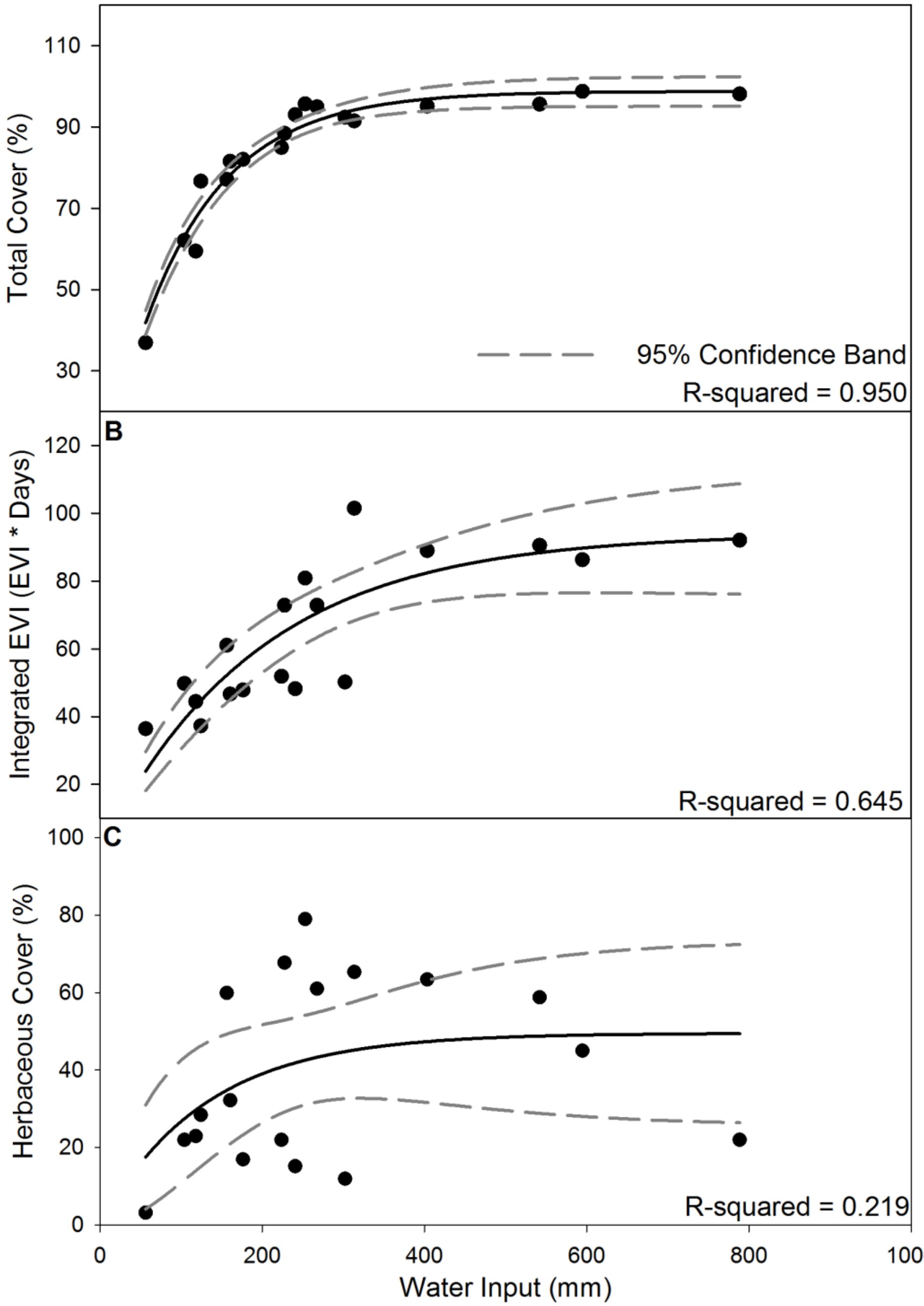

Figure 3.7: (A) Points are water input (mm) vs total cover (%); black line represents the saturating relationship between water input (mm) and total cover (%): $total\ cover\ (\%)\ = 98.786(1 - e^{(-0.010\,*\,water\ input\ (mm))})$ (R^2 = 0.95; 56 mm - 789 mm annual water input) determined through regression; dashed gray lines represent the 95% confidence band of the regression. (B) Points are water input (mm) vs Integrated EVI (EVI * Days); black line represents the saturating relationship between water input (mm) and total cover (%):

$Integrated\ EVI\ (EVI * Days)\ = 94.046(1 - e^{(-0.005 * water\ input\ (mm))})$ ($R^2 = 0.67$; 56 mm - 789 mm annual water input) determined through regression; dashed gray lines represent the 95% confidence band of the regression. (C) Points are water input (mm) vs herbaceous fractional cover (%); black line represents the saturating relationship between water input (mm) and herbaceous cover (%): $herbaceous\ cover\ (\%)\ =\ 49.500(1 - e^{(-0.008 * water\ input\ (mm))})$ ($R^2 = 0.22$; 56 mm - 789 mm annual water input) determined through regression; dashed gray lines represent the 95% confidence band of the regression.

Finally, we calculated the relationship between herbaceous cover and water input (**Figure 3.7c**) and found that $herbaceous\ cover\ (\%)\ =\ 49.500(1 - e^{(-0.008 * water\ input\ (mm))})$ ($R^2 = 0.22$). Residuals were normalized to a water input of 600 mm, and analyzed by year post-fire and water treatment (**Figure 3.8e**) and by water treatment alone (**Figure 3.8f**). When grouped by year post-fire, residuals showed a trend that was generally similar to the integrated EVI residuals, but with a much larger magnitude overall (**Figure 3.8e**). The herbaceous cover residuals for the second year (2008-2009) were highest, ranging from 0.443 for the added-water and 0.622 for the restricted-water treatments. Residuals were lowest in the fifth year (2011-2012) for added- and ambient-water treatments, -0.689 and -0.419 respectively, and in the seventh year (2013-2014) for the restricted-water treatment at -0.398. Residuals shifted from positive to negative for the added- and ambient-water treatments by year four and for the restricted-water treatments by year five, which is consistent with the prolonged high herbaceous cover in the restricted-water treatment that appeared in the vegetative composition observations (**Figure 3.5b**). The magnitude of this shift was greatest in the added-water treatment. The residuals calculated based on water treatments were 0.145, 0.082, and -0.261 for restricted-, ambient-, and added-water treatments, respectively. Integrated EVI reflects the combined effects of vegetation extent, duration, and leaf type, and the three sets of residuals paint a consistent picture, with the shifts in residual integrated EVI (**Figure 3.8c,d**) indicating trends in herbaceous cover (**Figure 3.8e,f**), despite constant total cover (**Figure 3.8a,b**).

3.5 Discussion

Coastal sage scrub ambient wildfire recovery

Coastal sage scrub fire recovery is characterized by a rapid reestablishment of vegetative cover, which is initially dominated by herbaceous annuals that gradually give way to perennial shrubs as crown-resprouters expand and seedlings grow, and concludes with a closed shrub canopy with herbaceous annuals dispersed throughout the understory (*Westman*, 1981; *Malanson and O'Leary*, 1982; *Westman*, 1982; *Keeley and Keeley*, 1984; *Malanson*, 1984; *Malanson and Westman*, 1985). We broke this pattern into three stages for discussion. During stage one, vegetative cover increases rapidly and is composed primarily of annual grasses and forbs; the end of this stage is signaled when total cover nears 100%. During stage two, the community is comprised of a mix of shrubs, subshrubs, and herbaceous annuals. Herbaceous cover declines and shrub cover increases. The end of this stage is signaled when shrub cover stabilizes. Stage three represents a mature ecosystem, where herbaceous annuals are present but dispersed, species characteristic of mid-succession, such as *Acmispon glaber*, have largely disappeared, and shrubs have established a closed canopy.

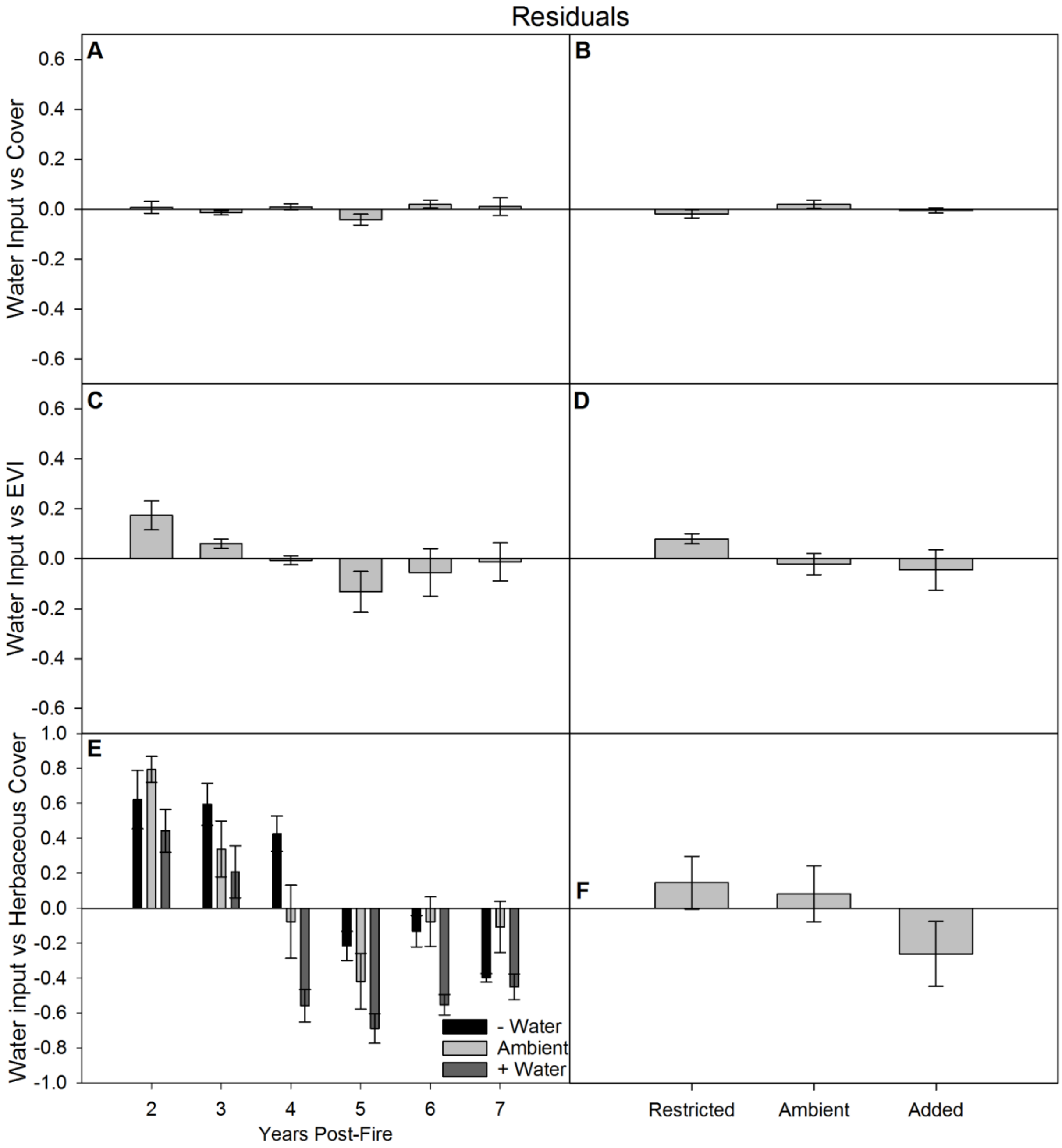

Figure 3.8: (A, B) Residual analysis of water input (mm) vs total vegetative cover (%) grouped by year post-fire (A) and water treatment (B). (C, D) Residual analysis of water input (mm) vs Integrated EVI (EVI * Days) grouped by year post-fire (C) and water treatment (D). (E, F) Residual analysis of water input (mm) vs herbaceous fractional cover (%) grouped by water treatment and year post-fire (E) and water treatment alone (F). All bars indicate mean residual ± standard error.

Our measurements began in the second growing season after the fire (2008-2009); total cover approached 100% in the ambient water treatment by this point (**Figure 3.3**) and recovery had reached stage two. Herbaceous cover was high at the beginning of the measurements, and steadily declined as shrub cover increased until year five (2011-2012), characteristic of stage two. Much of the shrub cover in stage two was accounted for by one subshrub species, *Acmispon glaber* (*Baldwin et al.*, 2012), an obligate seeder and nitrogen fixer that plays an important role in CSS mid-succession (Chapter 4). *Acmispon glaber* dies back almost entirely by the end of stage two; the presence of this subshrub may account for the peak in shrub cover between years three and five (2010-2012) and its senescence may account for the slight drop in shrub cover the following year. Herbaceous annuals in the understory may be better able to access sunlight following *A. glaber* senescence, accounting for the slight uptick in herbaceous cover. However, year five (2011-2012) also marked the beginning of a multiyear drought (**Figure 3.2**), and interannual water input variation may also explain these trends.

The patterns of recovery appear in the EVI observations as well (**Figure 3.3**). Integrated EVI is high through year four (2010-2011); this is likely due to two mechanisms. First, EVI tracks overall vegetative cover, which was high through year four. Second, EVI is particularly sensitive to herbaceous cover (*Huete et al.*, 2002). Integrated EVI fell dramatically between years four and five (2010-2012); herbaceous cover reached its minimum in year five (2011-2012), and total cover began to fall this year as well. These two mechanisms may have combined to create the large drop in integrated EVI between these two years. The slow decline subsequent to year five may be explained by the continued decrease of total cover with the multi-year dry period.

Shifts in amplitude of succession

Shifts in the amplitude of variation during succession would appear as an increase or decrease in the magnitude of measurements of ecosystem structure and function relative to ambient conditions (**Figure 3.1a, c**). There is strong evidence for a decrease in the amplitude of the successional signal in total cover (**Figure 3.4a**) and integrated EVI (**Figure 3.4b**) in the restricted-water treatment. Total cover was significantly lower in the restricted-water treatments (**Figure 3.4a**) with the exception of year four (2010-2011), which was so wet that these plots received nearly as much water input as the long-term average ambient water input (**Figure 3.2**). Integrated EVI was lower under restricted-water conditions than added- or ambient-water conditions through year five (2011-2012), despite sufficient water in year four to drive total vegetative cover close to 100% (**Figure 3.4b**). This signals a decrease in amplitude during recovery under dry conditions, as EVI indicates lower vegetation density in the restricted-water treatment than in the added- and ambient-water treatments.

Total cover and integrated EVI data did not show substantial evidence of an increase in successional variation in the added-water treatment relative to ambient. This lack of response may reflect a saturation of the effect of water input (**Figure 3.7a,b**), which reaches a threshold beyond which additional water addition cannot increase total cover (**Figure 3.6a**). Both the added- and ambient-water treatments received sufficient water input to drive vegetative cover to near-complete closure throughout most of the experiment, and an amplification of total cover with water addition was not possible. Similarly, integrated EVI exhibits a saturating relationship with water input (**Figure 3.6b**), which is likely related to vegetation density. Throughout most of the experiment (2009-2013), both the added- and ambient-water treatments received sufficient water input to drive up vegetation density enough to saturate the EVI signal for the current successional stage. Integrated EVI was higher in the added-water treatment than in the ambient-water treatment during the 2008-2009 and 2013-2014 growing seasons (**Figure 3.4b**), offering some evidence for an increase in amplitude during these years; notably, these were two of the driest years of the experiment, and water input in the ambient-water treatment appears to have been low enough to reduce vegetation density and thus decrease EVI.

