

Drivers, mechanisms, and thresholds of woody encroachment in mesic grasslands

by

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B.S., Brigham Young University-Idaho, 2009

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AN ABSTRACT OF A DISSERTATION

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## Abstract

Over the past 130 years in the North American tallgrass prairie, dramatic changes in grassland extent, structure and function have resulted from cessation of fire, extirpation of native herbivores (grazers and browsers), and the fragmentation of the landscape. One consequence of these changes is woody encroachment, the increased cover and abundance of woody species in grasslands. Woody encroachment is a worldwide phenomenon, resulting from global drivers (increased CO<sub>2</sub> concentrations [CO<sub>2</sub>], changes in climate) and local drivers (i.e. land-use history, habitat fragmentation, changes in herbivore diversity, and land management practices). In this dissertation, I investigated the role of fire and browsing (local drivers) on woody plant ecophysiology (Chapter 2 & 3). I then addressed how elevated [CO<sub>2</sub>], and drought (global drivers) impact the growth and physiology of woody plant seedlings (Chapter 4). Chapter 5 reports on breakpoint models to identify temporal and spatial thresholds in ecosystems to help improve adaptive management. In Chapter 2, I observed that fire and repeated browsing significantly decreased *Cornus drummondii* canopy cover, ramet density, and root nonstructural carbohydrates. These results suggest the significance of both fire and browsing on reducing *C. drummondii* dominance in the tallgrass prairie. In Chapter 3, I tested the limited leaf homeothermy hypothesis (LLHH) which posits that leaves can thermoregulate during periods of high temperatures to maximize carbon gain. I used *C. drummondii* shrub islands to test LLHH. T<sub>leaf</sub> was lower during the hottest parts of the day, had minimal spatial variability within the shrub islands, and had little to no variation between browsed and unbrowsed shrub islands. This regulation of T<sub>leaf</sub> by *C. drummondii* suggests support for the LLHH via high rates of transpiration and low water-use efficiency. In Chapter 4, I investigated how increased [CO<sub>2</sub>] and water stress impacted the growth and physiology of four woody encroaching species (*C.*

*drummondii*, *Rhus glabra*, *Gleditsia tricanthos*, *Juniperus osteosperma*). I found that elevated [CO<sub>2</sub>] ameliorated the conditions of drought for all species through tight regulation of stomatal conductance. Starch concentrations within leaf and stem tissues had variable responses to treatments based on the species. However, I did not observe any increases in total biomass in response to increased [CO<sub>2</sub>]. These results demonstrate that these seedlings were resilient to water stress in conjunction with elevated [CO<sub>2</sub>]. In Chapter 5, I developed a method to quantitatively estimate temporal and spatial thresholds using Bayesian breakpoint models. Both models estimated breakpoints and corresponding uncertainties. Breakpoints and the latent spatial interpolation of breakpoints were mapped. Mapping of spatial breakpoints will allow managers to track where thresholds were crossed to help allocate resources. Overall, the results from my dissertation highlight the key roles of local and global drivers on woody plant ecophysiology, and the mechanisms contributing to their ability to maximize carbon gain in fluctuating environmental conditions. My work also provided a framework for linking the knowledge of drivers and mechanisms to create quantitative models that can inform when and where thresholds occur for adaptive management of grassland ecosystems.

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## Abstract

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## **Dedication**

I would like to dedicate this dissertation to my loving wife, Emily, who has supported me through this crazy dream to become a rangeland ecologist. Emily kept me focused on the fact that perpetual grad life is not an end goal. She is strong and patient, a perfect role model for my girls. I would also like to dedicate my dissertation to my three wonderful daughters who have stomped around Konza, helping me collect data, or set up experiments during the summer. I hope they see that they can be curious about the world around them and with hard work achieve whatever they want. Never stop being curious!

# Chapter 1 - Introduction

## Overview

Grasslands cover 30% of Earth's terrestrial surface and provide key services to humanity including cycling nutrients, water, and carbon, providing habitat for wildlife, and forage for livestock (White et al. 2000, Anderson 2006, Sherow 2007). In North America, grasslands once covered 40% of the continent, but urbanization, row-crop agriculture, and mismanaged lands have reduced the extent of this ecosystem by 79% (Dix 1964, White et al. 2000, Brown and Makings 2014). The remaining native grasslands of North America are used predominately for livestock grazing (Anadón et al. 2014), but are slowly transitioning into shrublands and woodlands through the encroachment of woody plants (Archer et al. 2017).

The term woody encroachment describes the increased abundance of woody plants, shrubs or trees in grasslands. The transition from grassland to shrubland or to woodland decrease species diversity (Ratajczak et al. 2012), changes ecosystem carbon and water dynamics (Gill et al. 2002a, Creamer et al. 2011, Kulmatiski and Beard 2013, Logan and Brunsell 2015), and decreases available forage for cattle (Allred et al. 2012, Anadón et al. 2014). The drivers associated with the transitions from grassland to shrubland or woodland are many and occur at global, regional, and local scales (Briggs et al. 2005, Saintilan and Rogers 2015, Archer et al. 2017, Venter et al. 2018). Determining which drivers and mechanisms are responsible for local woody encroachment is crucial to grassland conservation.

Global and regional drivers each influence the rate and trajectory of woody encroachment in grasslands, but local drivers likely influence grassland dynamics most significantly (Archer et al. 1995, Venter et al. 2018). These local drivers include increased woody plant propagule sources, land-use legacies and management practices (i.e., cessation of fire, changes in herbivore

diversity and density, over-grazing), and social perceptions (i.e., prescribed fires are dangerous, prescribed fires cause unnecessary pollution, a grass and tree mix provides increased habitat for animals, etc.) (Archer et al. 1995, Briggs et al. 2005, Allred et al. 2012, Leis et al. 2017). In North American grasslands, herbivory is a major local driver for the maintenance of these systems (Shaw and Lee 1997, Knapp et al. 1999, Bakker et al. 2016). However, in the mid- to late-1800's during westward expansion by European settlers in the Great Plains of North America, many large native ungulate herbivores (grazers and browsers) were completely extirpated from the landscape (Shaw and Lee 1997, Flores 2016). Extirpation of large native ungulate herbivores resulted in increased forage availability for the developing domestic livestock industry in the United States. Around the same time as the extirpation of the native ungulates, fire frequency (another major local driver of grasslands) decreased substantially in and around military forts, towns, and homesteads. Fires historically had kept woody plant propagules from expanding out of the riparian forests and woodlands into the grasslands (Gleason 1913). As Europeans homesteaded across the Great Plains, they planted trees and shrubs (Sherow 2007), adding woody plant propagule sources to a dramatically changing landscape.

The tallgrass prairie, a mesic grassland in the eastern Great Plains, was one of the first grasslands that European settlers homesteaded. Historically, the tallgrass prairie was once 677,000 km<sup>2</sup>, but today only 21,548 km<sup>2</sup> remains making it the most endangered grassland and biome worldwide (White et al. 2000, Hoekstra et al. 2004). The largest remnants of contiguous tallgrass prairie are located in the Flint Hills of Kansas and Oklahoma (Knapp et al. 1998). In the Flint Hills, and elsewhere in the tallgrass prairie, woody plants are increasing in cover and abundance, providing increased pressure on this ecosystem (Bragg et al. 1976, Briggs et al. 2005,

Knapp et al. 2008, Mcculley and Jackson 2012). The dominant woody species expanding are *Juniperus virginiana* (eastern red cedar), *Cornus drummondii* (rough-leaf dogwood), *Rhus glabra* (smooth sumac), and *Gleditsia triacanthos* (honey locust) (Bragg et al. 1976, Briggs et al. 2002, Ratajczak et al. 2016, Leis et al. 2017). Two hypothesized local drivers for expansion of woody plants in the Flint Hills have been the lack of frequent fires and improper grazing management.

Within the Flint Hills of eastern Kansas, the Konza Prairie Biological Station (KPBS) manages intact native tallgrass prairie. In 1977, KPBS researchers established a landscape-scale experiment that manipulates fire frequencies (annual, biennial, 4-yr, and 20-yr) to understand the role of fire in this ecosystem. In 1987 bison (*Bos bison*) were introduced to KPBS to study the role of native grazers in this ecosystem. Results from this long-term KPBS fire and grazing experiment show that frequently-burned watersheds (annual, biennial) restrict woody plants establishment and persistence. In the infrequent-fire watersheds (4-yr and 20-yr) woody plant cover has increased 50% since 1983 demonstrating the significant role fire has in maintaining this grassland (Briggs et al. 2002, Ratajczak et al. 2014a). The interaction of bison grazing with infrequent fires did not halt the expansion of woody plants (Briggs et al. 2002). These results demonstrate that additional drivers regulate grassland structure and woody encroachment beyond fire and grazing.

To determine which potential drivers regulate woody plant expansion, it is necessary to understand life history traits and physiological traits of the expanding woody plant species. Woody plants that have expanded the most are those that have drupe or berry-like (cones) fruits that entice consumption by animals, predominately birds (Holthuijzen and Sharik 1985, Willson and Whelan 1993). Once consumed, birds and other animals transport the seeds to new locations

via defecation, furthering the expansion of woody plants. Seeds passed through animal digestive tracts are scarified which aids in germination. Aside from sexual reproduction, many woody plants in the tallgrass prairie also resprout (i.e. *G. triacanthos*, *Ulmus americana*) or are clonal resprouting species (i.e. *C. drummondii*, *R. glabra*) (The Great Plains Flora Association (U.S.) 1986). Resprouting and clonal resprouting (hereafter, clonal) woody species have adapted to be resilient to disturbances (i.e. fire and herbivory) through the storage of non-structural carbohydrate (NSC) in root and modified underground stem tissues (Fick and Sosebee 1981, Janicke and Fick 1998, Bond and Midgley 2003b, Clarke et al. 2013, Pausas and Keeley 2014). Following disturbance, the resprouting and clonal species reallocate NSCs for regrowth from adventitious buds or auxiliary buds, increasing stem/ramet density aboveground (Lett and Knapp 2003, Heisler et al. 2004, Hajny et al. 2011a). Increases in stem/ramet density shade out grasses, creating discontinuity in grass cover which leads to decreased fire intensity and frequency, ultimately promoting further woody plant expansion (positive feedbacks) (Heisler et al. 2004, Ratajczak et al. 2011).

The ecophysiology of woody plants also has an important role in their persistence in grasslands and allows them to be decoupled from some typical system drivers (i.e. seasonal drought and water stress), re-enforcing the positive feedbacks. Woody plants have long taproots that access water from deep within the soil profile, which allows for a consistent source of water even during droughts (Nippert and Knapp 2007, Eggemeyer et al. 2008, O'Keefe and Nippert 2017). This deep-soil water use reduces competition between woody plants and shallow-rooted grass species for water resources. It also allows for high rates of transpiration at the leaf-level that can translate to higher evapotranspiration rates at the canopy and watershed scales (Brunsell et al. 2013, Logan and Brunsell 2015, Muench et al. 2016, O'Keefe and Nippert 2018). As



previously described, a combination of ecophysiological and life history traits facilitates persistence of woody plants in grasslands. Through a detailed understanding of these traits and responses of woody plants to changes in grassland drivers, adaptive management can be developed to determine what other drivers and mechanisms are necessary for removing woody plants and improving conservation of tallgrass prairie.

## **Objectives and hypotheses**

This research had several goals. The first goal was to understand how two major local drivers, fire and browsing, impact clonal resprouting shrubs in a mesic grassland. Specifically, I was interested in understanding the underlying physiological mechanisms allowing clonal resprouting woody plants to persist after disturbances (i.e. fire and browsing) in a mesic grassland (chapters 2-3). The second goal was to understand how elevated CO<sub>2</sub> concentrations ([CO<sub>2</sub>]) and drought impact the growth and physiology of seedlings and juveniles of several woody encroaching species. I was interested in understanding the underlying physiological mechanisms that promote woody plant growth and storage of starch under future climate conditions (i.e., elevated [CO<sub>2</sub>] and drought) (chapter 4). The final goal of my dissertation was to quantitatively determine where ecological breakpoints occur temporally and spatially to aid in adaptive management of ecosystems. Specifically, I wanted to model the uncertainties surrounding breakpoints to create a spatially interpolatable map of breakpoints (chapter 5).

### **Chapter 2: A missing driver in North American grasslands**

Fire and herbivory are key drivers of grassland dynamics. Typically, research on 'herbivory' in North American grasslands emphasizes only grazing when, in reality, the suite of large ungulate herbivores were historically present included grazers (feeding primarily on grasses) and browsers (grass and woody plants consumed). If browsing is an important driver in

mesic grasslands, then the reintroduction of browsing in a woody encroached mesic grassland should decrease woody plant cover and long-term success. In conjunction with browsing, periodic fire in a woody encroached grassland should reduce woody plant cover more than each driver by itself. To determine the effects of browsing and fire on woody plants, I measured woody plant cover, ramet density, leaf-level gas exchange, and root nonstructural carbohydrates to test the following hypotheses:

- 1) Browsing of clonal resprouting shrubs will open canopy cover and decrease ramet density which will reduce light limitation and increase grass growth. Increased grass growth will promote connectivity of fine fuels for increased intensity of prescribed fires.
- 2) Browsing will cause decreased root nonstructural carbohydrates (NSC).
- 3) Fire and browsing combined will decrease canopy cover, ramet density and NSCs in clonal resprouting shrubs in mesic grasslands, because stored energy reserves required for maintenance or regrowth will be depleted.

### **Chapter 3: Limited Leaf Homeothermy Hypothesis**

Plants are often considered poikilothermic, with leaf temperatures matching ambient air temperatures. Numerous studies since the early 20<sup>th</sup> century have discussed the potential of leaf thermoregulation as a mechanism to maximize physiological performance in vascular plants. Building upon academic discussion on the potential existence of leaf thermoregulation, the limited leaf homeothermy hypothesis (LLHH) posits that leaves thermoregulate during specific periods of the day to maximize carbon gain. To test the LLHH and its mechanisms, I measured leaf temperature, leaf-level gas exchange, and  $\delta^{13}\text{C}$  on *C. drummondii* shrub islands. If support for the LLHH in *C. drummondii* exists, then I expect the following hypotheses to be supported:

- 1) Leaf temperatures should be equal to air temperature in the morning and cooler than air temperatures in the afternoon during high air temperatures.
- 2) Leaf temperatures should be cooler than air temperature during the hottest periods of the growing season.
- 3) Leaf temperatures should not vary throughout the spatial extent of shrub islands even with the natural variations in air temperature surrounding the perimeter of the shrub island.
- 4) Leaf temperatures should be cooler than air temperature following fire.
- 5) Browsing will open up shrub island canopies to increase solar radiation, which should reduce variation in leaf temperatures between browsed and unbrowsed shrub islands because of increased transpiration by browsed shrub islands.

#### **Chapter 4: Elevated [CO<sub>2</sub>] and drought on woody plant seedlings**

A commonly suggested global driver of woody encroachment is increased CO<sub>2</sub> concentrations ([CO<sub>2</sub>]), which has coincided with the timeline of woody plants expanding. Increased [CO<sub>2</sub>] promotes C<sub>3</sub> plant growth through increased rates of carbon assimilation, while improving water use efficiencies via greater stomatal regulation (Curtis 1996, Leakey et al. 2009). Predictions of global climate change in grassland regions include increased drought frequencies in addition to elevated [CO<sub>2</sub>]. Increased frequency and intensity of drought will impact many woody plants species at the seedling and juvenile stage before their roots can access deep soil water. The seedling and juvenile stages of woody plants are important stages in the success of woody plant species establishing in grasslands. Seedlings and juveniles are the most vulnerable to abiotic and biotic stressors. In this chapter I investigated the effects of elevated [CO<sub>2</sub>] and drought on seedlings and juveniles of several woody encroaching species. I measured leaf-level gas

exchange,  $\Delta^{13}\text{C}$ , tissue specific biomass and starch concentrations to test the following hypotheses:

- 1) Elevated  $[\text{CO}_2]$  will increase total biomass of woody plant seedlings and juveniles through increased photosynthetic rates.
- 2) Elevated  $[\text{CO}_2]$  will increase storage of starch in juvenile stem and root tissues compared to ambient  $[\text{CO}_2]$ .
- 3) Water stress will decrease starch concentrations in juvenile stem and root tissues compared to well-watered conditions.
- 4) Elevated  $[\text{CO}_2]$  will increase photosynthetic rates but allow for lower stomatal conductance resulting in increased water use efficiency among woody species.

## **Chapter 5: Quantitatively determining breakpoints**

Ecologists and land managers are often interested in determining when and where thresholds exist within ecosystems. However, being able to quantitatively determine the breakpoint of thresholds is difficult. One reason for the difficulty in predicting thresholds is because current methodologies do not allow for estimation of uncertainties surrounding the breakpoint without post-hoc analyses, or the ability to incorporate spatial data. The construction of Bayesian breakpoint models is one method to improve breakpoint models for determining uncertainties and incorporate spatial data. To improve our ability to estimate thresholds, I created temporal and spatial Bayesian breakpoint models to estimate when breakpoints (posterior distributions) occur and where they occur (combining posterior distributions from multiple sites and kriging them for spatial interpolation). I tested the Bayesian breakpoint models against two data sets where I addressed these hypotheses:

- 1) In the PVC02 dataset woody plant cover should become the dominant functional plant cover type in the infrequently-burned watersheds regardless of grazing treatment (grazed vs ungrazed).
- 2) In the pelagic bioluminescent source data set, breakpoints (depths at which bioluminescent sources are near zero) should be interpolatable across the set spatial scale, with decreased uncertainty near sampled sites.

## **Chapter 6 Management of woody plants in temperate grasslands**

Woody encroachment in grasslands is a worldwide issue. Each location that is experiencing woody encroachment has a different land management history, but the goals remain the same. The goal is to have a productive and functioning grassland without an overabundance of woody plants present. This last chapter synthesizes the need to focus on functional group (i.e., resprouting woody plants) and not on a single species and I provide some thoughts on the best methods to effectively treat the encroached grassland.

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## **Chapter 2 - Browsing and fire decreases dominance of a resprouting shrub in woody encroached grassland**

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### **Abstract**

North American grasslands have experienced increased relative abundance of shrubs and trees over the last 150 years. Alterations in herbivore composition, abundance and grazing pressure along with changes in fire frequency are drivers that can regulate the transition from grassland to shrubland or woodland (a process known as woody encroachment). Historically, North American grasslands had a suite of large herbivores that grazed and/or browsed (i.e. bison, elk, pronghorn, deer), as well as frequent and intense fires. In the tallgrass prairie, many of the large native ungulates were extirpated by the 1860's corresponding with increased homesteading (which led to decreased fire frequencies and intensities). Changes in the frequency and intensity of these two drivers (browsing and fire) has coincided with woody encroachment in tallgrass prairie. Within tallgrass prairie, woody encroachment can be categorized in to two groups: non-resprouting species that can be killed with fire, and resprouting species that cannot be killed with fire. Resprouting species require additional active management strategies to decrease abundance and eventually be removed from the ecosystem. In this study we investigated plant cover, ramet density and physiological effects of continuous simulated browsing and prescribed fire on *Cornus drummondii* C.A. Mey, a resprouting clonal native shrub species. Browsing reduced *C. drummondii* canopy cover and increased grass cover. We also observed decreased ramet density that allowed for more infilling of grasses. Photosynthetic rates between browsed and unbrowsed

shrubs did not increase in 2015 or 2016. In 2017, photosynthetic rates for browsed shrubs were higher in the unburned site than the unbrowsed shrubs at the end of the growing season. Additionally, after the prescribed fire, browsed shrubs had ~90% decreased cover, ~50% reduced ramet density, and grass cover increased by ~80%. In the roots of browsed shrubs after the prescribed fire, non-structural carbohydrates (NSC) experienced a 2-fold reduction in glucose and a 3-fold reduction in both sucrose and starch. The combined effects of browsing and fire show strong potential as a successful management tool to decrease the abundance of clonal-resprouting woody plants in mesic grasslands and illustrate the potential significance of browsers as a key driver in this ecosystem.

**Keywords:** Tallgrass Prairie; shrub encroachment; resprouting/clonal; browsing; fire; mesic grasslands; Konza Prairie; *Cornus drummondii*; nonstructural carbohydrates

## Introduction

Woody encroachment, the expansion of shrubs and trees into grasslands, is a global phenomenon occurring in many grasslands, savannas and steppes (Knapp et al. 2008, Saintilan and Rogers 2015, Archer et al. 2017, Stevens et al. 2017). Causes of woody encroachment are often broken down into three hierarchical scales of drivers: 1) global drivers such as elevated [CO<sub>2</sub>]; 2) regional drivers (e.g. precipitation timing and amount, temporal temperature changes); and 3) local drivers such as land management history, changes in fire frequencies, land fragmentation and removal of native herbivores (Archer et al. 1995, Van Auken 2009, Wigley et al. 2010, Stevens et al. 2017, Venter et al. 2018). Each biome undergoing woody encroachment has a suite of these interacting drivers that influence the rate of woody encroachment. While global and

regional drivers are important for forecasting future ecosystem patterns, identifying local drivers is paramount in the development of potential management strategies.

North American grasslands evolved with fire and a suite of herbivores (i.e. grazers, browsers and mixed feeders) that would have been similar to modern day African grasslands (Sherow 2007, Allen and Palmer 2011, Ripple et al. 2015, Bakker et al. 2016, Flores 2016). After the mass extinction of the Pleistocene megafauna, remnant species remained in North American grasslands such as the bison (*Bos bison*, grazer), pronghorn (*Antilocapra americana*, browser), elk (*Cervus elaphus*, mixed), mule deer (*Odocoileus hemionus*, browser) and white tail deer (*Odocoileus virginianus*, browser) (Rickel 2005, Flores 2016). However, these species were nearly extirpated throughout their historic grassland ranges by the end of the 19<sup>th</sup> century through westward expansion of European settlers (Shaw and Lee 1997, Conard et al. 2006, Sherow 2007, Flores 2016). These mammalian herbivores were replaced with cattle, a grazer, which left a void in the browsing and mixed feeder niches. The loss of browsers may be a key facilitator of woody plant colonization and establishment in these grasslands. In African grasslands, it has been shown through observation and experimental studies that without browsers or mixed feeders woody plants successfully establish (Roques et al. 2001, Holdo et al. 2009, Ward 2015, Goheen et al. 2018). When cattle are present, but browser or mixed-feeder species are not, woody plant establishment may increase because of decreased herbaceous cover and increased light availability (Augustine and McNaughton 2004, Hempson et al. 2017). The top-down effect of browsing removes woody seedlings and decreases growth of established woody plants.

Similar to herbivory, fire removes plant material and is a major driver of grassland structure and function. Fire is crucial for maintaining and facilitating grass dominated herbaceous communities by removing plant litter, increasing light availability, stimulating grass

regeneration via belowground buds, warming soils and eliminating woody plant seedlings (Hulbert 1988, Van Auken 2000, Archibald et al. 2005, Benson and Hartnett 2006, Bond 2008, Archer et al. 2017). However, the cessation of frequent fire allows woody plant species to establish and expand, infilling grasslands and sometimes resulting in a transition to a new ecological state (Allen and Palmer 2011, Ratajczak et al. 2016, Miller et al. 2017). Many woody plants that have encroached in grasslands are capable of resprouting after disturbances, including periodic fires (Bell 2001, Bond and Midgley 2003a, Lett and Knapp 2003, Hajny et al. 2011a, Robertson and Hmielowski 2014). Resprouting woody plants store carbon belowground in root tissues as starch, and maintain a reserve pool of belowground buds that can then be used for regrowth after a disturbance such as herbivory or fire (Janicke and Fick 1998, Bell 2001, Schutz et al. 2011, Moreira et al. 2012, Pausas et al. 2016). This regrowth often occurs in the same growing season and corresponds with increasing stem or ramet densities (Hajny et al. 2011a). Increases in woody plant cover often create positive feedbacks that further decouple the grassland from historic drivers and lead to an alternative stable state (i.e., shrubland, woodland) (Ratajczak et al. 2014a).

In the tallgrass prairie, the role of fire as a key driver of system dynamics has long been recognized (Gleason 1913, Weaver and Aldous 1935, Henderson 1982, Gibson and Hulbert 1987, Briggs et al. 2005, Allen and Palmer 2011). In this ecosystem fire frequencies >3 years (historic mean fire frequency 3.76 years (Allen and Palmer 2011)) are no longer sufficient to mitigate woody establishment because of low intensity fires, and fire is typically ineffective at removing resprouting woody plants once established (Briggs et al. 2005, Ratajczak et al. 2014b, 2017b, Twidwell et al. 2016, Miller et al. 2017). If fire alone is ineffective at eliminating resprouting woody plants, then finding another ecological driver that acts in conjunction with fire



may be necessary for managing woody plants in mesic temperate grasslands. We proposed to test the hypothesis that browsing in conjunction with fire may be a suitable prescription for the removal of resprouting woody plants from an encroached grassland. We specifically wanted to address three questions: 1) Does browsing a resprouting woody plant allow for increases in herbaceous understory beneath the woody plant canopy to create a buildup of fine fuel for prescribed fires? 2) Does browsing decrease carbon storage in the form of non-structural carbohydrates in resprouting woody plant roots by the end of a growing season? 3) Does the combination of browsing and fire decrease or eliminate resprouting woody plants in woody encroached grasslands? To answer these three questions, we experimentally investigated the combined importance of browsing and fire on the plant community in a woody encroached grassland as well as their effects on the demography and physiology of *Cornus drummondii* C.A. Mey. (roughleaf dogwood), a C<sub>3</sub> clonal resprouting shrub. *C. drummondii* and other resprouting woody plants have expanded and continue to expand into the tallgrass prairie despite a reintroduction of fire frequencies similar to presumed historic frequencies (Briggs et al. 2002, Ratajczak et al. 2014a). *C. drummondii* shrubs were selected in two locations at the Konza Prairie Biological Station (KPBS), one site with a 4-year fire frequency and the other with a 20-year fire frequency. We imposed a monthly simulated browsing treatment where we randomly removed 50% of new meristematic growth throughout the growing season on half of the selected *C. drummondii* shrubs for 2 years prior to a prescribed fire in the 4-year fire frequency location. The simulated browsing treatment continued for an additional year after the prescribed fire for both locations studied.

## Methods

### Site description

Research was conducted during the 2015 to 2017 growing seasons at the Konza Prairie Biological Station (KPBS), a 3,487-ha native C<sub>4</sub> dominated grassland in northeastern Kansas, USA (39°05' N, 96°35' W). KPBS is located within the Flint Hills region, one of the largest continuous expanses of unplowed tallgrass prairies left in North America. It remained unplowed due to the shallow rocky soils and steep-sided hills. The climate in the tallgrass prairie at KPBS is characteristic of mid-continental climates with high inter-annual variability in precipitation. Long-term mean annual precipitation for KPBS is 806.9 mm (1982-2017) with 79% occurring during the growing season (April-September). For research and management purposes, KPBS is divided into watershed units with varying fire frequencies (1, 2, 4, or 20 years). The majority of prescribed fire treatments occur during the spring.

### Study design

To assess the effects of browsing and fire on resprouting woody plants we focused on *C. drummondii*, a C<sub>3</sub> resprouting clonal shrub that expands laterally to create shrub islands. The shrub grows through lateral rhizomes before a bud sends up a ramet. These ramets can grow upwards to be 1-2.5 m in height depending on soil profile. Due to the height of the ramets, these shrub islands reduce light to the understory which depresses herbaceous vegetation growth (Ratajczak et al. 2011). Within these shrub islands there can also be multiple woody species present (e.g., *Symphoricarpos orbiculatus* Moench, *Gleditsia triacanthos* L., and *Prunus americana* Marshall) but only one species is dominant.

In 2015, 40 randomly stratified locations were chosen with half in a 4-yr burn treatment ( $n = 20$ ) and half in an unburned treatment ( $n = 20$ ). Each of the locations had a *C. drummondii*

shrub island present that was randomly assigned to a browse treatment (browsed  $n = 20$ , unbrowsed  $n = 20$ ). The simulated browse treatment consisted of removing 50% of new meristematic growth randomly in the shrub islands through pinching or pulling off the plant tissue. All plant tissue that was removed from the shrub islands was deposited outside of the study area. The browse treatment occurred monthly through the growing season (May – September).

In the spring of 2017 (*13 April 2017*) a prescribed burn was applied to the 4-yr burn treatment. Our study area experienced a full headfire which top-killed all browsed shrub island ramets and top-killed a majority of control shrub islands. The browse treatment resumed after the prescribed fire when new growth occurred, and leaves were fully expanded.

### **Plant Community Composition**

Each August all shrub islands were surveyed for plant community composition and cover at their center mid-point using a 10 m<sup>2</sup> circular plot. The circular plots did not exceed the boundary of the shrub islands. All plants within the circular plot were identified down to species level and cover was estimated using a modified Daubenmire cover scale (Bailey and Poulton 1968). The modified Daubenmire cover scale size classes were as follows: 0-1, 1-5, 5-25, 25-50, 50-75, 75-95, and 95-100%.

### **Ramet Density**

At the end of each growing season, ramet density was determined by measuring the area of the *C. drummondii* shrub island and then counting each ramet within the shrub islands. Due to the irregular growth pattern of the clonal shrub islands, we calculated area of the shrub islands by dividing each clone into 1m wide lanes centered along the island's long axis. We then measured the distance between the distal most ramets of each lane. This distance was used to calculate the

area of each lane. Shrub island area was represented by the sum of all lane areas. We selected a wide range of shrub areas with the smallest being 8.8 m<sup>2</sup> to the largest at 139.7 m<sup>2</sup>. After determining the area of the shrub island, we divided the total number of ramets within the shrub islands by their respective areas. This protocol allowed us to measure the density of ramets for each individual shrub island.

### **Leaf Photosynthesis**

We measured net photosynthesis using a LI-6400XT open gas exchange system with a red/blue light source and a CO<sub>2</sub> injector (LI-COR Inc., Lincoln, NE). We set the light source within the leaf chamber to 2000 μmol m<sup>-2</sup> s<sup>-1</sup> and the CO<sub>2</sub> reference level to 400 μmol mol<sup>-1</sup>. Measurements were made throughout the growing season (May-August) from 1000-hr to 1500-hr on new fully expanded leaves. Two measurements were recorded per shrub island, one at the periphery of the shrub island and the second at the center of the shrub island to measure potential variation in photosynthesis within the shrub islands. Net photosynthetic rates did not differ significantly ( $P > 0.05$ ) between the inside and outside of the shrub islands so the photosynthetic rates were treated as subsamples and averaged for each shrub island prior to statistical analysis.

### **Non-structural Carbohydrate Analysis**

*Cornus drummondii* root samples were collected at the end of the growing season after leaf senescence to analyze for non-structural carbohydrates (NSC). Roots were harvested by locating three ramets at the northern, center, and southern parts of the shrub island. Soil from around the ramets was removed until fine and lateral roots were found. Once root tissues were uncovered 10 cm of root tissue was excised from each ramet, no rhizomes were used for analysis, and root tissue was pooled for each shrub island. We combined lateral and fine root tissues from each shrub island and placed the roots in a cooler. All roots were washed in distilled water to remove

all soil particles and then microwaved for 90 seconds to halt enzymatic activity (Landhäusser et al. 2018). After microwaving, roots were oven dried at 65 °C for 72 hours. All root samples were milled to 40 mesh (400 µm) prior to ball milling (Wig-L-Bug®) and stored in glass vials in a -20 °C freezer until NSC analysis. For each root sample, 20 mg of root tissue was suspended in 0.66 ml of 80% ethanol in a 2.5 ml microcentrifuge tube. Tubes were placed in a dry bath incubator at 80 °C for 20 minutes (Hendrix 1993, Landhäusser et al. 2018). Supernatant was placed in a separate tube and the extraction was repeated an additional two times. The ethanol extract was used to determine root glucose and sucrose concentrations. To quantify root glucose and sucrose concentrations we used the Total Starch Assay Kit from Megazyme Co. (Wicklow, Ireland). We used a 96-well plate and added 20 µl of sample ethanol extractant into 3 wells (sucrose, glucose, blank). For each root sample, analyses were performed in triplicate to establish technical replicates. Ethanol was evaporated in a drying oven at 55 °C for 20 minutes after which 20 µl of DI H<sub>2</sub>O was used to dissolve the extract. Samples being analyzed for sucrose had 10 µl of invertase added and incubated at 37 °C for 10 minutes. After the incubation 200 µl of GOPOD reaction mix (glucose oxidase/peroxidase reagent with O-dianisidine) was added to the sucrose, glucose sample wells as well as the standards wells. We incubated the samples for another 20 minutes at room temperature, placed the plate in a spectrophotometer, and read the absorbance at 510 nm. Concentrations of glucose and sucrose were determined using glucose and sucrose standard curves.

Starch was analyzed using the ethanol extracted tissue samples from the glucose and sucrose analysis. The extracted tissues had 1 ml of DI H<sub>2</sub>O added to the microcentrifuge tube and was then autoclaved for 1 hour at 135 °C. After the samples were autoclaved, they were placed in a drying oven at 65 °C for 12 hours. Starch concentrations of root tissue were quantified using

the Total Starch Assay Kit from Megazyme Co. (Wicklow, Ireland). Ethanol extracted root tissue samples were digested in 1 ml of  $\alpha$ -amylase, boiled for 20 minutes and then cooled for 10 minutes. Each root tissue sample then had 15  $\mu$ l of amyloglucosidase added. The samples were then placed in a 50 °C shaking water bath for 45 minutes. Using a 96-well plate, 20  $\mu$ l samples were plated out and 200  $\mu$ l of GOPOD reaction mix was added. The samples were incubated for 20 minutes at room temperature and then placed in a spectrophotometer to be read at 510 nm. Starch concentrations were quantified using a starch (maize) standard curve. Throughout the entire process, a positive control sample of *C. drummondii* root tissue (quantified using the same and a different method in separate labs) was used with known concentrations of glucose, sucrose and starch to verify analytical results.

Because *C. drummondii* is clonal and exhibits strong responses in shrub island size following fire and browsing (Lett et al. 2004). In our analysis and presentation of NSC data we multiply root NSC concentrations to their respective ramet densities. We assume that with a decrease in ramet density there will be a decrease in root density, which could result in decreased NSC concentrations. *C. drummondii* shrub islands have near equal above-ground to belowground biomass proportion with the majority of root biomass near the soil surface (sample size 1, unpublished data).

### **Statistical Analysis**

All the data met the assumptions of normality for repeated measures linear mixed effects models for all response variables (plant cover, ramet density, glucose, sucrose, and starch). The fixed effects in each model were browsing treatment and year with interaction of browsing treatment by year. Our random effect for these models was shrub island number to account for the variation between the different shrub islands as well as to account for the repeated measures on

each shrub island. The repeated measures mixed effects model for net photosynthetic rate and leaf nitrogen content had an additional fixed effect of date sampled added to the model due to the repeated sampling within and between years. If the interaction term of browsing and date sampled was significant then continued analysis of that specific year was performed. All analyses were done in Program R v3.4.3 (R Core Team 2012) with the “lme4” package v1.1-17 (Bates et al. 2015a) for linear mixed models, repeated measure ANOVAs in “car” (Fox and Weisberg 2011) and figures were made with “ggplot2” v2.2.1 (Wickham 2009).

## Results

Simulated browsing treatments were effective in reducing *C. drummondii* cover in both fire treatments (4-yr burn and unburned), however differences in the magnitude of the responses between the two fire treatments varied according to the measurement type and scale of inquiry.

### **Browsing and fire effects on community plant cover**

Browsing and browsing x year were significant in the 4-yr burn for *C. drummondii* cover (browsing  $P < 0.001$ ; browsing x year  $P < 0.001$ ) and grass cover (browsing  $P < 0.001$ ; browsing x year  $P < 0.001$ ). *C. drummondii* cover in the browsed shrub islands were 20 % lower than the control shrub islands in the first year (2015) (Fig. 2.1a,  $P = 0.008$ ). Grasses responded to the browse treatment with 43% higher cover in 2015 (Fig. 2.1c,  $P < 0.001$ ). By the end of 2016 and in the absence of fire there was no additional reduction in *C. drummondii* cover, which remained 20% lower than the control shrub islands ( $P = 0.008$ ). Grass cover was 67% higher in the browsed shrub islands compared to the control ( $P < 0.001$ ). In the spring of 2017 prior to leaf bud burst, the prescribed fire resulted in 100% top-kill of the browsed shrub islands and 75% top-kill of the control shrub islands. By the end of the 2017 growing season, we saw a ~90%

reduction in *C. drummondii* cover in browsed shrub islands ( $P < 0.001$ ) and grass cover was 77% higher in relation to the control shrub islands ( $P < 0.001$ ).

The unburned treatment experienced no statistically significant changes in shrub cover ( $P = 0.096$ ) or grass cover ( $P = 0.211$ ) due to browsing for any of the years sampled (Fig. 2.1b,d).

### **Ramet density in response to browsing and fire**

Ramet density mimicked patterns of *C. drummondii* cover in the 4-yr burn treatment with statistically significant responses by the browsing treatment and browsing x year ( $P = 0.005$ ,  $P < 0.001$  respectively). In 2015 and 2016, there was no statistically significant reduction of ramets in the browsed shrub islands compared to the control shrub islands (Fig. 2.2a). However, in 2017 after the prescribed fire, *C. drummondii* ramets increased in control shrub islands up to  $16.74 \pm 1.40$  ramets  $m^{-2}$  while in the browsed shrub islands ramets decreased to  $7.43 \pm 1.01$   $m^{-2}$  ( $P < 0.001$ ).

We did not observe a strong browsing treatment effect on ramet density in the unburned treatment ( $P = 0.225$ ), but we did see a browsing x year interaction (Fig. 2.2b;  $P = 0.042$ ).

### **Photosynthetic rate response to browsing and fire**

Browsing did not have a strong effect on the net photosynthetic rate of *C. drummondii* (4-yr burn,  $P = 0.248$ ; Unburned,  $P = 0.069$ ), but browsing x date sampled did show a significant interaction for both fire frequencies (Fig. 2.3, 4-yr burn,  $P = 0.012$ ; Unburned,  $P = 0.006$ ). In 2017 we observed opposite responses to browsing between the 4-yr burn and unburned sites. Following the 2017 prescribed fire in the 4-yr burn location, new leaves in the browsed shrub islands had lower net photosynthetic rates across the growing season compared to the control shrub islands (Fig. 2.3,  $P < 0.001$ ). This pattern contrasted with the unburned treatment, where



net photosynthetic rates increased in the browsed shrub islands compared to the control shrub islands (Fig 2.3,  $P < 0.005$ ).

### **Non-Structural Carbohydrate (NSC) responses to browsing and fire**

The effects of browsing and year on NSC varied depending on the forms of NSC measured (i.e. glucose, sucrose and starch) and the fire treatment (4-yr burn and unburned) (Fig. 2.4, Supplementary Table 2.1). In the 4-yr burn treatment we observed no statistically significant effects on glucose concentration between the browsed shrub islands ( $16.56 \pm 3.48 \text{ mg g}^{-1}$ ) and the control shrub islands in 2016 ( $13.78 \pm 2.39 \text{ mg g}^{-1}$ ), but in 2017 glucose concentrations increased 2-fold in the control shrub islands and decreased by 30 % in the browsed shrub islands relative to concentrations in 2016, resulting in a significant difference between treatments ( $25.37 \pm 2.21 \text{ mg g}^{-1}$  vs  $11.58 \pm 1.90 \text{ mg g}^{-1}$ ; Fig. 2.4a,  $P = 0.002$ ). In 2016, *C. drummondii* sucrose concentrations in the 4-yr burn treatment were not statistically significant in the browsed shrub islands ( $6.79 \pm 1.32 \text{ mg g}^{-1}$ ) compared to control shrub islands ( $9.24 \pm 3.27 \text{ mg g}^{-1}$ ). In 2017, sucrose concentrations were 3-fold higher in control shrub islands relative to browsed shrub islands ( $7.97 \pm 1.64 \text{ mg g}^{-1}$  vs  $24.49 \pm 5.41 \text{ mg g}^{-1}$ , Fig. 2.4c,  $P = 0.002$ ). *C. drummondii* starch concentrations in 2016 in the 4-yr burn treatment were not statistically different between the browsed shrub islands and the control shrub islands ( $399.78 \pm 64.47 \text{ mg g}^{-1}$  vs  $530.70 \pm 52.97 \text{ mg g}^{-1}$ ), while in 2017 starch concentrations were 3-fold higher in the control shrub islands compared to the browsed shrub islands, relative to concentrations in 2016, resulting in a significant difference between treatments ( $198.70 \pm 45.73 \text{ mg g}^{-1}$  vs  $648.00 \pm 91.90 \text{ mg g}^{-1}$ ; Fig. 2.4e,  $P < 0.001$ ).

In the unburned treatment, where only the browsing treatment occurred (no prescribed fire), we observed little to no difference in the amounts of glucose, sucrose and starch between

the browsed and control shrub islands (Table A.1; Fig. 2.4b, 2.4d, 2.4f). There was some variability between 2016 and 2017 in all the NSC forms sampled.