Changes in the amplitude variation during succession also appear in the observations of plant type (**Figures 3.5, 3.6**). Shrub cover differed substantially between the three water treatments and was related to water input (**Figure 3.5a**). Shrub cover in the added-water treatment was consistently higher and shrub cover in the restricted-water treatment was consistently lower than in the ambient-water treatment; this is consistent with a shift in the amplitude of shrub abundance with water input. Added nitrogen under restricted-water conditions resulted in a decrease in amplitude of shrub cover (**Figure 3.6a**). In general, the added-nitrogen treatments led to reduced shrub cover relative to the ambient-nitrogen treatments (**Figure 3.6b,c**), though this effect was small compared to the effect of the water treatments. Herbaceous cover was consistently higher in the added-nitrogen treatments across all water treatments; this effect was largest in the restricted- and ambient-water treatments between 2008 and 2011 (**Figure 3.6**).

Shifts in rate of succession

Shifts in the rate of succession should appear as phase shifts relative to ambient conditions. A transition from herbaceous to shrub-dominated communities is characteristic of stage two of CSS succession; the timing of this shift was altered relative to ambient conditions by our water treatments. This transition occurred between the third and fourth (2009-2010 and

2010-2011) growing seasons under ambient conditions (**Figure 3.6b,c**), and closer to the third growing season in the added-water treatment (**Figure 3.6a**). Trends in herbaceous cover (**Figure 3.5b**) and in the residuals calculated from the relationship between water and herbaceous cover further support this acceleration (**Figure 3.8e**). This shift is much larger in magnitude in the added-water treatment than under ambient-water conditions; herbaceous cover under ambient-water conditions is not significantly different than the predicted value in the fourth year post-fire. This pattern is consistent with the herbaceous cover decline characteristic of stage two of CSS succession (*Westman*, 1981; *O'Leary*, 1990) and suggests that the added-water plots progressed through the second stage of succession faster than the ambient plots.

Restricted water slowed succession relative to ambient conditions; this was also apparent in herbaceous cover trends and departures from predicted cover based on water input. Herbaceous cover was higher under restricted-water conditions than ambient during the third and fourth years post-fire (2009-2011, **Figure 3.5b**). This suggests a delay in the transition from herbaceous to shrub-dominated communities. The end of stage one of succession is characterized by a peak in herbaceous cover (*Westman*, 1981; *O'Leary*, 1990), which does not occur until the third year post-fire (2009-2010); herbaceous cover under ambient-water conditions declined after the second year post-fire (**Figure 3.5b**). A residual analysis of the relationship between water input and herbaceous cover shows a deceleration of succession in the restricted-water treatment as well (**Figure 3.8e**). Herbaceous cover remains higher than predicted until the fifth year (2011-2012). The integrated EVI residuals averaged across the six years of study also suggest a deceleration of succession under restricted-water conditions (**Figure 3.8d**). The best explanation for the higher measured integrated EVI than the predicted value under restricted-water conditions is that the community in this treatment was dominated by herbaceous annuals for a longer period than under ambient conditions; this is consistent with a slower emergence from stage two of succession and an overall deceleration of succession.

Shifts in vegetation type with drought and nitrogen addition

Southern California is projected to become more arid and to experience greater precipitation variability with global climate change (*Hayhoe et al.*, 2004; *Seager et al.*, 2007; *Loarie et al.*, 2008; *AghaKouchak et al.*, 2014; *Romero-Lankao, et al.*, 2014; *Berg and Hall*, 2015; *Diffenbaugh et al.*, 2015; *Hall et al.*, 2018; *Swain et al.*, 2018). Our results indicate this trend may alter coastal sage scrub fire recovery. Shrubs are capable of accessing deeper water stores than herbaceous annuals (Chapter 2; see also *Jackson et al.*, 1999; *Schenk and Jackson,* 2002), but this water is not unlimited, and under conditions of prolonged drought, shrublands may struggle to recover, shrub mortality will increase, and conversion to invasive grassland is likely (*Langan et al.*, 1997; *Keeley et al.*, 2005b; *Sandel and Dangremond*, 2012; *Rapacciuolo et al.*, 2014). Alteration of the fire regime may negatively impact CSS recovery (*Zedler et al.*, 1983; *Baker*, 2006; *Enright et al.*, 2011; *Jin et al.*, 2015; *Keeley and Syphard*, 2016); the CSS community is able to reestablish following fire in large part due to the survival of shrub root systems that enable crown resprouting (*Malanson and O'Leary*, 1982; *Malanson and Westman*, 1985). An increase in wildfire frequency, particularly when coupled with more frequent drought, may increase shrub mortality (*Zedler et al.*, 1983; *Whisenant*, 1990). Most extant coastal sage scrubland occurs near urban centers and thus experience high nitrogen deposition (*Fenn et al.*, 2003; *Talluto and Suding*, 2008; *Fenn et al.*, 2010). Additional nitrogen under restricted-water conditions markedly slowed shrub recovery, and resulted in negligible shrub growth (**Figure**

3.6a). This trend may indicate ecosystem retrogression or the beginning of ecosystem type conversion to invasive grassland.

The restricted-water, added-nitrogen treatment resulted in a decline in total and shrub cover and the absence of herbaceous cover by the end of the study (**Figures 3.4, 3.6**); a key question moving forward is whether these plots have effectively shifted to grassland, or whether the observed effects are reversible and shrubland would reemerge if the treatments were terminated. Previous work (see Chapter 2) suggests that invasive Eurasian grasslands and native CSS are alternative stable states under the same climatic regime due to differing growth patterns and water-use strategies. If the majority of the shrubs in this treatment have died and the community has shifted to a grassland, it is unlikely that the coastal sage scrub community will recover. However, this work also suggests that CSS is resilient to drought. If shrub cover has decreased through canopy thinning and aboveground dieback but retains intact root systems and can thus access deeper water stores, the CSS community may be able to recover following the end of this drought. The combination of restricted water and added nitrogen clearly favors herbaceous plants at the expense of shrubs; further work is needed to investigate when this shift becomes irreversible.

CHAPTER 4

Evidence for and controls on a transient maximum of productivity during post-fire succession in a semiarid shrubland

4.1 Abstract

Increased resource availability and reduced plant competition after fire create a window during which rapidly growing, shorter-lived species capitalize on the availability of nutrients, light, and space; this can cause a period of particularly high primary productivity. This transient productivity maximum is important because it allows an ecosystem to rapidly reestablish function and cover, minimizes nutrient loss, and creates a microenvironment that favors the species that compose the mature ecosystem. Species that are sensitive to the abundance of specific resources may have difficulty establishing during fire recovery under altered resource conditions, leading to a shift in subsequent community composition; this has implications for subsequent ecosystem processes if these species play a key role in the structure or function of the recovering ecosystem. We established a precipitation and nitrogen manipulation experiment in a seasonally-dry shrubland immediately following fire to determine whether a transient productivity maximum occurs in this ecosystem and to explore the impacts of altered resources on the phenomenon. We found that ambient productivity was higher than predicted by water input during mid-succession, indicating a transient productivity maximum. The transient productivity maximum occurred regardless of water and nitrogen treatments, suggesting that it was likely driven by light availability and competition for space. Nitrogen addition and water restriction shifted the vegetation type responsible for the transient productivity maximum from

the native nitrogen-fixing subshrub *Acmispon glaber* to invasive Eurasian annual grasses. This suggests that *A. glaber* is sensitive to drought and nitrogen deposition, and the projected increases in these factors could reduce the establishment of this species, with cascading effects on this ecosystem.

4.2 Introduction

Fire-adapted ecosystems often follow characteristic recovery patterns after large-scale disturbances (*Habeck and Mutch*, 1973; *Agee*, 1998; *Chapin et al.*, 2011; *Bonan*, 2015). Fire removes the vegetation canopy, reduces plant competitors, and increases the availability of resources such as light, water, and nutrients. The lack of vegetation after fire creates a window during which rapidly growing, shorter-lived species that are capable of rapid growth under high-resource conditions capitalize on the availability of nutrients, light, and space; this may cause a period of high ecosystem productivity (*Seastedt and Knapp*, 1993; *Knapp and Smith*, 2001; *Chapin et al.*, 2011; *Bonan*, 2015). The intense competition for abundant resources and space during recovery is broadly characteristic of secondary succession, which suggests that this phenomenon may occur in a range of ecosystems. A transient productivity peak has been described in many ecosystems, including Canadian Boreal forest (*Goulden et al.*, 2011) and North American tallgrass prairie (*Seastedt and Knapp*, 1993; *Blair*, 1997).

The transient productivity maximum is important because it allows an ecosystem to rapidly reestablish function and cover, leads to tighter nutrient cycling by reducing erosion and nutrient leaching, and sets the stage for the mature ecosystem, either by allowing species that will become dominant to capture space, or by creating a microenvironment that ultimately leads to the success of these species (*Seastedt and Knapp*, 1993; *Chapin et al.*, 2011). Different species and vegetation types within an ecosystem have differing abilities to respond rapidly to high resource availability, with some species displaying a greater response than others (*Grime*, 1977; *Tilman*, 1982; *Tilman*, 1988; *Baer, et al.*, 2003). Species that are sensitive to the abundance of specific resources may have difficulty establishing during recovery under altered resource conditions, leading to a shift in subsequent community composition. Some of these vulnerable species may play a key role in the structure or function of recovering or mature ecosystems, with implications for subsequent ecosystem processes, particularly since the period of ecosystem disturbance and recovery is thought to represent a window when ecosystems may become particularly vulnerable to habitat degradation or the establishment of invasive species (*D'Antonio and Vitousek*, 1992; *Blair*, 1997; *Mack and D'Antonio*, 1998; *Brook et al.*, 2008; *Seastedt and Pyšek*, 2011; *Keeley and Brennan*, 2012).

Southern California's coastal sage scrub (CSS) is a fire-adapted ecosystem that follows a characteristic recovery pattern following fire (see chapter 3, also *Westman*, 1981; *Malanson and O'Leary*, 1982; *Westman*, 1982; *Keeley and Keeley*, 1984; *Malanson*, 1984; *Malanson and Westman*, 1985). The post-fire lack of vegetation creates a situation in which early fire-following vegetation, mainly herbaceous annual grasses and forbs, capitalizes on light and nutrient availability, leading to rapid growth. Highly productive mid-successional vegetation types, particularly woody subshrubs, begin to appear two to three years following fire in CSS and persist for three to five years (*Montalvo and Beyers*, 2010; *Nilsen and Schlesinger*, 1981; *Nilsen and Muller*, 1981). The high productivity of these subshrubs allows them to compete with the herbaceous annuals for resources and the dense canopy produced by these subshrubs reduces understory light availability and allows slower-growing perennial shrubs to establish. Initial presence of perennial shrubs is low following fire in CSS, but steadily increases through a combination of resprouting and seedling establishment. Slower-growing perennials eventually reach maturity and intermediate successors die off, resulting in a mature ecosystem by five to seven years following the fire. A transient productivity maximum may occur during CSS mid-succession due to the high presence of rapidly growing herbaceous annuals and the establishment of productive woody subshrubs. This transient maximum ends when the community progresses to late-stage succession, with the concurrent dominance of slower-growing woody perennials, disappearance of highly productive subshrubs, and diminishing presence and density of herbaceous annuals.

We manipulated water and nitrogen inputs at a site in the Santa Ana Mountains of southern California to examine the role the transient maximum plays in the post-fire recovery of CSS and to assess the impacts of climate change and nitrogen deposition on CSS. The site burned in a wildfire in 2007, immediately after which we constructed well-defined experimental plots. The plots have been well-monitored and have undergone consistent precipitation and nitrogen treatments since 2008, allowing us to study the relationships between ecosystem processes and early- to mid-succession. We focused on three questions: is there a transient maximum of productivity during CSS post-fire succession? What is responsible for the peak in CSS productivity during early to mid-succession? How do altered water and nitrogen inputs affect the transient maximum in CSS?

4.3 Methods

Study location

We manipulated precipitation and nitrogen input in adjacent grassland and shrubland communities in the foothills of the Santa Ana Mountains, at Loma Ridge, within the Irvine Ranch Conservancy land (117.704^{o} W, 33.742^{o} N). The site, which sits at 350 m of elevation on a gentle northwest-facing slope, is a mosaic of annual grassland and deciduous shrubland whose borders have remained well-defined and largely immobile over the past 80 years, as documented in aerial photographs. The site experiences a Mediterranean climate, with a winter wet season and a summer dry season. Annual mean precipitation (1902-2014) is 327 mm, falling primarily between November and April. Ambient precipitation was slightly below average during the first two years of the experiment (264 and 253 mm in 2007-2008 and 2008-2009, respectively), increasing to 403 mm during the third year (2009-2010) and 595 mm during the fourth year (2010-2011). Years five through seven (2011-2014) marked the beginning of a prolonged drought, with precipitation falling from 224 mm in year five to a low of 124 mm in year seven (**Figure 4.1**). Temperatures during the winter wet season range from an average high of 21.0^{o} C to an average low of 6.2^{o} C. The site receives negligible precipitation during the summer (May through October) drought, with temperatures ranging from a high of 27.3^{o} C to a low of 13.1^{o} C (Tustin Irvine Ranch weather, 1902-2003, http://www.wrcc.dri.edu). Long-term temperature records and with the presence of *Malosma laurina*, a frost-intolerant species, indicate that the temperature rarely drops below 0^{o} C.

Coastal sage scrublands burn frequently; the experimental site burned in 2007, 1998, 1967, 1948, and 1914 (CAL FIRE Fire and Resource Assessment Program, http://frap.cdf.ca.gov/). We applied a controlled burn to half of the experimental plots in February 2007, and the remainder of the site burned in the Santiago wildfire in October 2007. We did not find significant differences between the biomass and species composition in the controlled burn relative to the wildfire, and pooled these plots in subsequent analyses.

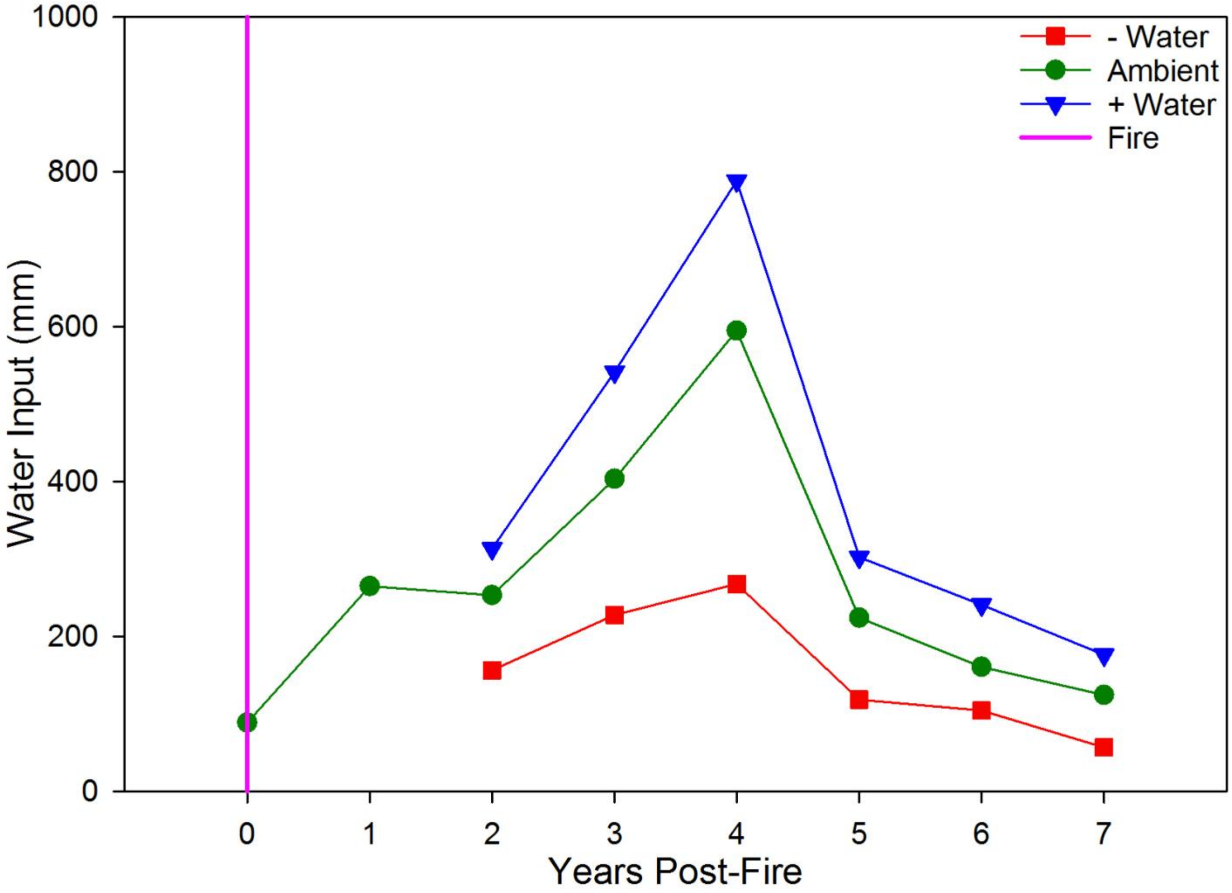

Figure 4.1: Annual ambient water input (mm) beginning in 2006-2007 (green) and water input in the added-water treatment (blue) and restricted-water treatment (red) beginning in 2008-2009, concurrent with the beginning of the water manipulations. The vertical line denotes the Santiago wildfire that occurred prior to the 2007-2008 growing season; x-axis denotes years subsequent to fire. Ambient precipitation record was obtained from Orange County Water District station 61 (33.720^{o} N 117.723^{o} W, http://www.ocpublicworks.com).