## Discussion

Here, we provide clear evidence for the interactive role of frequent fire and browsing as a strong top-down control on woody vegetation in the tallgrass prairie. As expected, simulated browsing removed enough leaf and new meristematic tissues that the closed canopies of *Cornus drummondii* shrub islands opened up and allowed grasses to increase in biomass and cover. The grasses within the shrub islands likely existed as dormant rhizomes before browsing, and changes in grass abundance were likely due to vegetative reproduction and not the germination of new seedlings (Benson and Hartnett 2006). With increased light and nutrient availability, grasses respond positively and quickly via tiller production from dormant buds (Lett and Knapp 2003, 2005, Vanderweide et al. 2014). The continuation of season-long removal of new growth over subsequent years led to decreases in *C. drummondii* ramet density and a buildup of fine fuels from grasses that, in the 4-yr burn treatment, allowed the prescribed fire to carry through each browsed shrub island for a 100% topkill (personal observation). The browsed shrub island responses following fire were an even further decrease in ramet density and an 88% reduction in *C. drummondii* cover and an increase of 80% grass cover by the end of the 2017 growing season (Fig 2.1a, c). However, the response to fire in the control shrub islands in the 4-yr fire treatment was a large increase in ramet density, similar to previous studies (McCarron and Knapp 2001, Heisler et al. 2004). In the unburned treatment, browsed *C. drummondii* shrub islands gradually decreased percent cover each year with a concurrent gradual increase in grass cover (Fig 2.1b, d). The slower decrease in shrub cover and increase in grass cover in the unburned treatment may result from no significant decrease in ramet density among browsed shrub islands during the first

2 years of the study. To explain the dramatic differences between the 4-yr burn and unburned treatments we propose that the species composition of woody plants present and competitive exclusion of subdominant woody species determines the efficacy of browsing (Augustine and McNaughton 2004, Ascoli et al. 2013, Roberts et al. 2014, Anderson et al. 2015). In the burned location, *C. drummondii* is the dominant woody plant on the landscape with *Rhus glabra* L (smooth sumac), another clonal resprouting shrub, mixing within the shrub islands. In the unburned location, there are more woody plant species that have infilled within the *C. drummondii* shrub islands (Briggs et al. 2005). Some of these woody species were not dominant at the start of the experiment, or even present, but by the end significant growth of these subdominant species had occurred within the shrub islands. A few of these species were *Symphoricarpos orbiculatus* Moench (coralberry), *Gleditsia triacanthos* L. (honeylocust) and *Prunus americana* Marshall (American plum), all resprouting and/or clonal woody plants. As *C. drummondii*'s influence was reduced, other woody species filled the available niche. Thus, successful adaptive management of woody plants must focus on functional groups (i.e. clonal woody plants, resprouting woody plants, non-resprouting plants), rather than species-specific removals.

Browsing did not increase leaf-level photosynthetic rates in *C. drummondii* shrub islands throughout the growing seasons of 2015 and 2016 as expected, but it did increase at the end of the 2017 growing season in the unburned treatment. Increased photosynthetic rates from browsing is consistent with other studies that observed increased photosynthetic rates under browsed conditions from native browsers (elk) in clonal or resprouting woody plants (Johnston et al. 2007, Rhodes et al. 2017). Increases in photosynthesis from herbivory is a mechanism that plants use to compensate for loss of tissue (Pinkard et al. 2011). In 2017, after the prescribed fire,

we expected to see continued increases in photosynthesis because of a release of available nitrogen and new ramet growth (Fig. 2.2) (Longstreth and Nobel 1980, Blair 1997). However, after the prescribed fire, only shrubs in the unbrowsed (control) treatments exhibited higher photosynthesis compared to previous years (Fig. 2.3), increasing NSC (glucose, sucrose and starch) for unbrowsed (control) shrubs in 2017 (Fig. 2.4). In contrast, browsed shrub island NSC was reduced by 200-300% following the prescribed fire (Fig. 2.4a), likely impacted by reduced photosynthetic rates (Fig. 2.3), reduced ramet density (Fig. 2.2) and reduced total leaf area (expressed as cover in Fig. 2.1). Independently, the effects of browsing or fire alone were insufficient to reduce ramet densities, photosynthesis or NSC reserves to produce large shrub ramet mortality. However, when browsing and fire were combined, the effects on ramet densities and root NSC were large and suggest a continued potential for long-term shrub mortality in this grassland.

### **Management Implications**

Woody encroachment is one of the greatest conservation threats to grasslands world-wide. The increase in dominance of woody plants, particularly resprouting woody species, may result from changes in many drivers including land use change, urban expansion, decreased fire frequency and severity, and decreased browsing herbivore pressure. Many grasslands experience frequent disturbance and require disturbance for the maintenance of the ecosystem state. However, clonal or resprouting woody plants have developed mechanisms to increase their competitive ability with grasses and ultimately alter disturbance patterns. These strategies of clonal woody shrubs include 1) access to water deep in the soil profile (Nippert et al. 2013b, Holdo et al. 2017), 2) stored energy reserves (NSC) in belowground tissues (Bond and Midgley 2003a, Bond 2008), 3) stored demographic potential in belowground bud banks (Clarke et al. 2013, Vanderweide et al.

2014), and 4) utilizing rapid vertical growth which results in shading out herbaceous competitors (Bond and Midgley 2003a). We have shown that of these three adaptive strategies shared by many clonal woody species, two can be negatively impacted via simulated browsing and prescribed fire. By decreasing the woody plants' abilities to adequately store energy belowground and improving the light environment for understory herbaceous species, simulated browsing decreased the dominance of the clonal woody species measured here, and promoted increased grass cover.

As land managers struggle to maintain both ecosystem function and profitability in the face of woody encroachment, finding effective tools for woody species mitigation is becoming increasingly important (Wilcox et al. 2018). Frequent disturbance of aboveground tissues to open up the canopy and increase light availability can be achieved with mechanical removal or by using browsers (Green and Newell 1982, Hart 2001, Lett and Knapp 2005). The data shown here illustrate that repeated disturbances that partially remove aboveground woody plant tissues negatively affects resprouting shrubs, while increasing grass cover. Our suggestion for land managers dealing with clonal resprouting shrubs in mesic temperate grasslands is the frequent removal of shrub aboveground biomass; total removal of aboveground biomass is not necessary. The method for removal of woody plant aboveground biomass can be through herd type browsers, mechanical removal, or both to increase light availability for grass growth. Once fine fuels are established, then fire can be reintroduced into the landscape for continued suppression and eventual mortality of the woody plants.

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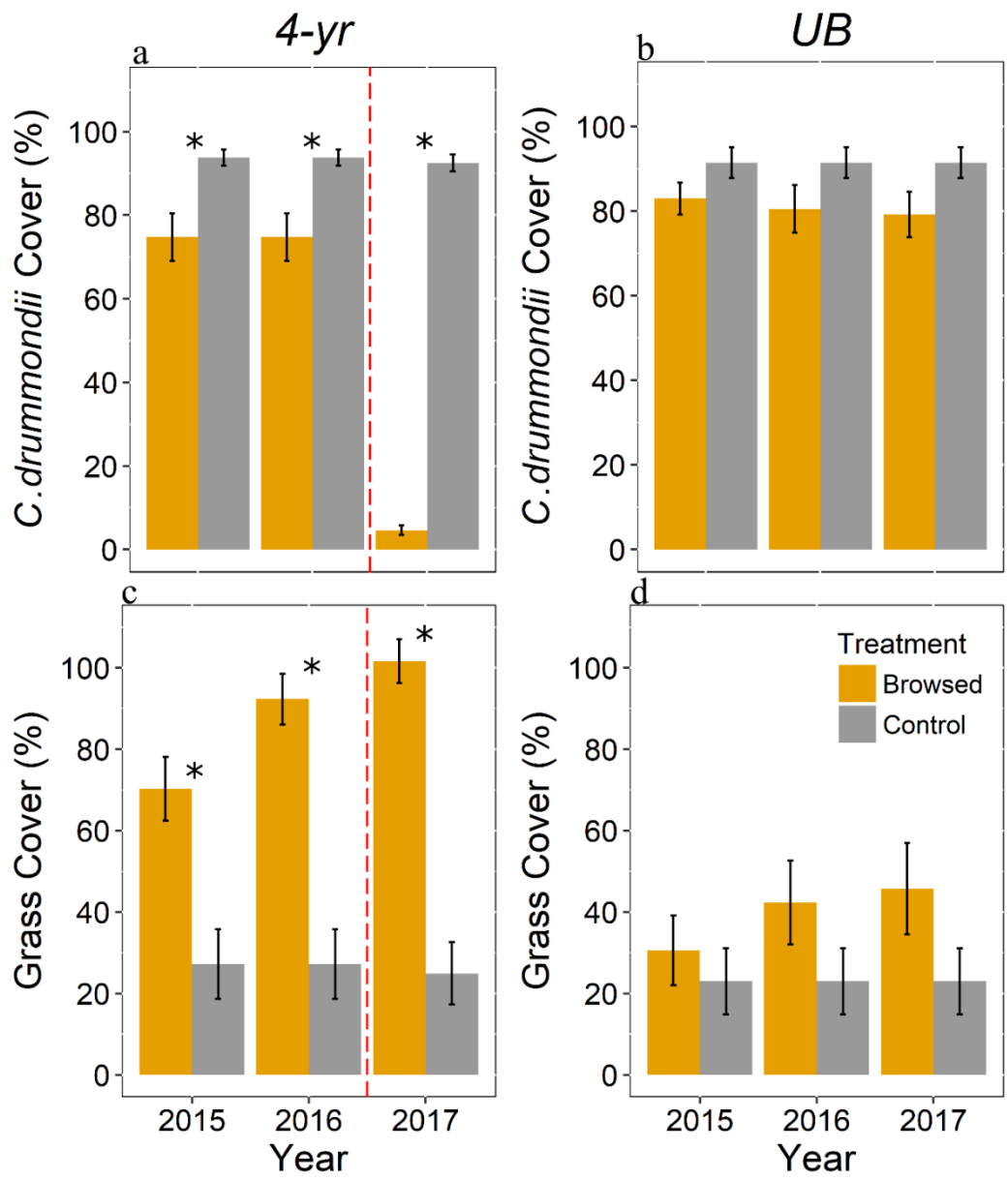
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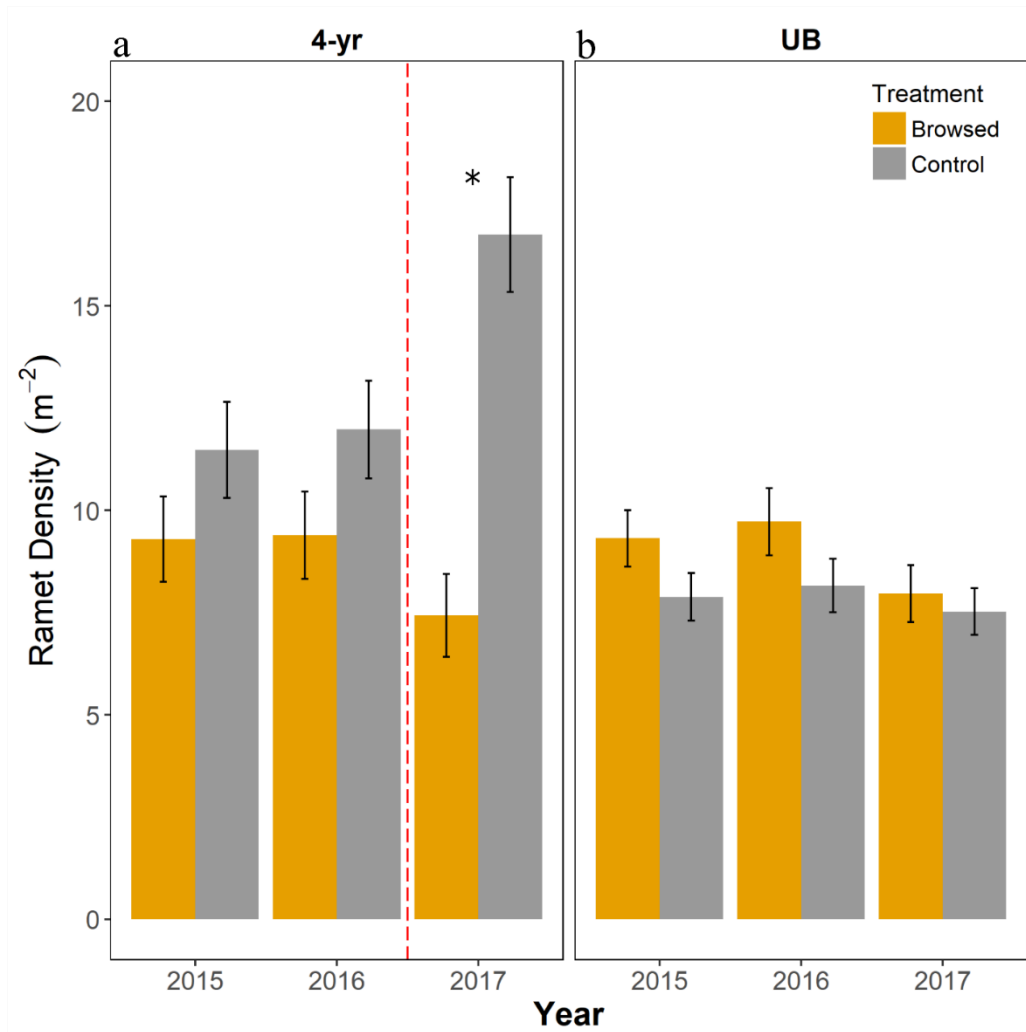
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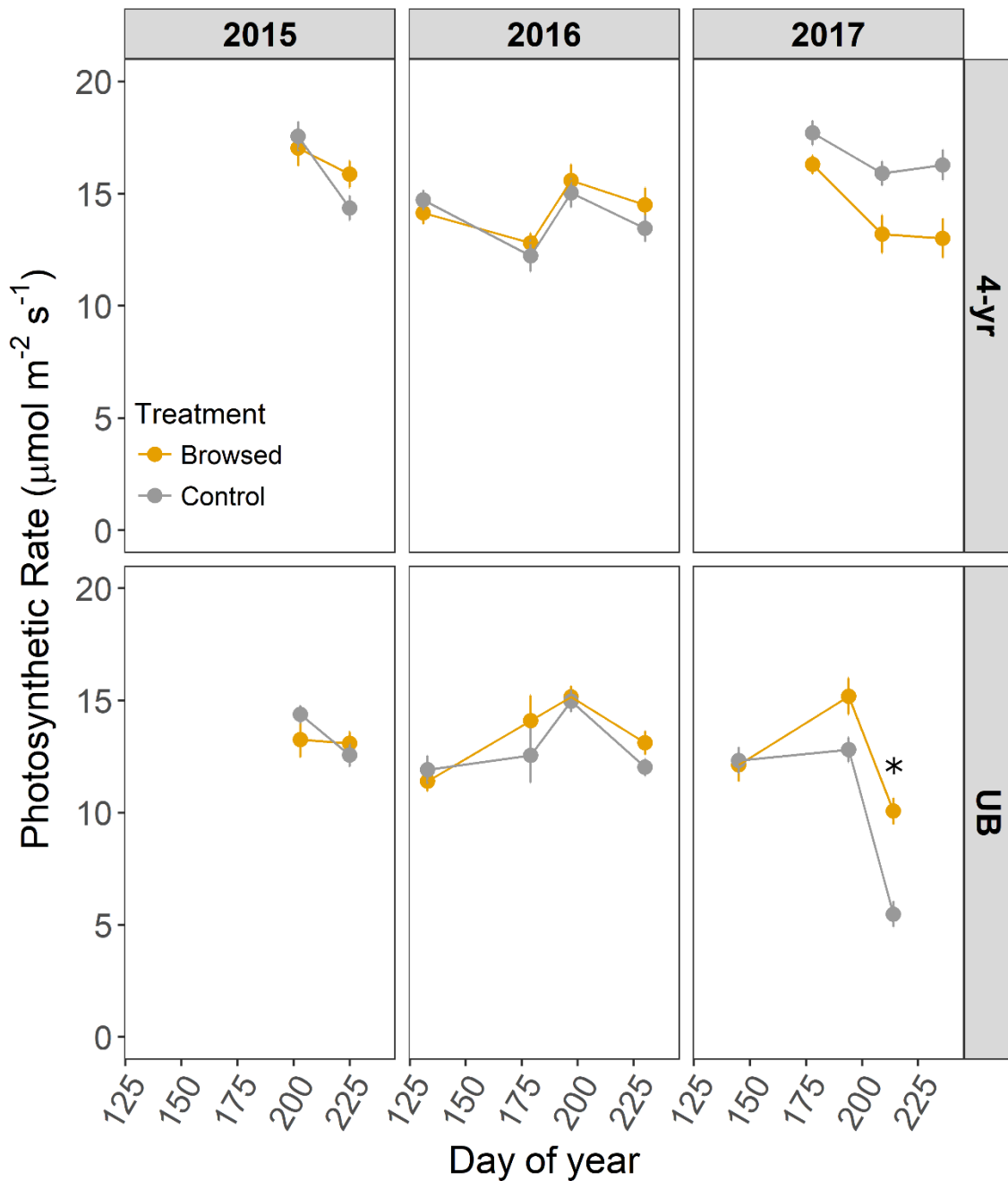
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**Figure 2.1** Effects of browsing on *Cornus drummondii* cover and grass cover in 4-yr burn and unburned (UB) locations from 2015 to 2017. In the 4-yr burned location a spring prescribed fire occurred in 2017 (red dashed line). Means are given with one SE around the mean as error bars. Significance is indicated by an asterisk ( $P < 0.05$ ).

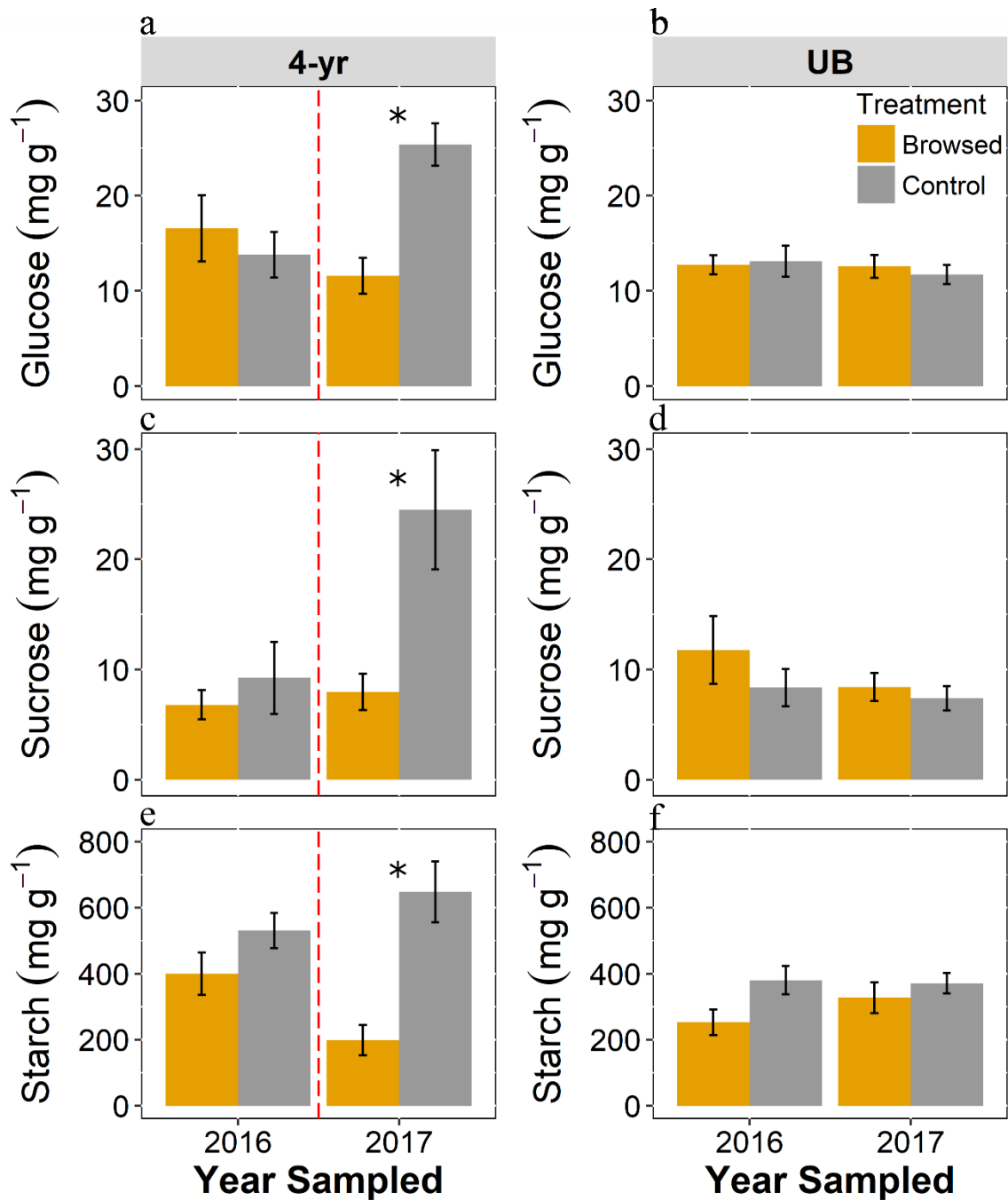


**Figure 2.2** Effects of browsing on *Cornus drummondii* ramet densities in 4-yr burned and unburned (UB) locations from 2015 to 2017. In the 4-yr burned location a spring prescribed fire occurred in 2017 (red dashed line). Means are given with one SE around the mean as error bars. Significance is indicated by an asterisk ( $P < 0.05$ ).



**Figure 2.3** Effects of browsing on the photosynthetic rates of *Cornus drummondii* in the 4-yr burned and unburned (UB) locations. Photosynthetic rates were measured during the growing season for 3 years (2015-2017). Means are given with one SE around the mean as error bars. Significance is indicated by an asterisk ( $P < 0.05$ ).





**Figure 2.4** Effects of browsing on *Cornus drummondii* root glucose, sucrose and starch in 4-yr burned and unburned (UB) locations in 2016 and 2017. In the 4-yr burned location a spring prescribed fire occurred in 2017 (red dashed line). Means are given with one SE around the mean as error bars. Significance is indicated by an asterisk ( $P < 0.05$ ).

# Chapter 3 - Leaf thermoregulation reduces thermal stress following browsing in a woody shrub species

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## Abstract

- Plants exist in a wide variety of environments, many with widely fluctuating air temperatures ( $T_{\text{air}}$ ). Plants are often considered poikilotherms, where leaf temperature ( $T_{\text{leaf}}$ ) matches ambient air temperatures. Photosynthesis is a temperature-sensitive biochemical process with temperature optima for most species. Daily or seasonal temperature fluctuations outside of these optima may reduce rates of photosynthesis and overall growth. The limited leaf homeothermy hypothesis (LLHH) posits that some species may regulate  $T_{\text{leaf}}$  lower than air temperatures to optimize leaf carbon gain.
- We tested for the LLHH in *Cornus drummondii*, a clonal resprouting shrub, through two growing seasons by observing  $T_{\text{leaf}}$  temperatures diurnally, across the growing season, and among different canopy locations. Additionally, we tested LLHH in responses to simulated repeated browsing and prescribed fire.
- $T_{\text{leaf}}$  were usually cooler or equal to air temperature during the warm daytime sampling periods, providing support for LLHH. As the growing seasons progressed  $T_{\text{leaf}}$  varied, weakly supporting LLHH. Within the shrubs,  $T_{\text{leaf}}$  did not vary with position within the canopy providing strong support for LLHH.

- *C. drummondii*  $T_{\text{leaf}}$  after the prescribed fire were lower than air temperature through the growing season, unlike the unburned *C. drummondii*  $T_{\text{leaf}}$  providing some support for the LLHH.  $T_{\text{leaf}}$  in browsed shrubs were similar to the  $T_{\text{leaf}}$  in unbrowsed shrubs.
- Increased transpiration rates are a mechanism responsible for LLHH in *C. drummondii*. Lower instantaneous WUE and seasonal patterns of leaf  $\delta^{13}\text{C}$  in browsed shrubs reflect the use of increased transpiration rates to alter the leaf latent energy budget. These results illustrate key mechanisms allowing this shrub species to persist within the temperate grassland and illustrate the potential impacts on the local hydrological cycle through increased transpirative demand.

**Key words:** leaf temperature, limited homeothermy hypothesis, thermoregulation, mesic grasslands, woody encroachment, *Cornus drummondii*, simulated browsing

## Introduction

The occurrence of leaf thermoregulation has been discussed since the 1920's and 1930's with a focus on identifying mechanisms that dictate how leaf temperatures are maintained either above, equal to, or below air temperature (Eaton and Belden 1929, Curtis 1936, Wallace and Clum 1938, Gates 1968, Michaletz et al. 2015). Typically, increased rates of transpiration are identified as the main physiological mechanism to change leaf temperature and vapor pressure deficit surrounding the leaf (Eaton and Belden 1929, Gates 1968). Other investigations concluded that the exchange of infrared radiation between the leaf and surrounding air within the boundary layer drives changes in leaf temperature (Curtis 1936, Wallace and Clum 1938). These early researchers led the way towards understanding environmental biophysics and physiological mechanisms that control leaf temperature. In 1988, Mahan and Upchurch proposed the "limited

leaf homeothermy hypothesis” which hypothesized that early morning leaf temperatures were controlled by the environment while leaf temperature at solar noon can be controlled by the plant to maximize energy gain (Mahan and Upchurch 1988, Upchurch and Mahan 1988). A key point from Mahan and Upchurch (1988) was that sufficient water availability was required to maintain leaf temperatures lower than air temperature. For this reason, reliable access to consistent sources of water are necessary for species that utilize limited homeothermy and active regulation of leaf transpiration as a mechanism to lower leaf temperatures.

Temperate grasslands are an ideal natural system to test the limited homeothermy hypothesis because these environments typically experience high variability in air temperature (Anderson 2006), soils with good water holding capacities (Zeglin et al. 2013), and bimodality of root systems among coexisting species results in water use from varying zones of the soil profile (Nippert and Holdo 2015). Woody plants in grasslands often have roots that reach deep soil layers and access the water from those layers (Nippert et al. 2013a, Holdo et al. 2017). In addition to climate variability, grasslands are also subject to frequent disturbance (Samson et al. 2004, Anderson 2006). Many woody plants in grasslands evolved to resprout after disturbances such as fire or herbivory, which allows them to continue to capture carbon and store it belowground in roots as starch (Bond and Midgley 2003a, Hoffmann et al. 2004, Zeppel et al. 2015). Fire and herbivory changes plant canopy architecture, aboveground biomass, and leaf area, all of which can affect leaf temperature (McNaughton 1983, Archibald and Bond 2003, Heisler et al. 2004, Johnston et al. 2007). If woody plants in grasslands are subject to these frequent disturbances and high air temperature, then the leaves of woody plant may follow the limited homeothermy hypothesis to maximize carbon gains.

To test this hypothesis, we used a simulated herbivory experiment in the tallgrass prairie of North America. Our study objective was to test the limited leaf homeothermy hypothesis in a clonal resprouting native shrub, *Cornus drummondii* C.A. Mey, that has increased in abundance in the central Great Plains of North America over the past 50 years. If support for LLHH exists within this clonal resprouting woody species in the tallgrass prairie, we will then identify the primary mechanisms allowing for leaf thermoregulation. Specifically, the following predictions were formulated as positive support for the limited leaf homeothermy hypothesis (hereafter LLHH): 1)  $T_{\text{leaf}}$  is equal to  $T_{\text{air}}$  during the night and early morning hours, and  $T_{\text{leaf}}$  is lower than  $T_{\text{air}}$  mid-day and in the afternoon. 2) Mid-day  $T_{\text{leaf}}$  will be more dissimilar to  $T_{\text{air}}$  as the growing season progresses. 3)  $T_{\text{leaf}}$  should not vary throughout the canopy (upper vs lower) or in a north to south gradient in the shrub even though  $T_{\text{air}}$  can vary around the periphery of shrubs. 4) Thermoregulation will be greater in burned areas compared to unburned, due to the warmer thermal environment in recently burned locations (and lower soil albedo). 5) Browsed shrubs will have lower  $T_{\text{leaf}}$  than unbrowsed shrubs because of an increased light environment, resulting in higher  $T_{\text{air}}$ .

## Methods

### Site description

Research was conducted in 2016 and 2017 at the Konza Prairie Biological Station (KPBS), a 3,487-ha native  $C_4$  grassland in northeastern Kansas, USA (39°05' N, 96°35' W). KPBS is located in the tallgrass prairie within the Flint Hills, one of the largest continuous stretches of unplowed prairies remaining in North America. The climate in the tallgrass prairie at KPBS is characteristic of mid-continental climates with high inter-annual variability in precipitation. Long-term mean annual precipitation for KPBS is 806.9 mm (1982-2017) with 79% occurring

during the growing season (April-September). KPBS is divided into watershed units, with varying spring fire frequencies (1, 2, 4, or 20 years) and season (spring, summer, fall, winter) prescribed to each watershed.

### **Study design**

This study measured responses by *Cornus drummondii*. *C. drummondii* is a C<sub>3</sub> clonal resprouting shrub that expands laterally through rhizomes. Ramets develop from buds on the rhizomes. Depending on the soil depth, these ramets can grow to be 1-2.5 m in height. Due to the height of the ramets, shrub islands reduce light to the understory which depresses herbaceous vegetation growth, alters the fire intensity, and creates a positive feedback that facilitates the shrub expansion across the landscape (Ratajczak et al. 2011).

In 2015, two watersheds at KPBS were chosen for implementation of a simulated browsing treatment. This included a watershed with a 4-yr spring fire frequency (watershed 4B, hereafter 4-yr) and an unburned watershed (20C, hereafter UB). Within each watershed, 20 shrub islands were randomly selected, stratified along a north to south gradient. Within each watershed, 10 shrub islands were randomly selected to receive the simulated browse treatment while the other 10 shrub islands were an 'unbrowsed' control. The simulated browse treatment consisted of removing 50% of new meristematic growth in the shrub islands through pinching or pulling off the plant tissue to mimic a large browsing mammal (Roberts et al. 2014). All plant tissues removed from the shrub islands were deposited outside of the study area. The browse treatments occurred monthly through the growing season (April – September) for multiple years.

In the spring of 2017 (13 April 2017) the 4-yr burn site had a prescribed fire. Our study area experienced a full headfire which top-killed all shrub island ramets in the browsed treatment

and top-killed most of the shrub islands in the control. The browse treatment resumed the following month (May 2017) when new shrub growth occurred, and leaves were fully expanded.

### **Leaf Temperature**

Leaf temperatures were measured at four times during a 24-hr period (i.e. 0600, 1200, 1800, 2400) using a MI-220 hand-held infrared radiometer with a 18° half-angle field of view (Apogee Instruments; Logan, UT, USA). We took leaf temperature at six spatial locations within each shrub island canopy to identify potential thermal variations resulting from diel patterns. The six spatial locations in each shrub island were split between upper and lower canopy positions, as well as northern-edge, center and southern-edge locations within the shrub (e.g. north-upper, north-lower, middle-upper, etc...). Measurements were not taken during rain events.

Additionally, if shrub island stature was less than 0.5 m then no lower canopy measures were made. Measurements were made multiple times throughout 2016 and 2017 growing seasons (May-August).

### **Leaf-level stomatal conductance and transpiration**

We measured stomatal conductance ( $g_s$ ) and transpiration rates ( $E$ ) using a LI-6400XT open gas exchange system with a red/blue light source and a CO<sub>2</sub> injector (LI-COR Inc., Lincoln, NE).

We set the light source within the leaf chamber to 2000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and the CO<sub>2</sub> reference level to 400  $\mu\text{mol mol}^{-1}$ . Measurements were made throughout the 2016 and 2017 growing seasons (May-August) from 1000-hr to 1500-hr on new fully expanded leaves. Two measurements were recorded as subsamples per shrub island, one at the periphery and the second at the center of the shrub island. Gas exchange measures of *C. drummondii* do not vary with spatial positions in the shrub (unpublished data), thus not as many measures were taken as with leaf temperature.

## **Stable Carbon Isotope Analysis**

New fully expanded leaf samples from within the shrub islands were collected and dried at 60°C in a drying oven for 48-hrs. The leaves were then ground using a Wig-L-Bug® ball mill (Dentsply Sirona; York, PA, USA). Isotopic analysis for  $\delta^{13}\text{C}$  was conducted using 2 mg of ground leaf tissue at the Stable Isotope Mass Spectrometry Lab (SIMSL) at KSU using a ThermoFinnigan Delta Plus mass spectrometer interfaced with a Carlo Erba elemental analyzer with a ConFlo II interface (Thermo Fisher Scientific Inc., Waltham, MA, USA). Isotopic ratios are expressed in per mil (‰) relative to VPDB (Vienna PDB). The long-term precision of this instrument using in-house quality-control standards is <0.07 ‰ for  $\delta^{13}\text{C}$ .

## **Leaf area**

Leaf area was measured by removing four mature leaves from each individual shrub island and placing them in a plastic bag with a moist paper towel. Each leaf was measured using the Leafscan iOS App (<http://www.leafscanapp.com>) to calculate two-dimensional leaf area.

## **Environmental Variables**

Environmental data were downloaded from an Ameriflux tower on Konza (Tower ID = KON) near our field sites (< 2.5 km from either watershed sampled). The data were parsed to correspond with the time points of the leaf temperature and soil moisture sampling. Air temperature was used with leaf temperature ( $T_{\text{leaf}} - T_{\text{air}}$ ) to test leaf thermoregulation and the limited homeothermy hypothesis.

## **Data Analysis**

We analyzed our data using linear mixed-effects repeated measure ANOVA models for all of our response variables ( $T_{\text{leaf}} - T_{\text{air}}$ ,  $E$ , WUE,  $\delta^{13}\text{C}$ ). The data met all assumptions for linear mixed-effects repeated measure ANOVA models. All statistical analyses were conducted and figures



were made in program R V3.4.3 using the packages “lme4” V1.1-19, “car” V3.0-2 and “ggplot2” V3.1.0 (Wickham 2009, Fox and Weisberg 2011, Bates et al. 2015a, R Core Team 2017). For each variable, we separated the data by year for analysis. Fixed effects were browse treatment (browsed or control) and day of year as an interaction for all explanatory variables with shrub island ID as our random effect. To assess the relationship between soil moisture and  $T_{\text{leaf}}-T_{\text{air}}$ , a simple linear regression was fit to all the data.

## Results

### Patterns of leaf temperature

Diurnal variations of  $T_{\text{leaf}}-T_{\text{air}}$  in *C. drummondii* shrub islands showed a general trend of  $T_{\text{leaf}}$  being lower than  $T_{\text{air}}$  during 0600-hr and 2400-hr (Figs. 3.1-3.4; not statistically significant).  $T_{\text{leaf}}$  were more variable during 1200-hr and 1800-hr.  $T_{\text{leaf}}$  were lower (Fig. 3.2), equal to (Figs. 3.1, 3.3, 3.4) and higher (Figs. 3.1, 3.3, 3.4) than the  $T_{\text{air}}$  (Tables 3.1-3.4).  $T_{\text{leaf}}$  in *C. drummondii* shrub islands also showed a general trend of being lower than  $T_{\text{air}}$  as the growing season progressed during both years (Figs. 3.2-3.4; not statistically significant). The  $T_{\text{leaf}}$  in the 4-yr burned treatment during 2016 were more variable from the beginning to the end the growing season.

$T_{\text{leaf}}$  within *C. drummondii* shrub islands varied minimally between the upper and lower canopy positions, regardless of watershed, day of year, or year (not statistically significant). Additionally,  $T_{\text{leaf}}$  between the north-side, center, and south-side of the shrub islands was not statistically significant with low variability (Figs. 3.1-3.4; Tables 3.1-3.4).

In 2016,  $T_{\text{leaf}}$  in the 4-yr burned treatment were lower than or equal to  $T_{\text{air}}$  during the 1200-hr and 1800-hr sampling periods for DOY 175 and 188 (not statistically significant). However, on DOY 202 and 216  $T_{\text{leaf}}$  were equal to or higher than  $T_{\text{air}}$  during those time periods

(Fig. 3.1; not statistically significant). After the prescribed fire in 2017,  $T_{\text{leaf}}$  were higher than or equal to  $T_{\text{air}}$  during 1200-hr and 1800-hr sampling periods for DOY 146 and 178.  $T_{\text{leaf}}$  was lower than or equal to  $T_{\text{air}}$  during DOY 209 and 235 for sampling periods 1200-hr and 1800-hr (Fig. 3.3; not statistically significant).

$T_{\text{leaf}} - T_{\text{air}}$  of browsed shrub islands were not statistically significantly different compared to the unbrowsed shrub islands. This pattern was uniform in both 4-yr and UB watersheds, across both years, and throughout the DOY sampled in each growing season (Figs. 3.1-3.4, Tables 3.1-3.4).

### **Leaf-level transpiration rates, WUE and $\delta^{13}\text{C}$**

In 2016, higher rates of leaf-level transpiration occurred in browsed *C. drummondii* shrub islands compared to unbrowsed shrub islands for both the 4-yr and UB through the whole growing season (Fig. 3.5a,d; 4-yr:  $P = 0.005$ , UB:  $P < 0.001$ ). Measurements conducted on DOY 179 exhibited the largest difference in transpiration between browsed and unbrowsed shrub islands for both sites. Transpiration rates were higher by 31% in the 4-yr ( $P = 0.029$ ; Table 3.5), and 57% increase in UB ( $P < 0.001$ ; Table 3.5) between browsed and unbrowsed shrub islands. Spring fire in the 4-yr altered transpiration rates for 2017. The new growth of stems and leaves in the 4-yr resulted in no differences in transpiration rates between browsed and unbrowsed shrub islands (Fig. 3.6a). However, browsed shrub islands in UB during the 2017 growing season had higher transpiration rates compared to the unbrowsed shrub islands (Fig. 3.6d;  $P < 0.001$ ). Measurements conducted on DOY 194 had 36% higher transpiration rates for browsed shrub islands compared to unbrowsed shrub islands ( $P = 0.001$ ; Table 3.6). Similarly, on DOY 214 browsed shrub islands had 144% higher transpiration rates compared to the unbrowsed shrub islands ( $P < 0.001$ ; Table 3.6).

Browsed shrub islands in 4-yr had lower leaf-level WUE through both growing seasons, but in 2017 after the prescribed fire it was lower than in 2016 (2016 = Fig. 3.5b,  $P = 0.075$ , Table 3.5; 2017 = Fig. 3.6b,  $P < 0.001$ , Table 3.6). Additionally, the browsed shrub islands in UB also had lower leaf-level WUE through both growing seasons (2016 = Fig. 3.5e,  $P < 0.001$ , Table 3.5; 2017 = Fig. 3.6e,  $P < 0.239$ , Table 3.6).

In 2016 both the 4-yr and UB browsed shrub islands had a decrease in  $\delta^{13}\text{C}$  leaf values from the start of the growing season to the end, while unbrowsed shrubs increased  $\delta^{13}\text{C}$  leaf values until the end of growing season (Fig. 3.5c,  $P < 0.001$ ; Fig. 3.5f,  $P < 0.001$ ; Table 3.7). In 2017 the 4-yr and UB browsed shrub islands decreased  $\delta^{13}\text{C}$  leaf values through the growing season while the unbrowsed shrub islands remained constant through the growing season (Fig. 3.6c,  $P = 0.033$ ; Fig. 3.6f,  $P < 0.001$ ; Table 3.8).

## Discussion

Plant leaves are often considered to be poikilothermic, unable to regulate temperature beyond the ambient environment (Curtis 1936, Campbell and Norman 1998). However, several studies have demonstrated that  $T_{\text{leaf}}$  can be cooler than the environment during the warmest parts of the day (Mahan and Upchurch 1988, Michaletz et al. 2015, Fauset et al. 2018). Regulation of  $T_{\text{leaf}}$  may provide important physiological benefits, by regulating thermal conditions around the leaf for a more conducive environment that results in higher rates of gas exchange. Here, we measured diel  $T_{\text{leaf}}$  in *C. drummondii* shrub islands in the tallgrass prairie to determine if and when the LLHH (Limited Leaf Homeothermy Hypothesis) is supported, and the likely mechanisms regulating this leaf process. Here, we show support for the LLHH through increased transpiration rates resulting in low instantaneous WUE, and low  $\delta^{13}\text{C}$  values.

The theory posits that when the LLHH is supported,  $T_{\text{leaf}}$  will be near ambient  $T_{\text{air}}$  in the night and early morning hours, but lower  $T_{\text{leaf}}$  than  $T_{\text{air}}$  during midday and afternoon (Upchurch and Mahan 1988, Yu et al. 2015, Mahan et al. 2016). Observations by Upchurch and Mahan (1988) on *Gossypium hirsutum* L. (cotton) found  $T_{\text{leaf}}$  lower than  $T_{\text{air}}$  from 1000-hrs to 1800-hrs which coincides with maximum daily global radiation. These results supported their LLHH hypothesis. Evidence for LLHH now exists for multiple species in several different ecosystem types. Yu et al (2015) observed *Artemisia ordosica* H. C. Fu. decreased leaf and stem temperatures during solar noon in a semiarid part of China. In the Brazilian Atlantic forest, Faust et al. (2018) reported that some tree species supported LLHH while others within the same communities did not regulate  $T_{\text{leaf}}$  (Fauset et al. 2018). In the study reported here,  $T_{\text{leaf}}$  within *C. drummondii* shrub islands were near  $T_{\text{air}}$  or lower during 0600-hr and 2400-hr, but during the 1200-hr and 1800-hr time periods  $T_{\text{leaf}}$  was often lower than  $T_{\text{air}}$ , providing support for the LLHH (Figs. 3.1-3.4). We also predicted that the difference between  $T_{\text{leaf}}$  and  $T_{\text{air}}$  would increase over the growing season because of seasonal increases in  $T_{\text{air}}$  at this location (Mahan et al. 2016).  $T_{\text{leaf}}$  in *C. drummondii* shrub islands were variable through the growing seasons, which weakly supported LLHH. To determine if *C. drummondii* strongly supports LLHH through the growing season more continuous measurements of  $T_{\text{leaf}}$  are needed in the shrub islands.

Microclimates around leaves within and around tree and shrub canopies can have large variations in  $T_{\text{air}}$  (Rey-Sánchez et al. 2016, Thompson et al. 2017). The variability of  $T_{\text{air}}$  with position in canopies requires regulation of  $T_{\text{leaf}}$  to maximize carbon gain. If LLHH is supported,  $T_{\text{leaf}}$  should be similar throughout the plant canopy regardless of spatial position (i.e. upper canopy vs lower) (Fauset et al. 2018).  $T_{\text{leaf}}$  temperatures within *C. drummondii* canopies were collected at the northern edge of the shrub, the center, and southern edge in both the upper and

lower canopy layers. At all these spatial locations within the shrub canopy  $T_{\text{leaf}}$  did not vary diurnally or during the growing season (Figs. 3.1-3.4). The low amount of variability in  $T_{\text{leaf}}$  among the spatial positions in the *C. drummondii* shrub islands may reflect key attributes of shrub clonality. Clonal plants have the ability to translocate water and nutrient resources to other ramets within the clone, which can help mitigate stress (Hartnett and Bazzaz 1983, Boggs 1997, Zhang et al. 2003, Luo et al. 2015). It is possible that this is a life history trait of clonal plants to deal with heterogeneous microclimates, but more research on other clonal plant species is needed for further understanding.

Disturbances such as fire or herbivory also change the microclimate surrounding individual plants through the removal of tissues and changes in plant architecture. Fire consumes plant material and produces darkened bare soil surfaces that increase near soil surface  $T_{\text{air}}$  because of a decreased albedo (Henderson 1982, Knapp 1984). With increased  $T_{\text{air}}$  around shrub islands,  $T_{\text{leaf}}$  should be cooler than  $T_{\text{air}}$  to support LLHH. In 2017, after the prescribed fire,  $T_{\text{leaf}}$  of the shrub islands in the 4-yr were equal to or lower than  $T_{\text{air}}$  (Fig. 3.3). In contrast to the post-fire growing season, data from 2016 showed  $T_{\text{leaf}}$  was higher than  $T_{\text{air}}$  (Fig. 3.1). The prescribed fire top-killed all of our shrub islands as new ramets and leaves were grown from stored carbon reserves in belowground root/rhizome tissues (Janicke and Fick 1998, Heisler et al. 2004). The flush of new growth from tissues would increase water uptake from functional rooting zones to support leaf-level gas exchange including stomatal conductance and photosynthesis (McCarron and Knapp 2003). The leaf-level gas exchange results shown here are similar to McCarron & Knapp (2003), with lower instantaneous WUE data and lower  $T_{\text{leaf}}$  than  $T_{\text{air}}$  in 2017 (Fig 3.6b). A previous study using *Andropogon gerardii*, a  $C_4$  grass, showed lower  $T_{\text{leaf}}$  in burned prairies than unburned prairies, but  $T_{\text{leaf}}$  was not lower than  $T_{\text{air}}$  within a given location (Knapp 1984). Lower

$T_{\text{leaf}}$  of both *C. drummondii* and *A. gerardii* after a fire may best be explained by increased leaf contact with wind, which would cause an increase in convective cooling on leaves (Schuepp 1993).

Herbivory, like fire, removes plant tissues and requires regrowth after the disturbance. Browsing is a specific form of herbivory that opens the canopy of woody plants through the removal of leaf and stem tissues. Once the canopy is open, increased solar radiation or light penetrates the canopy layers reaching the soil (Lett and Knapp 2005, Ratajczak et al. 2011). Increased solar radiation would increase  $T_{\text{air}}$  within shrub islands potentially elevating  $T_{\text{leaf}}$ . If  $T_{\text{leaf}}$  is lower or equal to  $T_{\text{air}}$  in browsed shrub islands but not unbrowsed shrub islands this would support LLHH. Browsed shrub island  $T_{\text{leaf}}$  did not vary from unbrowsed shrub island  $T_{\text{leaf}}$  diurnally, through the growing season, or spatially within shrub island canopies, providing strong support for the LLHH (Figs. 3.1-3.4). Determining the physiological mechanisms that underpin LLHH by browsed shrub islands is necessary to understand how  $T_{\text{leaf}}$  is regulated by these clonal shrubs.

### **Mechanisms for LLHH in browsed shrub island**

Herbivory (or browsing) of woody plants impacts many facets of plant growth such as canopy architecture via changes in apical dominance of tree saplings or shrubs (McNaughton 1983, Augustine and McNaughton 2004, Staver and Bond 2014), decreased leaf area with thicker leaves (McNaughton 1983, Johnston et al. 2007, Hartnett et al. 2012, Rhodes et al. 2017), and elevated photosynthetic and transpiration rates (McNaughton 1983, Johnston et al. 2007). Decreased stem length and leaf area along with increased transpiration rates increases the boundary layer resistance surrounding the leaves. Increased boundary layer resistance creates a microclimate that allows for maximized carbon assimilation for regrowth and storage of

photosynthates. The combination of compensatory growth with the limited homeothermy hypothesis best explains the results observed here. In our browsed shrub islands, we observed compensatory growth (Chapter 2), with a reduction of ~30% in leaf area for both sites, and increased transpiration rates (Figs 3.5a,d; 3.6a,d). These results in browsed shrub islands are similar to other studies measuring leaf physiological responses to browsing (Johnston et al. 2007, Pittermann et al. 2014). Peinetti *et al.* (2001) found that browsing of willows by elk did not result in differences in transpiration or WUE (A/E). However, elk densities were not high in locations browsed during the growing season suggesting that low or moderate browsing pressure may not induce changes in WUE (Peinetti et al. 2001). Unlike Peinetti et al. (2001) we observed decreased instantaneous WUE and smaller  $\delta^{13}\text{C}$  values in the browsed shrubs for both sites regardless of year (Figs 3.5b,c,e,f; 3.6b,c,e,f), signifying increased stomatal conductance allowing increased rates of  $\text{CO}_2$  and water vapor exchange. These data in combination with  $T_{\text{leaf}}$  data describes a mechanism whereby *C. drummondii* that has been previously browsed/defoliated compensates for the reduced leaf area by increasing leaf transpiration to maintain a relatively constant  $T_{\text{leaf}}$ .

Overall, these results illustrate key mechanisms allowing *C. drummondii* to persist within the temperate grassland and highlight the potential impacts on the local hydrological cycle through increased transpirative demand. High leaf-level transpiration rates regulating  $T_{\text{leaf}}$  of *C. drummondii* allows the shrub to maintain higher photosynthetic rates under stressful conditions like browsing, fire or drought. Increased rates of transpiration through the growing season requires access to consistent water sources, and in the tallgrass prairie that is located in the deep soil layers (Macpherson 1996, Nippert and Knapp 2007). *C. drummondii* relies on deep soil moisture which provides consistent water for higher transpiration rates even under drought

conditions (Ratajezak et al. 2011, Logan and Brunsell 2015, Muench et al. 2016). These traits combined with the ability to regulate  $T_{\text{leaf}}$  makes *C. drummondii* very resilient to disturbances (herbivory and fire) and climate variability (drought, high air temperature), further perpetuating its persistence within the tallgrass prairie.

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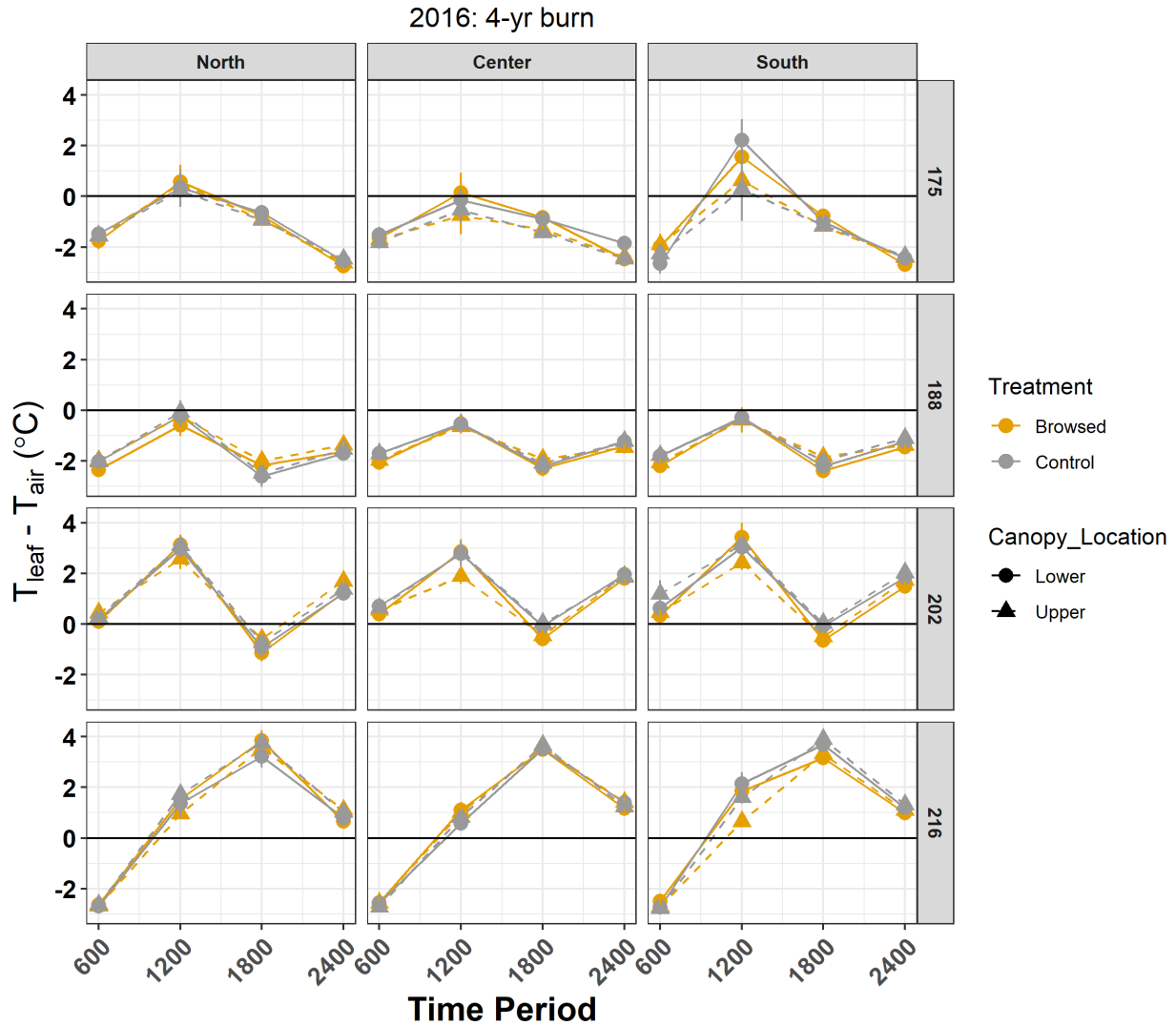
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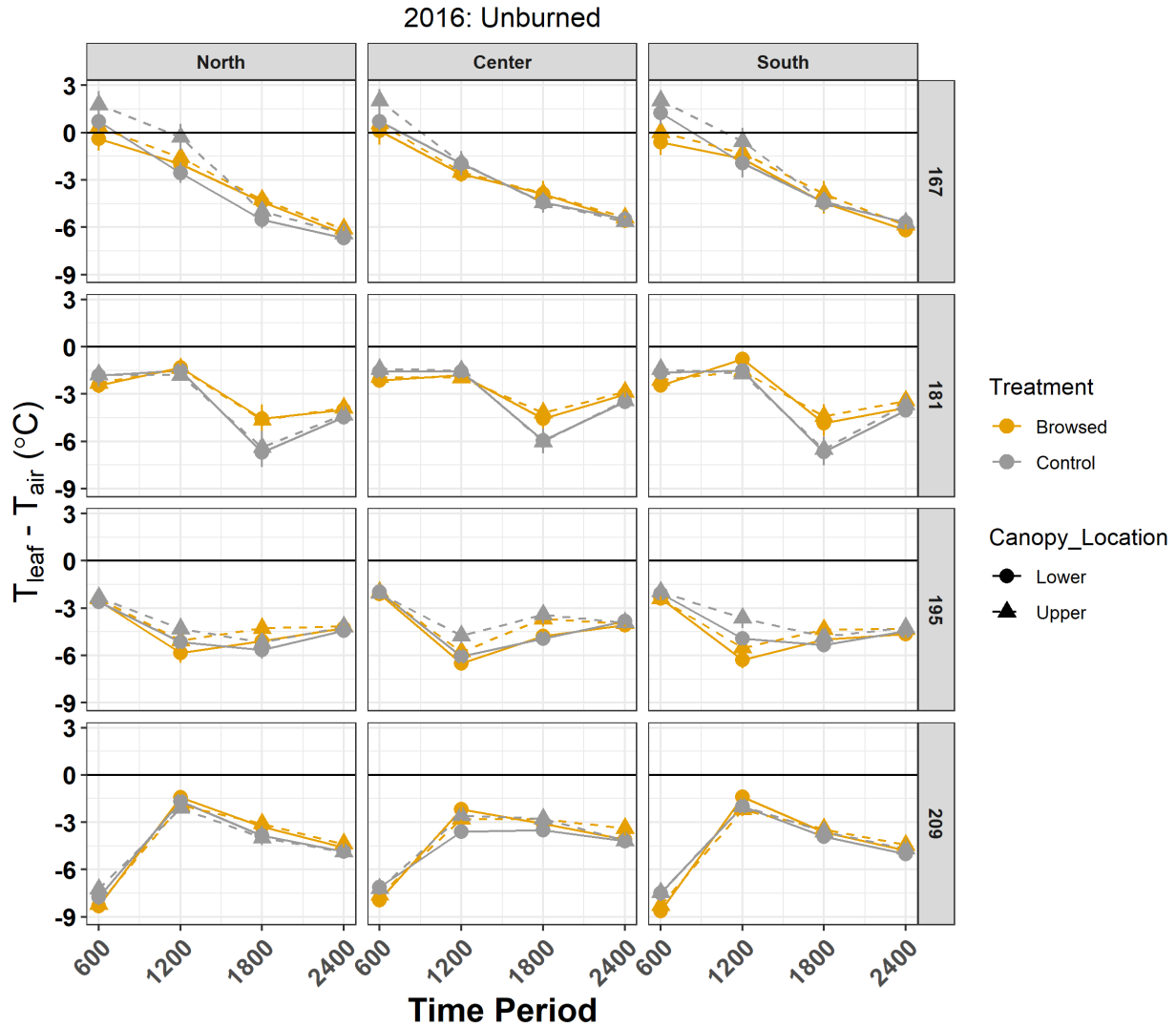
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**Figure 3.1.** 4-yr  $T_{\text{leaf}}-T_{\text{air}}$  (mean  $\pm$  1 SE) of *C. drummondii* shrub islands through the diel period in 2016. Circle and triangle icons represent  $T_{\text{leaf}}-T_{\text{air}}$  in lower and upper canopy position (respectively) in the shrub islands. Yellow symbols are for the browsed shrub islands, while the grey symbols are the control or unbrowsed shrub islands. The vertical columns are the cardinal direction sampling location within the shrub islands, and the horizontal rows are the DOY. Significance levels were determined by an  $\alpha = 0.05$ , all significant results ( $P < 0.05$ ) have an ‘\*’.





**Figure 3.2 UB  $T_{\text{leaf}}-T_{\text{air}}$  (mean  $\pm$  1 SE) of *C. drummondii* shrub islands through the diel period in 2016. Circle and triangle icons represent  $T_{\text{leaf}}-T_{\text{air}}$  in lower and upper canopy position (respectively) in the shrub islands. Yellow symbols are for the browsed shrub islands, while the grey symbols are the control or unbrowsed shrub islands. The vertical columns are the cardinal direction sampling location within the shrub islands, and the horizontal rows are the DOY. Significance levels were determined by an  $\alpha = 0.05$ , all significant results ( $P < 0.05$ ) have an ‘\*’.**

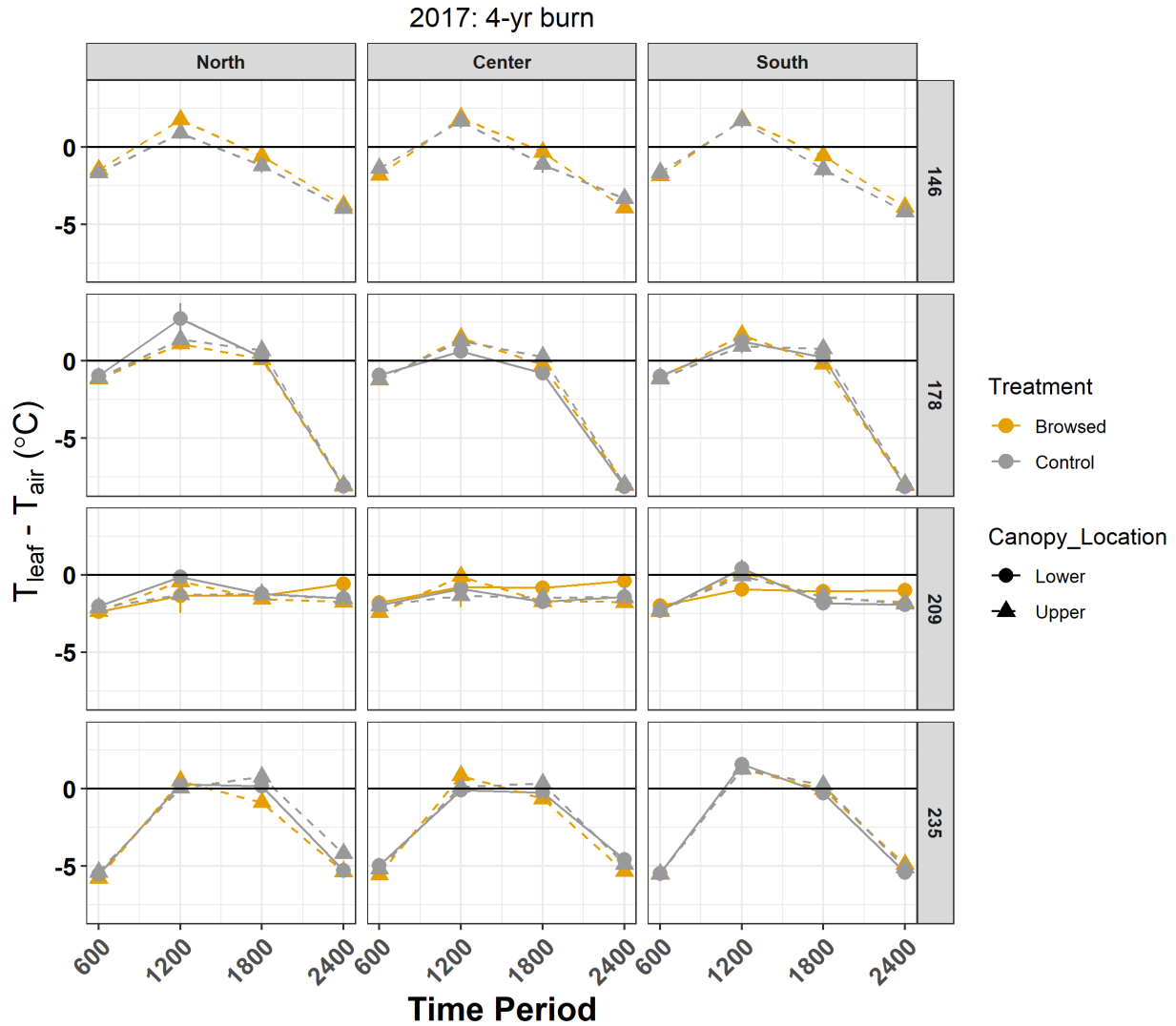
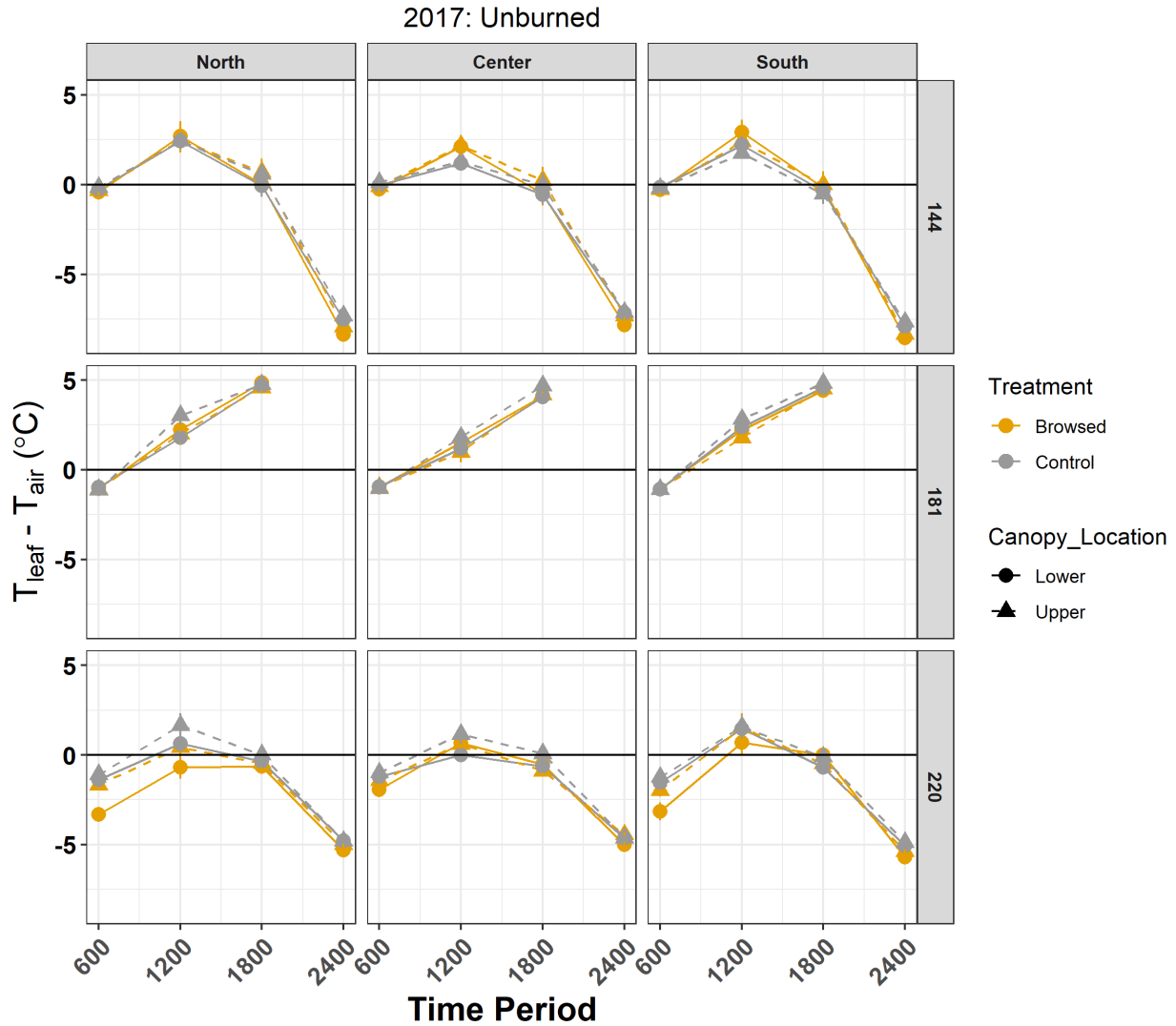
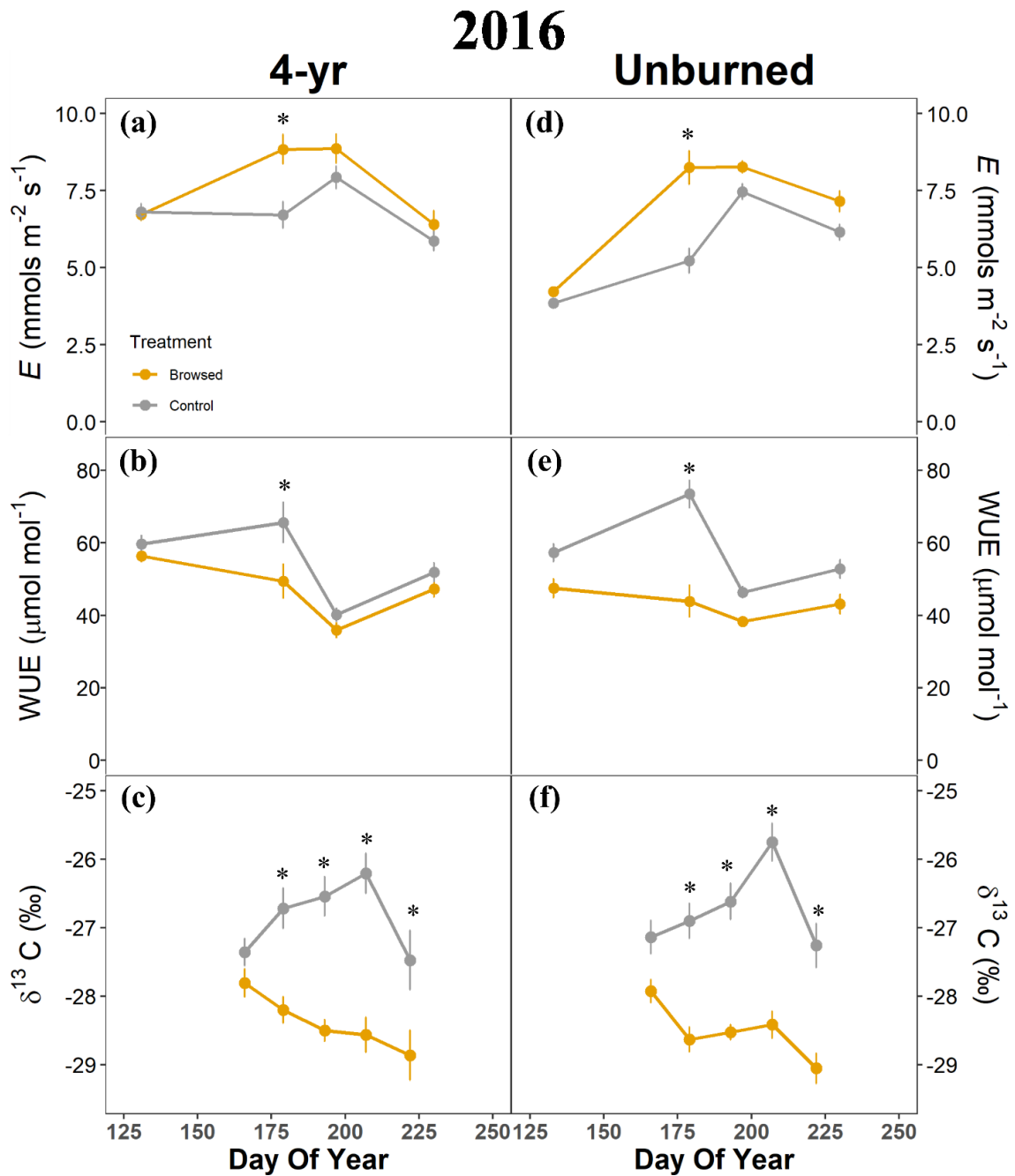


Figure 3.3 4-yr  $T_{\text{leaf}} - T_{\text{air}}$  (mean  $\pm$  1 SE) of *C. drummondii* shrub islands through the diel period in 2017. Circle and triangle icons represent  $T_{\text{leaf}} - T_{\text{air}}$  in lower and upper canopy position (respectively) in the shrub islands. Yellow symbols are for the browsed shrub islands, while the grey symbols are the control or unbrowsed shrub islands. The vertical columns are the cardinal direction sampling location within the shrub islands, and the horizontal rows are the DOY. Significance levels were determined by an  $\alpha = 0.05$ , all significant results ( $P < 0.05$ ) have an “\*”.



**Figure 3.4 UB  $T_{\text{leaf}} - T_{\text{air}}$  (mean  $\pm$  1 SE) of *C. drummondii* shrub islands through the diel period in 2017. Circle and triangle icons represent  $T_{\text{leaf}} - T_{\text{air}}$  in lower and upper canopy position (respectively) in the shrub islands. Yellow symbols are for the browsed shrub islands, while the grey symbols are the control or unbrowsed shrub islands. The vertical columns are the cardinal direction sampling location within the shrub islands, and the horizontal rows are the DOY. Significance levels were determined by an  $\alpha = 0.05$ , all significant results ( $P < 0.05$ ) have an “\*”.**



**Figure 3.5** 4-yr and UB transpiration rates, intrinsic WUE, and  $\delta^{13}\text{C}$  values (mean  $\pm$  1 SE) of *C. drummondii* shrub islands through the 2016 growing season. Yellow symbols are for the browsed shrub islands, while the grey symbols are the control or unbrowsed shrub islands. Significance levels were determined by an  $\alpha = 0.05$ , all significant results ( $P < 0.05$ ) have an “\*”.

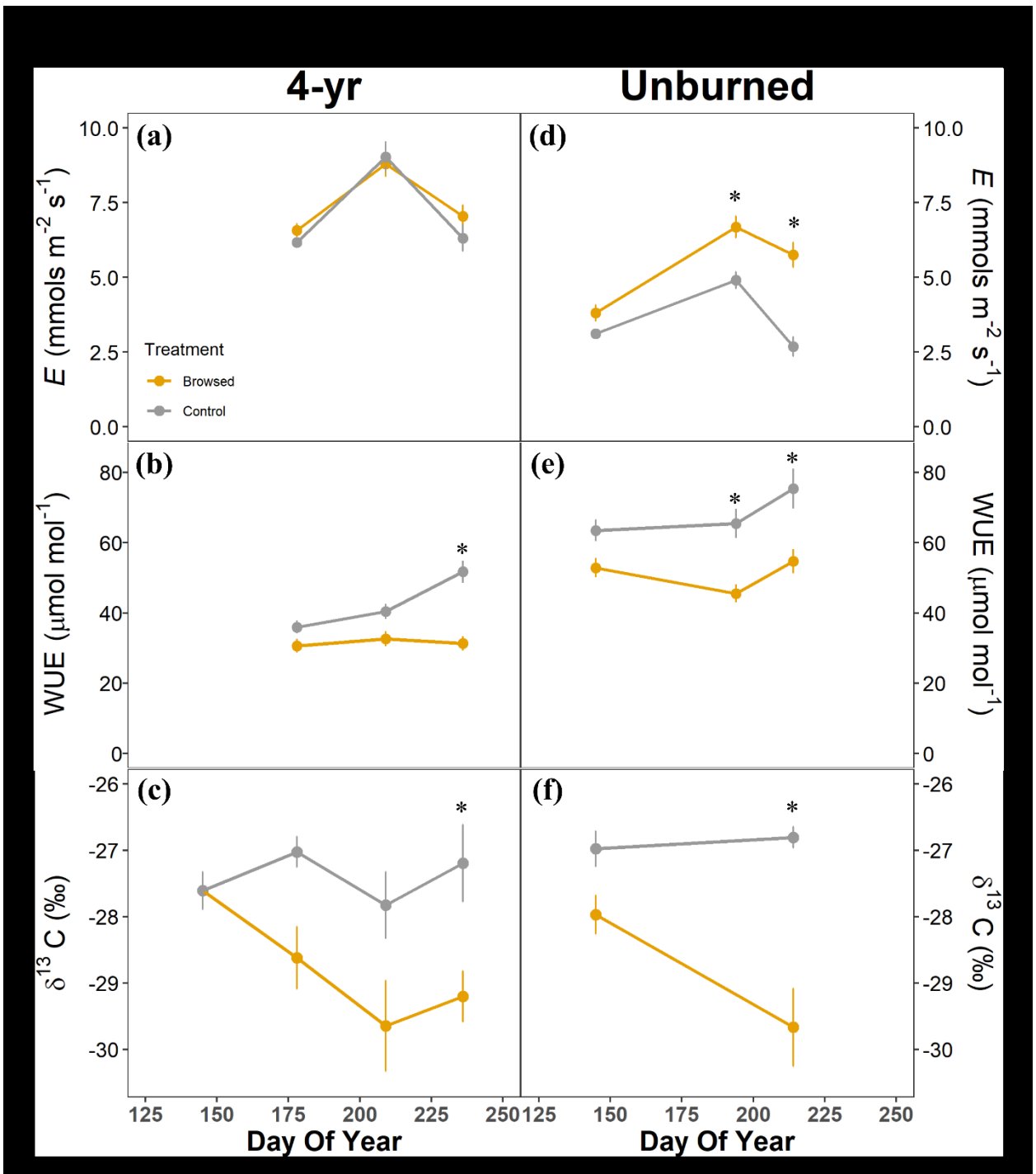


Figure 3.6 4-yr and UB transpiration rates, intrinsic WUE, and  $\delta^{13}\text{C}$  values (mean  $\pm$  1 SE) of *C. drummondii* shrub islands through the 2017 growing season. Yellow symbols are for the browsed shrub islands, while the grey symbols are the control or unbrowsed shrub islands. Significance levels were determined by an  $\alpha = 0.05$ , all significant results ( $P < 0.05$ ) have an “\*”.

**Table 3.1 Statistical results of  $T_{\text{leaf}}-T_{\text{air}}$  analyses. Shown are Chi square, degrees of freedom and P-values for  $T_{\text{leaf}}-T_{\text{air}}$  measured in 2016 at the 4-yr C. *drummondii* shrub islands. Factors within the analysis include browse treatment (Treatment), diel time period (Time\_Period), cardinal direction gradient (Sample\_Location), upper or lower canopy position (Canopy\_Locations), and Julian day of year sampled (DOY) and their interactions. Significance at the  $\alpha = 0.05$  is indicated with asterisks.**

<b>4-yr burn:2016</b>			
<u>Response: Leaf.air</u>	<u>Chisq</u>	<u>Df</u>	<u>Pr(&gt;Chisq)</u>
(Intercept)	5.528	1	0.019 *
Treatment	0.740	1	0.390
Time_Period	52.528	1	< 0.001 ***
Sample_Location	0.052	2	0.974
Canopy_Location	0.541	1	0.462
DOY	65.374	3	< 0.001 ***
Treatment:Time_Period	1.355	1	0.244
Treatment:Sample_Location	0.168	2	0.920
Time_Period:Sample_Location	0.302	2	0.860
Treatment:Canopy_Location	0.668	1	0.414
Time_Period:Canopy_Location	0.164	1	0.685
Sample_Location:Canopy_Location	0.054	2	0.973
Treatment:DOY	0.157	3	0.984
Time_Period:DOY	56.191	3	< 0.001 ***
Sample_Location:DOY	0.243	6	1.000
Canopy_Location:DOY	0.544	3	0.909
Treatment:Time_Period:Sample_Location	0.110	2	0.946
Treatment:Time_Period:Canopy_Location	0.199	1	0.656
Treatment:Sample_Location:Canopy_Location	0.040	2	0.980
Time_Period:Sample_Location:Canopy_Location	0.028	2	0.986
Treatment:Time_Period:DOY	0.538	3	0.911
Treatment:Sample_Location:DOY	0.392	6	0.999
Time_Period:Sample_Location:DOY	0.291	6	1.000
Treatment:Canopy_Location:DOY	0.523	3	0.914
Time_Period:Canopy_Location:DOY	0.233	3	0.972
Sample_Location:Canopy_Location:DOY	0.106	6	1.000
Treatment:Time_Period:Sample_Location:Canopy_Location	0.013	2	0.993
Treatment:Time_Period:Sample_Location:DOY	0.174	6	1.000
Treatment:Time_Period:Canopy_Location:DOY	0.271	3	0.965
Treatment:Sample_Location:Canopy_Location:DOY	0.201	6	1.000
Time_Period:Sample_Location:Canopy_Location:DOY	0.102	6	1.000
Treatment:Time_Period:Sample_Location:Canopy_Location:DO	0.209	6	1.000

Analysis of Deviance Table (Type III Wald chisquare tests)  
 Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

**Table 3.2 Statistical results of  $T_{\text{leaf}}-T_{\text{air}}$  analyses. Shown are Chi square, degrees of freedom and P-values for  $T_{\text{leaf}}-T_{\text{air}}$  measured in 2016 at the UB *C. drummondii* shrub islands. Factors within the analysis include browse treatment (Treatment), diel time period (Time\_Period), cardinal direction gradient (Sample\_Location), upper or lower canopy position (Canopy\_Location), and Julian day of year sampled (DOY) and their interactions. Significance at the  $\alpha = 0.05$  is indicated with asterisks.**

**Unburned: 2016**

<u>Response: Leaf.air</u>	<u>Chisq</u>	<u>Df</u>	<u>Pr(&gt;Chisq)</u>
(Intercept)	5.528	1	0.019 *
Treatment	0.740	1	0.390
Time_Period	52.528	1	< 0.001 ***
Sample_Location	0.052	2	0.974
Canopy_Location	0.541	1	0.462
DOY	65.374	3	< 0.001 ***
Treatment:Time_Period	1.355	1	0.244
Treatment:Sample_Location	0.168	2	0.920
Time_Period:Sample_Location	0.302	2	0.860
Treatment:Canopy_Location	0.668	1	0.414
Time_Period:Canopy_Location	0.164	1	0.685
Sample_Location:Canopy_Location	0.054	2	0.973
Treatment:DOY	0.157	3	0.984
Time_Period:DOY	56.191	3	< 0.001 ***
Sample_Location:DOY	0.243	6	1.000
Canopy_Location:DOY	0.544	3	0.909
Treatment:Time_Period:Sample_Location	0.110	2	0.946
Treatment:Time_Period:Canopy_Location	0.199	1	0.656
Treatment:Sample_Location:Canopy_Location	0.040	2	0.980
Time_Period:Sample_Location:Canopy_Location	0.028	2	0.986
Treatment:Time_Period:DOY	0.538	3	0.911
Treatment:Sample_Location:DOY	0.392	6	0.999
Time_Period:Sample_Location:DOY	0.291	6	1.000
Treatment:Canopy_Location:DOY	0.523	3	0.914
Time_Period:Canopy_Location:DOY	0.233	3	0.972
Sample_Location:Canopy_Location:DOY	0.106	6	1.000
Treatment:Time_Period:Sample_Location:Canopy_Location	0.013	2	0.993
Treatment:Time_Period:Sample_Location:DOY	0.174	6	1.000
Treatment:Time_Period:Canopy_Location:DOY	0.271	3	0.965
Treatment:Sample_Location:Canopy_Location:DOY	0.201	6	1.000
Time_Period:Sample_Location:Canopy_Location:DOY	0.102	6	1.000
Treatment:Time_Period:Sample_Location:Canopy_Location:DO	0.209	6	1.000

Analysis of Deviance Table (Type III Wald chisquare tests)  
 Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

**Table 3.3 Statistical results of  $T_{\text{leaf}}-T_{\text{air}}$  analyses. Shown are Chi square, degrees of freedom and P-values for  $T_{\text{leaf}}-T_{\text{air}}$  measured in 2017 at the 4-yr *C. drummondii* shrub islands. Factors within the analysis include browse treatment (Treatment), diel time period (Time\_Period), cardinal direction gradient (Sample\_Location), upper or lower canopy position (Canopy\_Locations), and Julian day of year sampled (DOY) and their interactions. Significance at the  $\alpha = 0.05$  is indicated with asterisks.**

<b>4-yr burn:2017</b>				
<u>Response: Leaf.air</u>		<u>Chisq</u>	<u>Df</u>	<u>Pr(&gt;Chisq)</u>
(Intercept)		0.022	1	0.882
Treatment		0.005	1	0.945
Time_Period		3.773	1	0.052
Sample_Location		0.325	2	0.850
Canopy_Location		0.009	1	0.926
DOY	1	8.416	3	< 0.001 ***
Treatment:Time_Period		0.002	1	0.970
Treatment:Sample_Location		0.198	2	0.906
Time_Period:Sample_Location		0.127	2	0.938
Treatment:Canopy_Location		0.044	1	0.834
Time_Period:Canopy_Location		0.006	1	0.939
Sample_Location:Canopy_Location		0.335	2	0.846
Treatment:DOY		0.432	3	0.933
Time_Period:DOY		0.863	3	< 0.001 ***
Sample_Location:DOY		0.345	6	0.999
Canopy_Location:DOY		0.715	3	0.870
Treatment:Time_Period:Sample_Location		0.188	2	0.910
Treatment:Time_Period:Canopy_Location		0.013	1	0.909
Treatment:Sample_Location:Canopy_Location		0.138	2	0.934
Time_Period:Sample_Location:Canopy_Location		0.104	2	0.950
Treatment:Time_Period:DOY		0.347	3	0.951
Treatment:Sample_Location:DOY		0.207	6	1.000
Time_Period:Sample_Location:DOY		0.287	6	1.000
Treatment:Canopy_Location:DOY		0.545	3	0.909
Time_Period:Canopy_Location:DOY		0.421	3	0.936
Sample_Location:Canopy_Location:DOY		0.429	6	0.999
Treatment:Time_Period:Sample_Location:Canopy_Location		0.158	2	0.924
Treatment:Time_Period:Sample_Location:DOY		0.069	6	1.000
Treatment:Time_Period:Canopy_Location:DOY		0.193	3	0.979
Treatment:Sample_Location:Canopy_Location:DOY		0.418	6	0.999
Time_Period:Sample_Location:Canopy_Location:DOY		0.139	6	1.000
Treatment:Time_Period:Sample_Location:Canopy_Location:DOY		0.191	6	1.000

Analysis of Deviance Table (Type III Wald chisquare tests)  
 Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1



**Table 3.4 Statistical results of  $T_{\text{leaf}}-T_{\text{air}}$  analyses. Shown are Chi square, degrees of freedom and P-values for  $T_{\text{leaf}}-T_{\text{air}}$  measured in 2017 at the UB *C. drummondii* shrub islands. Factors within the analysis include browse treatment (Treatment), diel time period (Time\_Period), cardinal direction gradient (Sample\_Location), upper or lower canopy position (Canopy\_Location), and Julian day of year sampled (DOY) and their interactions. Significance at the  $\alpha = 0.05$  is indicated with asterisks.**

<b>Unburned: 2017</b>			
<b>Response: Leaf.air</b>	<b>Chisq</b>	<b>Df</b>	<b>Pr(&gt;Chisq)</b>
(Intercept)	33.165	1	< 0.001 ***
Treatment	0.090	1	0.765
Time_Period	67.620	1	< 0.001 ***
Sample_Location	0.358	2	0.836
Canopy_Location	0.034	1	0.854
DOY	43.382	2	< 0.001 ***
Treatment:Time_Period	0.221	1	0.638
Treatment:Sample_Location	0.013	2	0.994
Time_Period:Sample_Location	0.324	2	0.850
Treatment:Canopy_Location	0.017	1	0.896
Time_Period:Canopy_Location	0.175	1	0.676
Sample_Location:Canopy_Location	0.023	2	0.989
Treatment:DOY	1.574	2	0.455
Time_Period:DOY	87.485	2	< 0.001 ***
Sample_Location:DOY	1.195	4	0.879
Canopy_Location:DOY	1.086	2	0.581
Treatment:Time_Period:Sample_Location	0.001	2	1.000
Treatment:Time_Period:Canopy_Location	0.021	1	0.885
Treatment:Sample_Location:Canopy_Location	0.021	2	0.990
Time_Period:Sample_Location:Canopy_Location	0.011	2	0.995
Treatment:Time_Period:DOY	0.972	2	0.615
Treatment:Sample_Location:DOY	0.588	4	0.964
Time_Period:Sample_Location:DOY	0.884	4	0.927
Treatment:Canopy_Location:DOY	0.256	2	0.880
Time_Period:Canopy_Location:DOY	0.818	2	0.665
Sample_Location:Canopy_Location:DOY	0.528	4	0.971
Treatment:Time_Period:Sample_Location:Canopy_Location	0.032	2	0.984
Treatment:Time_Period:Sample_Location:DOY	0.342	4	0.987
Treatment:Time_Period:Canopy_Location:DOY	0.201	2	0.905
Treatment:Sample_Location:Canopy_Location:DOY	0.347	4	0.987
Time_Period:Sample_Location:Canopy_Location:DOY	0.301	4	0.990
Treatment:Time_Period:Sample_Location:Canopy_Location:DOY	0.211	4	0.995