Experimental design and water treatments

The manipulations consist of twenty-four 18.29 x 12.19 m plots in the coastal sage scrub and twenty-four 9.14 x 6.10 m plots in the grassland. Eight plots in both the grassland and shrubland were randomly selected to receive 40% additional water input while another eight were randomly selected to receive 40% restricted water. The plots were split lengthwise, with one side of each plot randomly selected to receive added nitrogen. Each half plot was further split into three subplots, 2 x 2 m in the grassland and 4 x 4 m in the shrubland. The southern, upslope side of each plot was subject to possible artifacts due to wind- and gravity-driven water input, and data collection focused on the lower two subplots in each plot.

The water restriction was achieved through the construction of frames with clear retractable polyethylene roofs. These roofs remained open for roughly 95% of the year to reduce potential temperature and humidity variation. Moreover, air temperature and relative humidity sensors installed in representative plots from the three water treatment types showed little difference in air temperature and relative humidity between the restricted-water plots and the other two treatments when the shelters were closed. These roofs were closed for a subset of storms to remove and store precipitation from the restricted-water plots; these closures were biased towards larger storms in order to reduce both precipitation frequency and intensity. Water collected from the restricted-water plots was stored in polyethylene tanks and later pumped through irrigation manifolds installed on the added-water plots. The water was applied to each added-water plot using a dense web of drip tubing, and the amount of water added was measured using Hersey positive-displacement water meters. The tanks have a water storage capacity of 5.1 cm; this was exceeded in 2010 and 2011 due to large storms. Some water was lost from the storage tanks during these events, so our actual water manipulations ended up off target: the restricted-water treatments were subject to a 51% reduction in water input and the added-water treatments received an additional 33% water input as compared to the ambient plots.

The high nitrogen deposition levels observed in southern California, particularly around the Los Angeles basin, were simulated through the addition of 6 gN m^{-2} yr^{-1} to the added-nitrogen plots. Loma Ridge currently receives approximately 1.5 gN m^{-2} yr^{-1} (*Fenn et al.*, 2010), and this addition pushed these treatments above the critical nitrogen load for coastal sage scrub.

This nitrogen application was conducted in two stages. 2 gN m^{-2} yr^{-1} fast-release fertilizer (15.5-0-0 calcium nitrate, 15.5% N, 0% P, 0% K, 19% Ca) was applied immediately prior to the first storm of the wet season to simulate the nitrogen flush that accompanies the first rain. The remainder of the nitrogen addition was applied approximately one month later as controlled release (4 month) fertilizer (14-0-0 calcium nitrate, 14% N, 0% P, 0% K, 19% Ca).

Field observations

Automated instrumentation arrays were installed in two plots from each water treatment in each community. These instruments were sampled every 30 minutes year-round. Each array consisted of eight Campbell Scientific CS616 soil moisture sensors, four in-house fabricated soil temperature sensors, two in-house fabricated NDVI sensors, two Campbell Scientific 506-L fuel moisture sensors, two Campbell Scientific LWS leaf wetness sensors, and an array of Campbell Scientific 229-L matric potential sensors installed at depths of 5, 10, 25, 50, and 100 cm, with an additional sensor at 200 cm in the shrubland plots only. Precipitation was measured at the site every 10 minutes with a single tipping-bucket rain gauge installed on level ground above the surrounding canopy with an unobstructed field of view of the sky.

Additional manual measurements were conducted throughout the year, including surface soil moisture, soil moisture depth profiles, and spectral reflectance (300-1200 nm) every two to three weeks during the growing season and every four to six weeks during the drying season. Surface soil moisture was further measured using permanent vertical TDR wave guides in four locations in each half-plot that were sampled with a handheld Campbell Hydrosense probe. Deeper moisture was measured in each plot with a CPN Hydroprobe 503DR neutron probe at 25 cm intervals in 2 m access tubes. Spectral reflectance was measured using a handheld spectrometer around the center subplot in each half plot. Twenty measurements were collected around each grassland subplot and thirty-six measurements were collected around each CSS subplot.

Ecosystem structure was measured annually at the end of each growing season. Each of the lower two subplots in each treatment plot was subdivided into 64 0.25 m^2 visual blocks, with each block representing 1.6% of the total area. The number of visual blocks occupied by a given species was recorded and normalized.

Herbaceous biomass was measured in all plots by harvesting herbaceous growth at four locations in the center subplot of each half-plot immediately following the peak growing season. Each harvested location measured 14 x 100 cm in the shrubland and 14 x 50 cm in the grassland. Different locations were sampled each year to avoid resampling bias. The harvested samples were dried at 65 ^oC for at least 48 hours and weighed.

A second harvest was conducted in July to account for late-season growth, primarily *Hirschfeldia incana, Hemizonia fasciculata, and Acmispon glaber*. The second harvest sampled locations that were adjacent to those sampled for herbaceous growth. The crown dimensions and height of each individual rooted within these frames were measured and each individual was dried and weighed. A cover transect was recorded in each half-plot concurrent with the late-season harvest to assess total cover of these three species, and a stem count was conducted in each half-plot. *Acmispon glaber* was the only common subshrub in our treatments; presence of other members of this vegetation type was minimal in all treatments, and will be referred to henceforth as *A. glaber* rather than identified by vegetation type.

Allometric equations based on crown volume and dry weight were determined in October, 2008 for *Artemisia californica, Salvia mellifera,* and *Malosma laurina* (**Table 4.1**).

1,600 shrubs throughout the shrubland plots were subsequently tagged and their crown dimensions and heights measured. These shrubs were surveyed for survival and their crown dimensions and height re-measured in September of subsequent years to determine shrub productivity for these species. Shrub cover and productivity, unless otherwise stated, is presented and discussed without the inclusion of the contribution from *A. glaber*, which will be presented separately.

Table 4.1: Linear allometric relationships between volume (cm^3) and mass (g) for the three most abundant shrubs at the study site (*Artemisia californica, Malosma laurina,* and *Salvia mellifera*). Ten samples of each species with a wide range of volumes were measured and harvested outside of the treatment plots in 2008. These shrubs were dried and weighed, and the measured volume and biomass were used to establish these allometric equations.

Species	**A**	**B**	**$M = A*V + B$**	**R^2**
A. californica	0.0002	37.577	$M = 0.0002V + 37.577$	0.8787
M. laurina	0.001	6.1763	$M = 0.001V + 6.1763$	0.8699
S. mellifera	0.0009	19.517	$M = 0.0009V + 19.517$	0.9536

The Landsat NDVI record for the site was determined from Collection 1, level 1 data. Low-cloud WRS-2 path 40, row 37 Surface Reflectance images were downloaded from USGS (https://espa.cr.usgs.gov). NDVI was calculated from the Red and NIR bands; the images were masked to exclude clouds and cloud shadows and the annual mean NDVI for the pixels at the site were calculated.

Precipitation record

Six nearby precipitation datasets were analyzed to determine the best precipitation record for Loma Ridge. Two nearby eddy covariance towers equipped with tipping-bucket rain gauges (Ameriflux sites US-SCg, 33.737^{o} N 117.695^{o} W and US-SCs, 33.734^{o} N 117.696^{o} W, http://ess.uci.edu/~california) provided records #1 and #2, which began in 2006. Record #3 was obtained from a third tipping-bucket rain gauge that was installed in a flat area with a low plant canopy and wide sky view adjacent to the manipulations site. Record #4 was obtained from a rain gauge installed in 2013 within the manipulations area. Records #5 and #6 were obtained from two Orange County Water District stations near the site, station 247 (33.745^{o} N 117.704^{o} W, http://www.ocpublicworks.com) and station 61 (33.720^{o} N 117.723^{o} W). The first three rain gauges were merged into a single complete record to fill gaps and periods with malfunctioning gauges, giving priority to record #3, followed by #2, then by #1. This composite record was compared with the two OCWD records (#5 and #6) and the final record from within the manipulations (#4), looking for continuity, duration, reliability of data, and proximity to the manipulations. The OCWD record from station 61 (record #6) was determined to be the longest, most homogeneous record, and subsequent analyses were conducted based on this dataset. Water input for the restricted-water treatment was calculated by subtracting the precipitation during storms when the treatment roofs were closed, and input for the added-water treatment by adding the amount of water applied (**Figure 4.1**).

4.4 Results

Ambient CSS fire recovery patterns

Landsat-derived NDVI indicated that overall cover and productivity were low in the first year following fire (**Figure 4.2a**). NDVI in non-wildfire years was controlled by both water input (**Figure 4.2b**) and successional stage (**Figure 4.2c**). A regression was performed on the relationship between precipitation and NDVI using an exponential rise to maximum ($NDVI = 0.5151(1 - e^{(-0.0087 * water\ input\ (mm))})$; $R^2 = 0.404$) (**Figure 4.2b**). Residuals were grouped by post-fire year. Residuals increased during years one through three, peaked in year four, then declined with considerable variability (**Figure 4.2c**).

Vegetative cover rapidly reestablished and remained high, reaching 96% in the second year following the fire, peaking at 99% in year four, and dropping to 77% by year seven (**Figure 4.3a**). Productivity peaked in the fourth year following fire at 712.8 g m^{-2}, then fell to 435.9 to 520.4 g m^{-2} in the subsequent three years (**Figure 4.3b**).

Herbaceous cover decreased from 79% in year two to 22% in year five, then stabilized (**Figure 4.3a**). Shrub cover increased steadily from 12% in year two to 41% in year seven. *Acmispon glaber* was the only common subshrub in our treatments; its cover increased from 5% in year two to a peak of 33% in year five, then fell to 11% and 8% the subsequent two years. Herbaceous productivity was highest during years two through four, totaling 135, 314, and 232 g m^{-2} respectively, then fell to 7 g m^{-2} in year five (**Figure 4.3b**). It increased to 86 and 57 g m^{-2} in the subsequent two years. Shrub productivity increased steadily from 248 g m^{-2} in year two to 389 g m^{-2} in year seven. *A. glaber* productivity was fairly consistent during years three, five, and six, ranging from 45 to 51 g m^{-2}, but peaked in year four at 123 g m^{-2}.

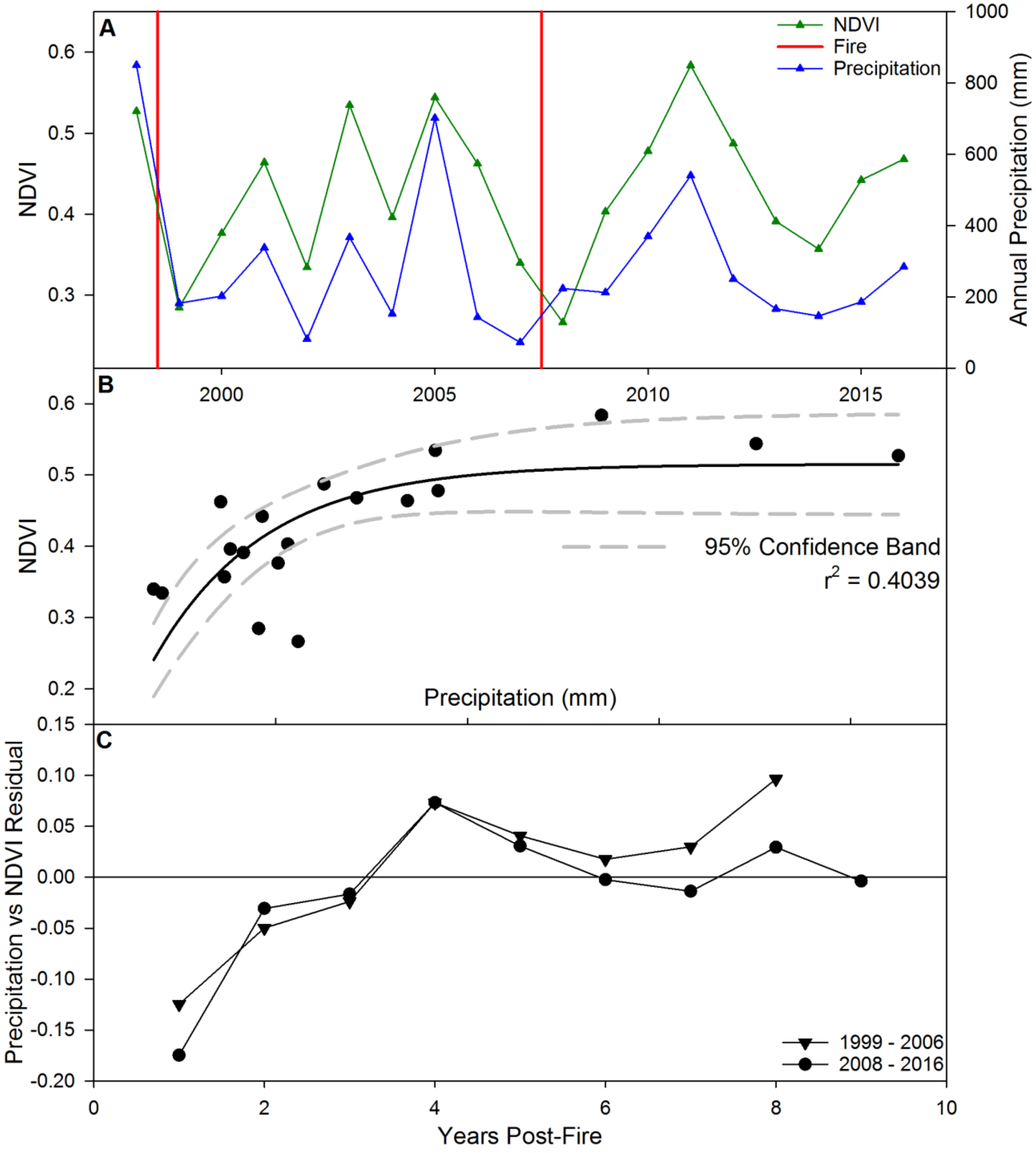

Figure 4.2: (A) NDVI (green) and precipitation (blue) time series from 1998-2016 (bottom); vertical red lines represent the 1998 and 2007 fires. Precipitation data was obtained from Orange County Water District station 61 (33.720° N 117.723° W, http://www.ocpublicworks.com). The Landsat NDVI record for the site was determined from Collection 1, level 1 data. Low-cloud WRS-2 path 40, row 37 Surface Reflectance images were downloaded from USGS (https://espa.cr.usgs.gov). NDVI was calculated from the Red and NIR bands; the images were masked to exclude clouds and cloud shadows and the annual mean NDVI for the pixels at the site were calculated. NDVI data was calculated for Landsat pixels corresponding with the

manipulation experiment. (B) Points are precipitation (mm) vs NDVI; black line represents the saturating relationship between water input (mm) and NDVI: $NDVI = 0.5151(1 - e^{(-0.0087 * water\ input\ (mm))})$ ($R^2 = 0.4039$; 72 mm - 850 mm annual water input) determined through regression; dashed gray lines represent the 95% confidence band of the regression. (C) Timeseries of precipitation vs NDVI residuals from one to eight years post-fire (2007 burn) and from one to nine years post-fire (1998 burn). Burn years were excluded from the timeseries to eliminate artifacts related to the timing of each burn.