Analysis of Deviance Table (Type III Wald chisquare tests)  
 Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

**Table 3.5 Statistical results of  $g_s$ ,  $E$  and WUE analyses for 2016. Shown are the mean and standard error values of each measurement type ( $g_s$ ,  $E$ , WUE) within watershed (4-yr, UB), for each browse treatment (Browsed, Control), and during which day of year. Significance at the  $\alpha = 0.05$  is indicated as being bolded.**

		2016					
Fire frequency		Browsed			Control		
		$g_s$ ( $\text{mol m}^{-2} \text{s}^{-1}$ )	$E$ ( $\text{mmol m}^{-2} \text{s}^{-1}$ )	WUE ( $\mu\text{mol mol}^{-1}$ )	$g_s$ ( $\text{mol m}^{-2} \text{s}^{-1}$ )	$E$ ( $\text{mmol m}^{-2} \text{s}^{-1}$ )	WUE ( $\mu\text{mol mol}^{-1}$ )
<b>4-yr</b>	131	0.25 ± 0.01	6.73 ± 0.20	56.42 ± 1.65	0.25 ± 0.01	6.81 ± 0.25	59.68 ± 2.19
	179	0.30 ± 0.03	<b>8.84 ± 0.48</b>	<b>49.37 ± 4.62</b>	0.21 ± 0.02	<b>6.71 ± 0.44</b>	<b>65.62 ± 5.46</b>
	197	0.46 ± 0.03	8.87 ± 0.48	35.88 ± 1.93	0.38 ± 0.01	7.93 ± 0.37	40.15 ± 1.72
	230	0.33 ± 0.03	6.40 ± 0.45	47.31 ± 2.26	0.28 ± 0.03	5.86 ± 0.32	51.89 ± 2.60
<b>Unburned</b>	133	0.25 ± 0.02	4.22 ± 0.15	47.45 ± 2.54	0.21 ± 0.01	3.85 ± 0.17	57.27 ± 2.38
	179	<b>0.37 ± 0.03</b>	<b>8.25 ± 0.55</b>	<b>43.88 ± 4.32</b>	<b>0.18 ± 0.02</b>	<b>5.23 ± 0.41</b>	<b>73.47 ± 3.71</b>
	197	0.40 ± 0.01	8.27 ± 0.19	38.33 ± 1.32	0.33 ± 0.02	7.47 ± 0.26	46.38 ± 1.48
	230	0.33 ± 0.02	7.15 ± 0.34	43.11 ± 2.68	0.24 ± 0.02	6.15 ± 0.26	52.77 ± 2.56

Bolded numbers indicates significance ( $P \leq 0.05$ )

**Table 3.6 Statistical results of  $g_s$ ,  $E$  and WUE analyses for 2017. Shown are the mean and standard error values of each measurement type ( $g_s$ ,  $E$ , WUE) within watershed (4-yr, UB), for each browse treatment (Browsed, Control), and during which day of year. Significance at the  $\alpha = 0.05$  is indicated as being bolded.**

2017							
Fire frequency		Browsed			Control		
		$g_s$ ( $\text{mol m}^{-2} \text{s}^{-1}$ )	$E$ ( $\text{mmol m}^{-2} \text{s}^{-1}$ )	WUE ( $\mu\text{mol mol}^{-1}$ )	$g_s$ ( $\text{mol m}^{-2} \text{s}^{-1}$ )	$E$ ( $\text{mmol m}^{-2} \text{s}^{-1}$ )	WUE ( $\mu\text{mol mol}^{-1}$ )
<b>4-yr</b>	178	0.56 ± 0.03	6.57 ± 0.22	30.68 ± 1.70	0.51 ± 0.03	6.18 ± 0.17	35.97 ± 1.60
	209	0.41 ± 0.03	8.80 ± 0.43	32.63 ± 1.92	0.41 ± 0.02	9.04 ± 0.50	40.42 ± 1.88
	236	0.43 ± 0.03	7.05 ± 0.36	<b>31.32 ± 1.75</b>	0.33 ± 0.02	6.32 ± 0.43	<b>51.73 ± 2.87</b>
<b>Unburned</b>	145	0.24 ± 0.02	3.80 ± 0.26	52.85 ± 2.52	0.20 ± 0.01	3.12 ± 0.14	63.47 ± 2.89
	194	<b>0.35 ± 0.03</b>	<b>6.69 ± 0.36</b>	<b>45.52 ± 2.31</b>	<b>0.22 ± 0.02</b>	<b>4.91 ± 0.28</b>	<b>65.45 ± 3.94</b>
	214	<b>0.20 ± 0.02</b>	<b>5.76 ± 0.42</b>	<b>54.71 ± 3.17</b>	<b>0.08 ± 0.01</b>	<b>2.68 ± 0.31</b>	<b>75.35 ± 5.41</b>

Bolded numbers indicates significance ( $P \leq 0.05$ )

**Table 3.7 Statistical results of  $\delta^{13}\text{C}$  analyses for 2016. Shown are the mean and standard error values of each  $\delta^{13}\text{C}$  value within each watershed (4-yr, UB), for browse treatment (Browsed, Control), and during which day of year. Significance at the  $\alpha = 0.05$  is indicated as being bolded.**

		2016	
Fire frequency	DOY	Browsed	Control
4-yr	166	-27.81 ± 0.21	-27.36 ± 0.20
	179	<b>-28.20 ± 0.19</b>	<b>-26.72 ± 0.30</b>
	193	<b>-28.50 ± 0.16</b>	<b>-26.54 ± 0.29</b>
	207	<b>-28.57 ± 0.26</b>	<b>-26.21 ± 0.29</b>
	222	<b>-28.86 ± 0.37</b>	<b>-27.48 ± 0.44</b>
Unburned	166	-27.93 ± 0.17	-27.14 ± 0.24
	179	<b>-28.63 ± 0.18</b>	<b>-26.90 ± 0.26</b>
	193	<b>-28.53 ± 0.11</b>	<b>-26.62 ± 0.27</b>
	207	<b>-28.42 ± 0.20</b>	<b>-25.75 ± 0.28</b>
	222	<b>-29.06 ± 0.22</b>	<b>-27.26 ± 0.32</b>

Bolded values indicate significance ( $P \leq 0.05$ )

**Table 3.8 Statistical results of  $\delta^{13}\text{C}$  analyses for 2017. Shown are the mean and standard error values of each  $\delta^{13}\text{C}$  value within each watershed (4-yr, UB), for browse treatment (Browsed, Control), and during which day of year. Significance at the  $\alpha = 0.05$  is indicated as being bolded.**

<b>2017</b>			
<b>Fire frequency</b>	<b>DOY</b>	<b>Browsed</b>	<b>Control</b>
4-yr	145	-27.61 ± 0.24	-27.61 ± 0.28
	178	-28.62 ± 0.47	-27.02 ± 0.23
	209	-29.65 ± 0.68	-27.83 ± 0.50
	236	<b>-29.20 ± 0.38</b>	<b>-27.19 ± 0.58</b>
Unburned	145	-27.97 ± 0.29	-26.98 ± 0.27
	214	<b>-29.67 ± 0.59</b>	<b>-26.81 ± 0.16</b>

Bolded values indicate significance ( $P \leq 0.05$ )

## Chapter 4 - Elevated CO<sub>2</sub> ameliorates effects of water stress on rangeland woody encroaching species

### Abstract

Many rangelands across the world are experiencing increases in woody plant cover and abundance, a process called woody plant encroachment. Woody plant encroachment has been occurring worldwide since the late-1800's which coincides temporally with the revolution and the advent of rising carbon dioxide concentrations ([CO<sub>2</sub>]) in the Earth's atmosphere. This correlation of rising [CO<sub>2</sub>] and woody plant encroachment has led to the hypothesis that C<sub>3</sub> woody plants are expanding as a byproduct of increased CO<sub>2</sub> fertilization. Current projections for North American rangelands predict a doubling of current [CO<sub>2</sub>] by 2100 and altered precipitation regimes that will reduce soil moisture. These climate changes will likely favor deep-rooted woody plants over shallow-rooted warm season grasses and exacerbate the spread of woody plants on the landscape. To test this prediction, we conducted a greenhouse study to determine how four juvenile species (*Cornus drummondii*, *Rhus glabra*, *Gleditsia triacanthos* and *Juniperus osteosperma*), that are woody encroachers in the Great Plains of the United States of America, would grow under elevated [CO<sub>2</sub>] and decreased soil moisture. We measured leaf gas exchange, water use efficiency, leaf  $\Delta^{13}\text{C}$ , total biomass, and tissue specific starch concentrations. After 5 months of monitoring, we found that all species increased photosynthetic rates, increased instantaneous water use efficiency, and increased starch concentrations in leaves exposed to elevated [CO<sub>2</sub>]. We also observed that with elevated [CO<sub>2</sub>] and water stress *G. triacanthos* and *C. drummondii* had increased photosynthetic rates because of a decrease in stomatal conductance. We found each woody species responded physiologically different to cope with the different environmental conditions. The physiological benefits of higher [CO<sub>2</sub>] on these

juvenile woody encroaching species undergoing drought, may lead to increased rates of juvenile establishment despite forecasts of adverse future drought conditions.

## **Introduction**

Rangelands cover 30% of the Earth's terrestrial surface, and provide many ecological services (floristic diversity, hydrological and biogeochemical cycle regulation) in addition to forage for grazing animals (Asner et al. 2004, Ellis and Ramankutty 2008, Dixon et al. 2014). Many rangelands globally are transitioning to shrublands and woodlands through a process called woody plant encroachment (Saintilan and Rogers 2015, Stevens et al. 2017). Woody plant encroachment is the increase of shrub or tree density and cover into rangelands (Briggs et al. 2005, Archer et al. 2017, Venter et al. 2018). Increases in woody plant density and cover in temperate grasslands alters nutrient and water cycles (Gill et al. 2002, Leffler et al. 2002, Brunsell et al. 2013, Yannarell et al. 2014, Logan and Brunsell 2015), changes fire regimes (Knapp et al. 2008, Holdo et al. 2009, Wigley et al. 2010), decreases species diversity (Van Auken 2009, Ratajczak et al. 2012, O'Connor and Chamane 2012), and decreases available livestock forage (Anadón et al. 2014). The phenomenon of woody plant encroachment has been attributed to many drivers; one global driver that impacts all rangelands is increased atmospheric CO<sub>2</sub> concentrations (hereafter [CO<sub>2</sub>])(Archer et al. 1995, 2017, Bond and Midgley 2000, Polley et al. 2002a).

Atmospheric [CO<sub>2</sub>] has risen from 280 ppm at the start of the industrial revolution to 405 ppm (2018), and are projected to exceed 800 ppm by the end of this century (IPCC 2013, Blunden et al. 2018). Rising [CO<sub>2</sub>] affects plants directly through increased plant growth, increased photosynthetic rates, decreased stomatal conductance, and improved water use efficiencies (WUE) (Bazzaz 1990, Curtis 1996, Curtis and Wang 1998, Leakey et al. 2009).

Increased [CO<sub>2</sub>] also favors C<sub>3</sub> plants over C<sub>4</sub> plants because of their ability to fix more carbon which can lead to increased storage of carbon in the form of non-structural carbohydrates (Curtis and Wang 1998, Bond and Midgley 2000, Leakey et al. 2009). These positive benefits of elevated [CO<sub>2</sub>] should favor C<sub>3</sub> woody plants in rangelands over C<sub>4</sub> grasses.

Experiments at the pot-level to field FACE (free-air carbon dioxide enrichment) facilities have documented the physiological mechanisms that promote C<sub>3</sub> woody plant expansion under elevated [CO<sub>2</sub>] (Polley et al. 1996, 1999, 2002a, 2002b, Morgan et al. 2007, Kgope et al. 2010). Similar to the aforementioned mechanisms, these studies observed increased photosynthetic rates that increase total plant biomass and non-structural carbohydrates within plant tissues in conjunction with elevated [CO<sub>2</sub>] (Picon et al. 1997, Curtis and Wang 1998, Ainsworth and Long 2004, Kgope et al. 2010, Clarke et al. 2016). These mechanisms are advantageous for woody plant establishment in rangelands because increased growth potential increases the likelihood to escape browsing and fire traps that typically regulate woody plants in grasslands (Bond and Midgley 2003, Staver and Bond 2014). However, many of these studies did not include additional predicted climate treatments such as increased temperature or water stress to observe the interactive effects with elevated [CO<sub>2</sub>].

Elevated [CO<sub>2</sub>] increases growth and improves WUE in woody plants that are expanding into rangelands, but do these responses ameliorate the effects of water stress? Droughts are predicted to increase in frequency and intensity in North America and across many rangelands worldwide (IPCC 2013, Polley et al. 2013, Cook et al. 2015). Decreased soil moisture limits pressure on recruitment, seedling and juvenile establishment, and growth of woody plants (Polley et al. 2002b, Hoffmann et al. 2004, Saintilan and Rogers 2015). To test how elevated [CO<sub>2</sub>] and water stress impacts woody encroaching species, we conducted a greenhouse



experiment to measure the growth and physiology of four woody plant encroaching species that span North American rangelands from the Great Plains (*Cornus drummondii* C.A. Mey., *Rhus glabra* L., *Gleditsia triacanthos* L.) to Great Basin (*Juniperus osteosperma* Torr.). Juvenile woody plant encroaching species were grown at elevated [CO<sub>2</sub>] (~800 ppm) and ambient [CO<sub>2</sub>] (~400 ppm). Each species was subjected to either chronic water stress or a control (well-watered) treatment for comparison. We hypothesized that elevated [CO<sub>2</sub>] would increase photosynthetic rates which would lead to increased total biomass and starch storage in stems and roots. We also hypothesized that elevated [CO<sub>2</sub>] would increase WUE, through increased photosynthetic rates and decreased stomatal conductance, which would ameliorate the effects of water stress on the juvenile woody plants.

## Methods

### *Study species and experimental design*

We grew our four study species *C. drummondii*, *R. glabra*, *G. triacanthos*, *J. osteosperma* (hereafter, dogwood, sumac, honey locust, and juniper respectively) in a greenhouse under ambient ( $414 \pm 31$  (SD) ppmv) and elevated ( $805 \pm 38$  ppmv) [CO<sub>2</sub>], and with two soil moisture conditions (water stressed and unstressed). Each of the four treatment combinations (two [CO<sub>2</sub>] X two soil moisture conditions) were replicated for each species ten times.

The experiment was arranged in blocked design with [CO<sub>2</sub>] treatments in separate greenhouse bays and the soil moisture treatment nested within the [CO<sub>2</sub>] treatment. One greenhouse bay received supplemental CO<sub>2</sub> inputs to maintain the elevated [CO<sub>2</sub>] treatment. Because we were limited to one greenhouse bay per treatment, we used a blocked experimental design for each [CO<sub>2</sub>] treatment. To decrease the likelihood of spurious effects of location, both greenhouse bays rotated [CO<sub>2</sub>] treatments biweekly. The woody plants were moved with their

corresponding [CO<sub>2</sub>] treatments to ensure a consistent treatment effect, while removing the potential for a greenhouse location effect.

Native soil was used for each species to mimic real plant-soil water interactions. For dogwood, sumac, and honey locust, soils were collected at the Konza Prairie Biological Station (KPBS) in the eastern portion of the tallgrass prairie. The soils from KPBS were Irwin silty clay loam. The soil for juniper came from Moffat County in northwest CO. These soils were a loamy sand (Chesus and Ocheltree 2018). Soil moisture conditions for each species were determined prior to the start of the drought treatment by pot weight, VWC, and evapotranspiration relationships. It was determined that the water stressed soils for junipers would have a VWC of < 10%, and that the other species would be at a VWC of < 20%. The control (well-watered) soils for all species would range between 35% and 50% VWC. Watering of treatments occurred once a week, with each pot weighed and water added to the 'target weight' determined by the pot weight and VWC relationship. After two months of growth in the greenhouse (Day 66) half of all the plants by species received the reduced water treatment that continued for 85 more days.

Each woody plant species was planted in 30 cm of their respective native soils in a 12.7 cm X 30.5 cm square tree pots. Honey locust and sumac plants were germinated from seeds collected from KPBS. Dogwood was difficult to get a high germination rate from seed collection, so first year ramet cuttings were planted. The ramet cuttings were propagated at the Missouri Department of Conservation White State Forestry Nursery and shipped to our greenhouse. Juniper seedlings were transplanted from the field in Moffat County, CO. Each species was grown for a month under ambient well-watered conditions to establish roots and leaves for those species germinated from seed. None of the transplanted species had taproots that extended below 15 cm of the soil surface. Honey locust and sumac seedlings were thinned to just one individual

per pot after a month of growth. No fertilizer was ever added to the plants during the experiment, but a pesticide (“Triple Action”, Ferti-loam) was added when mites were discovered on several junipers, and a fungicide (“Infuse”, Bonide) for several sumac plants that had mildew during the experiment.

#### *Leaf-level gas exchange*

Leaf-level gas exchange measurements were made on 4 plants of each woody plant species per CO<sub>2</sub> and water stress treatment every two weeks for the full duration of the experiment. Gas exchange measurements were made on fully expanded leaves using a Li-6400XT portable photosynthesis system, with red/blue light source and the CO<sub>2</sub> injector (LI-COR Inc., Lincoln, NE). Leaves that did not fill the Li-6400XT cuvette were imaged, leaf area was calculated using imageJ software (Ferreira and Rasband 2012), and corrected in the gas exchange file.

Measurements were made from 1000-hrs to 1600-hrs. The light source of the Li-6400XT was set to a light intensity of 1200  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and the CO<sub>2</sub> concentrations were adjusted to match the appropriate greenhouse CO<sub>2</sub> treatments (400ppm, 800ppm). Instantaneous water use efficiency (WUE) was calculated post-hoc as the ratio of photosynthetic rate divided by stomatal conductance to yield WUE expressed as  $\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ .

#### *Biomass and tissue preparation*

At the end of the experiment all plant tissues were harvested and prepared for further analyses. Leaves were removed and placed in labelled plastic bags, as were the stems of each species. Roots were harvested by gently emptying the pot into a sieve and rinsed with water until soil particulates were removed. All tissues were then microwaved for 90 seconds to halt enzymatic activity for starch quantification. After all tissues were microwaved, they were then transferred to appropriately labelled paper bags and placed within a drying oven at 60°C for 48-hrs. Once all

plant tissues were dried, biomass was recorded for leaves, stems, and roots. The dried plant material was then stored accordingly for further molecular analyses.

#### *$\Delta^{13}\text{C}_{\text{leaf}}$ isotopic analysis*

Dried leaf samples were ground using a Wig-L-Bug® ball mill (Dentsply Sirona; York, PA, USA) to be analyzed for  $\delta^{13}\text{C}$  to evaluate intrinsic WUE. Isotopic and leaf elemental analysis was conducted on 2 mg ground leaf tissue at the Stable Isotope Mass Spectrometry Lab (SIMSL) at KSU using standard methods on a ThermoFinnigan Delta Plus mass spectrometer interfaced with a Carlo Erba elemental analyzer with ConFlo II interface (Thermo Fisher Scientific Inc., Waltham, MA, USA). The carbon isotopic ratio was expressed relative to the standard Vienna Pee Dee Belemnite (VPDB). Measured values of  $\delta^{13}\text{C}$  were compared to a known value of an internal laboratory standard (SD < 0.07 ‰). These measured values of  $\delta^{13}\text{C}_{\text{leaf}}$  then needed to be corrected for the atmospheric  $\delta^{13}\text{C}_{\text{air}}$  in the glasshouse which is required to calculate  $\Delta^{13}\text{C}_{\text{leaf}}$ . The elevated [ $\text{CO}_2$ ] treatment within the glasshouses were maintained with  $\text{CO}_2$  sources that were depleted of  $\delta^{13}\text{C}$  ( $\delta^{13}\text{C} \approx -47.1$  ‰ to  $-45.2$  ‰). We calculated atmospheric  $\delta^{13}\text{C}$  of both glasshouses by taking several air samples in vacuumed air tight glass vials from within the center of each glasshouse. The air samples were analyzed on a Piccaro G2101-i cavity ringdown spectrometer to determine the  $\delta^{13}\text{C}_{\text{sample}}$ . These  $\delta^{13}\text{C}$  values were then adjusted for the volume of sample and container to calculate  $\delta^{13}\text{C}_{\text{air}}$  for use in calculating  $\Delta^{13}\text{C}_{\text{leaf}}$ .

#### *Starch analysis*

All dried plant tissues (leaves, stems, and roots) were ground using a Wig-L-Bug® ball mill (Dentsply Sirona; York, PA, USA); stems and roots were milled first to 40 mesh (400  $\mu\text{m}$ ) prior to ball milling. The ground tissues were stored in glass vials in a  $-20$  °C freezer until starch analysis. For starch analysis, 20 mg of each plant tissue type had the simple sugars extracted

according to the ethanol extraction method (Hendrix 1993). The ethanol extracted tissue samples were immersed in 1 ml of water in a 2 ml microcentrifuge tube and autoclaved for 1 hour at 135 °C. Samples were then transferred to a drying oven to be dried at 60 °C. Starch concentrations were quantified using the Total Starch Assay Kit (Total Starch Assay Kit, Megazyme Co., Ireland). The plant tissues were digested in 1 ml of  $\alpha$ -amylase, boiled for 20 minutes, and then cooled for 10 minutes, followed by an addition of 15  $\mu$ l amyloglucosidase. The samples were mixed in a shaking water bath at 50 °C for 45 minutes. Samples were then plated out in 96-well plates, and then 200  $\mu$ l of GOPOD reaction mix was added to the samples. After 20 minutes of incubation at room temperature, absorbance was read at 510 nm on a 96-well plate reader spectrophotometer. Starch concentrations were quantified using a starch (maize) standard curve. Also, a positive control sample of *C. drummondii* root tissue with known concentrations of starch (quantified from separate methods in separate labs) was used to verify the precision of this protocol.

#### *Data analysis*

An ANCOVA analyses was conducted for each species present to address the physiological effects of [CO<sub>2</sub>] and water stress on photosynthetic rates and stomatal conductance. All other seedling measurements were compared among treatments with linear mixed-effects ANOVAs and linear mixed-effects repeated measure ANOVAs. Fixed effects for all analyses were [CO<sub>2</sub>] treatment, water stress treatment, and interactions. Block was considered a random effect. For the repeated measure ANOVA ‘day of experiment’ was added to account for the variability of repeated measures. All assumptions were met for the statistical analyses performed, and if needed basic data transformations were done to meet the assumptions of ANOVAs. Statistical significance was set at an  $\alpha$  of 0.05 *a priori*. All figures and statistical analyses were done in

Program R with packages lmer, lmerTest and ggplot ((Wickham 2009, Bates et al. 2015, R Core Team 2017).

## Results

### *Leaf gas exchange*

Instantaneous photosynthetic rates compared to stomatal conductance for each species had strong interactions among each treatment combination (Fig. 4.1). Stomatal conductance as a covariate was statistically significant for all species ( $P < 0.001$ ). Dogwood had lower photosynthetic rates with lower stomatal conductance under ambient  $[\text{CO}_2]$  while water stressed compared to the control with ambient  $[\text{CO}_2]$  and well-watered ( $P = 0.022$ ). Dogwood had increased photosynthetic rates with lower stomatal conductance with elevated  $[\text{CO}_2]$  and under water stress compared to the control ( $P = 0.030$ ). Other treatment combinations for dogwood were not statistically significant. Sumac had higher photosynthetic rates with lower stomatal conductance in conjunction with elevated  $[\text{CO}_2]$  compared to the control treatment ( $P = 0.001$ ), but no other treatment combinations were statistically significant. Honey locust had a significant  $[\text{CO}_2]$  direct effect with increased photosynthesis ( $P = 0.006$ ), as well as increased photosynthetic rates and lower stomatal conductance with elevated  $[\text{CO}_2]$  compared to the control treatment ( $P < 0.001$ ). Additionally, honey locust increased photosynthetic rates with lower stomatal conductance in conjunction with elevated  $[\text{CO}_2]$  and with water stress compared to the control treatment ( $P = 0.010$ ). Other treatment combinations for honey locust were not significant. Juniper increased photosynthetic rates with lower stomatal conductance in conjunction with elevated  $[\text{CO}_2]$  compared to the control treatment ( $P < 0.001$ ). All other treatment combinations were not significant.

Photosynthetic rates measured every few weeks after the start of the water stress treatment increased for all woody species subjected to elevated [CO<sub>2</sub>] compared to the ambient [CO<sub>2</sub>] treatment (Fig 4.2; dogwood, P = 0.001; sumac, P < 0.001; honey locust, P < 0.001; juniper, P < 0.001). The main effects of water stress did not statistically affect dogwood and sumac photosynthetic rates over the duration of the experiment from day 66 to day 149, however, both honey locust and juniper did have lower photosynthetic rates while water stressed compared to the control well-watered individuals (honey locust, P < 0.001; juniper, P = 0.021). For all woody species there was no statistically significant interaction between the [CO<sub>2</sub>] and water stress treatments.

Instantaneous water-use efficiency (A/g<sub>s</sub>) from day 66 to day 149 was higher for woody species with elevated [CO<sub>2</sub>] than the ambient [CO<sub>2</sub>] (Fig. 4.3; dogwood, P < 0.001; sumac, P < 0.001; honey locust, P < 0.001; juniper, P < 0.001). Water stress improved the instantaneous water-use efficiency of honey locust (P = 0.011) and juniper (P < 0.001) but not dogwood (P = 0.259) and sumac (P = 0.096). Dogwood, sumac and juniper instantaneous water-use efficiency did not have a statistically significant response to the interaction of [CO<sub>2</sub>] and water stress. Honey locust did have improved instantaneous water-use efficiency with elevated [CO<sub>2</sub>] and water stress compared to the control treatment (P = 0.022).

#### *Carbon isotopes*

The  $\Delta^{13}\text{C}$  values of leaf tissues for each woody species was not significant for any of the direct effects of [CO<sub>2</sub>] or water treatments, or for the combination of the [CO<sub>2</sub>] and water treatments (Fig. 4.4).

#### *Biomass*

Total biomass (root, shoot, leaf) for each woody species was not statistically significant for any [CO<sub>2</sub>] and water treatments, or [CO<sub>2</sub>] and water treatment combinations. Also, proportionally it was not statistically significant among tissue types for the [CO<sub>2</sub>] and water treatments, or [CO<sub>2</sub>] and water treatment combinations (Figs. 4.5, 4.6).

#### *Tissue specific starch*

Dogwood root starch concentrations increased by ~20 mg g<sup>-1</sup> in the water stressed treatment (minus = 66.44 ± 4.79 mg g<sup>-1</sup>, control = 46.08 ± 3.92 mg g<sup>-1</sup>; P = 0.004), but a statistically significant [CO<sub>2</sub>] or interaction effect was not present (Fig 4.7). All other species (sumac, honey locust, and juniper) did not have statistically significant differences between treatment combinations for root starch.

Sumac stem starch had a ~4 mg g<sup>-1</sup> increase in conjunction with elevated [CO<sub>2</sub>] (400 ppm = 61.07 ± 1.73 mg g<sup>-1</sup>, 800 ppm = 65.42 ± 2.01 mg g<sup>-1</sup>; P = 0.005), while water stress decreased stem starch by ~10 mg g<sup>-1</sup> (minus = 57.60 ± 1.36 mg g<sup>-1</sup>, control = 67.72 ± 1.49 mg g<sup>-1</sup>; P < 0.001). A statistically significant interaction between water stress and [CO<sub>2</sub>] on stem starch for sumac was not present (Fig 4.8). Honey locust stem starch increased by ~16 mg g<sup>-1</sup> under water stress compared to the control (minus = 93.79 ± 1.72 mg g<sup>-1</sup>, control = 77.25 ± 2.71 mg g<sup>-1</sup>; P < 0.001), but no statistically significant [CO<sub>2</sub>] or interaction effect was not present (Fig. 4.8). Dogwood and juniper had no statistically significant results for stem starch concentrations.

Dogwood leaf starch concentrations increased five-fold in conjunction with elevated [CO<sub>2</sub>] (400 ppm = 4.60 ± 1.39 mg g<sup>-1</sup>, 800 ppm = 25.25 ± 6.55 mg g<sup>-1</sup>; P = 0.006), but no water stress or interaction effect was present (Fig. 4.9). Sumac leaf starch concentrations doubled with elevated [CO<sub>2</sub>] (400 ppm = 31.28 ± 5.61 mg g<sup>-1</sup>, 800 ppm = 67.63 ± 4.59 mg g<sup>-1</sup>; P = 0.032), the water stress treatment was not statistically significant. There was a statistically significant



interaction between [CO<sub>2</sub>] and water stress for sumac plants, elevated [CO<sub>2</sub>] and water stress increased leaf starch concentrations compared to the other treatment combinations (P = 0.044; Fig. 4.9). Honey locust plants under water stress had ~20 mg g<sup>-1</sup> less leaf starch compared to the control plants (minus = 61.59 ± 5.67 mg g<sup>-1</sup>, control = 81.05 ± 2.65 mg g<sup>-1</sup>; P < 0.001). No statistically significant direct effect from elevated [CO<sub>2</sub>] was present in the data, but there was a statistically significant interaction between water stress and [CO<sub>2</sub>] treatments. Honey locust leaf starch concentrations were higher with elevated [CO<sub>2</sub>] and water stress (P = 0.031; Fig. 4.9). Juniper leaf starch concentrations were increased almost 3-fold with elevated [CO<sub>2</sub>] (400 ppm = 8.02 ± 1.46 mg g<sup>-1</sup>, 800 ppm = 23.12 ± 3.57 mg g<sup>-1</sup>; P = 0.004; Fig. 4.9). The water stress treatment and the interactions between treatments were not statistically significant for juniper leaf starch concentrations.

## Discussion

Woody plants in grasslands have several key demographic bottlenecks to overcome, one main bottleneck is juvenile survival (Wigley et al. 2009, Holdo et al. 2014). The juvenile stage is a key ontogenetic stage for woody plants in rangelands because of the need to escape biotic and abiotic pressures (Boege and Marquis 2005, Wigley et al. 2009, Hartnett et al. 2012, Clarke et al. 2013). Juvenile woody plants exposed to elevated [CO<sub>2</sub>] increase photosynthetic rates and water-use efficiencies (WUE) which can lead to increased growth, biomass, survival and establishment success (Polley et al. 2002b, Leakey et al. 2009, Kgope et al. 2010, Clarke et al. 2016). But does increased growth and improved WUE from elevated [CO<sub>2</sub>] mitigate the effects of water stress on juvenile woody plants? In this study we explored this question and our results provide evidence that elevated [CO<sub>2</sub>] ameliorates the effects of chronic water stress on juvenile woody plants through improved leaf-level gas exchange and starch allocation.

Elevated [CO<sub>2</sub>] improves leaf-level physiology in C<sub>3</sub> plants through increased [CO<sub>2</sub>] within the intercellular spaces of the leaves, which results in increased photosynthetic rates (Lambers et al. 2008, Leakey et al. 2009, Kelly et al. 2016). The increased [CO<sub>2</sub>] also decreases stomatal conductance which lowers transpiration rates and improves the WUE of plants (Bazzaz 1990, Polley et al. 1996, Kelly et al. 2016). Our results show all four juvenile woody plant species (dogwood, sumac, honey locust and juniper) increased photosynthetic rates with elevated [CO<sub>2</sub>] because of decreased stomatal conductance (Fig. 4.1), which concurs with results from other studies and meta-analyses (Curtis 1996, Curtis and Wang 1998, Polley et al. 2003, Leakey et al. 2009, Kelly et al. 2016). When the juvenile plants experienced several months of chronic water stress, honey locust and dogwood had increased photosynthetic rates with decreased stomatal conductance (Fig. 4.1). While sumac and juniper did not have as strong a response to elevated [CO<sub>2</sub>] and water stress (Fig. 4.1, not statistically significant). One explanation for our results is the plants had tighter stomatal regulation, not lower intercellular [CO<sub>2</sub>] because of adjustments made to leaf area which would also cause increased photosynthetic rates (Kelly et al. 2016). The tight regulation of stomatal conductance with elevated [CO<sub>2</sub>] and chronic water stress is a physiological trait that will allow these species to persist and potentially continue to further establishment and success in rangelands in the future.

Elevated [CO<sub>2</sub>] improves intrinsic water-use efficiency of C<sub>3</sub> plants through increased photosynthetic rates and/or decreased stomatal conductance (Polley et al. 1992, Curtis 1996, Leakey et al. 2009). Our results showed that each juvenile woody plant species had improved intrinsic WUE (A/g<sub>s</sub>) due to elevated [CO<sub>2</sub>] (Fig. 4.3), which can be attributed to the higher photosynthetic rates as well as decreased stomatal conductance (Fig. 4.1). Honey locust and juniper both had higher intrinsic WUE with chronic water stress. This result is not surprising as

both species are known for their drought tolerances (Graves et al. 1991, Linton et al. 1998, Polley et al. 2002b). Also, honey locust was the only species that the interaction of elevated  $[\text{CO}_2]$  and chronic water stress improved WUE (Fig. 4.3). The potential reason for honey locust having improved WUE with elevated  $[\text{CO}_2]$  and chronic water stress could be attributable to the small leaflets of the compound leaf structure as well as its ability to increase solutes in leaves to maintain turgor at low water potentials (Graves et al. 1991). However, when we sampled the  $\delta^{13}\text{C}$  of the leaves of each species there was no effect of  $[\text{CO}_2]$  and/or chronic water stress with any of the juvenile woody plant species (Fig. 4.4). There was increased variability within each species, especially honey locust, between the different  $[\text{CO}_2]$  and water stress treatments. A potential reason for not observing differences in  $\delta^{13}\text{C}$  values could be attributable to an artifact of heating the greenhouses with propane. The use of fossil fuels to heat the greenhouses would cause a more depleted  $\delta^{13}\text{C}$  value in the greenhouse air. Regardless of the greenhouse air artifact it is apparent that the WUE of all four juvenile woody species demonstrates the ability for these plants to withstand chronic water stress.

Higher rates of photosynthesis can result in increased storage of carbon as nonstructural carbohydrates (NSC), this is generally the trend for resprouting woody plants which allocate more NSCs and biomass belowground than non-resprouting woody plants (Bond and Midgley 2003b, Clarke and Knox 2009, Pausas et al. 2016). Resprouting woody plants grown at elevated  $[\text{CO}_2]$  have increased NSC concentrations in root tissues compared to ambient  $[\text{CO}_2]$  (Bond and Midgley 2000, Kgope et al. 2010, Clarke et al. 2016). Woody plants that experience water stress can remobilize NSCs to increase osmolytes in leaves to lower water potentials, it can also be used as a carbon source to maintain respiration (Graves et al. 1991, Adams et al. 2013, Martínez-Vilalta et al. 2016). However, tissue specific starch re-allocation with elevated  $[\text{CO}_2]$  and/or

water stress is still part of a large discussion among physiologists (Dietze et al. 2014, Zeppel et al. 2015, Bachofen et al. 2018). We found that starch concentrations did not increase because of elevated  $[\text{CO}_2]$  in the roots of any of our woody plants (Fig. 4.7), nor in the stems except for sumac which did increase starch concentrations slightly (Fig. 4.8). Leaf starch concentrations did increase in all species of woody plants with elevated  $[\text{CO}_2]$  (Fig. 4.9). Of particular interest is the response that the juvenile plants experiencing water stress had varied starch concentrations and allocations. Water stressed dogwood plants had higher starch concentrations in the root tissue compared to the unstressed plants, which could be a mechanism for the plant to prepare for new leaves when conditions improve (Pausas et al. 2016, Klimešová et al. 2018). Sumac had decreased stem starch concentrations while water stressed, while honey locust increased stem starch concentrations (Fig. 4.8). These differences demonstrate how different each species responds to water stress. The differences between sumac and honey locust in stem starch concentrations might be explained in conjunction with the leaf starch concentrations for both species (Fig. 4.9). Sumac had decreased stem starch concentrations but there was more starch in its leaves while grown in elevated  $[\text{CO}_2]$ , otherwise the leaf starch levels were lower than the individuals not water stressed. Honey locust leaves had decreased starch concentrations with chronic water stress, but in the elevated  $[\text{CO}_2]$  treatment it was higher than individuals water stressed and grown at ambient  $[\text{CO}_2]$ . Lower starch concentrations with water stress could be a result of a breakdown of starch molecules to more soluble sugar molecules (i.e., sucrose, fructose, glucose) that would increase the concentration of osmolytes in the tissues to help mitigate the effects of water stress (Graves et al. 1991, Martínez-Vilalta et al. 2016, Pausas et al. 2016). The increase in osmolytes would allow for drought avoidance in the plants, unlike the juniper in our study which is considered drought tolerant and anisohydric (Linton et al. 1998).

Overall, the responses of starch concentrations to elevated [CO<sub>2</sub>] and/or water stress were not as expected with regard to the resprouting woody species storing starch in root tissues.

Juvenile woody plants transition from the ontogenetic stage of seedlings with high root:shoot because of fast aboveground growth transitions to slower growth that results with more carbohydrate storage (Boege and Marquis 2005, Klimešová et al. 2018). This transition from seedling to juvenile stages result in an increase biomass. Numerous studies and meta-analyses have shown the elevated [CO<sub>2</sub>] increases biomass of C<sub>3</sub> plant species, including woody plants (Bazzaz 1990, Curtis and Wang 1998, Polley et al. 2002a, Leakey et al. 2009, Kgope et al. 2010). Our study did not observe the typical trend in increased total biomass or proportional biomass based on tissue type (roots, stems, leaves) with elevated [CO<sub>2</sub>] (Fig. 4.5 & 4.6), even though we observed increased photosynthetic rates and improved WUE for the duration of the study (Figs. 4.6 & 4.7). We expected an increase in belowground biomass relative to aboveground biomass with elevated [CO<sub>2</sub>], because the roots would act as a sink for stored carbohydrates (Curtis and Wang 1998, Clarke et al. 2016). Our study is not the only study to observe a non-statistically significant [CO<sub>2</sub>] treatment response to biomass. The Nevada Desert FACE Facility did not see a cumulative effect of elevated [CO<sub>2</sub>] on the biomass of *Larrea tridentate*, *Ambrosia dumosa*, *Lycium andersonii* and *Lycium pallidum* over the 10-year duration of the experiment (Newingham et al. 2014). Newingham et al. determined that because of low precipitation, low leaf area, the mature nature of the shrubs and an ecosystem in a long-term equilibrium state the treatment effects of elevated [CO<sub>2</sub>] had no quantitative effect. Another study in Australia found mixed results with total biomass between multiple resprouting and non-resprouting species. The researchers found that some non-resprouting woody plants had increased total biomass with elevated [CO<sub>2</sub>], while the resprouting species did not have an

increase in total biomass (Clarke et al. 2016). However, Clarke et al. did find that the resprouting woody species did allocate more biomass belowground. The no effect of [CO<sub>2</sub>] on total biomass in our experiment could be a result of these resprouting species still in the seedling stage or as juveniles still have a relatively fast growth rate. For the juniper it is most likely because it is a slow growing drought adapted species.

### *Conclusion*

Global climate change effects on North American rangeland woody encroaching species will include water stress through frequent intense droughts (Tegen et al. 2004, Polley et al. 2013, Cook et al. 2015), elevated [CO<sub>2</sub>] (IPCC 2013), and increased heat stress (Hamerlynck et al. 2000, Adams et al. 2009, Huang et al. 2015). Our results suggest that elevated [CO<sub>2</sub>] does ameliorate the effects of water stress on these juvenile woody plants. It also adds information to our understanding of the physiological mechanisms that allow woody plants to establish and encroach into rangelands. Each of the species in this study had tight control of their stomata to improve WUE, and increased starch storage within leaf tissues when subjected to elevated [CO<sub>2</sub>] and water stress. These physiological traits will continue to perpetuate the expansion of these woody plant species in their respective rangelands in the future.

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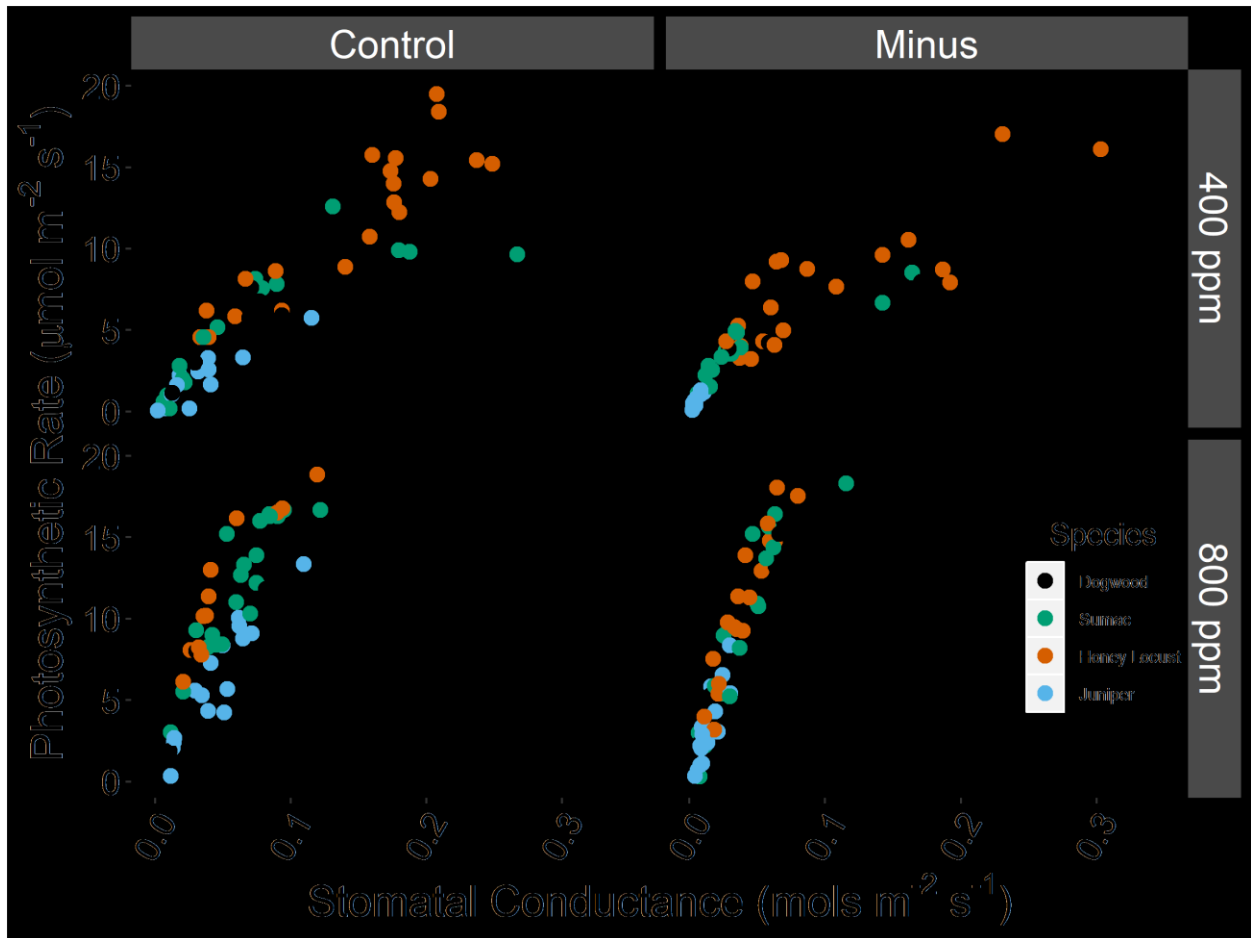
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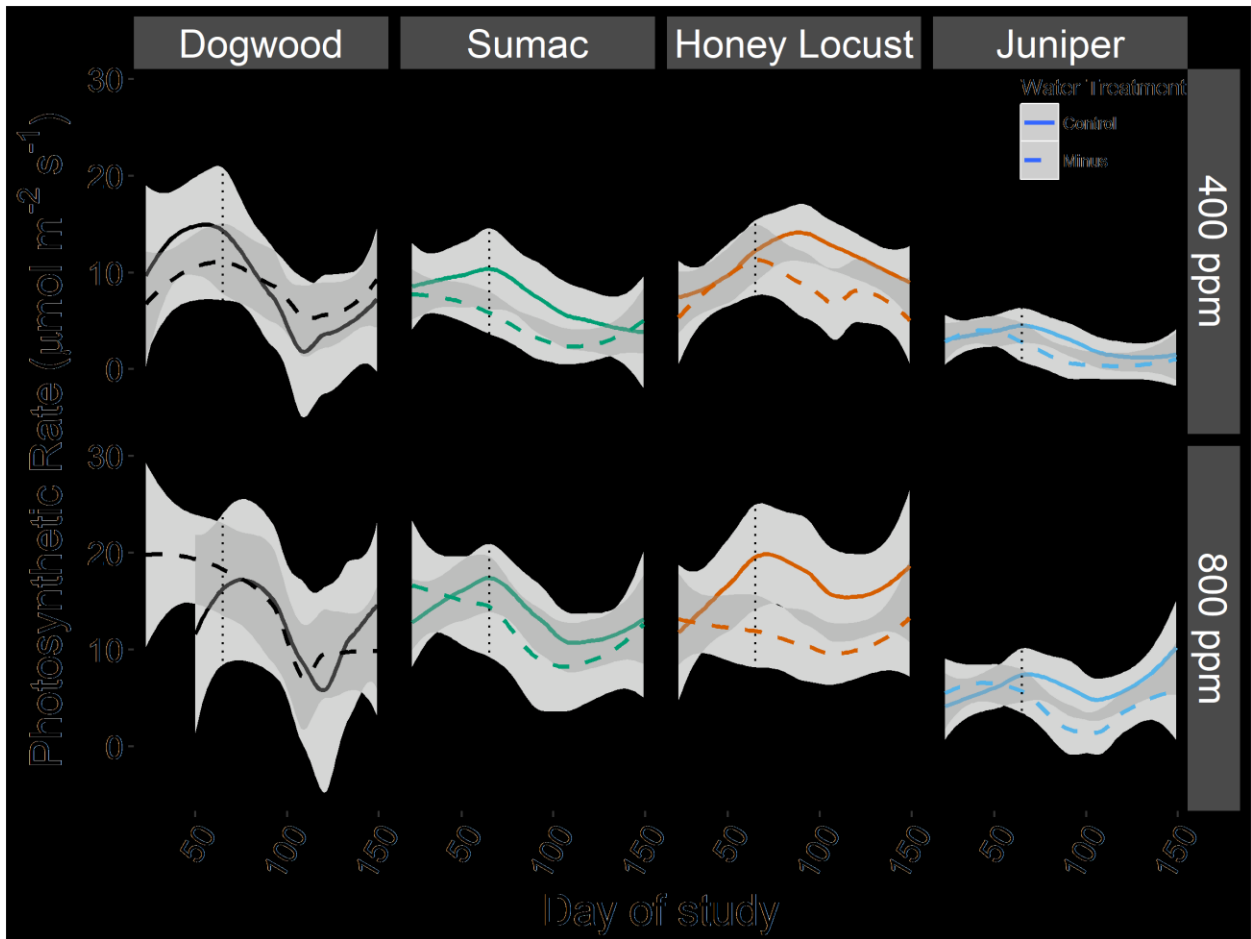
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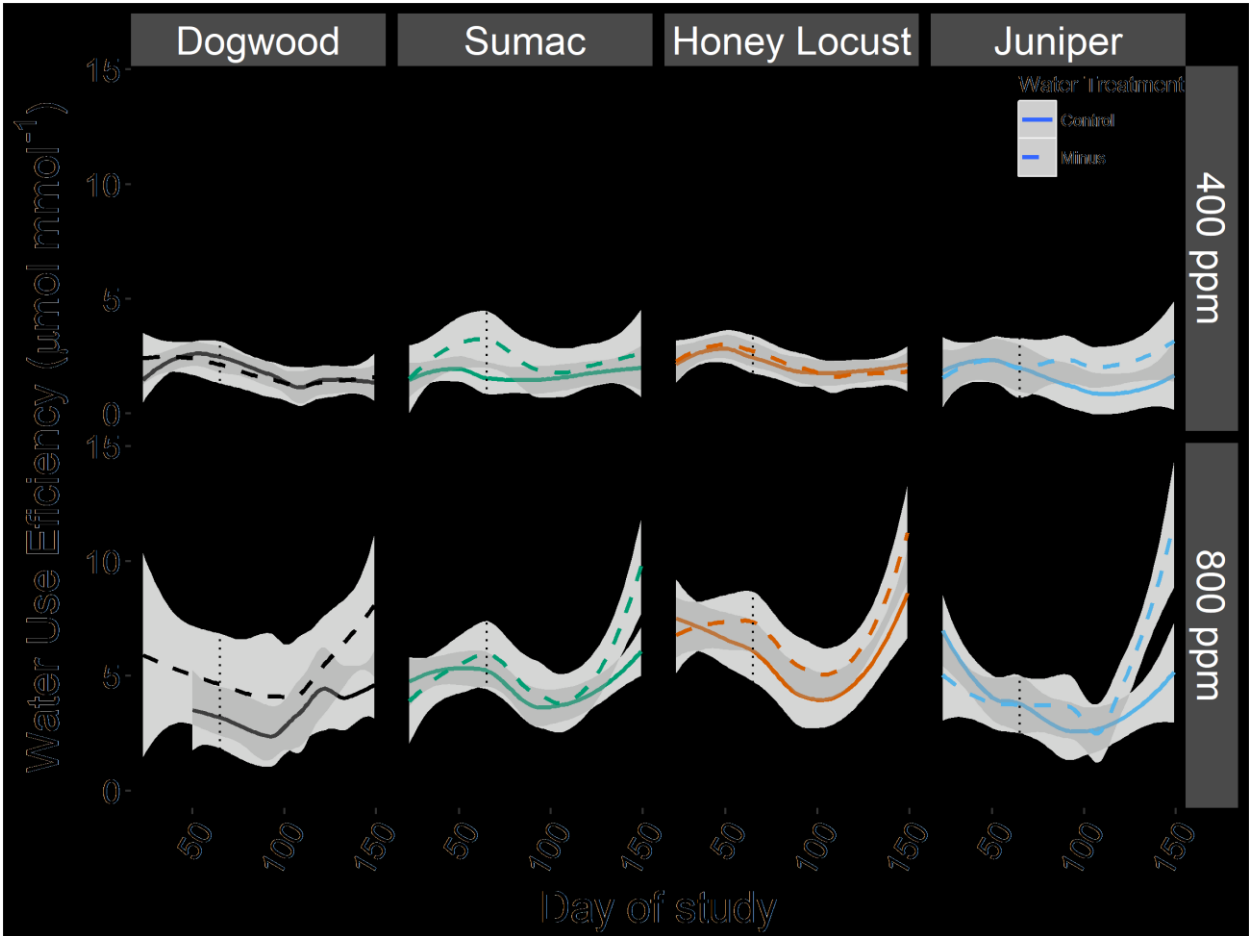


**Figure 4.1.** Instantaneous photosynthetic rate and stomatal conductance for each treatment combination by species. The columns represent the water stress treatment and rows are the [CO<sub>2</sub>] treatments. Each circle represents a single measurement. All measurements were taken after day 66 of the experiment.

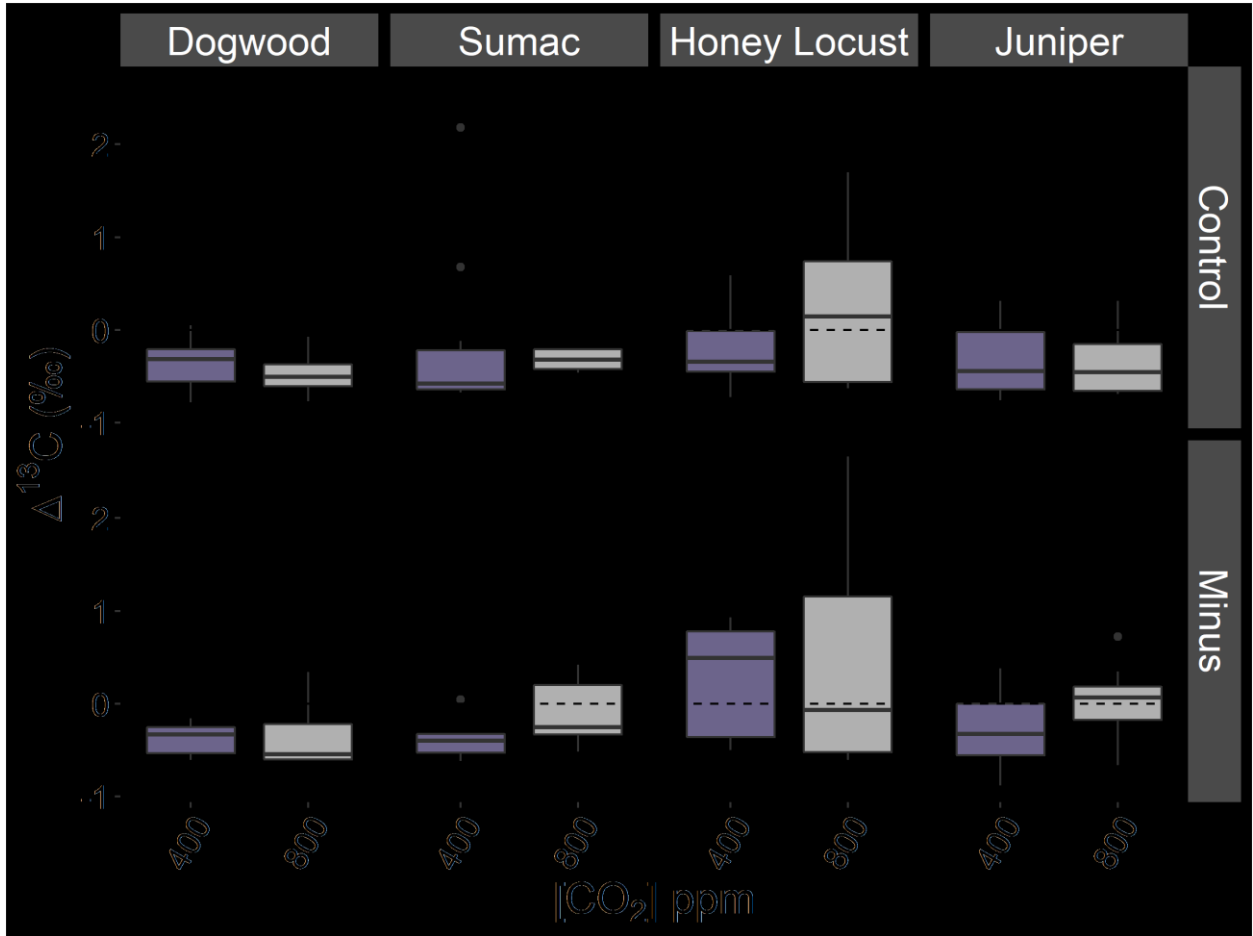




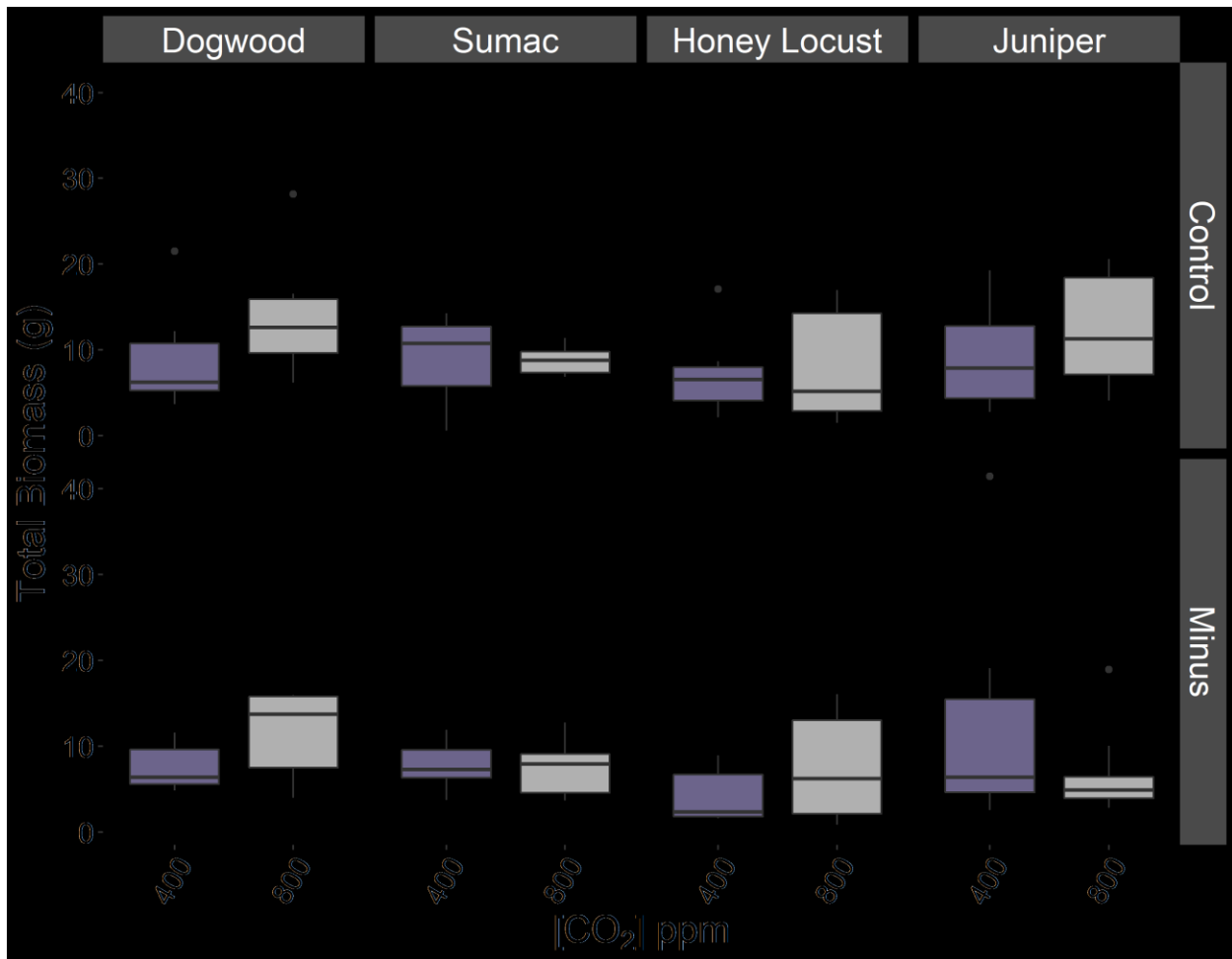
**Figure 4.2.** Instantaneous photosynthetic rates of each species by treatment (data has been smoothed for interpretation of trends). Woody plant species are columns and [CO<sub>2</sub>] treatments are the rows of this figure. Within the figure water stress treatments are the dashed lines, and the control treatments are the solid lines. The grey polygons surrounding the lines are 95% confidence intervals. The dotted vertical line represents the day when the water stress treatments began.



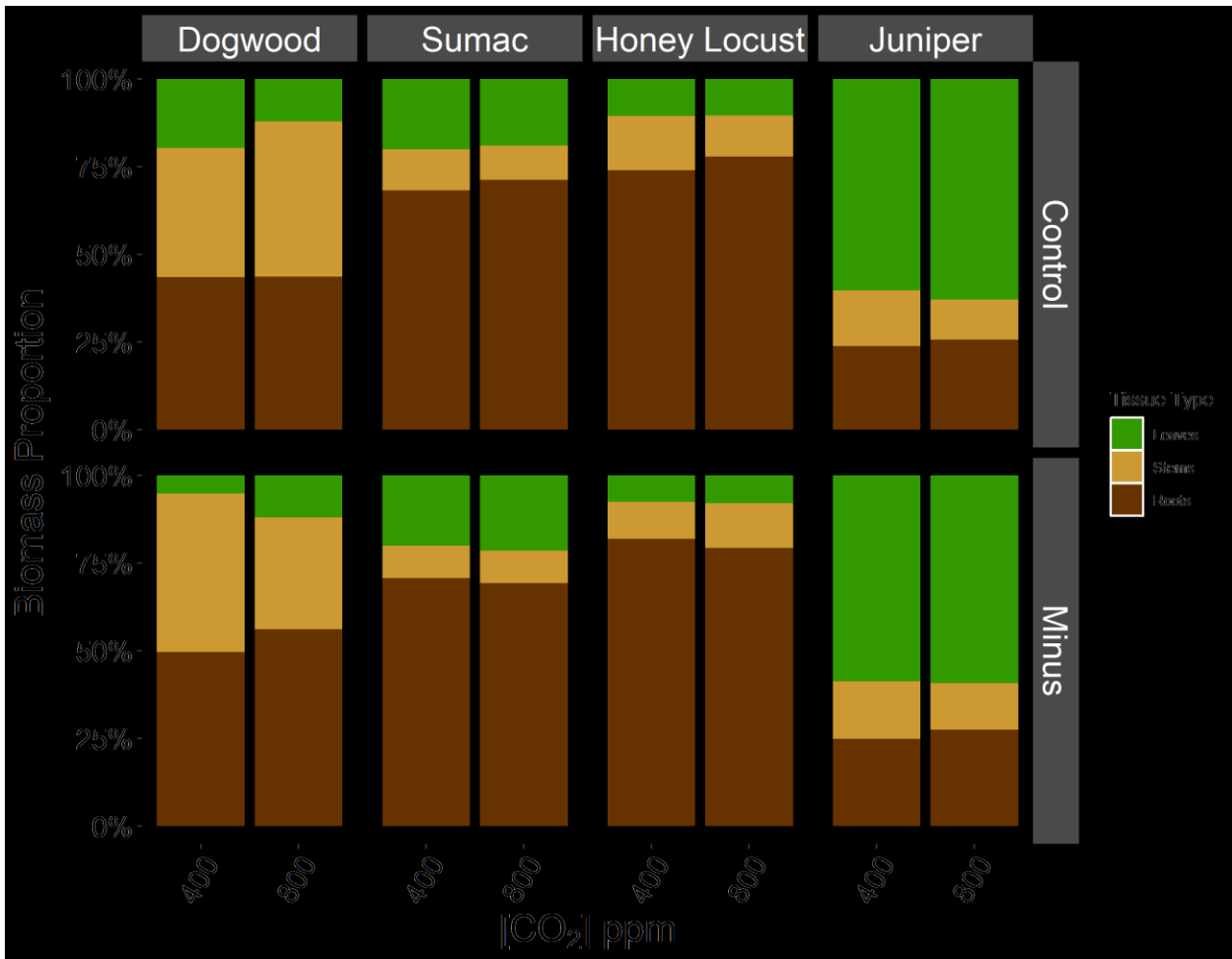
**Figure 4.3.** Instantaneous water use efficiency ( $A/g_s$ ) results (data has been smoothed for interpretation of trends). Woody plant species are columns and  $[CO_2]$  treatments are the rows of this figure. Within the figure water stress treatments are the dashed lines, and the control treatments are the solid lines. The grey polygons surrounding the lines are 95% confidence intervals. The dotted vertical line represents the day when the water stress treatments began.



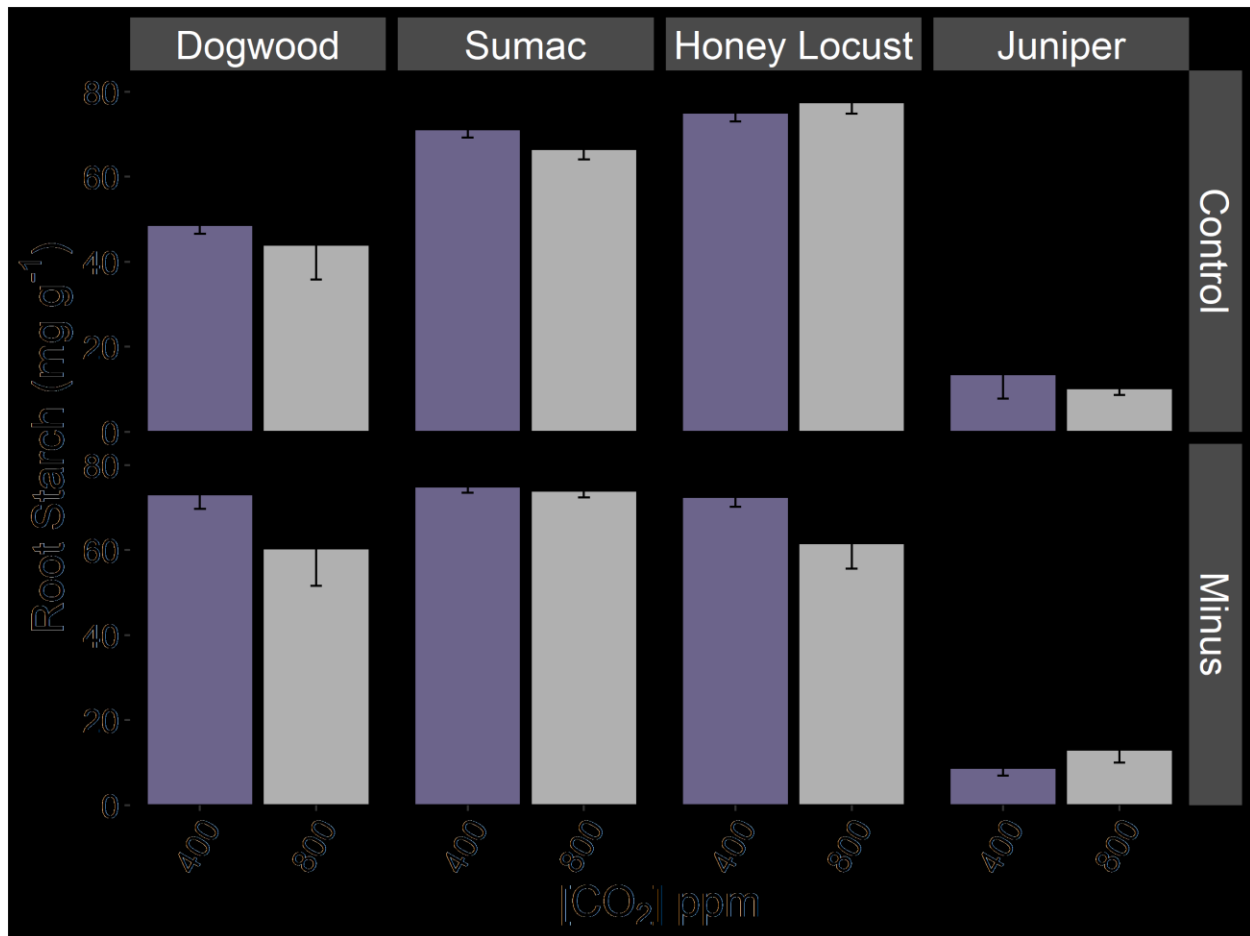
**Figure 4.4. A boxplot of  $\Delta^{13}\text{C}_{\text{leaf}}$  of each woody plant species by treatment. Woody plant species are separated by columns and the water stress treatments are separated by rows (water stressed = minus). The purple boxes are ambient  $[\text{CO}_2]$  (400 ppm) and the grey boxes are elevated  $[\text{CO}_2]$  (800 ppm). Whiskers contain  $Q1 - 1.5 \times \text{IQR}$  to  $Q3 + 1.5 \times \text{IQR}$  of data points (Q, quartile, IQR, interquartile range) and outliers are displayed by dots.**



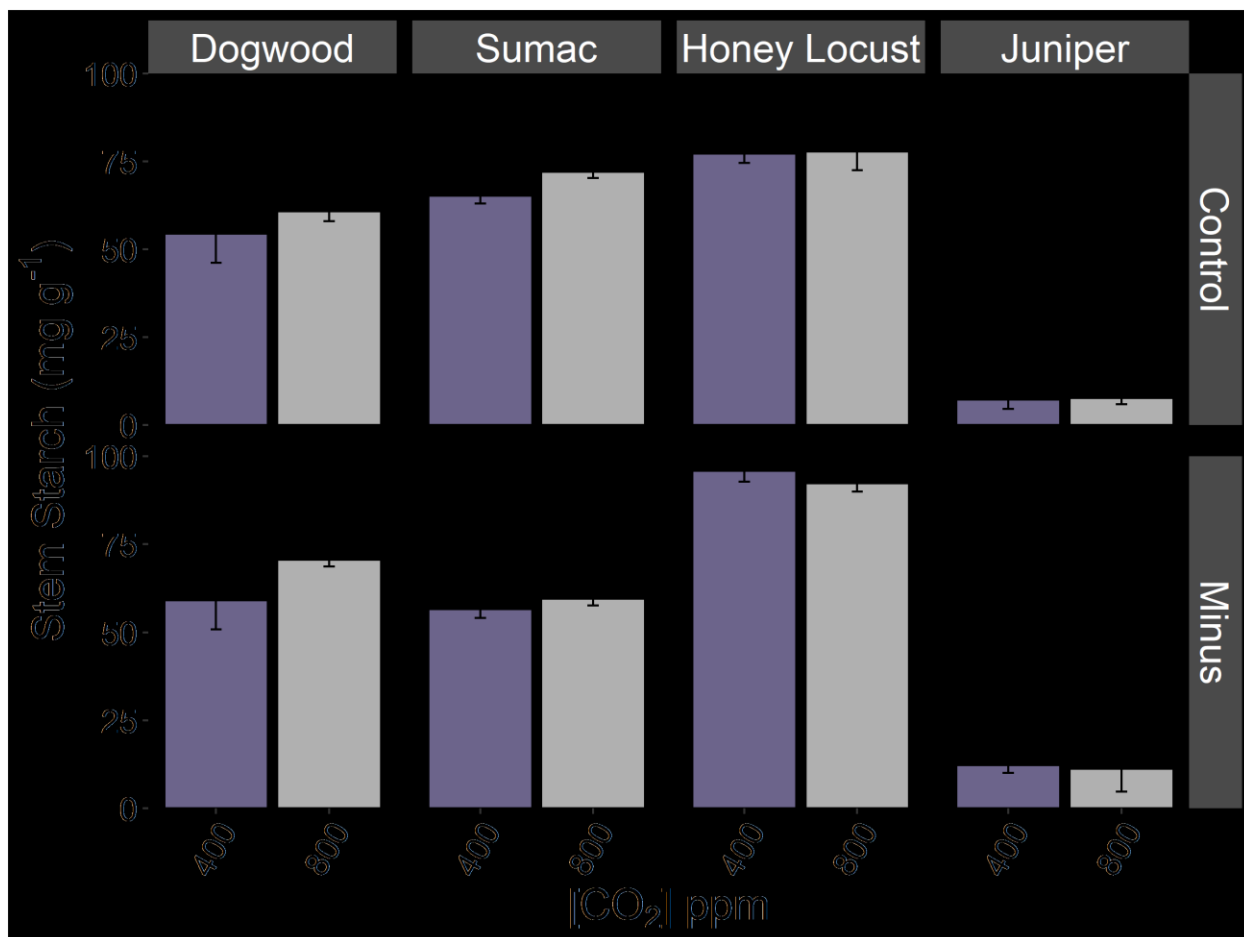
**Figure 4.5. Total biomass (roots, stems, leaves) of each species. Woody plant species are separated by columns and the water stress treatments are separated by rows (water stressed = minus) in this figure. The purple boxes are ambient [CO<sub>2</sub>] (400 ppm) and the grey boxes are elevated [CO<sub>2</sub>] (800 ppm). Whiskers contain Q1– 1.5 x IQR to Q3 + 1.5 x IQR of data points (Q, quartile, IQR, interquartile range) and outliers are displayed by dots.**



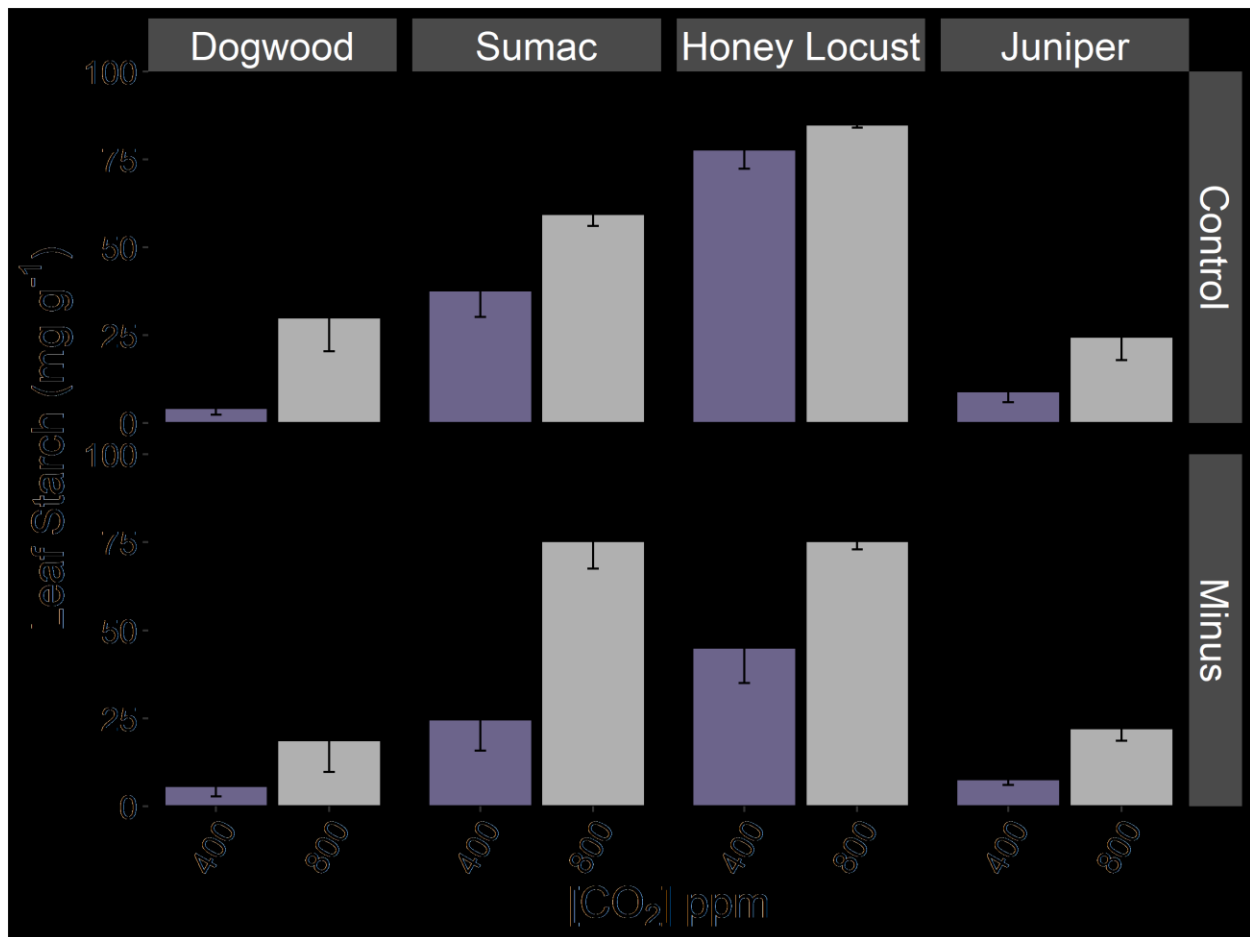
**Figure 4.6. Total biomass of each species broken down by tissue type for each treatment combination. Woody plant species are separated by columns and the water stress treatments are separated by rows (water stressed = minus) in this figure.**



**Figure 4.7.** Mean root starch concentrations ( $\text{mg g}^{-1}$ ) of each woody plant species ( $\pm\text{SE}$ ). Woody plant species are separated by columns and the water stress treatments are separated by rows (water stressed = minus) in this figure. The purple bars are ambient  $[\text{CO}_2]$  (400 ppm) and the grey bars are elevated  $[\text{CO}_2]$  (800 ppm).



**Figure 4.8. Mean stem starch concentrations (mg g<sup>-1</sup>) of each woody plant species ( $\pm$ SE). Woody plant species are separated by columns and the water stress treatments are separated by rows (water stressed = minus) in this figure. The purple bars are ambient [CO<sub>2</sub>] (400 ppm) and the grey bars are elevated [CO<sub>2</sub>] (800 ppm).**



**Figure 4.9.** Mean leaf starch concentrations ( $\text{mg g}^{-1}$ ) of each woody plant species ( $\pm\text{SE}$ ). Woody plant species are separated by columns and the water stress treatments are separated by rows (water stressed = minus) in this figure. The purple bars are ambient  $[\text{CO}_2]$  (400 ppm) and the grey bars are elevated  $[\text{CO}_2]$  (800 ppm).



## **Chapter 5 - Identifying ecological breakpoints using Bayesian hierarchical temporal and spatial piecewise regression**

*This chapter has been formatted for the journal "Ecology" as a statistical report*

### **Abstract**

Ecologists and natural resource managers are interested in identifying when and where thresholds occur in ecosystems. Crossing of thresholds (i.e., breakpoints) often result in a change from one ecological state to another. Breakpoint equations are one method that allows for the identification of thresholds. Traditional breakpoint equations estimate a breakpoint location but do not quantify the uncertainty. Breakpoint equations combined within Bayesian hierarchical models give estimations of breakpoints with corresponding uncertainties at any temporal or spatial scale. Bayesian hierarchical breakpoint models also improve the ability of estimation and predicting breakpoints. In this paper we show how to build Bayesian hierarchical breakpoint models and demonstrate two examples. First, a Bayesian hierarchical temporal breakpoint model is developed to analyze when breakpoints occur in a grassland transitioning to a woody dominated state. The second model, a Bayesian hierarchical spatial breakpoint model is used to determine at what depth bioluminescent sources are no longer detected. The Bayesian hierarchical temporal breakpoint model estimated the years that woody plant cover became the dominant plant functional cover type in several different fire and grazing treatments. In the Bayesian hierarchical spatial breakpoint model, estimated breakpoints from each sampled spatial location are spatially interpolated to estimate breakpoints outside of the sampling locations. In addition to these Bayesian hierarchical breakpoint models we provide recommendations for

improving Bayesian hierarchical breakpoint models to aid in conservation and adaptive management of ecosystems.

**Key-words:** Bayesian statistics; breakpoint analysis; spatial breakpoints; temporal breakpoints; ecological threshold; beta distribution; woody encroachment; pelagic bioluminescence

## Introduction

Ecological thresholds are locations (spatial, temporal, or spatio-temporal) where abrupt changes occur that cause non-linear responses to drivers (biotic or abiotic) (Groffman et al. 2006). Ecological thresholds often correspond with transitions to a new stable or quasi-stable states, as have been shown through theoretical and empirical studies (Holling 1973, Noy-Meir 1975, May 1977, Gunderson 2000, Folke et al. 2004, Scheffer et al. 2009). Ecological thresholds occur in all ecosystems, and can be observed at multiple levels of organization, from the population to whole ecosystem (Bestelmeyer et al. 2011, Foley et al. 2015). Understanding how to appropriately identify thresholds and to predict where and when these thresholds occur is paramount to understanding how systems change, as well as how to adaptively manage these systems.

In the last decade, several review papers have discussed the best statistical methods to analyze non-linear data that contain ecological thresholds (Dodds et al. 2010, Bestelmeyer et al. 2011, Toms and Villard 2015, Foley et al. 2015). One statistical method often used in determining thresholds are breakpoint equations (Toms and Lesperance 2003, Toms and Villard 2015). Breakpoints occur when the relationship between the response and explanatory variables

change at a specific point in space and/or time. The simplest breakpoint equation has two straight lines with an abrupt vertical break, it is not necessary for the lines to join around the breakpoint (Equation 1).

$$f(x, \theta, \beta) = \begin{cases} \beta_0 + \beta_1 x & \text{if } x \leq \theta \\ \beta_2 + \beta_3 x & \text{if } x > \theta \end{cases} \quad (1)$$

In breakpoint equation 1,  $f(x, \theta, \beta)$  is the value of observations,  $x$  is the corresponding explanatory variable,  $\theta$  is the breakpoint (threshold). Breakpoints can be abrupt, or they can exhibit a gradual change (Fig. 5.1). Regardless of the breakpoint being abrupt or gradual, our ability to estimate or predict where and when these changes occur in ecological data can have large implication for conservation and adaptive management.

Despite the need to estimate and predict thresholds in ecology, breakpoint analyses are relatively uncommon in the literature compared to Bayesian analyses (Fig. 5.2). The paucity of breakpoint analyses in ecological literature, even though the results are important for managers, could be explained that current breakpoint equations do not give directionality, explain mechanisms, or give predictions (Dodds et al. 2010, Foley et al. 2015). Bayesian models can provide flexibility and quantify uncertainties to improve breakpoint equations (Wade 2000, Cressie and Wikle 2011, Hooten and Hobbs 2015). From a literature search, there was one study that incorporated a breakpoint equation into a Bayesian model (Lee et al. 2017). By using a Bayesian breakpoint model, Lee et al. were able to model the probability and prediction of when extinctions occurred for the Barbary lion (2017). Bayesian breakpoint models have the potential to move ecological understanding of thresholds forward.

The aim of this paper is to demonstrate that combining breakpoint equations within Bayesian hierarchical models creates a viable solution to determine breakpoints temporally and

spatially, and estimate the uncertainties surrounding breakpoints. We first provide a brief introduction to Bayesian hierarchical models. Then we demonstrate how to build a temporal Bayesian hierarchical breakpoint model to identify when breakpoints occurred to transition a mesic grassland to a woody plant dominated grassland. Third, we demonstrate how to build a spatial Bayesian hierarchical breakpoint model to identify the depth of where pelagic bioluminescent sources are no longer detected. Finally, we discuss future opportunities and adjustments to the Bayesian hierarchical breakpoint models for adaptive management.

### **Bayesian Models**

Bayesian statistical models are commonplace for modelling ecological data and will continue to be developed within the field (Fig. 5.2). Bayesian models are used to calculate the probability (joint distributions) of random variables from the given data (Wade 2000). If complicated processes are needed to be modelled, instead of trying to specify a single distribution it is easier to decompose (breakdown) the distribution into several smaller components (Wikle 2003). These types of Bayesian models are called Bayesian hierarchical models and generally are arranged in three levels:

- 1) Data model: [data | process, parameters]
- 2) Process model: [process | parameters]
- 3) Parameter model: [parameters]

The data model specifies the distribution of data given a process and parameters that help specify the distribution. The process model describes the uncertainties with the chosen parameters, and within the parameter model each parameter's uncertainties are modelled. Each level within the hierarchy can have sub-levels, thus providing opportunities to model additional processes, parameters, or uncertainties. The point of the hierarchical specification is to obtain the posterior

distributions of each process parameter as well as the uncertainties of each parameter to better understand the complicated processes being modelled.

### **Temporal Bayesian breakpoint model**

The temporal Bayesian breakpoint model is built in a Bayesian hierarchical framework. To describe the development of the Bayesian hierarchical temporal breakpoint model we used the plant community composition data set (PVC02) from the Konza Prairie LTER program. We wanted to know at what year(s) do woody plants become the dominant plant cover type in the tallgrass prairie. We also wanted to know how fire frequency or grazing impact the location of the breakpoint. (A brief description of woody plant dominance in the tallgrass prairie, the method of preparing the data for analysis, and corresponding R code is provided in Appendix B.) Woody plant cover was used to determine the breakpoint of when woody plants achieve dominance in the tallgrass prairie. The woody plant cover data are a continuous proportion-type data (bounded between 0 and 1) and temporally explicit. This Bayesian hierarchical model only uses the process and parameter models.