Effects of altered water and nitrogen availability on the transient productivity maximum

Our experimental design had six treatments: added-water, added-nitrogen (AN), added-water, ambient-nitrogen (AX), restricted-water, added-nitrogen (RN), restricted-water, ambient-nitrogen (RX), ambient-water, added-nitrogen (XN), and ambient-water, ambient-nitrogen (control, XX). Total productivity displayed low variation between treatments or between years in years two, five, six, and seven (**Figure 4.4d**). Characteristic ranges during these years were 366 - 504 g m^{-2} in RX, 334 - 495 g m^{-2} in RN, 413 - 524 g m^{-2} in the XN, 427 - 502 g m^{-2} in the AX, and 498 - 627 g m^{-2} in the AN treatments. Productivity peaked in years three and four at 666 - 734 g m^{-2} and 666.8 - 703 g m^{-2} in the RX and RN treatments, 785 - 792 g m^{-2} in the XN treatment, and 801 - 736 and 926 - 876 g m^{-2} in the AX and AN treatments. Herbaceous productivity varied from 81 - 208 g m^{-2} among treatments in year two, with lowest productivity in RX and RN treatments, comparable productivity between XN and AX treatments, and highest productivity in AN treatments (**Figure 4.4a**). Productivity peaked in most treatments the subsequent year and remained high the following year, 304 and 348 g m^{-2} and 355 and 328 g m^{-2} in RX and RN treatments, 457 and 325 g m^{-2} in the XN treatment, and 376 and 176 g m^{-2} and 535 and 282 g m^{-2} in the AX and AN treatments, respectively.

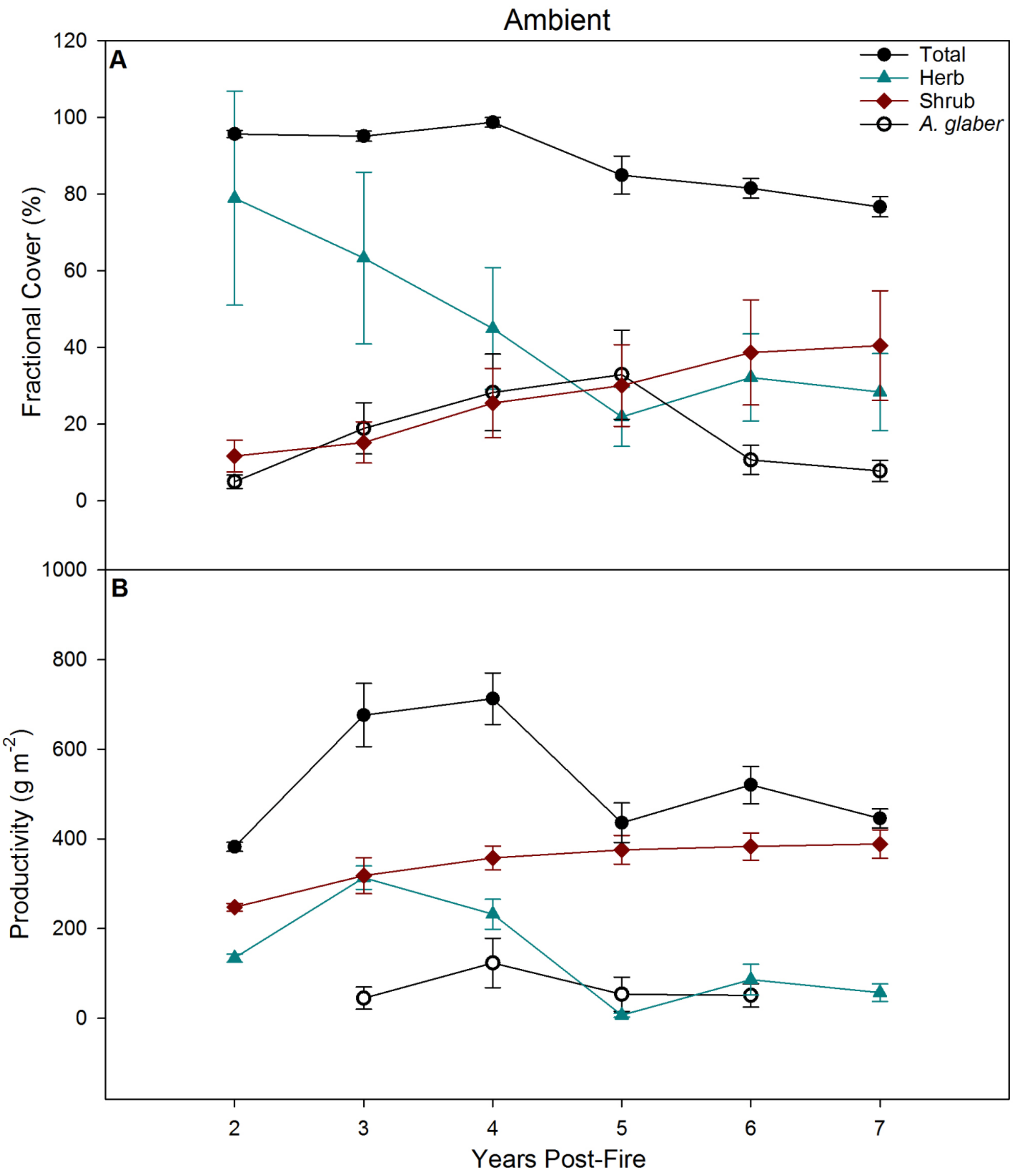

Figure 4.3: (A) Ambient total cover (%, black solid circles) and fractional cover (%) of shrubs (dark red), herbaceous annuals (cyan), and *A. glaber* (black open circles) throughout the study period, years two through seven post-fire. (B) Ambient total productivity (g m^{-2}) and productivity of shrubs, herbaceous annuals, and *A. glaber* throughout the study period, years two through seven post-fire; points represent mean ± standard error.

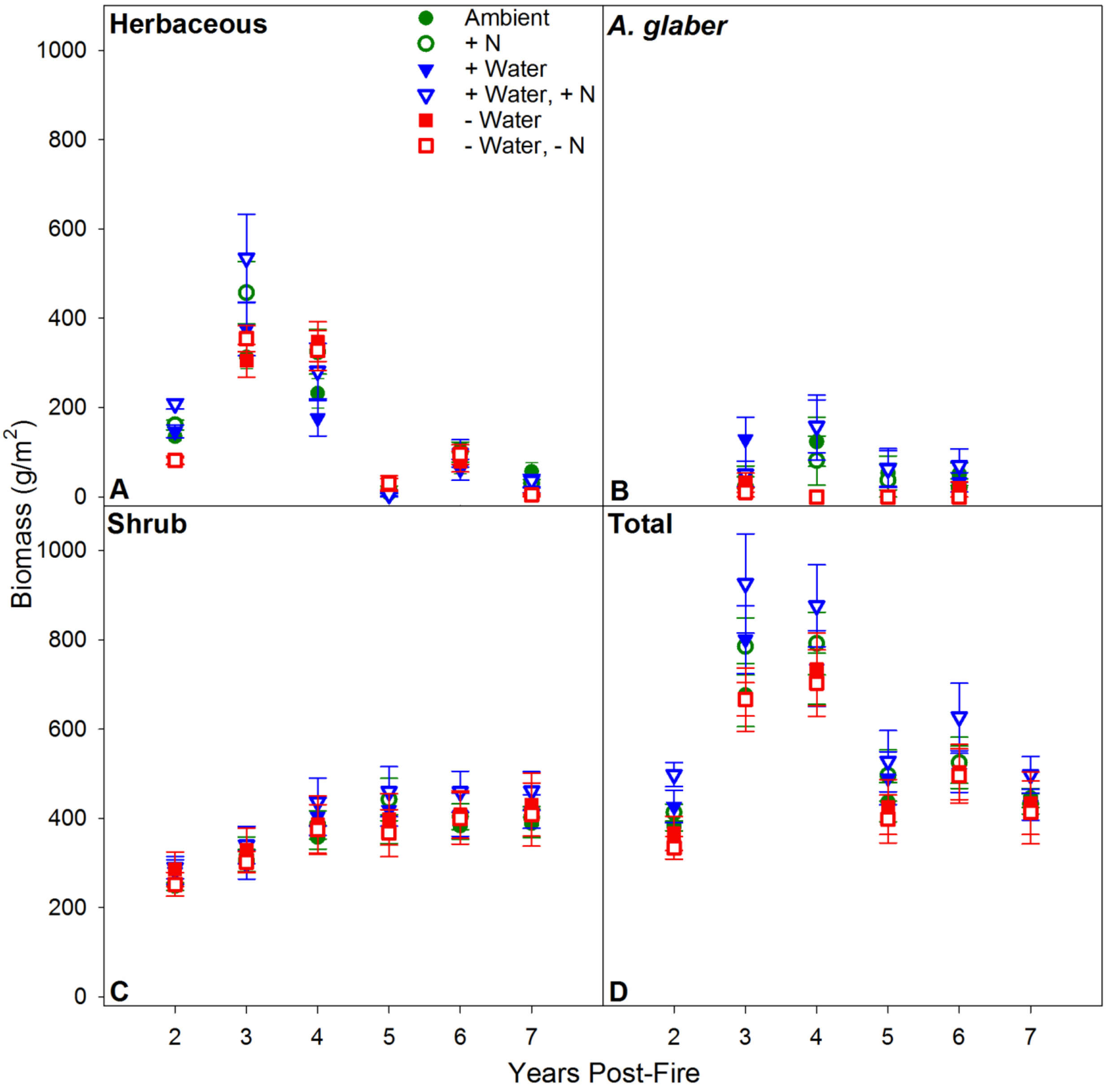

Figure 4.4: (A) Herbaceous aboveground NPP (g m^{-2}) by treatment, determined by annual harvest of a subset of each experimental plot. (B) *A. glaber* aboveground biomass increment (g m^{-2}) by treatment, determined by annual harvest of *A. glaber* individuals rooted within a subset of each experimental plot. (C) Shrub aboveground productivity (g m^{-2}) by treatment, determined through annual measurements of crown volume and the allometric relationships in **Table 1.** (D) Total annual aboveground productivity (g m^{-2}) calculated as the sum of herbaceous NPP (A), *A. glaber* biomass increment (B), and shrub productivity (C). Points represent mean ± standard error.

A. glaber productivity remained below 22 g m^{-2} in the RX and RN treatments in all years (**Figure 4.4b**). Productivity peaked in year three in the XN, AX, and AN treatments, at 81, 156, and 158 g m^{-2} respectively. *A. glaber* productivity was high in the AX treatment in year two, 129 g m^{-2}, but did not exceed 70 g m^{-2} in the AX and AN treatments or 38 g m^{-2} in the XN treatment in other years. Shrub productivity did not vary greatly among treatments, and steadily increased from 251 g m^{-2} (XN) to 290 g m^{-2} (AN) in year two to 401 g m^{-2} (XN) to 461 g m^{-2} (AN) in year seven (**Figure 4.4c**).

Regressions of the relationship between water input and productivity were performed using an exponential rise to maximum (**Figure 4.5a,b**). Treatments were grouped by the nitrogen treatment. The regression under ambient-nitrogen conditions produced the relationship $productivity\ (g\ m^{-2}) = 687.263(1 - e^{(-0.0073 * water\ input\ (mm))})$ with an R^2 of 0.342 and the regression under added-nitrogen conditions produced the relationship $productivity\ (g\ m^{-2}) = 877.145(1 - e^{(-0.0048 * water\ input\ (mm))})$ with an R^2 of 0.642. Residuals were binned by year post-fire (**Figure 4.5c,d**). Residuals were consistently negative in the second and fifth year and positive in the third, fourth, sixth, and seventh years post-fire. The magnitude of the residuals was greatest in years two through five and approached zero by year seven in both nitrogen treatments.

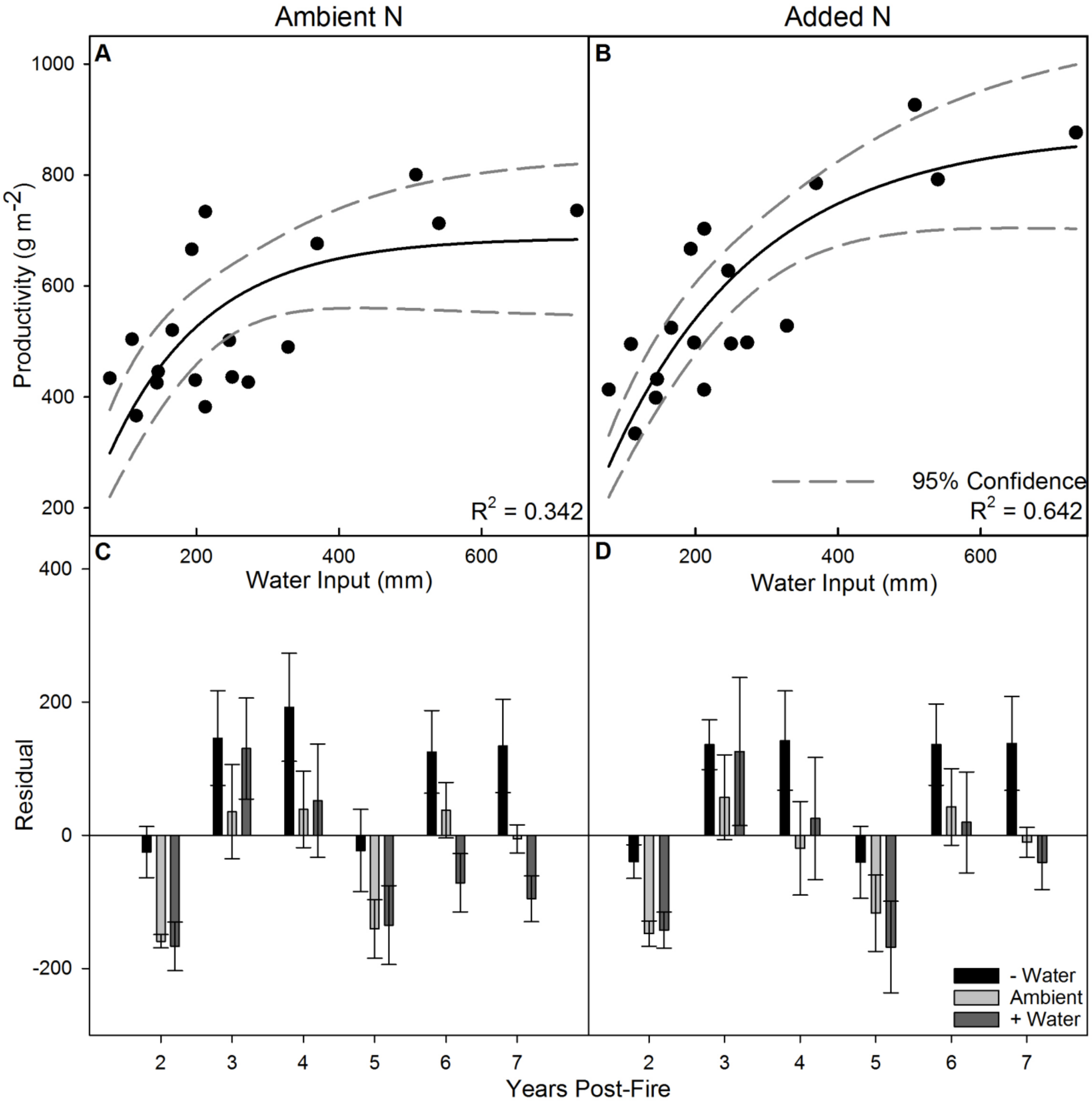

Figure 4.5: (A) Points are water input (mm) vs productivity (g m^{-2}) under ambient-nitrogen conditions; black line represents the saturating relationship between water input and productivity: $productivity\ (g\ m^{-2})\ =\ 687.263(1\ -\ e^{(-0.0073\ *\ water\ input\ (mm))})$(R^2 = 0.342; 56 mm - 789 mm annual water input) determined through regression; dashed gray lines represent the 95% confidence band of the regression. (B) Points are water input (mm) vs productivity (g m^{-2}) under added-nitrogen conditions; black line represents the saturating relationship between water input and productivity: $productivity\ (g\ m^{-2})\ =\ 877.145(1\ -\ e^{(-0.0048\ *\ water\ input\ (mm))})$ (R^2 = 0.642; 56 mm - 789 mm annual water input) determined through regression; dashed gray lines represent the 95% confidence band of the regression. (C, D) Residual analysis of water input (mm) vs productivity

(g m^{-2}) grouped by ambient-nitrogen water treatment and year post-fire (C) and by added-nitrogen water treatment and year post-fire (D). All bars indicate mean residual ± standard error.

Effects of altered water and nitrogen availability on species composition

Neither restricted-water treatment developed significant *A. glaber* cover (**Figure 4.6a, 4.7a,b**). *A. glaber* cover was comparable between the AX and the AN treatments (**Figure 4.6a, 4.7e,f**); it rose from 4% cover in year two to a peak during years four and five (24% and 26%, AN, and 29% for both years, AX) then fell to 2% and 8% cover by year seven in the AN and AX treatments, respectively, corresponding to a difference of 30% cover relative to the control (**Figure 4.7a**). *A. glaber* cover was substantially higher in the control than in the XN treatment, increasing steadily from 5% in year two to 33% in year five, then falling below 11% in subsequent years in the control but increasing from 1% in year two to 11% in year five and falling below 8% in subsequent years in the XN treatment (**Figure 4.6b**); the difference between *A. glaber* cover in the control and the XN treatment reached 22% cover in year five (**Figure 4.8b**).

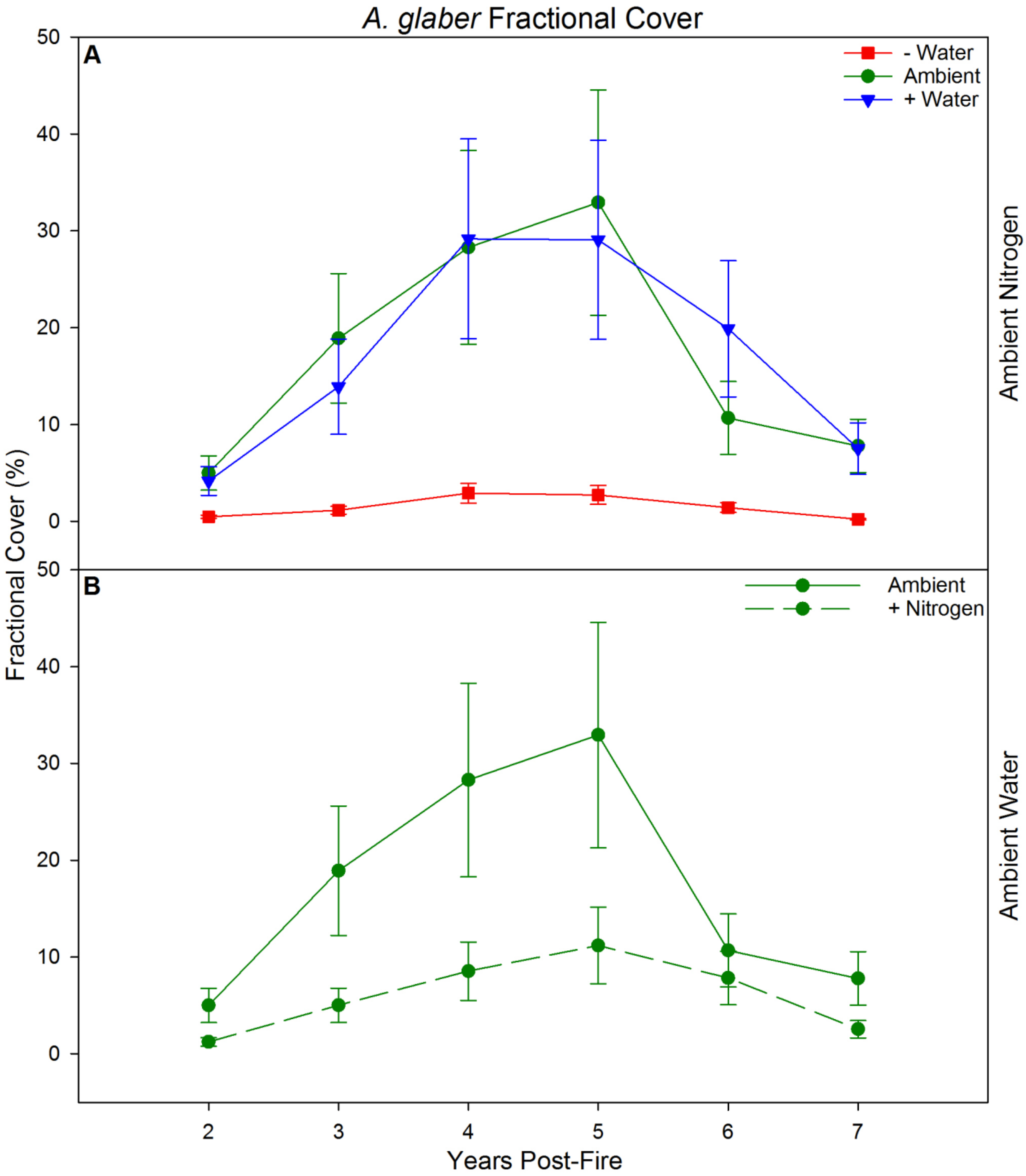

Figure 4.6: (A) *A. glaber* fractional cover (%) throughout the study period (two to seven years post-fire) in the restricted (red), ambient (green), and added (blue) water treatments. (B) *A. glaber* fractional cover (%) throughout the study period in the ambient (solid line) and ambient-water, added-nitrogen treatment (dashed line); points represent mean ± standard error.

Shrub cover was lower under RN conditions than under RX conditions, increasing from 17% in year two to 39% in year six then falling to 34% in year seven in the RX treatment, and increasing from 10% in year two to a peak of 23% in year five then a subsequent decrease to 14% in year seven in the RN treatment (**Figure 4.7a,b**). Shrub cover was comparable between the XX and XN treatments, increasing from 12% and 11% in year two to 41% and 45% in year seven, respectively (**Figure 4.7c,d**). Shrub cover was also comparable between the AX and AN treatments, increasing from 22% in both treatments in year two to 58% in the AX and 61% in the AN treatment in year seven (**Figure 4.7e,f**). Shrub cover was notably higher under added-water conditions than in the control, with a difference ranging between 8% and 21% cover throughout the study (**Figure 4.8c,d**).

Herbaceous cover decreased from a maximum of 68% and 77% in the RX and RN treatments respectively in year three to 23% and 25% in year five, stabilized for a year, then fell to 3% and 4% in year seven (**Figure 4.7a,b**). Herbaceous cover was comparable between the control and XN treatments, decreasing from 79% and 84% in year two to 22% and 24% by year five, then stabilized between 22% and 34% (**Figure 4.7c,d**). Herbaceous cover in the AX and AN treatments decreased from 65% and 71% to 12% and 10% between years two and five, then stabilized between 15% and 24% the subsequent two years (**Figure 4.7e,f**). There was less herbaceous cover in the AX and the AN treatments than in the XX treatments throughout the study, with a difference ranging between 3% and 23% cover. The RX and RN treatments had less herbaceous cover than the control during years two, six, and seven, 19% and 11%, 10% and 2%, and 25% and 24% respectively during these three years (**Figure 4.8e,f**). Herbaceous cover was higher in the RX and RN treatments than in the control during years three through five, with the difference peaking in year four at 16% and 26% cover, respectively.

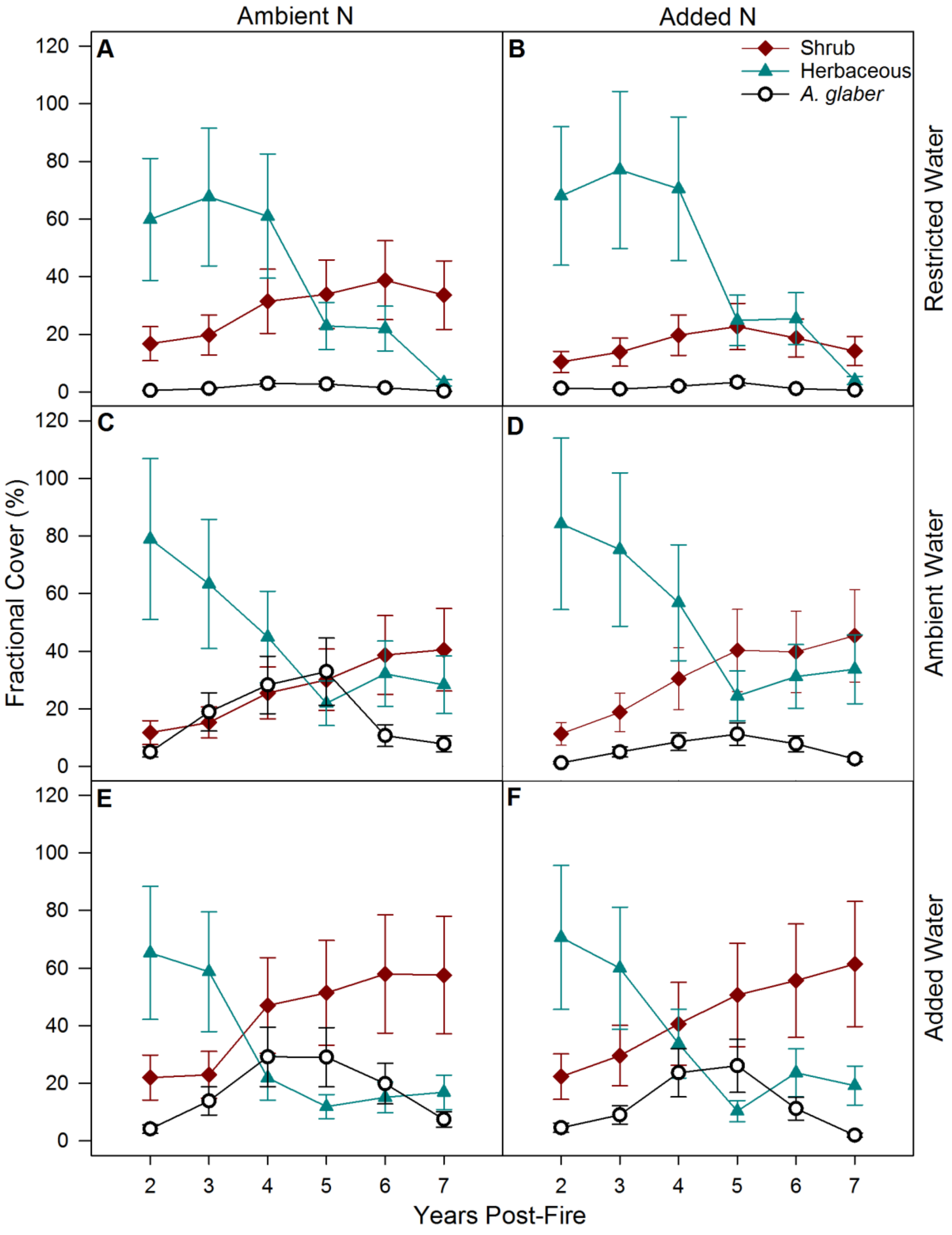

Figure 4.7: Fractional cover (%) by treatment of shrubs (dark red), herbaceous annuals (cyan), and *A. glaber* (black open circles) throughout the study period, years two through seven post-fire. (A) restricted water, ambient nitrogen; (B) restricted water, added nitrogen; (C) ambient water, ambient nitrogen; (D) ambient water, added nitrogen; (E) added water, ambient nitrogen; (F) added water, added nitrogen. Points represent mean ± standard error.

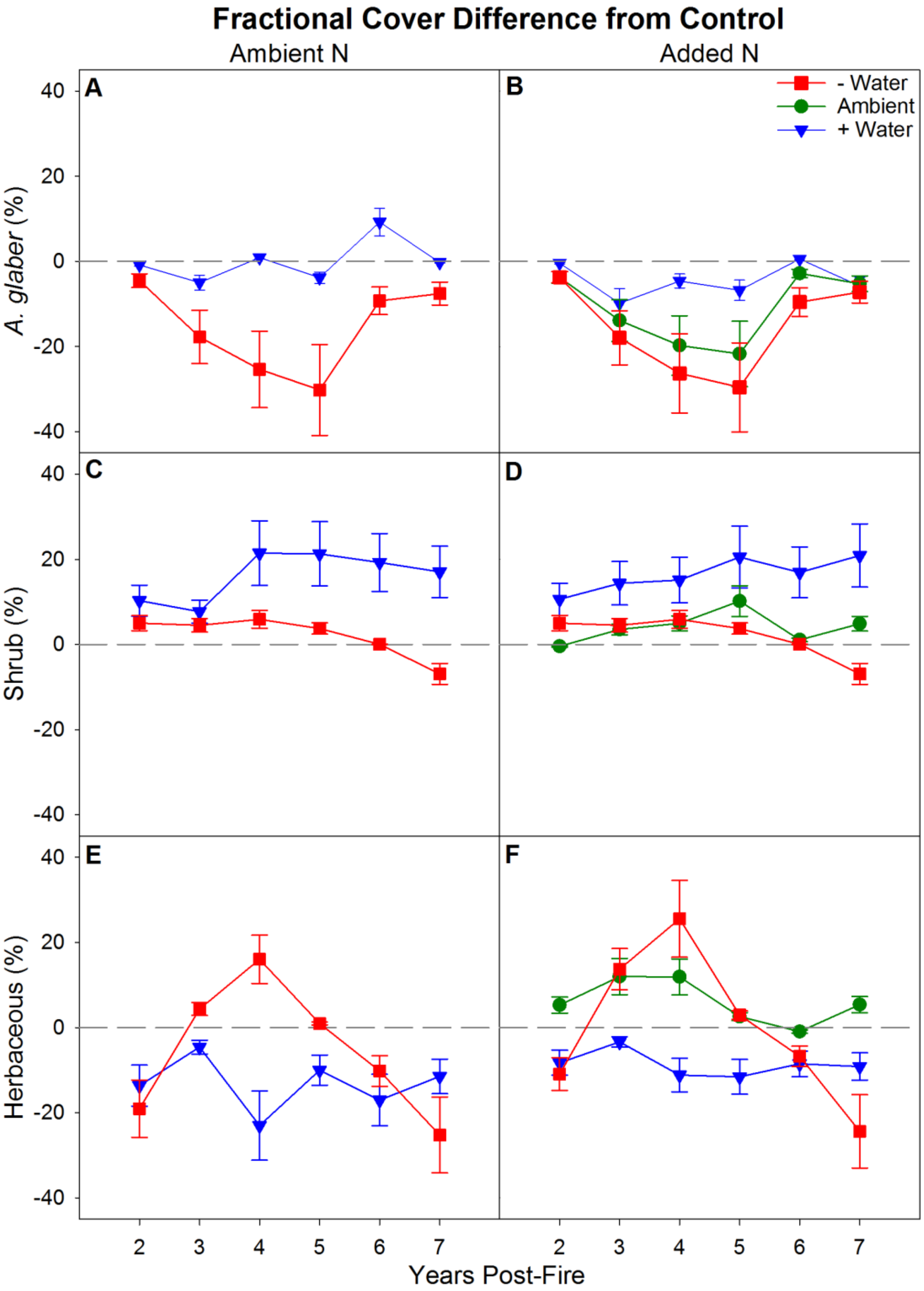

Figure 4.8: Differences in *A. glaber*, shrub, and herbaceous annual fractional cover (%) between water and nitrogen treatments and ambient. (A) *A. glaber* fractional cover difference (%) from ambient for the ambient-nitrogen, restricted-water (red) and ambient-nitrogen, added-water (blue) treatments. (B) *A. glaber* fractional cover difference (%) from ambient for the added-nitrogen, restricted-water (red), added-nitrogen, ambient-water (green), and added-nitrogen,