The process model is  $y$  as the observed woody plant cover. The observed woody plant cover has a beta distribution with the expected value of woody plant cover ( $\mu$ ), and the dispersion parameter (i.e., breakpoint) ( $\phi$ ):

$$y \sim \mathbf{Beta}(\mu, \phi). \quad (2)$$

Within the process model the expected values of woody plant cover ( $\mu$ ) are a functional, a logit transformation function on the function of  $f(\mathbf{x}, \boldsymbol{\beta}, \theta)$ :

$$\mu = \mathbf{logit}(f(\mathbf{x}, \boldsymbol{\beta}, \theta)) \quad (3)$$

where  $\mathbf{x}$  is time,  $\boldsymbol{\beta}$  are the parameters around the breakpoints, and  $\theta$  are the year(s) (breakpoints) where woody plant cover became the dominant plant functional cover type.

The standard parameter model (priors):

$$\boldsymbol{\phi} \sim IG(2.1, 1) \quad (4)$$

$$\boldsymbol{\beta} \sim N(\mathbf{0}, \sigma_{\boldsymbol{\beta}}^2) \quad (5)$$

$$\boldsymbol{\theta} \sim norm(t, 2018) \quad (6)$$

Where  $\phi$ , the uncertainty parameter, is an inverse gamma distribution (IG).  $\boldsymbol{\beta}$ , the intercepts and slopes around the breakpoints, are normally distributed with a ‘vague’ hyper parameter  $\sigma_{\boldsymbol{\beta}}^2$ , that had a prior value of 100.  $\theta$ , the breakpoints, are a uniform distribution with ‘t’ being the year vegetation sampling started at each watershed, and 2018 being the most current year with data available.

Five Bayesian hierarchical temporal breakpoint models were run with a MCMC sampling of 60,000 iterations, the model tuning parameters used an ‘adaptive random walk Metropolis-Hastings’ algorithm to improve the tuning of parameters (Givens and Hoeting 2012). A Metropolis-Hastings algorithm was implemented within the MCMC because full conditionals were not available for each estimated parameter. Convergence of each model was determined visually through trace plots (Hobbs and Hooten 2015). Parameter means and uncertainties were estimated after a burn-in of 20,000 iterations.

The Bayesian hierarchical temporal breakpoint model estimated breakpoints for each fire frequency and grazing treatment and gave realistic predictions of woody plant cover for each treatment (Fig. 5.3). Woody plant cover breakpoints were very similar for all sites and occurred in 1999 (Table 5.1). The one site that was different was the unburned and ungrazed site whose breakpoint was in 2004 (Table 5.1). The predicted woody cover estimates suggest that when woody plant cover exceeds 15-30%, depending on fire frequency and whether it was grazed, it begins to transition to woody-plant dominated watershed (Fig. 5.3). These predicted woody-plant

cover estimates are slightly lower than some of observational and modelled studies on transitions to shrubland or woodland states (Holdo et al. 2009, Ratajczak et al. 2016, 2017, Archer et al. 2017). These results demonstrate that maybe the conversion from grassland state to woody dominated state occurs at a lower woody plant cover than previously reported.

### **Spatial Bayesian breakpoint model**

The spatially varying breakpoint equation is built within a Bayesian hierarchical model. The Bayesian hierarchical spatial breakpoint model used the pelagic bioluminescent data set from Gillibrand et al (2007). The purpose of building this Bayesian hierarchical model was to determine at what depths the bioluminescent sources are no longer detectable and interpolate those depths across spatial locations between the sampling stations. The Bayesian hierarchical model had one hierarchical level, the process model and parameter model. However, within the parameter model there were several sub-models present. To answer our question, the process model is log transformed on  $\mathbf{y}$ , where  $\mathbf{y}$  is the observed bioluminescence sources. The data are continuous and spatially explicit where  $i$  is the observation number and  $j$  is the station identifier. Bioluminescent sources have a normal distribution with spatially varying intercepts and slopes ( $\beta$ ) around the breakpoints ( $\theta$ ):

$$\mathbf{Log}(y_{ij} + 0.05) \sim N(\beta_0 + X_{ij}(\theta_j)\beta_1 + X_{ij}(\theta_j)^2\beta_2 + \alpha_j, \sigma_E^2\mathbf{I}) \quad (6)$$

The process model also includes a spatial random effect ( $\alpha$ ), and an error term to determine the uncertainties within the model ( $\sigma_E^2\mathbf{I}$ ).

In the parameter model the betas were all normally distributed and a ‘vague’ hyperparameter ( $\sigma_\beta^2$ ) initial value set at 1000 (Model 7).

$$\beta \sim N(\mathbf{0}, \sigma_\beta^2) \quad (7)$$

The breakpoint parameter,  $\theta$ , is estimated from a logit-link function that incorporates the deepest sea floor depth from all spatial locations as the numerator, the denominator has the parameter  $\phi$  incorporated into the logistic function:

$$\theta = \frac{\textit{deepest depth of sea floor}}{\mathbf{1} + \exp^{-\phi}} \quad (8)$$

The parameter  $\phi$  is the individual breakpoint for a single sampling station, it is a multivariate normal distribution with the mean depth of observed bioluminescent sources with a corresponding uncertainty estimation ( $\sigma_\phi^2$ ) from a correlation matrix ( $\mathbf{C}(\rho_\phi)$ ):

$$\phi \sim \textit{MVN}(\boldsymbol{\mu}_\phi, \sigma_\phi^2 \mathbf{C}(\rho_\phi)) \quad (9)$$

The spatial random effect ( $\boldsymbol{\alpha}$ ) is a Gaussian process multivariate normal distribution and the spatial uncertainties ( $\sigma_\alpha^2$ ) estimated with a correlation matrix ( $\mathbf{C}(\rho_\alpha)$ ) (Cressie and Wikle 2011):

$$\boldsymbol{\alpha} \sim \textit{MVN}(\mathbf{0}, \sigma_\alpha^2 \mathbf{C}(\rho_\alpha)) \quad (10)$$

The error term ( $\sigma_E^2$ ) was estimated using an inverse gamma distribution and identity matrix ( $\mathbf{I}$ ):

$$\sigma_E^2 \sim \textit{IG}(2, \mathbf{1}, \mathbf{1}, I) \quad (11)$$

All other parameters listed within the parameter models are ‘vague’ hyperparameters and were given individual initial values which are listed in the R code in Appendix B.

The Bayesian hierarchical spatial breakpoint model was run with a MCMC sampling of 40,000 iterations, the model tuning parameters used an ‘adaptive random walk metropolis-hastings’ algorithm to improve tuning of parameters (Givens and Hoeting 2012). A Metropolis-Hastings algorithm was implemented within the MCMC because full conditionals were not available for each parameter and hyperparameter that was estimated. Convergence of each model was determined visually through trace plots (Hobbs and Hooten 2015). Parameter means and uncertainties were estimated after a burn-in of 10,000 iterations.



The Bayesian hierarchical spatial breakpoint model estimated breakpoints and uncertainties for each station (Fig. 4). Model estimates of breakpoints, uncertainties, and predictions of bioluminescent sources for each station were observed (Appendix B). As an example, station #15 had a mean breakpoint  $\sim 2117$  m (95% CI = 2008.19 m – 2224.64 m) (Fig. 1a). The predictions of the bioluminescent sources match well with the observed data. There was variability among the depths of each spatial breakpoint, but most breakpoints were located between 3000 m and 4000 m (Fig. 1b,c). The map of breakpoint depths shows the estimated breakpoints from each station as well as the spatial interpolation of breakpoints across the spatial extent of the map (Fig. 1c). The estimated breakpoint depths are predominantly within the range of depths from the observed values in Gillibrand et al (2007).

### **Concluding remarks**

Conservationists and managers of ecosystems often want to know when and where thresholds occur so they can improve their adaptive management strategies (Suding and Hobbs 2009, Toms and Villard 2015, Foley et al. 2015). Estimating temporal and spatial breakpoints can provide insight into ecosystem functioning, potential community dynamics, or species-specific requirements for management (Huggett 2005, Reyer et al. 2015). Current methods for the determination of ecological breakpoints can identify breakpoints and with post-hoc analyses estimate the variance around the breakpoint (Toms and Lesperance 2003). Combining breakpoint models within a Bayesian hierarchical framework allows for improved breakpoint inferences, as well as more accurate predictions (Wade 2000, Ketz et al. 2016, Lee et al. 2017).

The results presented from the temporal and spatial Bayesian hierarchical breakpoint models developed here were able to estimate breakpoints from their posterior distributions with corresponding uncertainties and predict 95% credible intervals surrounding the true data (Figs.

3;4). These results are encouraging because it is now possible to obtain a breakpoint from the mean of the posterior distribution as well as know the uncertainties surrounding that mean. Also, using the posterior distribution of breakpoints it is possible to predict credible intervals that can inform where data should be located. These predicted credible intervals can also aid in creating forecast models for determining future breakpoints (Wikle 2003, Luo et al. 2011, Dietze et al. 2018).

Temporal and spatial Bayesian hierarchical breakpoint models are just platforms for improving how we quantitatively estimate breakpoints. These models have the capability to fit any data distribution or include covariates because they have a Bayesian hierarchical model framework (Baker and King 2010, Hooten and Hobbs 2015, Wikle et al. 2019). For example, improvements to the woody expansion Bayesian hierarchical temporal breakpoint model could include adding covariates such as traits from individual woody plant species to observe which species cause increases in plant cover over time. The inclusion of covariates within these models will improve inferences made on ecological drivers or processes (Dietze et al. 2018). Another step toward improving these models will be to include both spatial and temporal parameters to create a spatio-temporal breakpoint model. Bayesian hierarchical spatio-temporal breakpoint models would allow for more accurate detection of when and where thresholds occur in systems. A good application would be invasive species management. Through Bayesian spatio-temporal breakpoint analyses, managers would be able to monitor treatment effects from invasive species management prescriptions. Results from these models would help inform how to allocate resources for management (Suding and Hobbs 2009). Creating and implementing Bayesian breakpoint models are not the only method to determine thresholds, but they do offer increased insights into potential drivers that cause the underlying thresholds.

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## **Data accessibility**

The Konza LTER plant composition data are archived at the Environmental Data Initiative (EDI) <https://doi.org/10.6073/pasta/f7b9965ec6efa5247a97059bcdaf4a1b> (Hartnett D., S. Collins. 2019). The pelagic bioluminescence data are found in Gillibrand et al. 2007 and as a text file at <http://www.highstat.com/index.php/mixed-effects-models-and-extensions-in-ecology-with-r>

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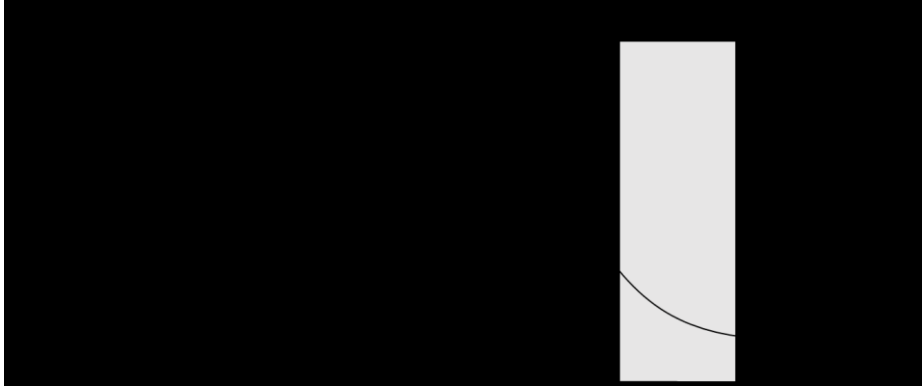


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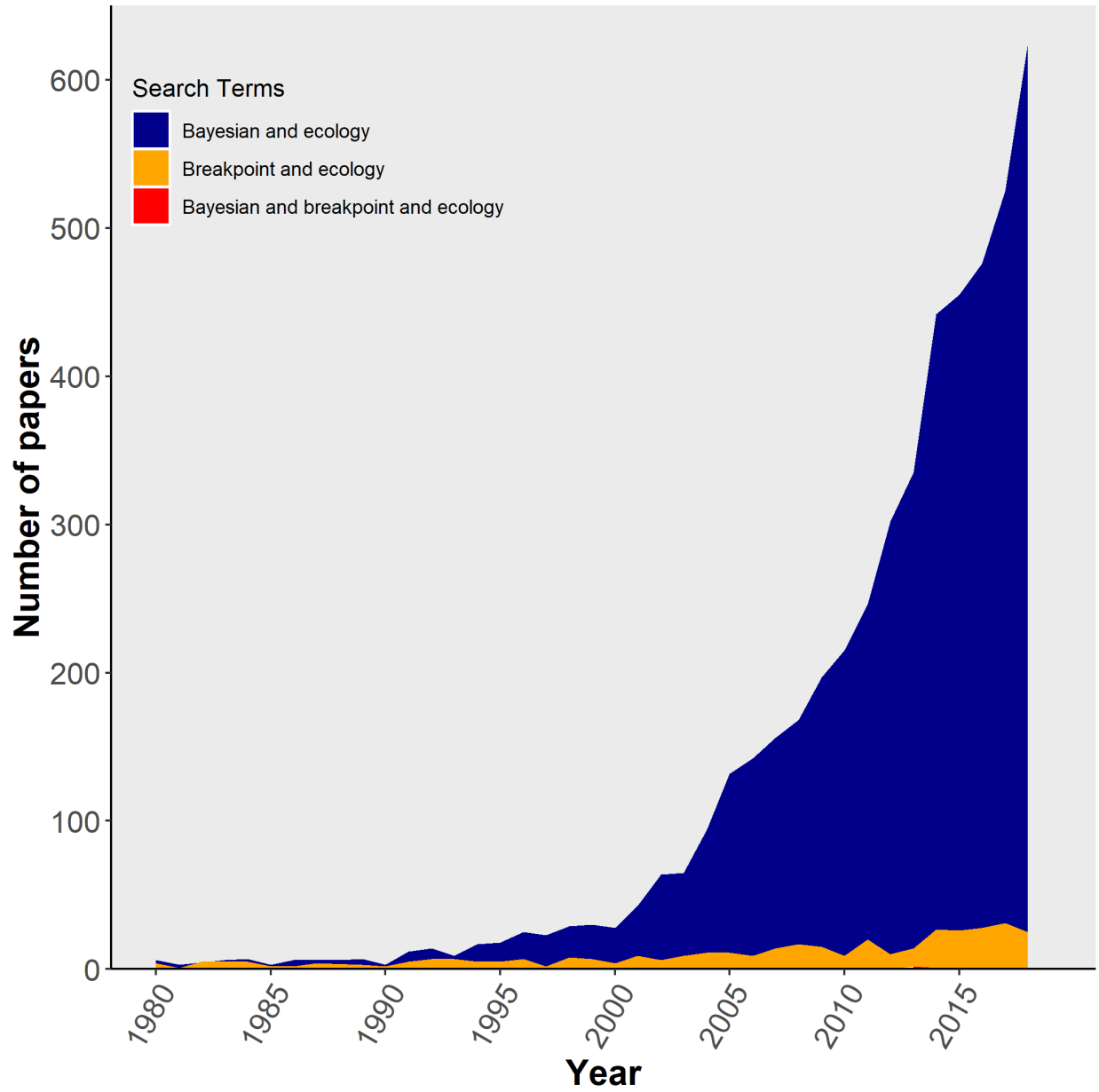
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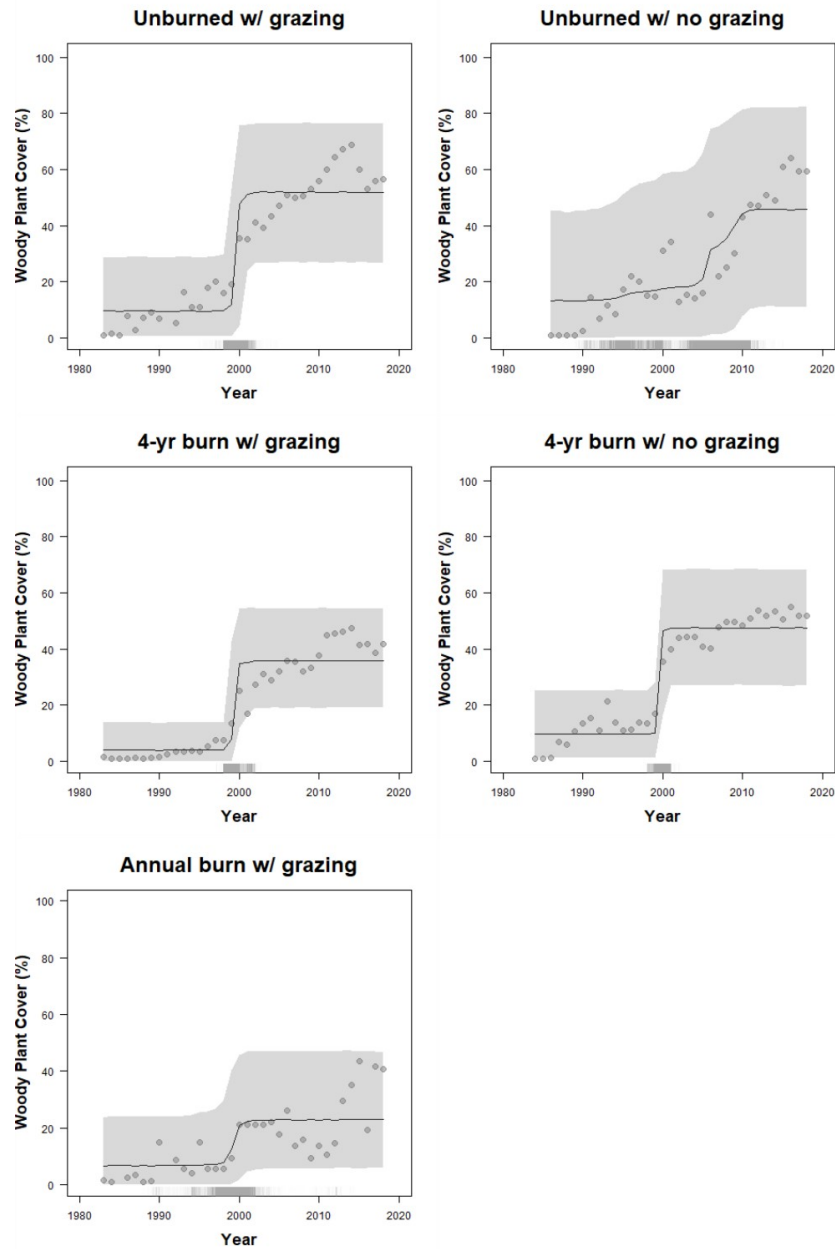
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**Figure 5.1. Examples of two different types of thresholds. (a) A breakpoint threshold with no transition and (b) a breakpoint threshold with a transition. The dotted line in (a) is the breakpoint. The grey area in (b) is the breakpoint in the transition area.**



**Figure 5.2. Results of a Web of Science search for number of articles per search string since 1980 to 2018. Bayesian and breakpoint and ecology only had one paper in 2017.**

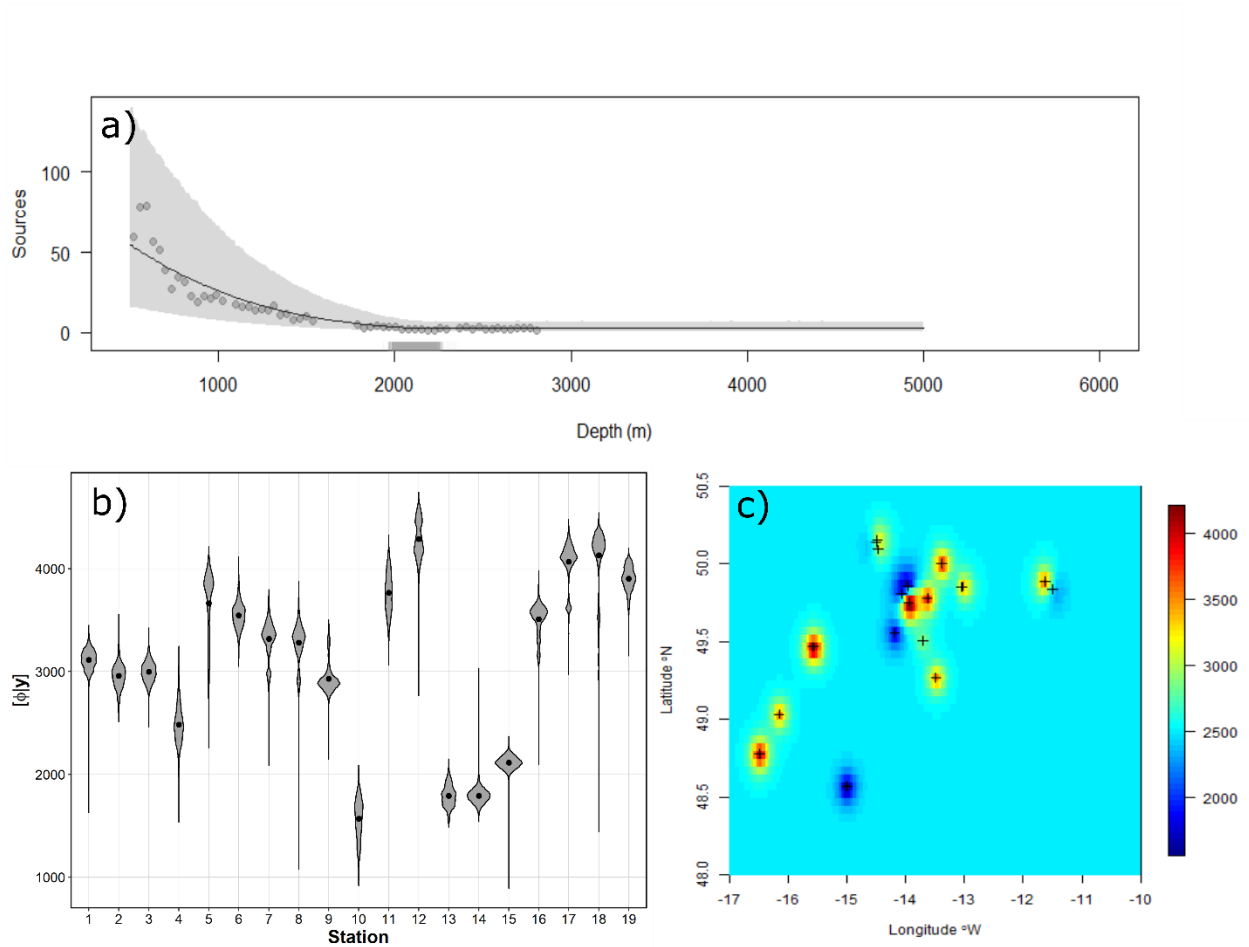


**Figure 5.3. The grey circles are the observed woody plant cover (%). The black line represents the predicted woody plant cover and associated 95% prediction intervals (grey shaded region) for the posterior distributions of the true woody plant cover (%) before and after the breakpoint on KPBS watersheds during 1983 – 2018. The grey rug represents the breakpoint (year(s)) when woody plant cover became dominant cover type. (For ease of interpretation and convention proportional data was multiplied by 100 to make it into percentages)**

**Table 5.1 Posterior means and 95% credible intervals of the breakpoints (years) for each KPBS watershed treatment.**

<b>Grassland treatments</b>	<b>Breakpoint (95% CI)</b>
Annually burned grazed	1999 (1996, 2001)
4-yr burned grazed	1999 (1998, 2000)
Unburned grazed	1999 (1998, 2001)
4-yr burned ungrazed	1999 (1998, 2000)
Unburned ungrazed	2004 (1992, 2010)





**Figure 5.4. Breakpoints of pelagic bioluminescent source data. a) Station 15 breakpoint at the depth of when bioluminescent sources are near zero. Grey circles are observed source data, with the black line as the predicted sources in the breakpoint model with the grey shading as the 95% credible interval surrounding the predicted sources. The grey rug is the estimated depth at which breakpoints likely are found. b) Violin plots of the estimated breakpoints for each station with the mean estimated breakpoint (black dot). c) The spatial breakpoint map showing the locations (latitude °N and longitude °W) of each station (black crosses) with the estimated breakpoint and corresponding latent spatially interpolated breakpoints.**

## **Chapter 6 - Management of woody plants in temperate grasslands**

Native woody plants in grasslands are extremely resilient to both biotic and abiotic stresses in their respective grasslands. Woody plants in grasslands have evolved life history and physiological strategies to coexist in a dynamic system where multiple disturbances (i.e., fire, herbivory, drought) strongly regulate the plant communities (McNaughton 1985, Brown and Archer 1999, Augustine and McNaughton 2004, Holdo et al. 2009, Ascoli et al. 2013). One life history trait exhibited by many woody plants in grasslands is the ability to resprout from belowground organs or epicormic buds on aboveground stems after a disturbance (Canadell and Lopez-Soria 1998, Hajny et al. 2011, Pausas and Keeley 2014, Pausas et al. 2016). Resprouting success post-disturbance comes from the woody plants' ability to store carbohydrates in stems, roots, or storage tissues (i.e., rhizomes, caudex, lignotubers) for reallocation (Bond and Midgley 2003, Clarke et al. 2016). Carbohydrate storage in stem and belowground tissues is a major physiological trait that gives resprouting plants an advantage over non-resprouting woody plants for post-disturbance survival and growth. Another physiological trait that many woody plants in grasslands have are roots that extend deep into the soil profile to access perennial water (Nippert and Knapp 2007, Eggemeyer et al. 2008, Nippert et al. 2013, Kulmatiski and Beard 2013, Holdo and Nippert 2015). As a functional group, resprouting woody plants have contributed to the woody encroachment issue that ranchers, pastoralists, land managers and conservationists are confronting in many of our grasslands today (Hoffmann et al. 2004, Briggs et al. 2005, Gignoux et al. 2009, Stevens et al. 2017, Manea and Leishman 2019).

In the United State of America, 355 million Ha (40%) of rangeland are experiencing woody encroachment (Pacala et al. 2001, Anadón et al. 2014) and continues to grow between 0.5% in xeric grasslands and 2.3% in mesic grasslands annually (Archer et al. 2017). One of the

main causes for growth of woody plants is the mismanagement of grasslands over a century (Samson et al. 2004, Sherow 2007, Archer and Predick 2014). The mismanagement of grasslands at the local level has limited or removed prescribed fire, focused on grazing only, and the lack of maintenance of field windbreaks has helped perpetuate woody plant encroachment (Holdo et al. 2009, Wilcox et al. 2018a, Donovan et al. 2018).

In 2012, Tanaka et al. reported that between 2005 and 2009 the Natural Resource Conservation Service (NRCS) spent \$129 million for brush management and prescribed fire in the United States which helped treat 34 million Ha. Of the \$129 million the NRCS used nationally, \$96 million was used to treat 18 million Ha in the Great Plains states, with the state of Kansas using \$4.5 million to treat less than 1 million Ha (Tanaka et al. 2012). The help from the NRCS is a start -- however the rate of increase is far exceeding our ability to effectively treat all the necessary areas cost effectively (Leis et al. 2017). In the Flint Hills, fire is still used as the primary treatment to maintain tallgrass prairie. It is predicted that 56% of the area will be converted to shrubland or woodland if more landowners/managers do not implement more frequent prescribed fires (Ratajczak et al. 2016). However, prescribed fire is only one of the tools necessary to remove woody plants. In the tallgrass prairie many woody plants resprout which requires additional active management strategies such as herbicide, bush cutting or logging, and browsing.

Since the late 1940's in the tallgrass prairie, landowners and land managers have used herbicides (i.e., picloram; triclopyr; 2,4-D or 2,4,5-T; dicamba) to control woody plants (Bovey et al. 1968, Bragg and Hulbert 1976, Scholtz et al. 2018). Herbicide applications were successful in eliminating some of the woody plants (resprouters and non-resprouters) but it did not eliminate all woody plants and it required repeat herbicide application (Bragg and Hulbert 1976).

Recent research has shown that the combination of herbicide application and prescribed fire does reduce woody plant expansion by 25%, but still does not eliminate the woody plants entirely (Scholtz et al. 2018). Like prescribed fire, herbicide is a tool that can be used to reduce woody plant abundance but because resprouting woody plants store carbohydrates it is necessary to understand their physiology to know when and how to decrease their stored carbohydrates to apply effective management treatments (Janicke and Fick 1998).

Management of resprouting woody plants requires a multifaceted approach. The use of all tools available (fire, herbicide, brush cutting/logging, browsing) with monitoring becomes necessary for adaptive management of woody encroached grasslands (Wilmer et al. 2017, Wilcox et al. 2018b). Success in grassland restoration from woody encroachment will be from implementing multiple tools and working with surrounding landowners/managers. One of the largest challenges is to create a continuous fuel load of grass beneath woody plants to carry a fire. Some methods to achieve this is browsing, brush cutting or mowing (Chapter 2, Packard and Mutel 2005, Allred et al. 2011, Archer et al. 2017). Once there is continuity in herbaceous fuels between woody plants, use of prescribed fire to eliminate woody plant aboveground biomass should be applied. After the fire, the continuation of browsing, brush cutting/mowing, or use of a systemic herbicide is necessary. These active treatments will take a few growing seasons but should result in large reductions in both resprouting and non-resprouting woody plants. The continued application of prescribed fire will further eliminate new cohorts of woody plants from establishing. Removing woody plants from encroached grasslands is expensive and time intensive. However, if we want to improve our grasslands for conservation, livelihoods and future generations it is imperative that restoration occurs now.

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## References

Please see individual chapters for references.

## Appendix A - For Chapter 2

**Table A.1 Type 3 ANOVA table of results for browse treatment effects on *Cornus drummondii* roots non-structural carbohydrates (glucose, sucrose and starch) for the 4-yr burned and unburned locations between years. Significance levels are indicated by an asterisk (\* P = 0.05, \*\* P = 0.001, \*\*\* P < 0.001).**

	NumDF	DenDF	F value	Pr(>F)	
<b>4-yr Burned</b>					
<i>Glucose</i>					
Browse trt	1	18.155	3.946	0.062	.
Year	1	18.066	1.594	0.223	
Browse trt x Year	1	18.066	11.652	0.003	**
<i>Sucrose</i>					
Browse trt	1	36.000	9.033	0.005	**
Year	1	36.000	9.912	0.003	**
Browse trt x Year	1	36.000	6.840	0.013	*
<i>Starch</i>					
Browse trt	1	18.000	17.895	0.001	***
Year	1	18.000	0.434	0.519	
Browse trt x Year	1	18.000	6.262	0.022	*
<b>Unburned</b>					
<i>Glucose</i>					
Browse trt	1	18.277	0.025	0.876	
Year	1	17.668	0.944	0.345	
Browse trt x Year	1	17.668	0.595	0.451	
<i>Sucrose</i>					
Browse trt	1	18.000	0.713	0.410	
Year	1	18.000	1.811	0.195	
Browse trt x Year	1	18.000	0.415	0.527	
<i>Starch</i>					
Browse trt	1	17.379	3.985	0.062	.
Year	1	17.195	0.708	0.412	
Browse trt x Year	1	17.195	1.403	0.252	

Type III Analysis of Variance Table with Satterthwaite's method

## Appendix B - For Chapter 5

### *Temporal Bayesian Breakpoint Model - Woody encroachment*

Woody encroachment, the expansion of trees and shrubs into grasslands, is a global phenomenon that produces non-linear data and thresholds (Bestelmeyer et al. 2011, Ratajczak et al. 2014b).

Woody encroachment data is often collected as percent tree/shrub cover, or density (number of individuals per unit area). Both data types are spatially and temporally explicit. For the purposes of this paper we will only be addressing the temporal structure of percent cover data. The data comes from the Konza Prairie Long Term Ecological Research (LTER) database. The Konza Prairie LTER is an NSF funded ecological research program located at the Konza Prairie Biological Station (KPBS) in the tallgrass prairie, a mesic grassland, in North America. KPBS is a 3,487 ha preserve for the tallgrass prairie that is also a landscape scale experiment with replicated watershed-level treatments manipulating fire frequency and ungulate grazing. Within a subset of these watershed treatments, plant community composition data is collected (PVC02), this is the data we used in our Bayesian hierarchical temporal breakpoint model. The plant community composition data has been collected every year since 1983. Plant community composition data was collected by use of a 10 m<sup>2</sup> circular frame and every plant species present was recorded with its cover class. The plant cover class was determined visually using a modified Daubenmire cover classification method (Bailey and Poulton 1968). Ratajczak et al (2014, 2017) showed that over several decades a mesic grassland converted to a shrubland or woodland through changes in fire frequency using this same data. We used this data to estimate when thresholds were crossed for these watersheds. The specific watersheds analyzed are a mix of ungrazed sites with fire frequencies of every 4 years (4b), and 20 years (20b), as well as grazed sites with an annual (n1b), 4-year (n4d), and 20-year (n20b) fire frequency. The reason

that we are not analyzing an annually burned site that is ungrazed is because there are no woody plants recorded over a 0.5 m in height (Ratajczak et al. 2014b).

To analyze this data set, we focused on similar woody encroaching species as Ratajczak et al (2017). The woody species present in the watersheds are: *Celtis occidentalis*, *Cercis canadensis*, *Cornus drummondii*, *Crataegus moll*, *Gleditsia triacanthos*, *Juniperus virginiana*, *Morus alba*, *Prunus americana*, *Rhus aromatica*, *Rhus glabra*, *Ulmus americana*, *Ulmus rubra*, and *Zanthoxylum americanum*. For each watershed we summed the cover of each woody species together and then set the maximum percent of cover as 99.999% and then divided the data by 100 to make it proportional (between 0 and 1). The processing of the data and the full analysis of the model can be found in the R code provided below.

### ***Spatial breakpoint model – Pelagic bioluminescent source depth***

The pelagic bioluminescent data set comes from a study done in the Porcupine Seabight and Porcupine Abyssal plain area of the NE Atlantic Ocean off of the coast of Ireland (Fig. B.1; Gillibrand et al. 2007). Bioluminescent organisms were measured at 19 sampling times and location during the spring and fall of 2001 and 2002. At each of these locations and times a measure of bioluminescent organisms was conducted from depths of 500 m to the sea floor (740 m – 4808 m). To measure the density of bioluminescent organisms a downward looking ISIT (intensified silicon intensified target) camera with a horizontal screen mounted onto an unmanned free-fall lander vehicle was used to collect the data. To analyze the bioluminescence source data, we log transformed it and added 0.05 to normalize data. The rest of the data processing and model analysis can be found in the R code provided below.



**Figure B.1** Spatial locations of bioluminescent sources sampling stations in the North Atlantic Ocean.

### *Implementation of models*

We used Program R V3.4.3 (R Core Team 2017) to conduct all data analyses. R packages and code for both Bayesian breakpoint models are provided in the R code below. Posterior means, 95% credible and predicted intervals are provided for all parameters and hyperparameters. These values can be calculated from the supplied R code. Model convergences were assessed visually using diagnostic plots for all parameters (Hooten and Hobbs 2015, Hooten and Hefley 2019, Wikle et al. 2019). Appropriate burn-ins were then assessed and implemented from the diagnostic plots. We are only reporting the estimated breakpoint values ( $[\theta|y]$ ) in the results sections of Chapter 5 because these are the breakpoints being estimated and thus the parameter of ecological importance.

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*R Code*

## **Bayesian hierarchical temporal breakpoint model R Code**

Packages needed for analysis

```
knitr::opts_chunk$set(message=FALSE, warning=FALSE, tidy=TRUE, cache=TRUE)
```

```
library(tidyverse)
```

```
## Registered S3 methods overwritten by 'ggplot2':
```

```
## method      from  
## [.quosures  rlang  
## c.quosures  rlang  
## print.quosures rlang
```

```
## -- Attaching packages ----- tidyverse 1.2.1 --
```

```
## v ggplot2 3.1.1   v purrr  0.3.2  
## v tibble  2.1.3   v dplyr  0.8.1  
## v tidyr   0.8.3   v stringr 1.4.0  
## v readr   1.3.1   v forcats 0.4.0
```

```
## -- Conflicts ----- tidyverse_conflicts() --
```

```
## x dplyr::filter() masks stats::filter()  
## x dplyr::lag()   masks stats::lag()
```

```
library(knitr)
```

```
library(latex2exp)
```

```
library(MASS)
```

```
##
```

```
## Attaching package: 'MASS'
```

```
## The following object is masked from 'package:dplyr':
```

```
##  
## select
```

```
library(mgcv)
```

```
## Loading required package: nlme
```

```
##
```

```
## Attaching package: 'nlme'
```

```
## The following object is masked from 'package:dplyr':
```

```
##  
## collapse
```

```
## This is mgcv 1.8-28. For overview type 'help("mgcv-package")'.
```

Bring in Konza species composition cover data from the Konza LTER database PVC02. Also bring in the species code list but that had to be downloaded first from the Konza prairie LTER website (<http://lter.konza.ksu.edu/content/pvc02-plant-species-composition-selected-watersheds-konza-prairie>).

```

# Konza plant composition data
plant.comp <- readr::read_csv("http://lter.konza.ksu.edu/sites/default/files/data/PVC021.csv",
  col_names = TRUE)
# Konza plant species list
spec.list <- read.csv("sp_list.csv", header = TRUE)

```

Plant composition cover data needs to be cleaned up and cover class values need to be changed to proportional cover values between 0 and 1. I am also just interested in 6 watersheds on Konza that have been used in previous woody encroachment studies.

Konza Watersheds \* Ungrazed + 1D -> Annually burned + 4B -> 4-yr burned + 20B ->

Unburned \* Grazed + n1B -> Annually burned + n4D -> 4-yr burned + n20B -> Unburned

```

# Plant composition dataset cleanup Remove unnecessary columns
plant.comp <- plant.comp[, -c(7, 11, 12, 14, 15)]

## Correct and convert data types
plant.comp$WaterShed <- as.factor(plant.comp$WaterShed)
plant.comp$Transect <- as.factor(plant.comp$Transect)

## Convert Daubenmire cover classes to midpoint percents and remove NA's
plant.comp <- plant.comp %>% mutate(Cover.percent = as.numeric(case_when(Cover ==
  1 ~ 0.01, Cover == 2 ~ 0.025, Cover == 3 ~ 0.15, Cover == 4 ~ 0.375, Cover ==
  5 ~ 0.625, Cover == 6 ~ 0.85, Cover == 7 ~ 0.975, TRUE ~ 0)))

## Filter out watersheds of interest, using same watershed from Ratajczak et
## al 2014 (Ecology)
plant.comp <- plant.comp %>% filter(WaterShed %in% c("001d", "004b", "020b",
  "n01b", "n04d", "n20b")) %>% droplevels()

```

Cleaning up the species list to make it joinable to plant.comp dataframe.

```

# Plant species list Remove unnecessary columns
spec.list <- spec.list[, -c(2, 3, 10)]

## Changing name to match plant composition dataset
names(spec.list)[1] <- "SpeCode"

## Remove NA's from data
spec.list[spec.list == "."] <- NA
spec.list <- na.omit(spec.list)

## Combine Genus and species names into 1 column
spec.list <- unite_(spec.list, "Genus_species", c("genus", "species"), sep = "_")
spec.list <- droplevels(spec.list)

```

Joining plant.comp and spec.list dfs by their species codes. I am also filtering by woody plants that occur on Konza that are larger than 0.5m in height. Also, we are filling in 0's for all woody species to get an accurate summation of the data.

```

plant.full <- plant.comp %>%
  dplyr::full_join(spec.list, by = "SpeCode") %>%
  filter(life.form=="w" & Genus_species %in% c("acer_negundo", "aesculus_glabra", "asimina_t
riloba", "carya_cordiformis", "celtis_occidentalis", "cercis_canadensis", "cornus_drummondii", "cr
ataegus_mollis", "euonymus_atropurpureus", "fraxinus_pennsylvanica", "gleditsia_triacanthos", "g
ymnocladus_dioicus", "juglans_nigra", "juniperus_virginiana", "maclura_pomifera", "morus_alba"
, "morus_rubra", "platanus_occidentalis", "populus_deltoides", "prunus_americana", "prunus_pumil
a", "prunus_virginiana", "pyrus_calleryana", "quercus_macrocarpa", "quercus_muehlenbergii", "rhu
s_aromatica", "rhus_glabra", "robinia_pseudo-acacia", "salix_amygdaloides", "salix_exigua", "salix
_nigra", "sambucus_canadensis", "tilia_americana", "ulmus_americana", "ulmus_rubra", "zanthoxy
lum_americanum")) %>%
  na.omit() %>%
  droplevels()

plant.full$Genus_species <- as.factor(plant.full$Genus_species)

plant.wide <- plant.full %>%
  mutate(i = row_number()) %>%
  spread(Genus_species, Cover.percent, fill = 0)

plant.comb <- plant.wide %>%
  gather(Genus_species, Cover.percent, 16:28)

```

Choose woody plants that are larger than 1m in height. I also only want a maximum of 100% cover to simplify model.

```

woody.plot <- plant.comb %>%
  group_by(RecYear, WaterShed, Transect, Plot) %>%
  summarize(cover = max(Cover.percent))%>%
  droplevels()
#summarize(cover = if_else(sum(Cover.percent) >= 0.999, 0.999, sum(Cover.percent)))%>%

woody.transect <- woody.plot %>%
  group_by(RecYear, WaterShed, Transect) %>%
  summarize(cover = mean(cover))%>%
  droplevels()

woody <- woody.transect %>%
  group_by(RecYear, WaterShed) %>%
  summarize(cover = mean(cover))%>%
  droplevels()

```

Plotting all of the different watersheds and how woody plant cover changes over time.



```
colnames(woody)[2] <- "watershed"
```

```
burn.annually <- rep(0,36)
```

```
years <- as.numeric(c(1983:2018))
```

```
par(mfrow = c(3,2))
```

```
plot(woody$RecYear[woody$watershed=="001d"], woody$cover[woody$watershed=="001d"],
las = 1, xlim = c(1983, 2018), ylim = c(0, 1), xlab = "Year", ylab = "Woody Cover (%)", col = rgb(0, 0, 0, 0.25), pch = 19, main = "Annually burned w/ no grazing")
```

```
points(years, burn.annually, col = rgb(0, 0, 0, 0.25), pch = 19)
```

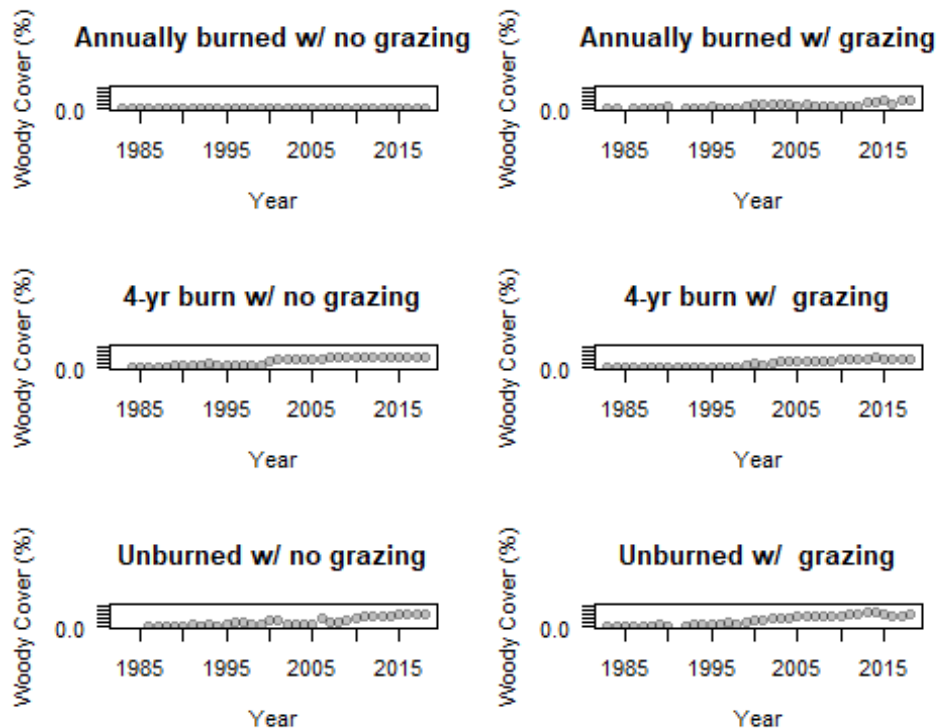
```
plot(woody$RecYear[woody$watershed=="n01b"], woody$cover[woody$watershed=="n01b"],
las = 1, xlim = c(1983, 2018), ylim = c(0, 1), xlab = "Year", ylab = "Woody Cover (%)", col = rgb(0, 0, 0, 0.25), pch = 19, main = "Annually burned w/ grazing")
```

```
plot(woody$RecYear[woody$watershed=="004b"], woody$cover[woody$watershed=="004b"],
las = 1, xlim = c(1983, 2018), ylim = c(0, 1), xlab = "Year", ylab = "Woody Cover (%)", col = rgb(0, 0, 0, 0.25), pch = 19, main = "4-yr burn w/ no grazing")
```

```
plot(woody$RecYear[woody$watershed=="n04d"], woody$cover[woody$watershed=="n04d"],
las = 1, xlim = c(1983, 2018), ylim = c(0, 1), xlab = "Year", ylab = "Woody Cover (%)", col = rgb(0, 0, 0, 0.25), pch = 19, main = "4-yr burn w/ grazing")
```

```
plot(woody$RecYear[woody$watershed=="020b"], woody$cover[woody$watershed=="020b"],
las = 1, xlim = c(1983, 2018), ylim = c(0, 1), xlab = "Year", ylab = "Woody Cover (%)", col = rgb(0, 0, 0, 0.25), pch = 19, main = "Unburned w/ no grazing")
```

```
plot(woody$RecYear[woody$watershed=="n20b"], woody$cover[woody$watershed=="n20b"],
las = 1, xlim = c(1983, 2018), ylim = c(0, 1), xlab = "Year", ylab = "Woody Cover (%)", col = rgb(0, 0, 0, 0.25), pch = 19, main = "Unburned w/ grazing")
```



I am taking out watershed 1D, annually burned ungrazed because it does not have any woody plants >1m present and it will not run well in the model.

Subsetting the data by watersheds.

```
woody.4b <- droplevels(woody[which(woody$watershed == "004b"), ])  
woody.20b <- droplevels(woody[which(woody$watershed == "020b"), ])  
woody.n01b <- droplevels(woody[which(woody$watershed == "n01b"), ])  
woody.n04d <- droplevels(woody[which(woody$watershed == "n04d"), ])  
woody.n20b <- droplevels(woody[which(woody$watershed == "n20b"), ])
```

Global functions

Beta distribution functions to run the models with  $\mu$  and  $\sigma^2$ . The equations for the shapes comes from page 326 in Stroup 2013 (Generalized Linear Mixed Models). The inverse gamma PDF comes from Hooten and Hefley 2019 (Bringing Bayesian Models to Life). Because we are using a beta distribution an inverse logit link function is necessary to use linear models.

```
r.beta <- function(n, mu, sigma2) {  
  shape1 <- mu * sigma2  
  shape2 <- (1 - mu) * sigma2  
  rbeta(n, shape1, shape2) #this is from r base  
}  
  
d.beta <- function(x, mu, sigma2, log) {  
  shape1 <- mu * sigma2  
  shape2 <- (1 - mu) * sigma2  
  dbeta(x, shape1 = shape1, shape2 = shape2, log = log) #this is from r base  
}  
  
# Inverse gamma pdf  
dIG <- function(x, q, r) {  
  (r^q/gamma(q)) * x^(-(q + 1)) * exp(-r/x)  
}  
  
# Inverse logit link function  
ilogit <- function(x) (1/(1 + exp(-x)))
```

MCMC sampling of Bayesian hierarchical temporal breakpoint model for Annually burned and grazed watershed

```
# Data setup  
y <- woody.n01b$cover  
X <- model.matrix(~woody.n01b$RecYear)
```

```

# Number of MCMC samples to draw
m.draws <- 60000

# Samples from the posterior that will be saved
samples <- matrix(, m.draws + 1, dim(X)[2] + 2)
colnames(samples) <- c(colnames(X), "sigma2", "phi")

# Starting values
samples[1, ] <- c(-2, 6, 10, 1998) #betas, sigma2

# Priors
sigma2.beta <- 10 #Prior variance for beta
q <- 2.1 #Inverse gamma prior with  $E() = r/(q-1)$  and  $Var() = r^2/((q-1)^2(q-2))$ 
r <- 1

# Tuning parameters
beta.tune <- 0.2
sigma2.tune <- 0.45
phi.tune <- 1/100

# MCMC algorithm
set.seed(1235)
for (k in 1:m.draws) {
  beta <- samples[k, 1:2]
  sigma2.e <- samples[k, 3]
  phi <- samples[k, 4]
  x.temp <- ifelse(woody.n01b$RecYear < phi, "a", "b")
  X <- model.matrix(~x.temp)

  # Sample beta
  beta.star <- mvrnorm(1, beta, beta.tune * solve(t(X) %*% X))

  mh1 <- sum(d.beta(y, ilogit(X %*% beta.star), sigma2.e, log = T)) + sum(dnorm(beta.star,
    0, sigma2.beta, log = T))
  mh2 <- sum(d.beta(y, ilogit(X %*% beta), sigma2.e, log = T)) + sum(dnorm(beta,
    0, sigma2.beta, log = T))

  R <- min(1, exp(mh1 - mh2))

  if (R > runif(1)) {
    beta <- beta.star
  }

  # Sample sigma2.e

```

```

sigma2.star <- rnorm(1, sigma2.e, sigma2.tune)
if (sigma2.star > 0) {

  mh1 <- sum(d.beta(y, ilogit(X %*% beta), sigma2.star, log = T)) + sum(log(dIG(sigma2.
star,
  q, r)))
  mh2 <- sum(d.beta(y, ilogit(X %*% beta), sigma2.e, log = T)) + sum(log(dIG(sigma2.e,
  q, r)))

  R <- min(1, exp(mh1 - mh2))
} else {
  R = 0
}

if (R > runif(1)) {
  sigma2.e <- sigma2.star
}

# Sample phi
phi.star <- rnorm(1, phi, phi.tune)
# phi.star <- rdunif(1, 1983, 2018)

# Change breakpoint year values for each watershed
if (phi.star > 1983 & phi.star < 2018) {
  x.temp.star <- ifelse(woody.n01b$RecYear < phi.star, "a", "b")
  X.star <- round(model.matrix(~x.temp.star))

  mh1 <- sum(d.beta(y, ilogit(X.star %*% beta), sigma2.e, log = T))
  mh2 <- sum(d.beta(y, ilogit(X %*% beta), sigma2.e, log = T))

  R <- min(1, exp(mh1 - mh2))
} else {
  R = 0
}

if (R > runif(1)) {
  phi <- phi.star
}

samples[k + 1, ] <- c(beta, sigma2.e, phi)
# if(k%%1000==0) print(k)

# Adaptive random walk M-H (see pg. 238-239 in Computational Statistics by
# Given & Hoeting). This is done because the univariate conditional density
# is not in closed form

```

```

T <- 100
if (k%%T == 0) {
  accept.rate <- length(which(abs(diff(samples[(T * (k/T - 1) + 1):(k),
    1:2])) > 0))/T
  beta.tune <- beta.tune * exp(ifelse(accept.rate > 0.44, min(0.01, 1/sqrt(k/T)),
    -min(0.01, 1/sqrt(k/T))))^2
  accept.rate <- length(which(abs(diff(samples[(T * (k/T - 1) + 1):(k),
    3])) > 0))/T
  sigma2.tune <- sigma2.tune * exp(ifelse(accept.rate > 0.44, min(0.01,
    1/sqrt(k/T)), -min(0.01, 1/sqrt(k/T))))^2
  accept.rate <- length(which(abs(diff(samples[(T * (k/T - 1) + 1):(k),
    4])) > 0))/T
  phi.tune <- phi.tune * exp(ifelse(accept.rate > 0.25, min(0.01, 1/sqrt(k/T)),
    -min(0.01, 1/sqrt(k/T))))^2
}
}

```

MCMC sampling acceptance rates of Metropolis-Hastings random walks for breakpoint equation parameters. Also trace plots presented to visually check convergence of MCMC sampling of the model.

```

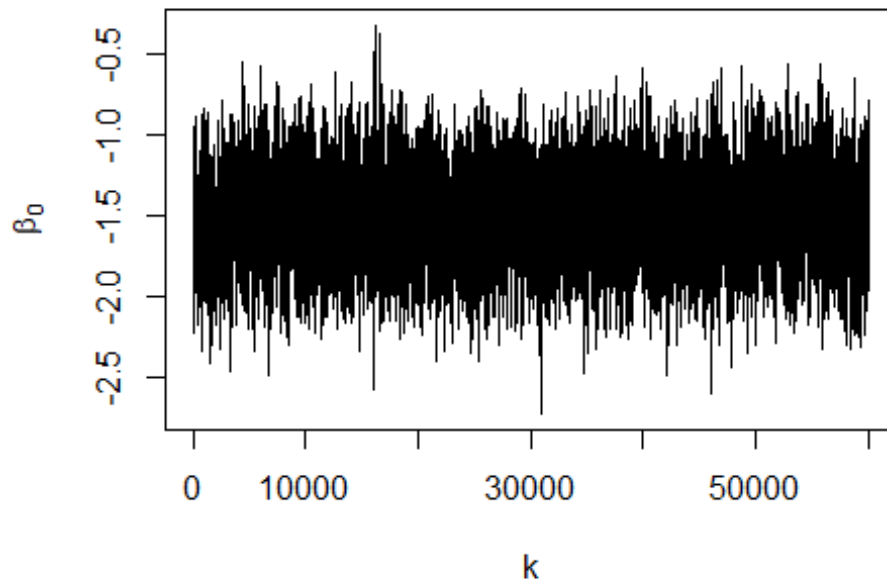
# Acceptance rates for M-H algorithm
length(which(abs(diff(samples[, 1])) > 0))/m.draws # betas
## [1] 0.3092333

length(which(abs(diff(samples[, 3])) > 0))/m.draws # sigma2
## [1] 0.4879

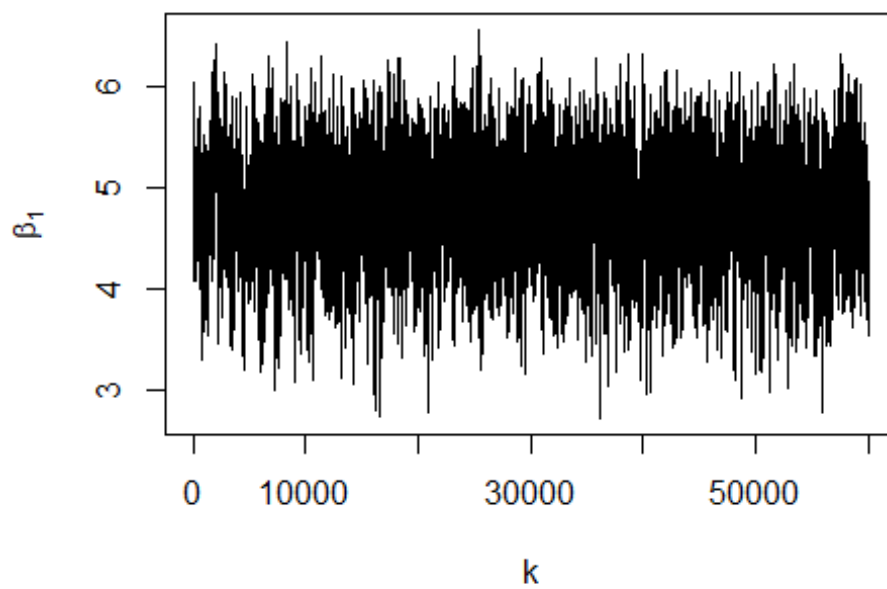
length(which(abs(diff(samples[, 4])) > 0))/m.draws # phi
## [1] 0.4934

# Trace Plots
plot(samples[, 1], typ = "l", xlab = "k", ylab = expression(beta[0]))

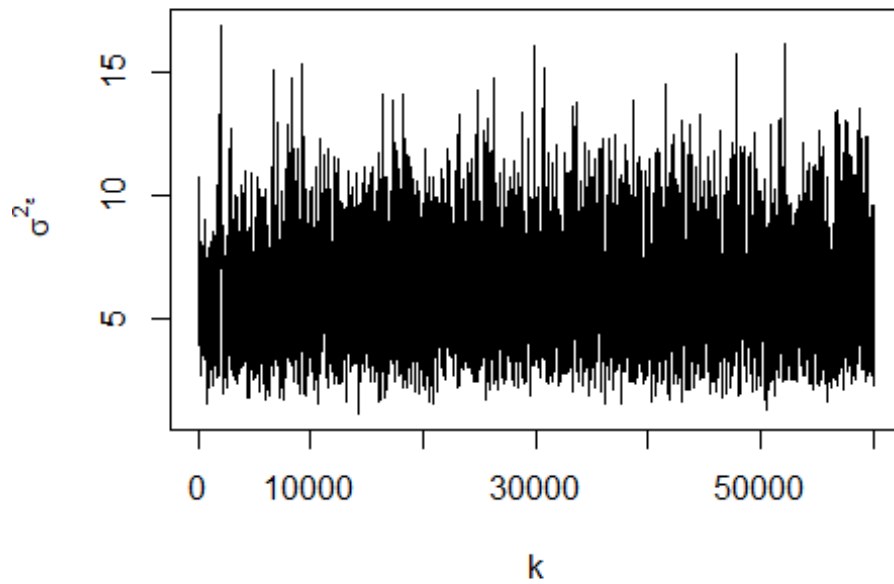
```



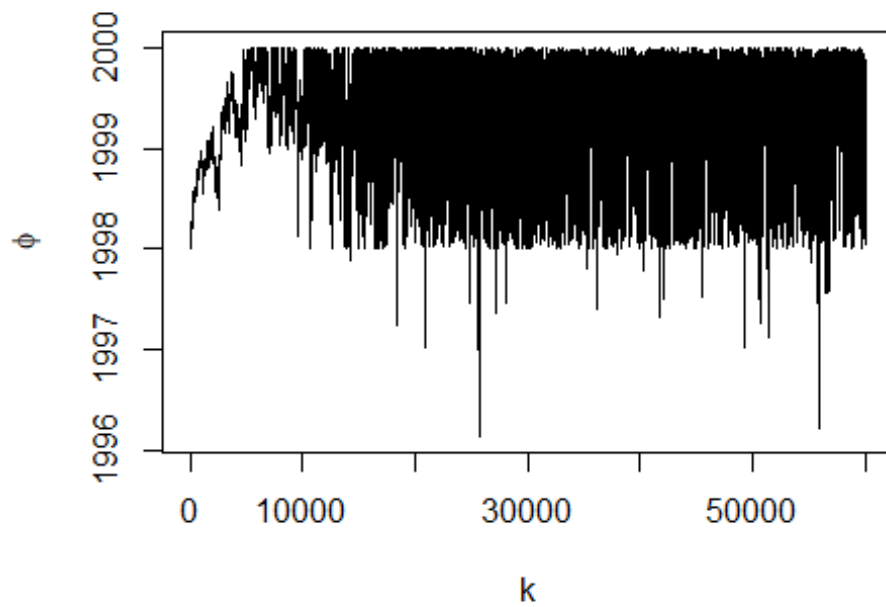
```
plot(samples[, 2], typ = "l", xlab = "k", ylab = expression(beta[1]))
```



```
plot(samples[, 3], typ = "l", xlab = "k", ylab = expression(sigma^2[epsilon]))
```



```
plot(samples[, 4], typ = "l", xlab = "k", ylab = expression(phi))
```



Output of results The mean  $E()$  of  $\beta$ 's and  $\sigma_\epsilon^2$ . Also presented are posterior distributions

of each parameter including the breakpoint.

```
burn.in <- 20000
# E() of beta and sigma2
colMeans(samples[-c(1:burn.in), ])

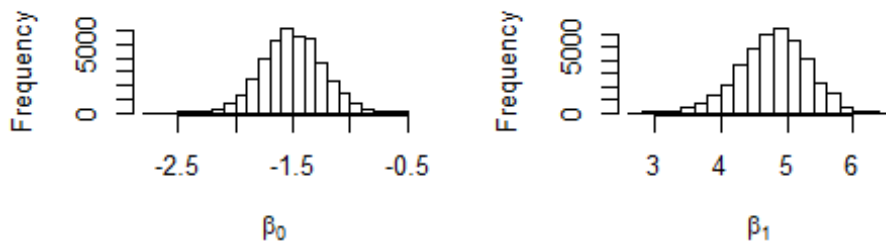
##      (Intercept) woody.n01b$RecYear      sigma2
##      -1.502160      4.798262      5.792058
##      phi
##      1999.358041

# 95% Equal-tailed CIs
apply(samples[-c(1:burn.in), ], 2, FUN = quantile, prob = c(0.025, 0.975))

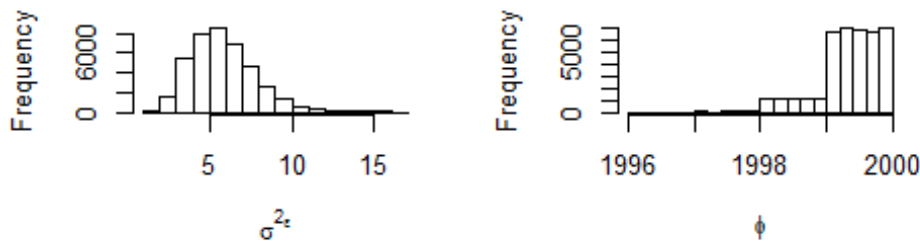
##      (Intercept) woody.n01b$RecYear      sigma2      phi
## 2.5% -2.0151899      3.728940 2.739699 1998.159
## 97.5% -0.9799642      5.746402 10.061184 1999.974

par(mfrow = c(2, 2))
hist(samples[-c(1:burn.in), 1], xlab = expression(beta[0]))
hist(samples[-c(1:burn.in), 2], xlab = expression(beta[1]))
hist(samples[-c(1:burn.in), 3], xlab = expression(sigma^2[epsilon]))
hist(samples[-c(1:burn.in), 4], xlab = expression(phi))
```

histogram of samples[-c(1:burn.in), 1] histogram of samples[-c(1:burn.in), 2]



histogram of samples[-c(1:burn.in), 3] histogram of samples[-c(1:burn.in), 4]



Final results of Bayesian hierarchical temporal breakpoint model for the Annually burned and grazed watershed.



```

# Posterior predictive distribution
burn.in <- 20000
RecYear.pred <- data.frame(RecYear = seq(1983, 2018, by = 1))
RecYear.pred <- data.frame(RecYear.pred[-c(3,9),])#woody.n01b missing two years in data
n.pred <- dim(RecYear.pred)[1]
y.pred <- matrix(, length(burn.in:m.draws), dim(RecYear.pred)[1])
ev.y.pred <- matrix(, length(burn.in:m.draws), dim(RecYear.pred)[1])

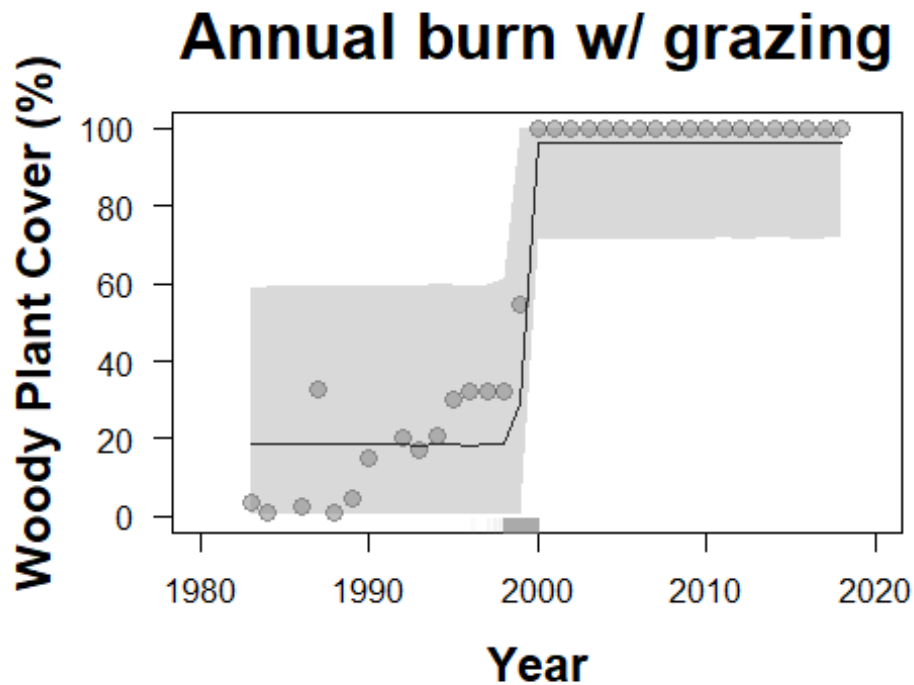
for (k in burn.in:m.draws) {
  beta <- samples[k, 1:2]
  sigma2.e <- samples[k, 3]
  phi <- samples[k, 4]

  x.temp.new <- ifelse(woody.n01b$RecYear < phi, "a", "b")
  X.new <- model.matrix(~x.temp.new)
  ev.y.pred[k - burn.in + 1, ] <- ilogit(X.new %*% beta)
  y.pred[k - burn.in + 1, ] <- r.beta(n.pred, ilogit(X.new %*% beta), sigma2.e)
  #if(k%%1000==0) print(k)
}

EV.z <- apply(y.pred,2,mean)
lwr.CI <- apply(y.pred, 2, FUN = quantile, prob = c(0.025))
upper.CI <- apply(y.pred, 2, FUN = quantile, prob = c(0.975))

#Plot of estimated breakpoint, and prediction
#png("woodyn01b_final.png")
par(mfrow = c(1, 1))
plot(woody.n01b$RecYear, woody.n01b$cover, las = 1,
  xlim=c(1980,2020), ylim = c(0,1),
  col = rgb(0,0, 0, 0.25), pch = 19, cex=1.25,
  xlab = "Year", ylab = "Woody Plant Cover (%)", cex.lab=1.5, font.lab=2, yaxt="n",
  main = "Annual burn w/ grazing", cex.main=2, font.main=2)
axis(2, at=pretty(0:1), lab=pretty(0:1) * 100, las=TRUE)
points(RecYear.pred$RecYear, EV.z, typ = "l")
polygon(c(RecYear.pred$RecYear, rev(RecYear.pred$RecYear)),
  c(lwr.CI, rev(upper.CI)), col = rgb(0.5, 0.5, 0.5, 0.3), border = NA)
rug(samples[-c(1:burn.in),4], col=rgb(0.5,0.5,0.5,0.01))

```



```
#dev.off()#close file
```

MCMC sampling of Bayesian hierarchical temporal breakpoint model for 4-yr burned and grazed watershed

```
# Data setup
```

```
y <- woody.n04d$cover
```

```
X <- model.matrix(~woody.n04d$RecYear)
```

```
# Number of MCMC samples to draw
```

```
m.draws <- 60000
```

```
# Samples from the posterior that will be saved
```

```
samples <- matrix(, m.draws + 1, dim(X)[2] + 2)
```

```
colnames(samples) <- c(colnames(X), "sigma2", "phi")
```

```
# Starting values
```

```
samples[1, ] <- c(-2, 6, 10, 1998) #betas, sigma2, and phi
```

```
# Priors
```

```
sigma2.beta <- 10 #Prior variance for beta
```

```
q <- 2.1 #Inverse gamma prior with E() = r/(q-1) and Var() = r^2/((q-1)^2(q-2))
```

```
r <- 1
```

```

# Tuning parameters
beta.tune <- 0.2
sigma2.tune <- 0.45
phi.tune <- 1/100

# MCMC algorithm
set.seed(1235)
for (k in 1:m.draws) {
  beta <- samples[k, 1:2]
  sigma2.e <- samples[k, 3]
  phi <- samples[k, 4]
  x.temp <- ifelse(woody.n04d$RecYear < phi, "a", "b")
  X <- model.matrix(~x.temp)

  # Sample beta
  beta.star <- mvrnorm(1, beta, beta.tune * solve(t(X) %*% X))

  mh1 <- sum(d.beta(y, ilogit(X %*% beta.star), sigma2.e, log = T)) + sum(dnorm(beta.star,
    0, sigma2.beta, log = T))
  mh2 <- sum(d.beta(y, ilogit(X %*% beta), sigma2.e, log = T)) + sum(dnorm(beta,
    0, sigma2.beta, log = T))

  R <- min(1, exp(mh1 - mh2))

  if (R > runif(1)) {
    beta <- beta.star
  }

  # Sample sigma2.e
  sigma2.star <- rnorm(1, sigma2.e, sigma2.tune)
  if (sigma2.star > 0) {

    mh1 <- sum(d.beta(y, ilogit(X %*% beta), sigma2.star, log = T)) + sum(log(dIG(sigma2.
star,
    q, r)))
    mh2 <- sum(d.beta(y, ilogit(X %*% beta), sigma2.e, log = T)) + sum(log(dIG(sigma2.e,
    q, r)))

    R <- min(1, exp(mh1 - mh2))
  } else {
    R = 0
  }

  if (R > runif(1)) {
    sigma2.e <- sigma2.star
  }
}

```

```

# Sample phi
phi.star <- rnorm(1, phi, phi.tune)
# phi.star <- rdunif(1, 1983, 2018)

# Change breakpoint year values for each watershed
if (phi.star > 1983 & phi.star < 2018) {
  x.temp.star <- ifelse(woody.n04d$RecYear < phi.star, "a", "b")
  X.star <- round(model.matrix(~x.temp.star))

  mh1 <- sum(d.beta(y, ilogit(X.star %*% beta), sigma2.e, log = T))
  mh2 <- sum(d.beta(y, ilogit(X %*% beta), sigma2.e, log = T))

  R <- min(1, exp(mh1 - mh2))
} else {
  R = 0
}

if (R > runif(1)) {
  phi <- phi.star
}

samples[k + 1, ] <- c(beta, sigma2.e, phi)
# if(k%%1000==0) print(k)

# Adaptive random walk M-H (see pg. 238-239 in Computational Statistics by
# Given & Hoeting). This is done because the univariate conditional density
# is not in closed form
T <- 100
if (k%%T == 0) {
  accept.rate <- length(which(abs(diff(samples[(T * (k/T - 1) + 1):(k),
1:2])) > 0))/T
  beta.tune <- beta.tune * exp(ifelse(accept.rate > 0.44, min(0.01, 1/sqrt(k/T)),
-min(0.01, 1/sqrt(k/T))))^2
  accept.rate <- length(which(abs(diff(samples[(T * (k/T - 1) + 1):(k),
3])) > 0))/T
  sigma2.tune <- sigma2.tune * exp(ifelse(accept.rate > 0.44, min(0.01,
1/sqrt(k/T)), -min(0.01, 1/sqrt(k/T))))^2
  accept.rate <- length(which(abs(diff(samples[(T * (k/T - 1) + 1):(k),
4])) > 0))/T
  phi.tune <- phi.tune * exp(ifelse(accept.rate > 0.25, min(0.01, 1/sqrt(k/T)),
-min(0.01, 1/sqrt(k/T))))^2
}
}

```

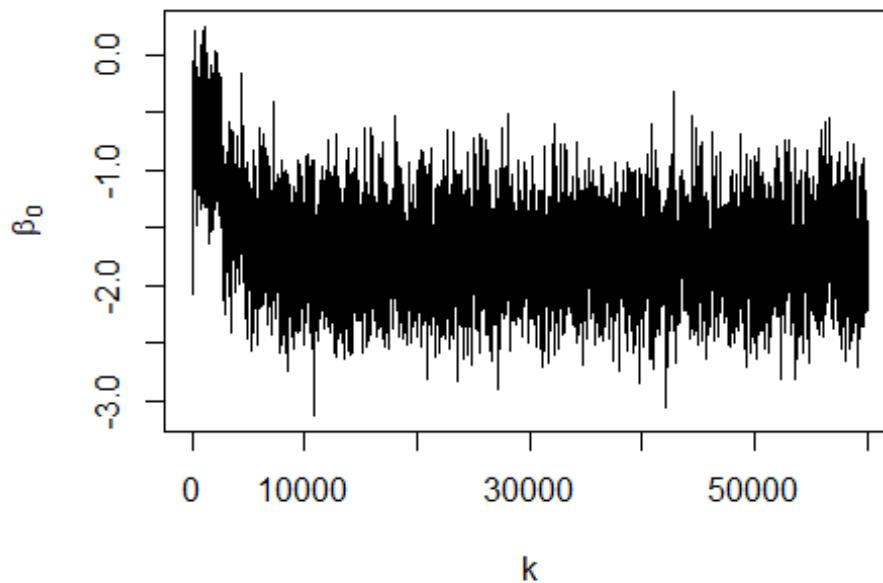
MCMC sampling acceptance rates of Metropolis-Hastings random walks for breakpoint equation parameters. Also trace plots presented to visually check convergence of MCMC sampling of the model.

```
# Acceptance rates for M-H algorithm
length(which(abs(diff(samples[, 1])) > 0))/m.draws # betas
## [1] 0.3123667

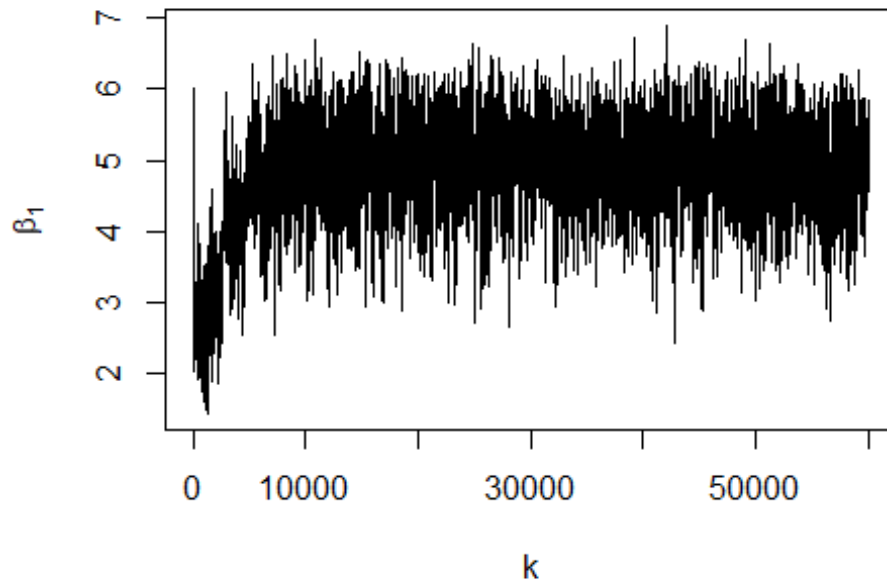
length(which(abs(diff(samples[, 3])) > 0))/m.draws # sigma2
## [1] 0.4692333

length(which(abs(diff(samples[, 4])) > 0))/m.draws # phi
## [1] 0.4936667

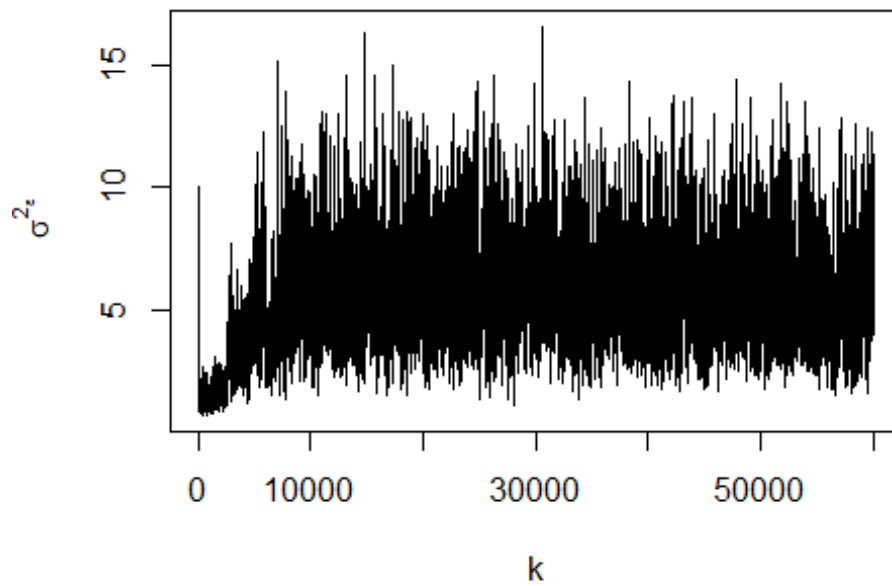
# Trace Plots
plot(samples[, 1], typ = "l", xlab = "k", ylab = expression(beta[0]))
```



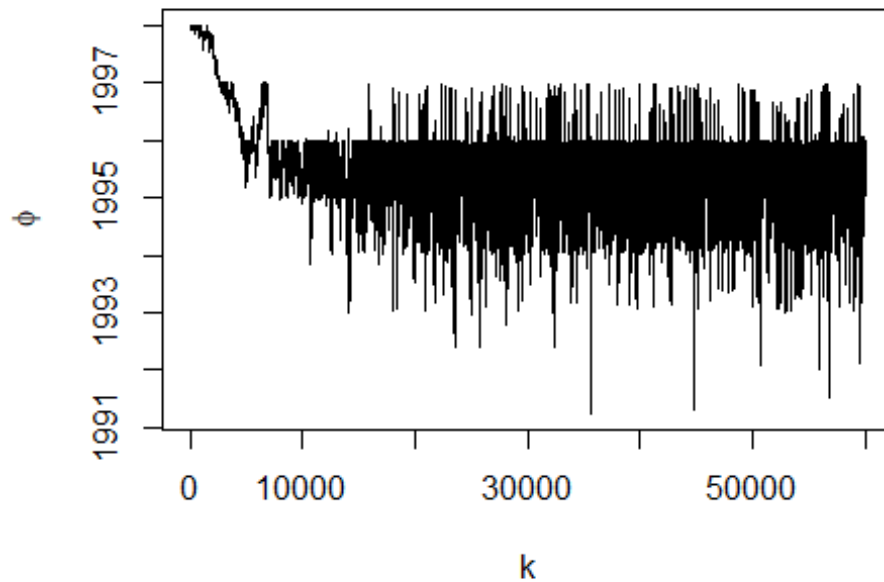
```
plot(samples[, 2], typ = "l", xlab = "k", ylab = expression(beta[1]))
```



```
plot(samples[, 3], typ = "l", xlab = "k", ylab = expression(sigma^2[epsilon]))
```



```
plot(samples[, 4], typ = "l", xlab = "k", ylab = expression(phi))
```



Output of results The mean  $E()$  of  $\beta$ 's and  $\sigma_\epsilon^2$ . Also presented are posterior distributions of each parameter including the breakpoint.

```
burn.in <- 20000
# E() of beta and sigma2
colMeans(samples[-c(1:burn.in), ])

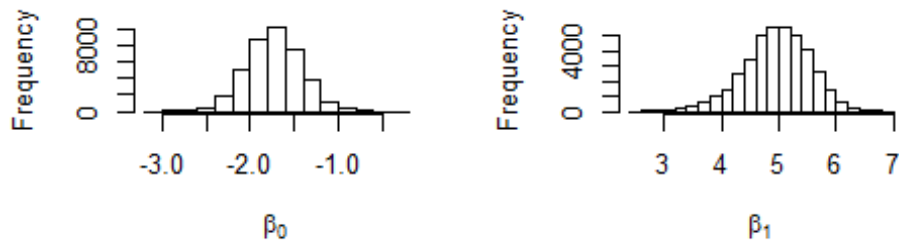
##      (Intercept) woody.n04d$RecYear      sigma2
##      -1.727093      4.962728      5.725804
##      phi
##      1995.399459

# 95% Equal-tailed CIs
apply(samples[-c(1:burn.in), ], 2, FUN = quantile, prob = c(0.025, 0.975))

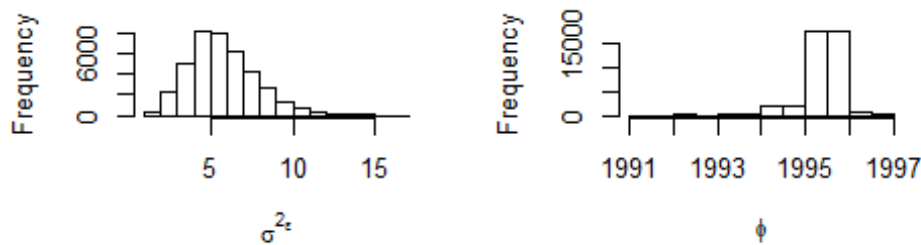
##      (Intercept) woody.n04d$RecYear      sigma2      phi
## 2.5%      -2.316713      3.746132      2.479485      1994.139
## 97.5%      -1.100169      5.977389      10.240580      1995.998

par(mfrow = c(2, 2))
hist(samples[-c(1:burn.in), 1], xlab = expression(beta[0]))
hist(samples[-c(1:burn.in), 2], xlab = expression(beta[1]))
hist(samples[-c(1:burn.in), 3], xlab = expression(sigma^2[epsilon]))
hist(samples[-c(1:burn.in), 4], xlab = expression(phi))
```

histogram of samples[-c(1:burn.in), burn.in:m.draws] for  $\beta_0$  and  $\beta_1$



histogram of samples[-c(1:burn.in), burn.in:m.draws] for  $\sigma^2_e$  and  $\phi$



Final results of Bayesian hierarchical temporal breakpoint model for the 4-yr burn and grazed watershed.

```
# Posterior predictive distribution
burn.in <- 20000
RecYear.pred <- data.frame(RecYear = seq(1983, 2018, by = 1))
n.pred <- dim(RecYear.pred)[1]
y.pred <- matrix(, length(burn.in:m.draws), dim(RecYear.pred)[1])
ev.y.pred <- matrix(, length(burn.in:m.draws), dim(RecYear.pred)[1])

for (k in burn.in:m.draws) {
  beta <- samples[k, 1:2]
  sigma2.e <- samples[k, 3]
  phi <- samples[k, 4]

  x.temp.new <- ifelse(woody.n04d$RecYear < phi, "a", "b")
  X.new <- model.matrix(~x.temp.new)
  ev.y.pred[k - burn.in + 1, ] <- ilogit(X.new %*% beta)
  y.pred[k - burn.in + 1, ] <- r.beta(n.pred, ilogit(X.new %*% beta), sigma2.e)
  #if(k%%1000==0) print(k)
}

EV.z <- apply(y.pred, 2, mean)
lwr.CI <- apply(y.pred, 2, FUN = quantile, prob = c(0.025))
```

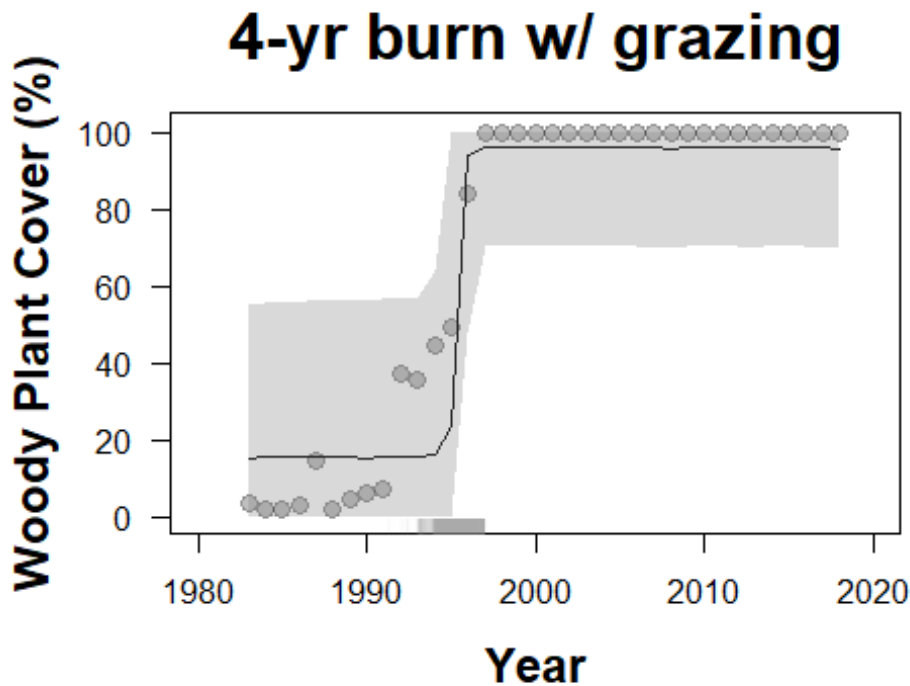


```

upper.CI <- apply(y.pred, 2, FUN = quantile, prob = c(0.975))

#Plot of estimated breakpoint, and prediction
#png("woodyn04d.png")
par(mfrow = c(1, 1))
plot(woody.n04d$RecYear, woody.n04d$cover, las = 1,
     xlim=c(1980,2020), ylim = c(0,1.01),
     col = rgb(0,0, 0, 0.25), pch = 19, cex=1.25,
     xlab = "Year", ylab = "Woody Plant Cover (%)", cex.lab=1.5, font.lab=2, yaxt="n",
     main = "4-yr burn w/ grazing", cex.main=2, font.main=2)
axis(2, at=pretty(0:1), lab=pretty(0:1) * 100, las=TRUE)
points(RecYear.pred$RecYear, EV.z, typ = "l")
polygon(c(RecYear.pred$RecYear, rev(RecYear.pred$RecYear)),
       c(lwr.CI, rev(upper.CI)), col = rgb(0.5, 0.5, 0.5, 0.3), border = NA)
rug(samples[-c(1:burn.in),4], col=rgb(0.5,0.5,0.5,0.01))