added-water (blue) treatments. (C) Shrub fractional cover difference (%) from ambient for the ambient-nitrogen, restricted-water (red) and ambient-nitrogen, added-water (blue) treatments. (D) Shrub fractional cover difference (%) from ambient for the added-nitrogen, restricted-water (red), added-nitrogen, ambient-water (green), and added-nitrogen, added-water (blue) treatments. (E) Herbaceous annual fractional cover difference (%) from ambient for the ambient-nitrogen, restricted-water (red) and ambient-nitrogen, added-water (blue) treatments. (F) Herbaceous annual fractional cover difference (%) from ambient for the added-nitrogen, restricted-water (red), added-nitrogen, ambient-water (green), and added-nitrogen, added-water (blue) treatments. Points represent mean ± standard error.

4.5 Discussion

Is there a transient productivity maximum during CSS fire succession?

Coastal sage scrub follows a characteristic post-fire recovery pattern (*Westman*, 1981; *Malanson and O'Leary*, 1982; *Westman*, 1982; *Keeley and Keeley*, 1984; *Malanson*, 1984; *Malanson and Westman*, 1985), which can be broken into three stages (see chapter 3). Early succession begins immediately after fire, is dominated by herbaceous annuals, and includes resprouting by surviving shrubs; this stage typically lasts one or two years. Mid-succession begins two to three years following fire, lasts three to five years, and is the expected period of transient productivity maximum. This stage is characterized by high herbaceous presence and the expansion of shrubs and subshrubs, particularly *Acmispon glaber*. Late succession begins five to seven years post-fire and represents a shrub community approaching maturity; this stage persists until the next disturbance.

Interannual water input and productivity are closely related in CSS. Both the Landsat NDVI and *in situ* productivity measurements revealed a successional signal superimposed on the relationship between water and productivity (**Figure 4.2, Figure 4.5a,b**). The data indicated substantially lower productivity during the first two years post-fire than predicted by water input, consistent with early succession. Ambient productivity in both the Landsat NDVI data (**Figure 4.2c**) and the *in situ* harvest and shrub productivity data (**Figure 4.5c,d**) was higher than predicted by water input in years three and four, indicating a transient productivity maximum. The return to levels of productivity predicted by water input in year five signaled the end of this maximum and progression of the ecosystem to a mature state.

How did altered water and nitrogen availability affect productivity and species composition?

Interannual precipitation variability (**Figure 4.1**) has a strong effect on cover and biomass (see chapter 2) and precipitation peaked during the third and fourth years post-fire, possibly confounding the transient maximum productivity signal. However, after detrending productivity and water input (**Figure 4.5a,b**) there was still strong evidence for an increase in productivity during mid-succession: productivity was higher than predicted regardless of water input in years three and four. There was some difference in the patterns of the transient maximum among the water treatments, but the strong transient signal evident in year three in the treatments representing the greatest extremes in precipitation variability, added- and restricted-water, suggests that the existence of the transient maximum was not dependent on water input. Likewise, there was evidence for a transient productivity maximum under both added- and ambient-nitrogen conditions (**Figure 4.5c,d**); a long-term increase in nitrogen did not eliminate the transient productivity maximum.

Although the transient maximum of productivity occurred regardless of treatment, the water and nitrogen manipulations had other effects on community structure and function. The most striking effect of nitrogen on succession was the difference in *A. glaber* presence between the control and XN treatments (**Figure 4.6b**). *A. glaber* accounted for 11.2% of community composition in the XN treatment during year five, compared with 32.9% of community composition the same year in the control. During stage two of succession, *A. glaber* cover under ambient conditions exceeded *A. glaber* cover in the XN treatment by a factor of 2.9 to 4.2; increased nitrogen appears to create conditions highly unfavorable to *A. glaber*.

Restricted water resulted in the slowest and added water resulted in the fastest decline of herbaceous cover among the water treatments (**Figure 4.7**). The rapid decline in herbaceous cover between years three and four in the added-water treatments was likely due to more rapid reestablishment of a closed shrub canopy in those treatments. The lack of a decline in herbaceous cover under restricted-water until year five was likely caused by an absence of shrub cover, allowing greater surface light penetration. Although shrub cover did not decrease significantly below ambient until year seven, the absence of *A. glaber* during stage two of succession delayed the reestablishment of a closed canopy in the restricted-water treatments. Ultimately, herbaceous cover likely declined more due to the drought that began in year five than due to the reestablishment of a closed shrub canopy. Added water resulted in higher total productivity than the other two water treatments throughout the study (**Figure 4.4**); the lowest productivity occurred in the restricted-water treatments. Productivity was highest in the AN treatment; this was driven by higher herbaceous productivity under added-nitrogen conditions, a phenomenon observed in all water treatments. Shrub and subshrub productivity did not differ markedly between the nitrogen treatments under added-water conditions. The low productivity under restricted-water conditions can be explained by the absence of *A. glaber* in these treatments, low herbaceous productivity during year three, and marginally lower shrub productivity throughout the study.

What causes the transient productivity maximum during CSS recovery?

Increased availability of light and the dominance of species that have been selected to rapidly capture unoccupied above and belowground space is likely responsible for a transient productivity maximum. Adding nitrogen did not substantially change the transient maximum (**Figure 4.5c,d**), which suggests that this maximum of productivity is not driven by increased nitrogen availability. Although there was variability of productivity with water input (**Figure 4.4**) due to ambient precipitation variability (**Figure 4.1**), detrended productivity and water input showed evidence for a transient productivity maximum over a broad range of water inputs.

While added nitrogen did not control the existence of a transient maximum of productivity during CSS fire succession, it did influence the vegetation type responsible for the phenomenon. The control treatment was characterized by an abundance of both herbaceous annuals and *A. glaber* during mid-succession (**Figure 4.3a**); both of these vegetation types are capable of rapid growth (*Nilsen and Schlesinger*, 1981; *Abraham et al.*, 2009; *Montalvo and Beyers*, 2010), and their presence contributed to the productivity maximum. The transient productivity maximum was not substantially different in treatments with little to no *A. glaber* presence (e.g., XN, RX, RN). The transient maximum was driven by rapid growth of the nitrogen-fixing *A. glaber* under ambient nitrogen, and by herbaceous annuals under added nitrogen. Added nitrogen apparently decreases the competitive advantage conferred to *A. glaber* and allows rapid growth by herbaceous annuals. Access to ample nitrogen is apparently needed to support the transient productivity maximum, which may be supplied by either biological nitrogen fixation or fertilization. The most likely cause of the transient maximum therefore appears to be increased access to light and the dominance of herbaceous annuals and perennial subshrubs that have evolved high degrees of competitiveness for available space.

The role of A. glaber in CSS fire recovery and implications for the future

A. glaber is an obligate seeder and typically establishes within the first two to three years following a fire. It is highly productive, and contributes substantially to cover and NPP from three to seven years after fire (*Nilsen and Muller*, 1981; *Nilsen and Schlesinger*, 1981; *Montalvo*, 2004; *Montalvo and Beyers*, 2010). *A. glaber* is an important member of the CSS community during this time for three reasons. First, *A. glaber* is an important nitrogen fixer in the CSS ecosystem (*Montalvo*, 2004; *Montalvo and Beyers*, 2010). Other nitrogen fixers characteristic of CSS succession include forbs such as *Lupinus* species and *Medicago polymorpha*; these establish quickly following the fire, but can be easily overtopped by annual grasses and perennial shrubs. *A. glaber* plays an important role during this period by continuing to develop the pool of bioavailable nitrogen while simultaneously out-competing invasive grasses for water and light. Second, its rapid establishment and broad cover serve to minimize soil nutrient loss due to runoff during the years immediately following a fire (*Nilsen and Schlesinger*, 1981). *A. glaber* quickly establishes extensive branched taproot systems (*Montalvo and Beyers*, 2010) that reach depths of 1.1 m, acting as a strong anchor that minimizes erosion (Hellmers et al., 1955; *Nilsen and Schlesinger*, 1981). Third, its rapid growth helps to rebuild the shrubland canopy and reestablish a micro-environment more favorable for native shrubs than invasive grasses. After senescence, *A. glaber* leaves a skeleton that continues to block sunlight, giving other slower-growing members of the coastal sage scrub community time to establish.

A. glaber was largely eliminated from the CSS community through nitrogen addition under ambient water input and through water restriction. *A. glaber* did not establish in the restricted-water treatments throughout the study (**Figure 4.6a**), and its presence was greatly diminished in the XN treatment relative to ambient conditions during the second stage of succession (**Figure 4.6b**). This suggests that *A. glaber* is highly sensitive to drought and nitrogen deposition, and an increase in these factors could prevent the establishment of this species, which may have cascading effects that increase vulnerability to invasion.

The slower overall reestablishment of shrubs under restricted-water conditions, the shrub die-back under restricted-water and restricted-nitrogen conditions, and the near-elimination of *A. glaber* by the addition of nitrogen under ambient-water conditions have possible consequences for CSS community composition in the future. Climate models project increased aridity and precipitation variability in the southwestern United States (*Hayhoe et al.*, 2004; *Seager et al.*, 2007; *Loarie et al.*, 2008; *AghaKouchak et al.*, 2014; *Romero-Lankao, et al.*, 2014; *Berg and Hall*, 2015; *Diffenbaugh et al.*, 2015; *Hall et al.*, 2018; *Swain et al.*, 2018). The majority of extant CSS is near large urban areas such as the foothills surrounding the Los Angeles basin; nitrogen deposition in these regions is high and may increase as the population of southern California grows (*Fenn et al.*, 2010). This combination of high nitrogen deposition and increased frequency and severity of drought may degrade coastal sage scrub communities, inhibit their ability to recover from fire, and accelerate invasion by annual Eurasian grasses (*Zedler et al.*, 1983; *Langan et al.*, 1997; *Fenn et al.*, 2003; *Keeley et al.*, 2005b; *Baker*, 2006; *Enright et al.*, 2011; *Sandel and Dangremond*, 2012; *Rapacciuolo et al.*, 2014; *Jin et al.*, 2015; *Keeley and Syphard*, 2016).

CHAPTER 5

Conclusions

This dissertation sought to improve our understanding of the mechanisms that enable coastal sage scrub (CSS) and invasive Eurasian grasslands to coexist, and forcings and factors that may favor ecosystem type conversion during the post-fire recovery period. This understanding is important, as humans activities are continuing to impact the biosphere in general and CSS habitat in particular. In extant CSS habitat, fire frequency is increasing (e.g., *Keeley and Davis*, 2007), drought frequency and severity are increasing (e.g., *Hall et al.*, 2018), and nitrogen deposition is increasing (e.g., *Fenn et al.*, 2010). This represents a fundamental shift in the disturbance regime and recovery conditions away from the historical regime to which CSS has adapted, and such shifts, concurrent with the presence of invasive communities, can lead to ecosystem degradation and type conversion.

5.1 Chapter synopses

Chapter two investigated the stable coexistence of CSS and Eurasian grassland communities under similar environmental conditions in a post-disturbance context. This coexistence relies on the different phenological patterns and water-use strategies employed by the two ecosystems; CSS tolerates invasive presence because the two communities rely on access to different water stores and timing of growth. CSS is deeply rooted and has an expanded growing season relative to annual grassland, which employs a “live fast, die young” growth pattern, rapidly withdrawing shallow water during the wet season. This chapter suggests that a significant enough change in the disturbance regime to preclude the survival of most CSS individuals may seriously hinder the ability of this ecosystem to recover from fire and drive the conversion from CSS to grassland.

Chapter three investigated patterns of CSS succession under several altered resource conditions. Altered water and nitrogen inputs drove changes in community structure and composition during succession and altered overall rates of succession, leading to faster or slower recovery to pre-fire conditions depending on the resource inputs. Under most conditions, CSS was able to return to a mature state by the end of the study period, but the combination of water restriction and nitrogen addition drove a reduction in shrub cover and resulted in a community that did not resemble a mature CSS ecosystem by the end of the experiment. This suggests a potential vulnerability to ecosystem type conversion during fire recovery under these resource conditions.

Chapter four investigated the existence and drivers of the mid-succession transient productivity maximum in the CSS ecosystem. This phenomenon was found to occur during CSS recovery independent of altered water or nitrogen inputs. However, altered water and nitrogen drove a shift in the vegetation type responsible for the transient maximum. In ambient CSS, the native nitrogen-fixing subshrub *Acmispon glaber* is responsible for this transient maximum; the addition of nitrogen and the restriction of water both eliminated this species from the community. Under these conditions, invasive herbaceous annuals were responsible for the transient productivity maximum. This suggests that altered resource availability may have important species-level effects during CSS recovery that have implications for the ecosystem as a whole.

5.2 Practical lessons

The field is a harsh environment for electronic instrumentation, and different field sites will pose different challenges for the researcher tasked with maintaining instrumentation. At Loma Ridge, a great deal of time was spent maintaining the automated instrumentation arrays; damage to these systems occurred mainly from animals. Coyotes and rodents in particular would frequently bite through instrument cables; depending on the type of instrument, this could either result in a dead instrument or a more major short that took a multiplexor or datalogger offline entirely.

Robust fuse systems with fuses at each multiplexor for systems where several multiplexors are read by one datalogger can go a long way towards minimizing the impact of shorts due to instrument damage. Flexible conduit can save many hours of time for the researcher if used to protect instrumentation cables; the type of conduit should be chosen to withstand environmental conditions at the field site and should be tough enough to resist animal chewing.

Care should be taken to prevent animal ingress into multiplexor and datalogger enclosures both for the safety of the researcher if the ingressing animal is dangerous, e.g., venomous snakes, spiders, scorpions, hornets, etc, and for the preservation of the data collection system. One mysterious infrequent but recurring short in an instrumentation array at Loma Ridge was traced back to a clutch of ant eggs laid on the circuit board within a multiplexor; when the humidity was high enough, these eggs became conductive enough to cause a short.

A good electrical ground goes a long way toward reducing noise in electronic signals. A robust grounding rod or grounding plate may make the difference between clear, reliable data and unusable noise. Consider the evolution of instrumentation arrays throughout the experiment as well; instrumentation that was not initially planned for was added to the arrays early in the experiment; a little bit of overkill with the electrical ground at the beginning should not significantly increase labor or monetary cost, and can greatly improve the robustness of an electrical system and its potential for expansion.

Measurements of ecosystem structure and function such as community composition and productivity can prove quite challenging to conduct, depending on the ecosystem. In a post-disturbance context, thought should be given to how these measurements may be affected as vegetation density and canopy height increase. The researcher should also consider how to carry out measurements to reduce interannual effects of the measurement; this is particularly a challenge when measuring productivity of perennial species. Allometry is a useful tool, but study design should account for seedling establishment and mortality throughout the experiment. Tower- or drone-based measurements of canopy height and density may yield an allometric solution to this problem. A machine-learning approach to analysis of aerial photographs may hold promise as a means to measure community composition.

5.3 Implications and future research directions

Human activities are expected to have a strong impact on the vegetation in southern California in the future. Southern California is among the regions in the continental United States that are projected to experience the greatest impacts of climate change by the end of the century (*Bell et al.*, 2004; *Hayhoe et al.*, 2004; *Seager et al.*, 2007; *Loarie et al.*, 2008; *AghaKouchak et al.*, 2014; *Romero-Lankao, et al.*, 2014; *Berg and Hall*, 2015; *Diffenbaugh et al.*, 2015; *Hall et al.*, 2018; *Swain et al.*, 2018); one of the projected impacts of climate change on southern California is an increase in frequency and intensity of drought. Southern California's population is projected to grow substantially as well, potentially increasing by 23% between 2010 and 2060

(*Johnson*, 1999; *Sanstad et al.*, 2009; California Department of Finance State Population Projections by County, http://www.dof.ca.gov). Increased drought combined with the increase in human ignitions that comes with a growing population will likely lead to an increase in fire frequency and intensity. Nitrogen deposition is also associated with population growth, and so will likely continue to rise in southern California as the population grows.

This research suggests that changes in fire frequency, water availability, and nitrogen deposition may all have profound impacts on the CSS community, and that the fire recovery period may represent a window of particularly high vulnerability to invasion. The existence of CSS in a region highly invaded by Eurasian annual grasses is in part attributable to the survival of the belowground component of CSS through fire, allowing the CSS community to access stable deeper water stores during the early to mid-successional period of dominance by invasive annuals, and to tolerate the presence of invasive annuals in the mature CSS community. Decreased water availability and increased nitrogen deposition affect the CSS community during fire recovery at both the community and the species level, and this research suggests that the combination of these two factors hinders the ability of CSS to recover from fire and may drive ecosystem type conversion to Eurasian grassland.

Perhaps the most pressing question for future research is whether or not the changes in the CSS community driven by restricted water and added nitrogen are reversible or irreversible. The restricted-water, added-nitrogen treatment had very little shrub presence and almost no herbaceous presence by the end of this study. If this treatment was stopped, what would be the community response? Has this treatment converted these plots to annual grassland, or have enough CSS roots remained alive yet dormant to yet enable a recovery to a CSS ecosystem?

A second important question for future research involves the physiological mechanisms through which an ecosystem type conversion can occur. Is it necessary to entirely kill a CSS community both above and belowground to drive an ecosystem type conversion, or can such a conversion occur through degradation but not elimination of the CSS? What factors are the most important drivers of such a conversion - is it depletion of belowground carbohydrate stores by more and more frequent fire recovery, drought stress, or a combination of the two that represents the greatest driver of shrub mortality and ecosystem type conversion?

Third, at the experimental site and in other Eurasian grasslands, a handful of CSS individuals have managed to establish, and once established, tend to thrive. What factors enable the establishment (or reestablishment) of CSS in a Eurasian grassland? What are the implications of this for restoration and management efforts moving forward?

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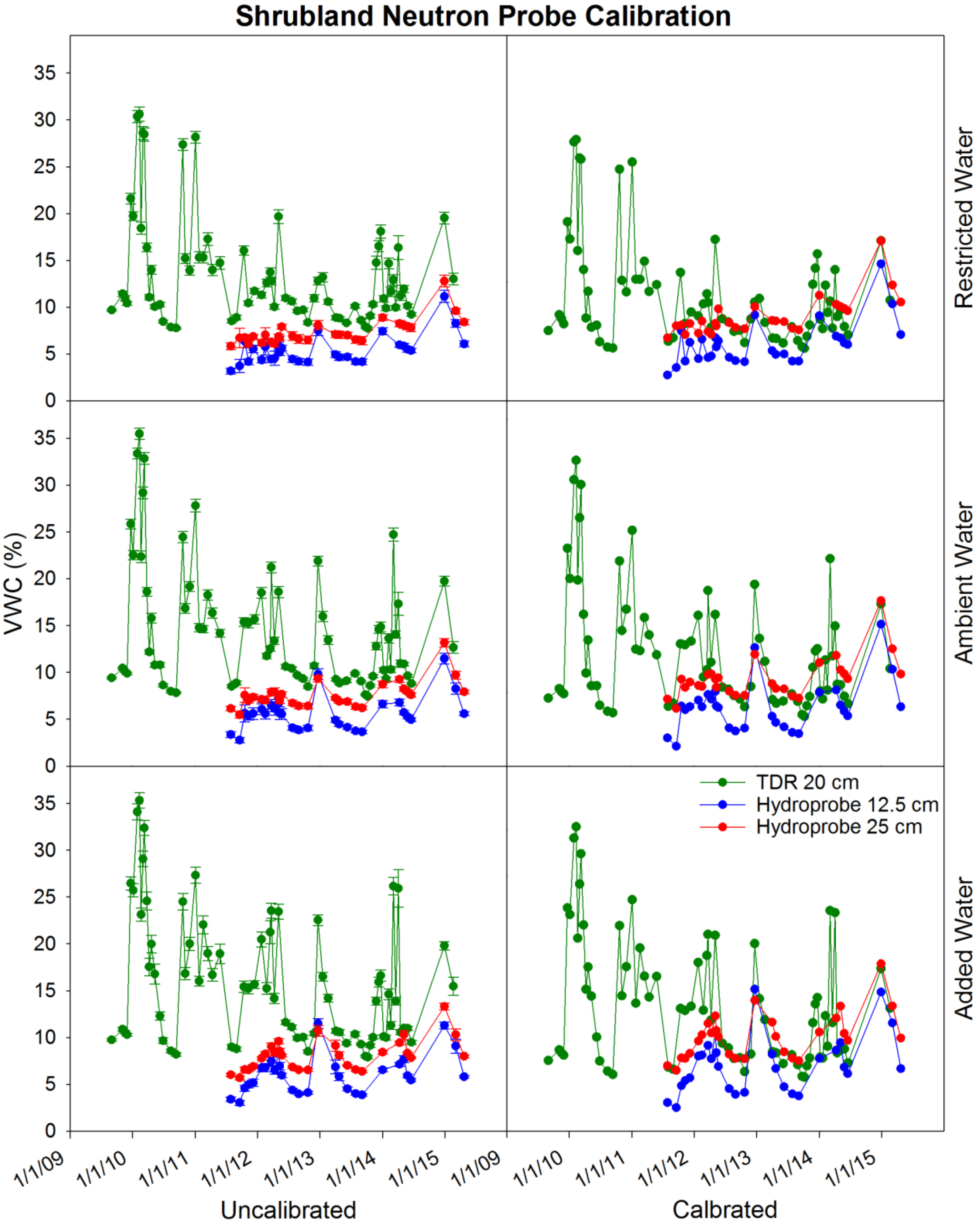
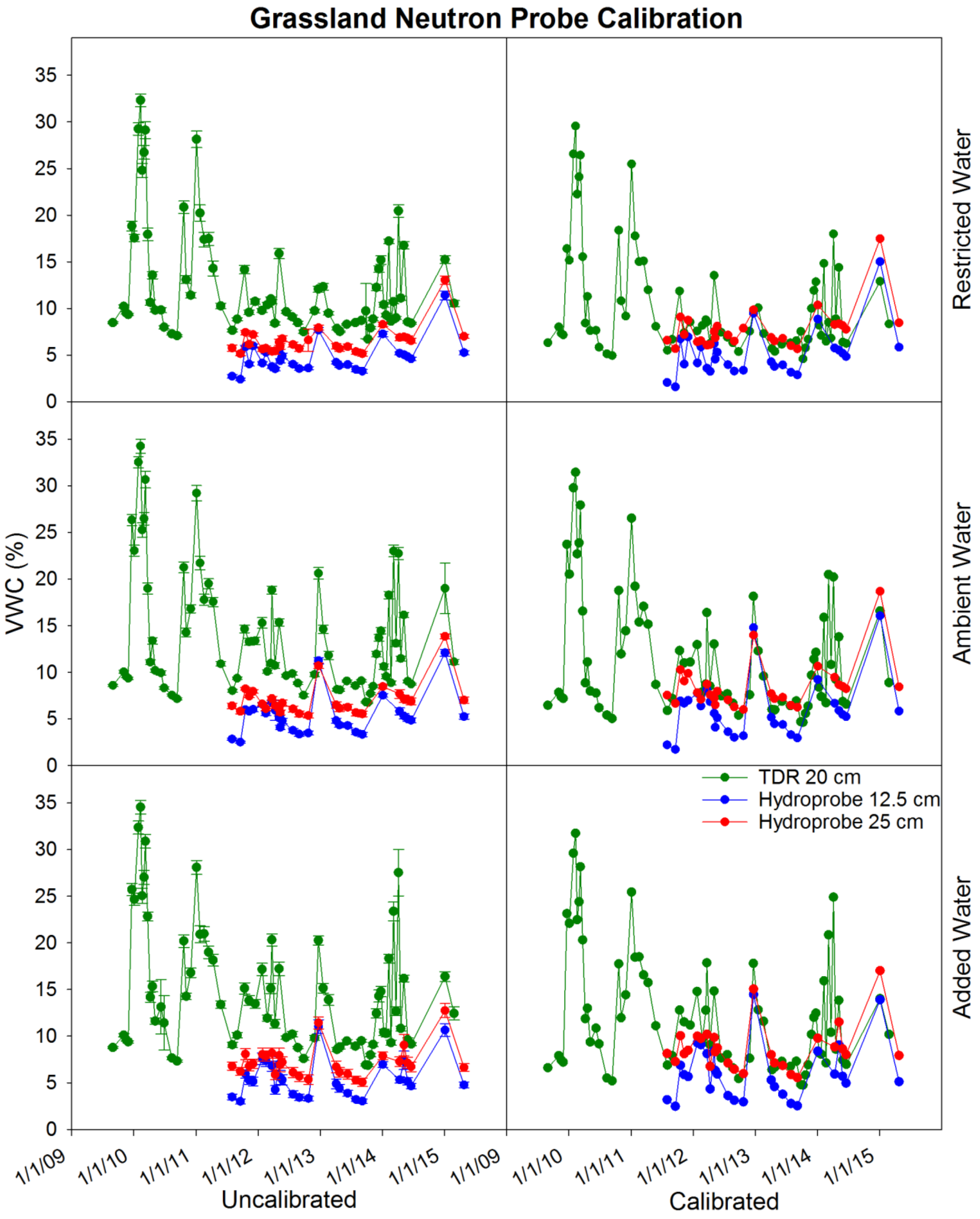
SUPPLEMENTARY FIGURES



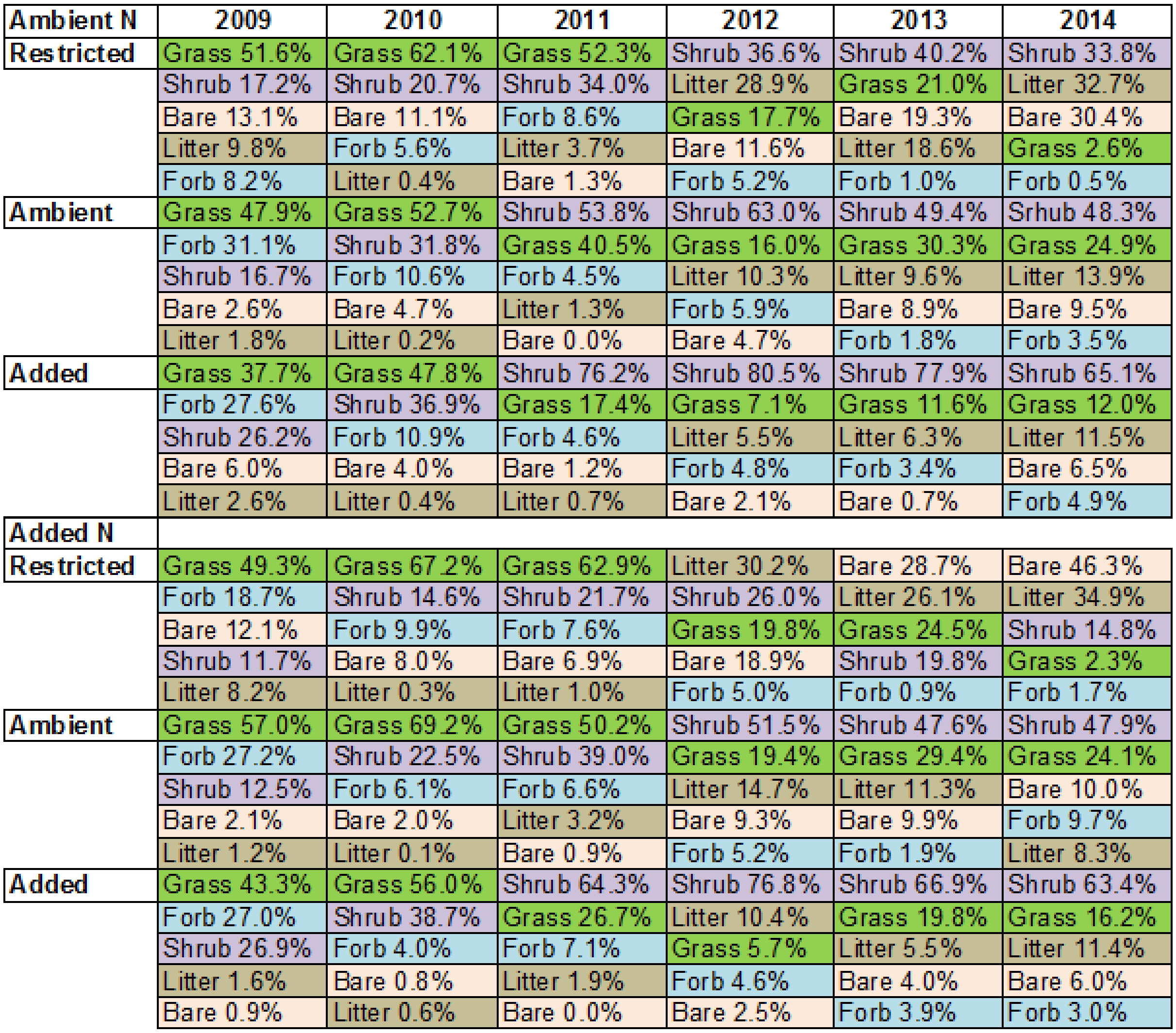
Supplementary Figure 2.1a



Supplementary Figure 1b

Supplementary Figure 1: Calibration results of the CPN Hydroprobe 503DR neutron probe in the shrubland (1a) and grassland (1b). Uncalibrated measurements are on the left and calibrated measurements are on the right for depths of 12.5 cm (blue) and 25 cm (red). Volumetric water content data collected over the top 20 cm using a Campbell Hydrosense sensor to measure TDR are included for comparison (green). Calibration was accomplished by comparing VWC measured by direct soil sampling with neutron probe measurements taken in the holes after soil samples were removed over a range of soil water content.

SUPPLEMENTARY TABLES



Ambient N	2009	2010	2011	2012	2013	2014
Restricted	Grass 51.6%	Grass 62.1%	Grass 52.3%	Shrub 36.6%	Shrub 40.2%	Shrub 33.8%
	Shrub 17.2%	Shrub 20.7%	Shrub 34.0%	Litter 28.9%	Grass 21.0%	Litter 32.7%
	Bare 13.1%	Bare 11.1%	Forb 8.6%	Grass 17.7%	Bare 19.3%	Bare 30.4%
	Litter 9.8%	Forb 5.6%	Litter 3.7%	Bare 11.6%	Litter 18.6%	Grass 2.6%
	Forb 8.2%	Litter 0.4%	Bare 1.3%	Forb 5.2%	Forb 1.0%	Forb 0.5%
Ambient	Grass 47.9%	Grass 52.7%	Shrub 53.8%	Shrub 63.0%	Shrub 49.4%	Srhub 48.3%
	Forb 31.1%	Shrub 31.8%	Grass 40.5%	Grass 16.0%	Grass 30.3%	Grass 24.9%
	Shrub 16.7%	Forb 10.6%	Forb 4.5%	Litter 10.3%	Litter 9.6%	Litter 13.9%
	Bare 2.6%	Bare 4.7%	Litter 1.3%	Forb 5.9%	Bare 8.9%	Bare 9.5%
	Litter 1.8%	Litter 0.2%	Bare 0.0%	Bare 4.7%	Forb 1.8%	Forb 3.5%
Added	Grass 37.7%	Grass 47.8%	Shrub 76.2%	Shrub 80.5%	Shrub 77.9%	Shrub 65.1%
	Forb 27.6%	Shrub 36.9%	Grass 17.4%	Grass 7.1%	Grass 11.6%	Grass 12.0%
	Shrub 26.2%	Forb 10.9%	Forb 4.6%	Litter 5.5%	Litter 6.3%	Litter 11.5%
	Bare 6.0%	Bare 4.0%	Bare 1.2%	Forb 4.8%	Forb 3.4%	Bare 6.5%
	Litter 2.6%	Litter 0.4%	Litter 0.7%	Bare 2.1%	Bare 0.7%	Forb 4.9%
Added N						
Restricted	Grass 49.3%	Grass 67.2%	Grass 62.9%	Litter 30.2%	Bare 28.7%	Bare 46.3%
	Forb 18.7%	Shrub 14.6%	Shrub 21.7%	Shrub 26.0%	Litter 26.1%	Litter 34.9%
	Bare 12.1%	Forb 9.9%	Forb 7.6%	Grass 19.8%	Grass 24.5%	Shrub 14.8%
	Shrub 11.7%	Bare 8.0%	Bare 6.9%	Bare 18.9%	Shrub 19.8%	Grass 2.3%
	Litter 8.2%	Litter 0.3%	Litter 1.0%	Forb 5.0%	Forb 0.9%	Forb 1.7%
Ambient	Grass 57.0%	Grass 69.2%	Grass 50.2%	Shrub 51.5%	Shrub 47.6%	Shrub 47.9%
	Forb 27.2%	Shrub 22.5%	Shrub 39.0%	Grass 19.4%	Grass 29.4%	Grass 24.1%
	Shrub 12.5%	Forb 6.1%	Forb 6.6%	Litter 14.7%	Litter 11.3%	Bare 10.0%
	Bare 2.1%	Bare 2.0%	Litter 3.2%	Bare 9.3%	Bare 9.9%	Forb 9.7%
	Litter 1.2%	Litter 0.1%	Bare 0.9%	Forb 5.2%	Forb 1.9%	Litter 8.3%
Added	Grass 43.3%	Grass 56.0%	Shrub 64.3%	Shrub 76.8%	Shrub 66.9%	Shrub 63.4%
	Forb 27.0%	Shrub 38.7%	Grass 26.7%	Litter 10.4%	Grass 19.8%	Grass 16.2%
	Shrub 26.9%	Forb 4.0%	Forb 7.1%	Grass 5.7%	Litter 5.5%	Litter 11.4%
	Litter 1.6%	Bare 0.8%	Litter 1.9%	Forb 4.6%	Bare 4.0%	Bare 6.0%
	Bare 0.9%	Litter 0.6%	Bare 0.0%	Bare 2.5%	Forb 3.9%	Forb 3.0%

Supplementary Table 1: Fractional cover (%) of grasses (green), forbs (blue), shrubs (lavender), litter (brown), and bare ground (cream) grouped vertically by water and nitrogen treatments and horizontally by water year, with 2009 corresponding to the second year post-fire and 2014 corresponding to the seventh year post-fire. Within each treatment, for each year, the five cover types are arranged in order of descending abundance.

Ambient N	2009	2010	2011
Ambient	B. madritensis 27.8%	B. madritensis 23.1%	A. glaber 28.3%
	L. bicolor 18.4%	A. glaber 18.9%	B. madritensis 18.0%
Shrub	E. condensatus 8.7%	E. condensatus 13.8%	S. mellifera 15.2%
Grass	H. fasciculata 6.1%	V. myuros 8.3%	E. condensatus 12.0%
Forb	S. lepida 5.8%	L. bicolor 6.8%	S. pulchra 7.0%
Bare	A. glaber 5.7%	S. lepida 6.8%	B. diandrus 6.4%
Litter	S. mellifera 5.4%	S. mellifera 6.7%	M. laurina 5.9%
	M. laurina 3.8%	M. laurina 4.7%	L. multiflorum 3.0%
	V. myuros 3.8%	Bare 4.7%	A. californica 2.7%
	E. cicutarium 3.0%	A. californica 2.5%	V. myuros 2.3%
Addition	B. madritensis 23.1%	B. madritensis 19.1%	A. glaber 29.2%
	L. bicolor 16.4%	V. myuros 16.5%	S. mellifera 22.7%
	S. mellifera 11.7%	A. glaber 13.9%	M. laurina 15.5%
	Bare 7.9%	S. mellifera 11.5%	E. condensatus 8.3%
	E. condensatus 7.7%	E. condesnatus 7.9%	A. californica 4.6%
	M. laurina 4.6%	L. bicolor 7.6%	B. madritensis 3.5%
	A. glaber 4.2%	M. laurina 5.5%	V. myuros 3.0%
	Litter 4.1%	Bare 4.6%	B. hordeaceus 2.7%
	V. myuros 2.9%	S. lepida 4.0%	H. squarrosa 2.3%
	S. lepida 2.8%	A. californica 2.9%	S. xanti 2.0%
Restriction	B. madritensis 33.5%	B. madtritensis 42.3%	B. madritensis 34.8%
	E. condensatus 15.3%	E. condensatus 12.9%	E. condensatus 13.5%
	Bare 15.0%	Bare 11.1%	S. mellifera 11.9%
	Litter 9.8%	V. myuros 6.6%	A. californica 7.4%
	L. bicolor 6.0%	S. mellifera 6.1%	M. laurina 5.9%
	S. mellifera 5.8%	A. californica 4.7%	H. squarrosa 4.2%
	H. squarrosa 4.2%	M. laurina 4.4%	Litter 3.7%
	A. californica 3.5%	H. squarrosa 2.9%	A. glaber 2.9%
	M. laurina 3.1%	S. lepida 2.8%	G. angustifolium 2.6%
	S. lepida 1.9%	M. fasciculatus 2.5%	E. cicutarium 2.6%

Supplementary Table 2a

Ambient N	**2012**	**2013**	**2014**
Ambient	A. glaber 32.9%	B. madritensis 21.4%	S. mellifera 20.3%
	S. mellifera 14.3%	S. mellifera 21.3%	B. madritensis 14.6%
Shrub	E. condensatus 11.7%	M. laurina 11.1%	Litter 13.9%
Grass	Litter 10.3%	A. glaber 10.7%	M. laurina 10.5%
Forb	M. laurina 8.6%	Litter 9.6%	E. condensatus 9.7%
Bare	Bare 4.7%	E. condensatus 8.9%	Bare 9.5%
Litter	A. californica 4.5%	Bare 8.9%	A. glaber 7.8%
	B. madritensis 3.7%	A. californica 5.1%	A. californica 7.5%
	M. fasciculatus 2.4%	S. lepida 1.7%	M. fasciculatus 2.3%
	S. xanti 2.3%	M. fasciculatus 1.0%	S. lepida 2.0%
Addition	A. glaber 29.1%	S. mellifera 31.1%	S. mellifera 31.6%
	S. mellifera 22.2%	A. glaber 19.9%	M. laurina 17.0%
	M. laurina 19.7%	M. laurina 18.3%	Litter 11.5%
	E. condensatus 7.0%	Litter 6.3%	A. glaber 7.5%
	Litter 5.5%	A. californica 6.3%	A. californica 6.7%
	A. californica 4.8%	B. madritensis 5.0%	Bare 6.5%
	S. xanti 3.1%	E. condensatus 4.1%	B. madritensis 5.1%
	Bare 2.1%	S. barbatus 2.5%	E. condensatus 4.8%
	S. mexicanus 1.9%	H. squarrosa 2.1%	S. barbatus 1.9%
	H. squarrosa 1.6%	S. lepida 1.7%	S. lepida 1.7%
Restriction	Litter 28.9%	Bare 19.3%	Litter 32.7%
	E. condensatus 15.0%	Litter 18.6%	Bare 30.4%
	S. mellifera 12.4%	B. madritensis 16.0%	S. mellifera 9.6%
	Bare 11.6%	S. mellifera 14.8%	A. californica 9.3%
	M. laurina 7.2%	A. californica 7.8%	M. laurina 7.6%
	A. californica 7.0%	M. laurina 7.6%	M. fasciculatus 4.7%
	H. squarrosa 4.5%	E. condensatus 6.7%	E. condensatus 2.5%
	M. fasciculatus 2.8%	M. fasciculatus 6.0%	H. squarrosa 2.5%
	A. glaber 2.7%	H. squarrosa 2.1%	B. madritensis 0.4%
	B. madritensis 2.6%	A. glaber 1.4%	A. glaber 0.2%

Supplementary Table 2b

Added N	**2009**	**2010**	**2011**
Ambient	B. madritensis 36.9%	B. madritensis 40.8%	E. condensatus 20.7%
	E. condensatus 16.4%	E. condensatus 16.5%	B. madritensis 16.6%
Shrub	H. fasciculata 15.7%	S. mellifera 7.9%	S. mellifera 12.6%
Grass	L. bicolor 8.7%	L. multiflorum 7.3%	M. laurina 9.6%
Forb	S. mellifera 5.9%	A. californica 6.4%	B. diandrus 8.8%
Bare	S. lepida 3.5%	M. laurina 5.2%	A. glaber 8.5%
Litter	Bare 3.3%	A. glaber 5.0%	A. californica 7.8%
	L. multiflorum 3.2%	S. lepida 3.8%	Litter 3.2%
	H. incana 2.8%	Bare 3.3%	B. hordeaceus 2.8%
	Litter 2.4%	V. myuros 2.5%	S. xanti 2.6%
Addition	B. madritensis 26.9%	B. madritensis 30.4%	A. glaber 23.7%
	S. mellifera 10.8%	E. condensatus 11.8%	S. mellifera 17.8%
	H. fasciculata 7.8%	M. laurina 10.2%	M. laurina 14.0%
	E. condensatus 7.3%	S. mellifera 10.1%	B. madritensis 10.3%
	E. cicutarium 7.1%	A. glaber 9.1%	E. condensatus 10.2%
	L. bicolor 5.5%	V. myuros 7.8%	A. californica 7.1%
	M. laurina 5.3%	A. californica 6.6%	S. xanti 7.0%
	S. lepida 4.9%	H. squarrosa 2.9%	A. barbata 3.2%
	A. glaber 4.6%	Litter 2.4%	B. diandrus 3.0%
	V. myuros 4.2%	B. diandrus 2.2%	Litter 1.9%
Restriction	B. madritensis 31.7%	B. madritensis 48.6%	B. madritensis 47.6%
	E. condensatus 13.6%	E. condensatus 14.2%	E. condensatus 9.9%
	Bare 12.1%	Bare 10.7%	S. mellifera 7.0%
	Litter 8.2%	S. mellifera 7.8%	Bare 6.9%
	S. mellifera 7.1%	A. californica 3.1%	A. californica 4.9%
	L. bicolor 5.8%	H. incana 2.6%	M. laurina 4.3%
	H. incana 5.6%	E. chrysanthemifolia 2.3%	M. fasciculatus 3.2%
	M. macrocarpus 4.0%	S. lepida 2.3%	S. lepida 2.6%
	C. macrostegia 3.7%	M. fasciculatus 1.9%	B. diandrus 2.6%
	V. myuros 2.3%	M. laurina 1.9%	C. macrostegia 2.1%

Supplementary Table 2c

Added N	**2012**	**2013**	**2014**
Ambient	Litter 14.7%	B. madritensis 17.9%	S. mellifera 18.6%
	S. mellifera 14.5%	S. mellifera 17.4%	B. madritensis 13.9%
Shrub	E. condensatus 13.8%	E. condensatus 11.5%	M. laurina 12.0%
Grass	A. californica 13.0%	Litter 11.3%	A. californica 11.7%
Forb	A. glaber 11.2%	Bare 9.9%	Bare 10.0%
Bare	M. laurina 9.9%	A. californica 9.8%	E. condensatus 10.0%
Litter	Bare 9.3%	M. laurina 8.9%	Litter 8.3%
	B. madritensis 5.7%	A. glaber 7.8%	S. lepida 3.6%
	M. fasciculatus 3.0%	M. fasciculatus 3.7%	M. fasciculatus 3.2%
	S. xanti 2.0%	S. lepida 1.3%	E. chrysanthemifolia 2.8%
Addition	A. glaber 26.1%	S. mellifera 24.2%	S. mellifera 25.6%
	S. mellifera 21.3%	M. laurina 17.6%	M. laurina 25.1%
	M. laurina 17.9%	B. madritensis 11.5%	Litter 11.4%
	Litter 10.4%	A. glaber 11.2%	B. madritensis 10.3%
	A. californica 10.2%	E. condensatus 8.3%	A. californica 6.9%
	E. condensatus 5.7%	A. californica 7.5%	Bare 6.0%
	S. xanti 4.8%	Litter 5.5%	E. condensatus 5.1%
	M. fasciculatus 2.6%	Bare 4.0%	H. squarrosa 2.1%
	Bare 2.5%	M. fasciculatus 3.8%	A. glaber 2.0%
	E. cicutarium 0.4%	H. squarrosa 2.5%	M. fasciculatus 1.7%
Restriction	Litter 30.2%	Bare 28.7%	Bare 46.3%
	Bare 18.9%	Litter 26.1%	Litter 34.9%
	E. condensatus 10.5%	B. madritensis 21.9%	S. mellifera 4.5%
	S. mellifera 9.2%	S. mellifera 7.8%	A. californica 4.5%
	B. madritensis 9.0%	M. laurina 4.9%	M. laurina 3.8%
	A. californica 5.9%	A. californica 4.0%	E. condensatus 2.2%
	M. laurina 4.9%	E. condensatus 3.4%	E. chrysanthemifolia 1.5%
	A. glaber 3.3%	M. fasciculatus 1.9%	M. fasciculatus 0.8%
	M. fasciculatus 2.7%	A. glaber 1.1%	B. madritensis 0.6%
	S. xanti 2.5%	R. integrifolia 0.7%	A. glaber 0.6%

Supplementary Table 2d

Supplementary Table 2: Ranked abundance of the ten largest components of ground cover by water and nitrogen treatment and by water year with 2009 corresponding to the second year post-fire and 2014 corresponding to the seventh year post-fire. Within each treatment, for each year, the entries are arranged in order of descending abundance. Color-coding indicates categorization as grass (green), forb (blue), shrub (lavender), litter (brown), and bare ground (cream).