```



```
#dev.off()
```

MCMC sampling of Bayesian hierarchical temporal breakpoint model for Unburned and grazed watershed

```

# Data setup
y <- woody.n20b$cover
X <- model.matrix(~woody.n20b$RecYear)

```

```
# Number of MCMC samples to draw
```

```

m.draws <- 60000

# Samples from the posterior that will be saved
samples <- matrix(, m.draws + 1, dim(X)[2] + 2)
colnames(samples) <- c(colnames(X), "sigma2", "phi")

# Starting values
samples[1, ] <- c(-2, 6, 10, 1991) #betas, sigma2, and phi

# Priors
sigma2.beta <- 10 #Prior variance for beta
q <- 2.1 #Inverse gamma prior with  $E() = r/(q-1)$  and  $Var() = r^2/((q-1)^2(q-2))$ 
r <- 1

# Tuning parameters
beta.tune <- 0.2
sigma2.tune <- 0.45
phi.tune <- 1/100

# MCMC algorithm
set.seed(1235)
for (k in 1:m.draws) {
  beta <- samples[k, 1:2]
  sigma2.e <- samples[k, 3]
  phi <- samples[k, 4]
  x.temp <- ifelse(woody.n20b$RecYear < phi, "a", "b")
  X <- model.matrix(~x.temp)

  # Sample beta
  beta.star <- mvrnorm(1, beta, beta.tune * solve(t(X) %*% X))

  mh1 <- sum(d.beta(y, ilogit(X %*% beta.star), sigma2.e, log = T)) + sum(dnorm(beta.star,
    0, sigma2.beta, log = T))
  mh2 <- sum(d.beta(y, ilogit(X %*% beta), sigma2.e, log = T)) + sum(dnorm(beta,
    0, sigma2.beta, log = T))

  R <- min(1, exp(mh1 - mh2))

  if (R > runif(1)) {
    beta <- beta.star
  }

  # Sample sigma2.e
  sigma2.star <- rnorm(1, sigma2.e, sigma2.tune)
  if (sigma2.star > 0) {

```

```

    mh1 <- sum(d.beta(y, ilogit(X %*% beta), sigma2.star, log = T)) + sum(log(dIG(sigma2.
star,
    q, r)))
    mh2 <- sum(d.beta(y, ilogit(X %*% beta), sigma2.e, log = T)) + sum(log(dIG(sigma2.e,
    q, r)))

    R <- min(1, exp(mh1 - mh2))
  } else {
    R = 0
  }

  if (R > runif(1)) {
    sigma2.e <- sigma2.star
  }

  # Sample phi
  phi.star <- rnorm(1, phi, phi.tune)
  # phi.star <- rdunif(1, 1983, 2018)

  # Change breakpoint year values for each watershed
  if (phi.star > 1983 & phi.star < 2018) {
    x.temp.star <- ifelse(woody.n20b$RecYear < phi.star, "a", "b")
    X.star <- round(model.matrix(~x.temp.star))

    mh1 <- sum(d.beta(y, ilogit(X.star %*% beta), sigma2.e, log = T))
    mh2 <- sum(d.beta(y, ilogit(X %*% beta), sigma2.e, log = T))

    R <- min(1, exp(mh1 - mh2))
  } else {
    R = 0
  }

  if (R > runif(1)) {
    phi <- phi.star
  }

  samples[k + 1, ] <- c(beta, sigma2.e, phi)
  # if(k%%1000==0) print(k)

  # Adaptive random walk M-H (see pg. 238-239 in Computational Statistics by
  # Given & Hoeting). This is done because the univariate conditional density
  # is not in closed form
  T <- 100
  if (k%%T == 0) {
    accept.rate <- length(which(abs(diff(samples[(T * (k/T - 1) + 1):(k,
1:2]))) > 0))/T

```

```

beta.tune <- beta.tune * exp(ifelse(accept.rate > 0.44, min(0.01, 1/sqrt(k/T)),
  -min(0.01, 1/sqrt(k/T))))^2
accept.rate <- length(which(abs(diff(samples[(T * (k/T - 1) + 1):(k),
  3])) > 0))/T
sigma2.tune <- sigma2.tune * exp(ifelse(accept.rate > 0.44, min(0.01,
  1/sqrt(k/T)), -min(0.01, 1/sqrt(k/T))))^2
accept.rate <- length(which(abs(diff(samples[(T * (k/T - 1) + 1):(k),
  4])) > 0))/T
phi.tune <- phi.tune * exp(ifelse(accept.rate > 0.25, min(0.01, 1/sqrt(k/T)),
  -min(0.01, 1/sqrt(k/T))))^2
}
}

```

MCMC sampling acceptance rates of Metropolis-Hastings random walks for breakpoint equation parameters. Also trace plots presented to visually check convergence of MCMC sampling of the model.

```

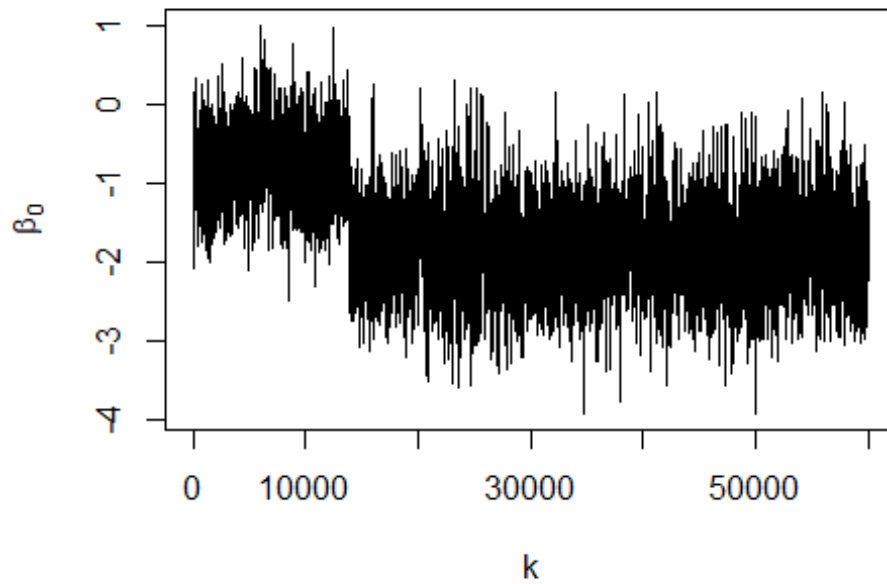
# Acceptance rates for M-H algorithm
length(which(abs(diff(samples[, 1])) > 0))/m.draws # betas
## [1] 0.32125

length(which(abs(diff(samples[, 3])) > 0))/m.draws # sigma2
## [1] 0.4685667

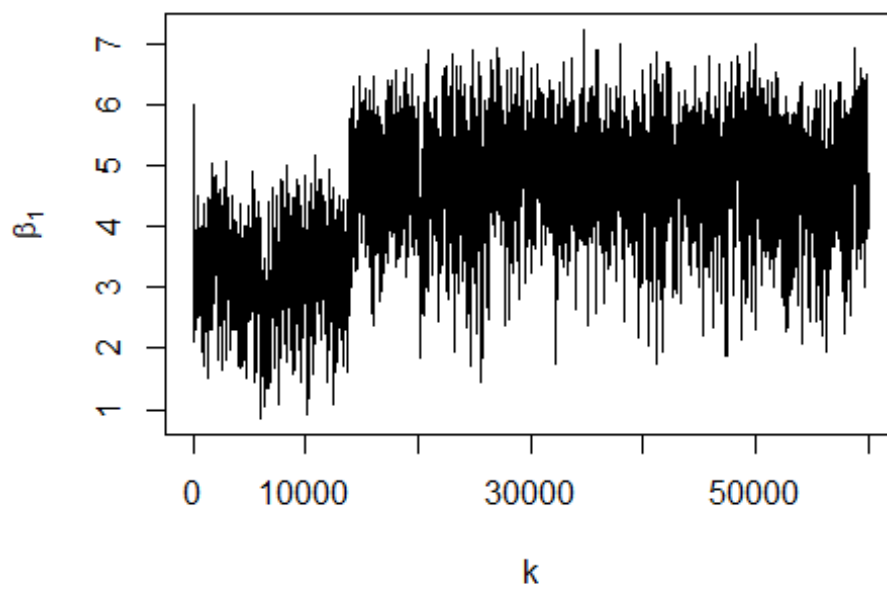
length(which(abs(diff(samples[, 4])) > 0))/m.draws # phi
## [1] 0.4946667

# Trace Plots
plot(samples[, 1], typ = "l", xlab = "k", ylab = expression(beta[0]))

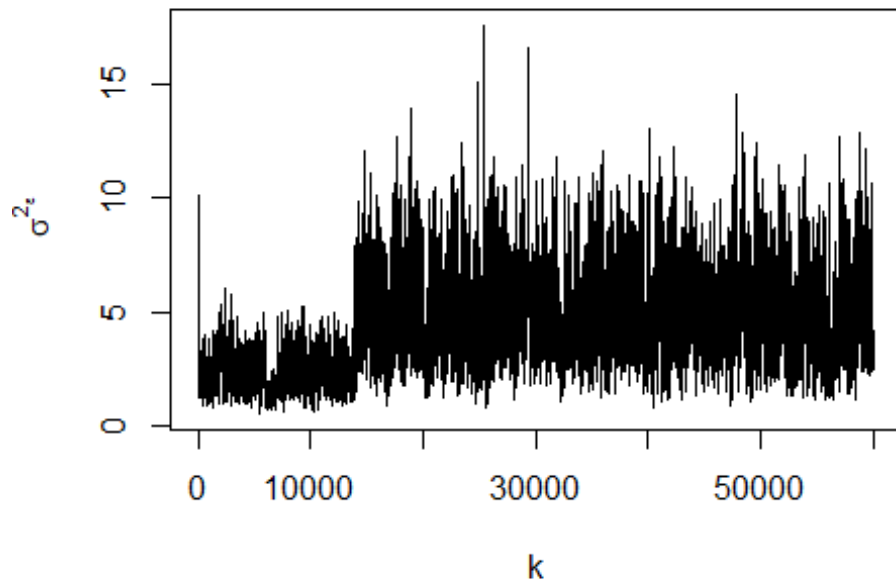
```



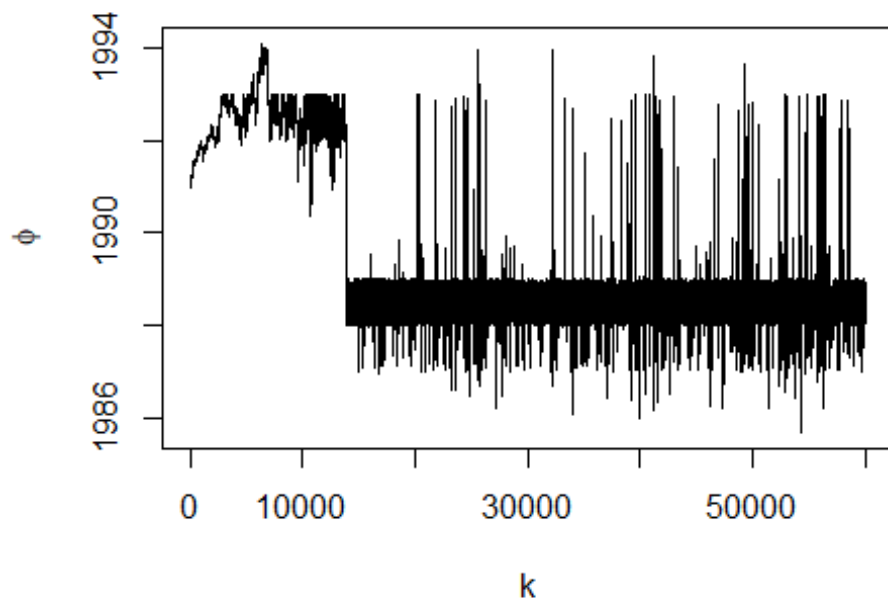
```
plot(samples[, 2], typ = "l", xlab = "k", ylab = expression(beta[1]))
```



```
plot(samples[, 3], typ = "l", xlab = "k", ylab = expression(sigma^2[epsilon]))
```



```
plot(samples[, 4], typ = "l", xlab = "k", ylab = expression(phi))
```



Output of results The mean  $E()$  of  $\beta$ 's and  $\sigma_\epsilon^2$ . Also presented are posterior distributions of each parameter including the breakpoint.

```
burn.in <- 20000
# E() of beta and sigma2
colMeans(samples[-c(1:burn.in), ])

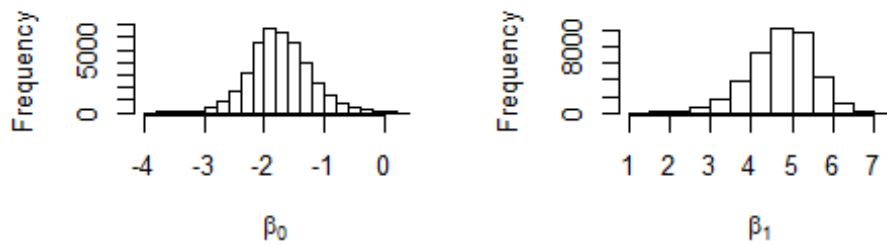
##      (Intercept) woody.n20b$RecYear      sigma2
##      -1.745338      4.733488      4.732533
##      phi
##      1988.600040

# 95% Equal-tailed CIs
apply(samples[-c(1:burn.in), ], 2, FUN = quantile, prob = c(0.025, 0.975))

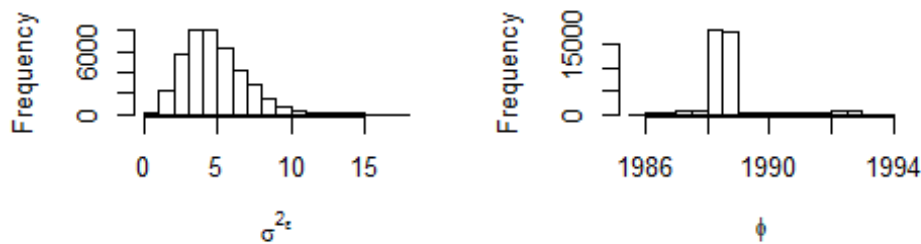
##      (Intercept) woody.n20b$RecYear sigma2 phi
## 2.5% -2.7208211      3.011418 1.643694 1987.540
## 97.5% -0.6644856      6.102950 9.142747 1992.132

par(mfrow = c(2, 2))
hist(samples[-c(1:burn.in), 1], xlab = expression(beta[0]))
hist(samples[-c(1:burn.in), 2], xlab = expression(beta[1]))
hist(samples[-c(1:burn.in), 3], xlab = expression(sigma^2[epsilon]))
hist(samples[-c(1:burn.in), 4], xlab = expression(phi))
```

histogram of samples[-c(1:burn.in), 1] histogram of samples[-c(1:burn.in), 2]



histogram of samples[-c(1:burn.in), 3] histogram of samples[-c(1:burn.in), 4]



Final results of Bayesian hierarchical temporal breakpoint model for the Unburned and grazed watershed.

```

# Posterior predictive distribution
burn.in <- 20000
RecYear.pred <- data.frame(RecYear = seq(1983, 2018, by = 1))
RecYear.pred <- data.frame(RecYear.pred[-9,])#woody.n20b missing one year in the data
n.pred <- dim(RecYear.pred)[1]
y.pred <- matrix(, length(burn.in:m.draws), dim(RecYear.pred)[1])
ev.y.pred <- matrix(, length(burn.in:m.draws), dim(RecYear.pred)[1])

for (k in burn.in:m.draws) {
  beta <- samples[k, 1:2]
  sigma2.e <- samples[k, 3]
  phi <- samples[k, 4]

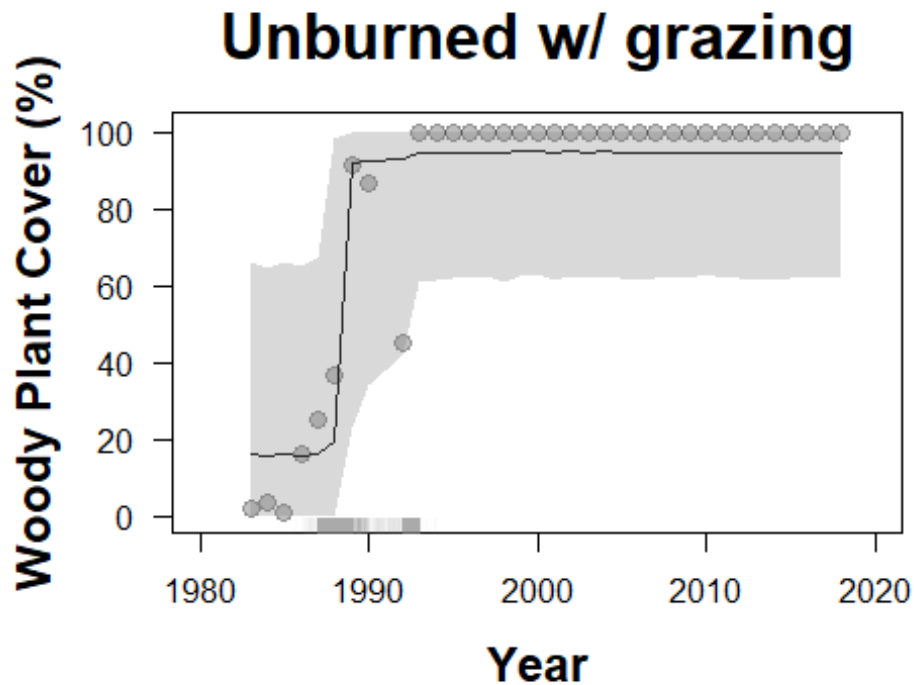
  x.temp.new <- ifelse(woody.n20b$RecYear < phi, "a", "b")
  X.new <- model.matrix(~x.temp.new)
  ev.y.pred[k - burn.in + 1, ] <- ilogit(X.new %*% beta)
  y.pred[k - burn.in + 1, ] <- r.beta(n.pred, ilogit(X.new %*% beta), sigma2.e)
  #if(k%%1000==0) print(k)
}

EV.z <- apply(y.pred,2,mean)
lwr.CI <- apply(y.pred, 2, FUN = quantile, prob = c(0.025))
upper.CI <- apply(y.pred, 2, FUN = quantile, prob = c(0.975))

#Plot of estimated breakpoint, and prediction
#png("woodyn20b.png")
par(mfrow = c(1, 1))
plot(woody.n20b$RecYear, woody.n20b$cover, las = 1,
      xlim=c(1980,2020), ylim = c(0,1.01),
      col = rgb(0,0, 0, 0.25), pch = 19, cex=1.25,
      xlab = "Year", ylab = "Woody Plant Cover (%)", cex.lab=1.5, font.lab=2, yaxt="n",
      main = "Unburned w/ grazing", cex.main=2, font.main=2)
axis(2, at=pretty(0:1), lab=pretty(0:1) * 100, las=TRUE)
points(RecYear.pred$RecYear, EV.z, typ = "l")
polygon(c(RecYear.pred$RecYear, rev(RecYear.pred$RecYear)),
        c(lwr.CI, rev(upper.CI)), col = rgb(0.5, 0.5, 0.5, 0.3), border = NA)
rug(samples[-c(1:burn.in),4], col=rgb(0.5,0.5,0.5,0.01))

```





```
#dev.off()
```

MCMC sampling of Bayesian hierarchical temporal breakpoint model for 4-yr burn and ungrazed watershed

```
# Data setup
```

```
y <- woody.4b$cover
```

```
X <- model.matrix(~woody.4b$RecYear)
```

```
# Number of MCMC samples to draw
```

```
m.draws <- 60000
```

```
# Samples from the posterior that will be saved
```

```
samples <- matrix(, m.draws + 1, dim(X)[2] + 2)
```

```
colnames(samples) <- c(colnames(X), "sigma2", "phi")
```

```
# Starting values
```

```
samples[1, ] <- c(-2, 6, 10, 1991) #betas, sigma2, and phi
```

```
# Priors
```

```
sigma2.beta <- 10 #Prior variance for beta
```

```
q <- 2.1 #Inverse gamma prior with E() = r/(q-1) and Var() = r^2/((q-1)^2(q-2))
```

```
r <- 1
```

```

# Tuning parameters
beta.tune <- 0.2
sigma2.tune <- 0.45
phi.tune <- 1/100

# MCMC algorithm
set.seed(1235)
for (k in 1:m.draws) {
  beta <- samples[k, 1:2]
  sigma2.e <- samples[k, 3]
  phi <- samples[k, 4]
  x.temp <- ifelse(woody.4b$RecYear < phi, "a", "b")
  X <- model.matrix(~x.temp)

  # Sample beta
  beta.star <- mvrnorm(1, beta, beta.tune * solve(t(X) %*% X))

  mh1 <- sum(d.beta(y, ilogit(X %*% beta.star), sigma2.e, log = T)) + sum(dnorm(beta.star,
    0, sigma2.beta, log = T))
  mh2 <- sum(d.beta(y, ilogit(X %*% beta), sigma2.e, log = T)) + sum(dnorm(beta,
    0, sigma2.beta, log = T))

  R <- min(1, exp(mh1 - mh2))

  if (R > runif(1)) {
    beta <- beta.star
  }

  # Sample sigma2.e
  sigma2.star <- rnorm(1, sigma2.e, sigma2.tune)
  if (sigma2.star > 0) {

    mh1 <- sum(d.beta(y, ilogit(X %*% beta), sigma2.star, log = T)) + sum(log(dIG(sigma2.
star,
    q, r)))
    mh2 <- sum(d.beta(y, ilogit(X %*% beta), sigma2.e, log = T)) + sum(log(dIG(sigma2.e,
    q, r)))

    R <- min(1, exp(mh1 - mh2))
  } else {
    R = 0
  }

  if (R > runif(1)) {
    sigma2.e <- sigma2.star
  }
}

```

```

# Sample phi
phi.star <- rnorm(1, phi, phi.tune)
# phi.star <- rdunif(1, 1983, 2018)

# Change breakpoint year values for each watershed
if (phi.star > 1984 & phi.star < 2018) {
  x.temp.star <- ifelse(woody.4b$RecYear < phi.star, "a", "b")
  X.star <- round(model.matrix(~x.temp.star))

  mh1 <- sum(d.beta(y, ilogit(X.star %*% beta), sigma2.e, log = T))
  mh2 <- sum(d.beta(y, ilogit(X %*% beta), sigma2.e, log = T))

  R <- min(1, exp(mh1 - mh2))
} else {
  R = 0
}

if (R > runif(1)) {
  phi <- phi.star
}

samples[k + 1, ] <- c(beta, sigma2.e, phi)
# if(k%%1000==0) print(k)

# Adaptive random walk M-H (see pg. 238-239 in Computational Statistics by
# Given & Hoeting). This is done because the univariate conditional density
# is not in closed form
T <- 100
if (k%%T == 0) {
  accept.rate <- length(which(abs(diff(samples[(T * (k/T - 1) + 1):(k),
1:2])) > 0))/T
  beta.tune <- beta.tune * exp(ifelse(accept.rate > 0.44, min(0.01, 1/sqrt(k/T)),
-min(0.01, 1/sqrt(k/T))))^2
  accept.rate <- length(which(abs(diff(samples[(T * (k/T - 1) + 1):(k),
3])) > 0))/T
  sigma2.tune <- sigma2.tune * exp(ifelse(accept.rate > 0.44, min(0.01,
1/sqrt(k/T)), -min(0.01, 1/sqrt(k/T))))^2
  accept.rate <- length(which(abs(diff(samples[(T * (k/T - 1) + 1):(k),
4])) > 0))/T
  phi.tune <- phi.tune * exp(ifelse(accept.rate > 0.25, min(0.01, 1/sqrt(k/T)),
-min(0.01, 1/sqrt(k/T))))^2
}
}

```

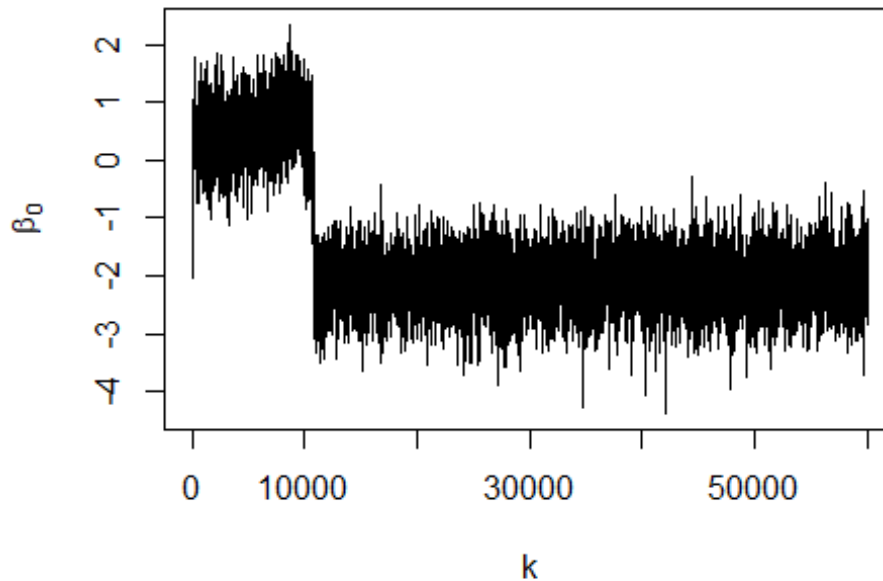
MCMC sampling acceptance rates of Metropolis-Hastings random walks for breakpoint equation parameters. Also trace plots presented to visually check convergence of MCMC sampling of the model.

```
# Acceptance rates for M-H algorithm
length(which(abs(diff(samples[, 1])) > 0))/m.draws # betas
## [1] 0.3195667

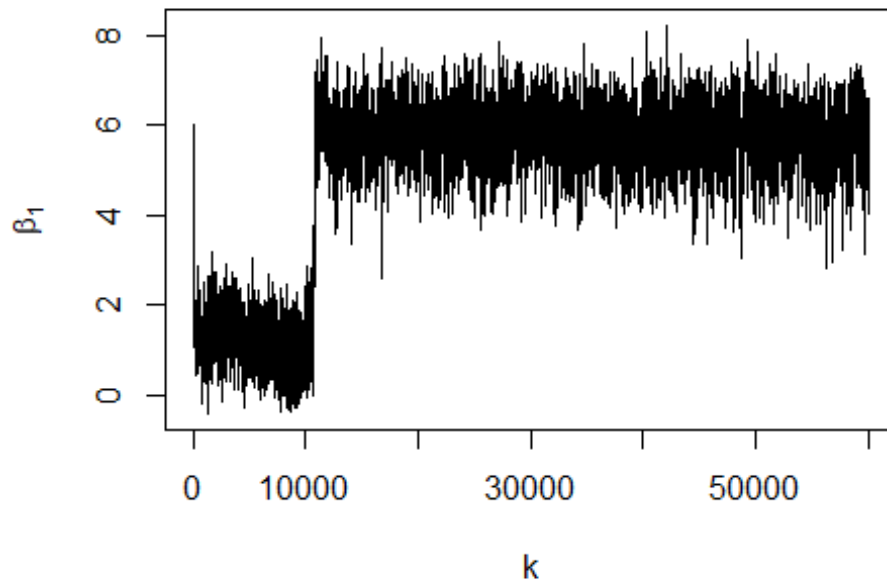
length(which(abs(diff(samples[, 3])) > 0))/m.draws # sigma2
## [1] 0.5117

length(which(abs(diff(samples[, 4])) > 0))/m.draws # phi
## [1] 0.4874167

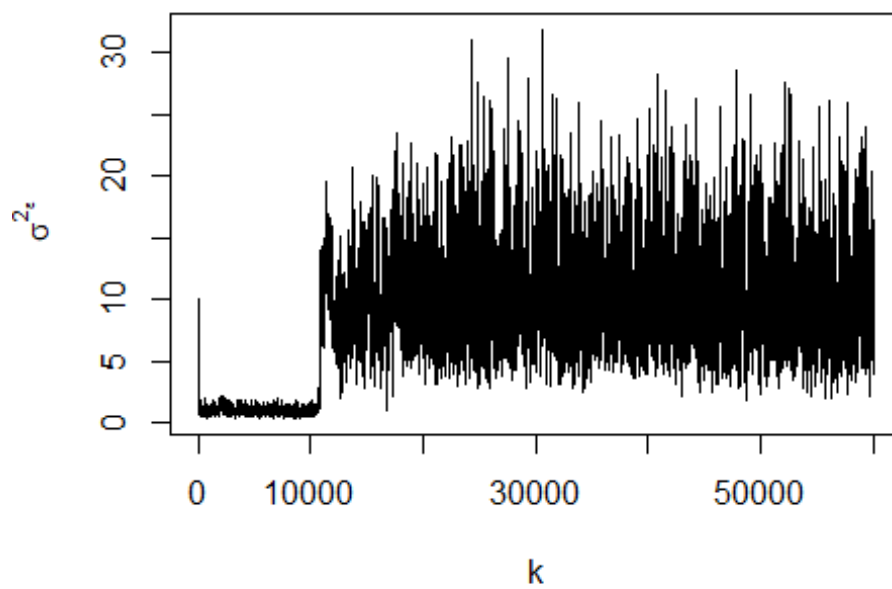
# Trace Plots
plot(samples[, 1], typ = "l", xlab = "k", ylab = expression(beta[0]))
```



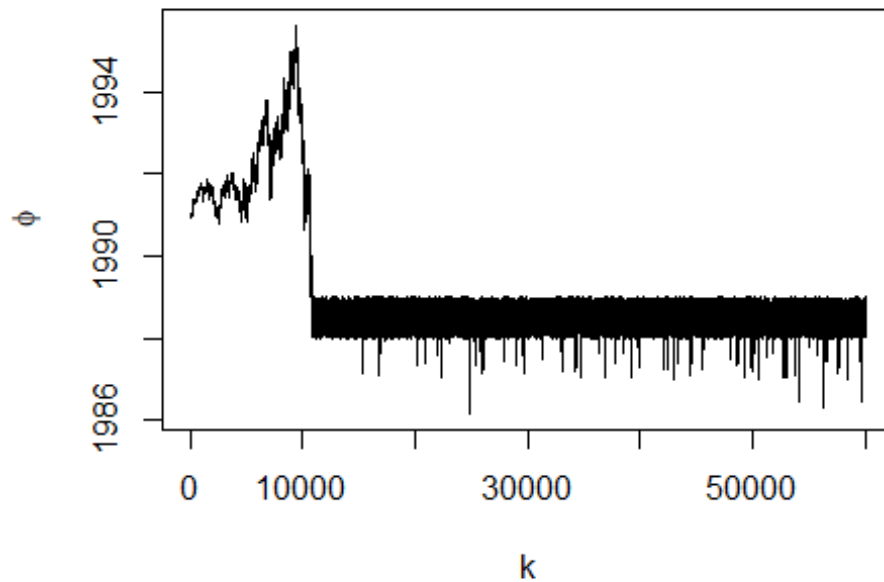
```
plot(samples[, 2], typ = "l", xlab = "k", ylab = expression(beta[1]))
```



```
plot(samples[, 3], typ = "l", xlab = "k", ylab = expression(sigma^2[epsilon]))
```



```
plot(samples[, 4], typ = "l", xlab = "k", ylab = expression(phi))
```



Output of results The mean  $E()$  of  $\beta$ 's and  $\sigma_\epsilon^2$ . Also presented are posterior distributions of each parameter including the breakpoint.

```

burn.in <- 20000
# E() of beta and sigma2
colMeans(samples[-c(1:burn.in), ])

## (Intercept) woody.4b$RecYear sigma2 phi
## -2.039266 5.752382 10.024496 1988.484619

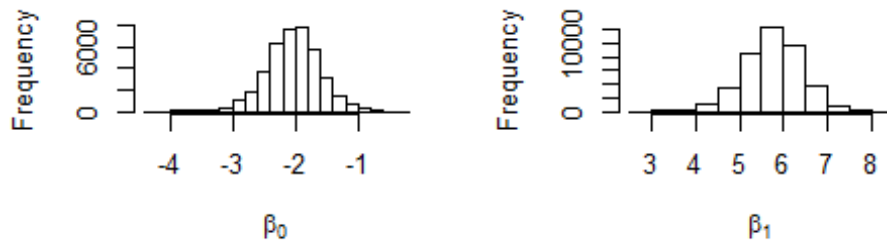
# 95% Equal-tailed CIs
apply(samples[-c(1:burn.in), ], 2, FUN = quantile, prob = c(0.025, 0.975))

## (Intercept) woody.4b$RecYear sigma2 phi
## 2.5% -2.916985 4.423258 3.805272 1988.014
## 97.5% -1.219668 6.913051 19.369836 1988.974

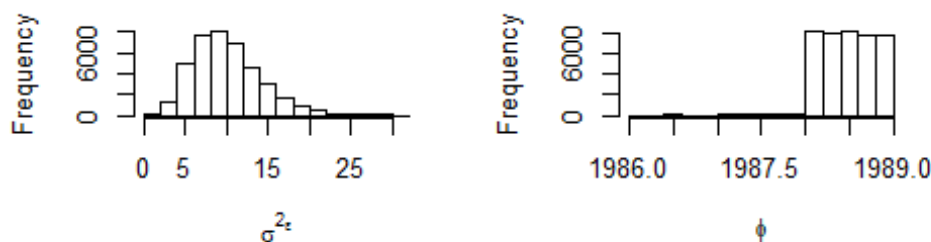
par(mfrow = c(2, 2))
hist(samples[-c(1:burn.in), 1], xlab = expression(beta[0]))
hist(samples[-c(1:burn.in), 2], xlab = expression(beta[1]))
hist(samples[-c(1:burn.in), 3], xlab = expression(sigma^2[epsilon]))
hist(samples[-c(1:burn.in), 4], xlab = expression(phi))

```

### histogram of samples[-c(1:burn.in)] histogram of samples[-c(1:burn.in)]



### histogram of samples[-c(1:burn.in)] histogram of samples[-c(1:burn.in)]



Final results of Bayesian hierarchical temporal breakpoint model for the 4-yr burn and ungrazed watershed.

```
# Posterior predictive distribution
burn.in <- 20000
RecYear.pred <- data.frame(RecYear = seq(1984, 2018, by = 1))#woody.4b starts at 1984
n.pred <- dim(RecYear.pred)[1]
y.pred <- matrix(, length(burn.in:m.draws), dim(RecYear.pred)[1])
ev.y.pred <- matrix(, length(burn.in:m.draws), dim(RecYear.pred)[1])

for (k in burn.in:m.draws) {
  beta <- samples[k, 1:2]
  sigma2.e <- samples[k, 3]
  phi <- samples[k, 4]

  x.temp.new <- ifelse(woody.4b$RecYear < phi, "a", "b")
  X.new <- model.matrix(~x.temp.new)
  ev.y.pred[k - burn.in + 1, ] <- ilogit(X.new %*% beta)
  y.pred[k - burn.in + 1, ] <- r.beta(n.pred, ilogit(X.new %*% beta), sigma2.e)
  #if(k%%1000==0) print(k)
}

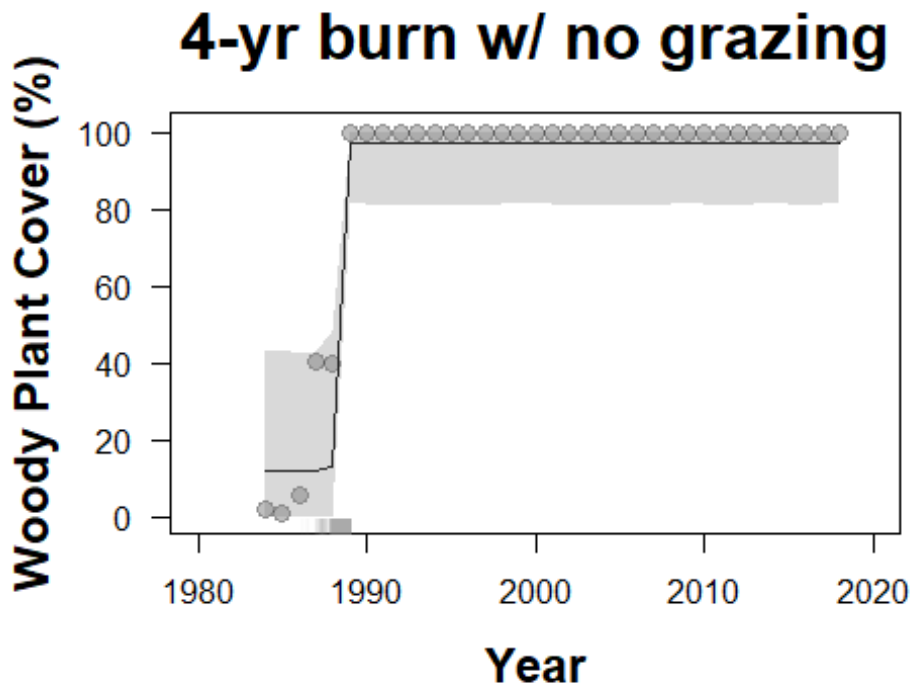
EV.z <- apply(y.pred,2,mean)
lwr.CI <- apply(y.pred, 2, FUN = quantile, prob = c(0.025))
```

```

upper.CI <- apply(y.pred, 2, FUN = quantile, prob = c(0.975))

#Plot of estimated breakpoint, and prediction
#png("woody4b.png")
par(mfrow = c(1, 1))
plot(woody.4b$RecYear, woody.4b$cover, las = 1,
     xlim=c(1980,2020), ylim = c(0,1.01),
     col = rgb(0,0, 0, 0.25), pch = 19, cex=1.25,
     xlab = "Year", ylab = "Woody Plant Cover (%)", cex.lab=1.5, font.lab=2, yaxt="n",
     main = "4-yr burn w/ no grazing", cex.main=2, font.main=2)
axis(2, at=pretty(0:1), lab=pretty(0:1) * 100, las=TRUE)
points(RecYear.pred$RecYear, EV.z, typ = "l")
polygon(c(RecYear.pred$RecYear, rev(RecYear.pred$RecYear)),
        c(lwr.CI, rev(upper.CI)), col = rgb(0.5, 0.5, 0.5, 0.3), border = NA)
rug(samples[-c(1:burn.in),4], col=rgb(0.5,0.5,0.5,0.01))

```



```
#dev.off()
```

MCMC sampling of Bayesian hierarchical temporal breakpoint model for Unburned and ungrazed watershed

```

#Data setup
y <- woody.20b$cover
X <- model.matrix(~woody.20b$RecYear)

```



```

# Number of MCMC samples to draw
m.draws <- 60000

# Samples from the posterior that will be saved
samples <- matrix(, m.draws + 1, dim(X)[2] + 2)
colnames(samples) <- c(colnames(X),"sigma2","phi")

# Starting values
samples[1,] <- c(-2,2,50,2000) #betas, sigma2, and phi

# Priors
sigma2.beta <- 10 #Prior variance for beta
q <- 2.1 #Inverse gamma prior with  $E() = r/(q-1)$  and  $Var() = r^2/((q-1)^2(q-2))$ 
r <- 1

# Tuning parameters
beta.tune <- 0.2
sigma2.tune <- 0.45
phi.tune <- 1/150

# MCMC algorithm
set.seed(1235)
for (k in 1:m.draws) {
  beta <- samples[k, 1:2]
  sigma2.e <- samples[k, 3]
  phi <- samples[k, 4]
  x.temp <- ifelse(woody.20b$RecYear < phi, "a", "b")
  X <- model.matrix(~x.temp)

  #Sample beta
  beta.star <- mvrnorm(1, beta, beta.tune * solve(t(X) %*% X))

  mh1 <- sum(d.beta(y, ilogit(X %*% beta.star), sigma2.e, log = T)) + sum(dnorm(beta.star, 0,
sigma2.beta, log = T))
  mh2 <- sum(d.beta(y, ilogit(X %*% beta), sigma2.e, log = T)) + sum(dnorm(beta, 0, sigma2.
beta, log = T))

  R <- min(1, exp(mh1-mh2))

  if(R > runif(1)){
    beta <- beta.star
  }

  #Sample sigma2.e
  sigma2.star <- rnorm(1, sigma2.e, sigma2.tune)
  if(sigma2.star > 0){

```

```

mh1 <- sum(d.beta(y, ilogit(X %*% beta), sigma2.star, log = T)) + sum(log(dIG(sigma2.star,
q, r)))
mh2 <- sum(d.beta(y, ilogit(X %*% beta), sigma2.e, log = T)) + sum(log(dIG(sigma2.e, q, r)
))

R <- min(1, exp(mh1 - mh2))
} else {R=0}

if(R > runif(1)){
  sigma2.e <- sigma2.star
}

#Sample phi
phi.star <- rnorm(1, phi, phi.tune)
#phi.star <- rdunif(1, 1983, 2018)

#Change breakpoint year values for each watershed
if(phi.star > 1986 & phi.star < 2018){
  x.temp.star <- ifelse(woody.20b$RecYear < phi.star, "a", "b")
  X.star <- round(model.matrix(~x.temp.star))

mh1 <- sum(d.beta(y, ilogit(X.star %*% beta), sigma2.e, log = T))
mh2 <- sum(d.beta(y, ilogit(X %*% beta), sigma2.e, log = T))

R <- min(1, exp(mh1-mh2))
} else {R=0}

if(R > runif(1)){
  phi <- phi.star
}

samples[k + 1, ] <- c(beta, sigma2.e, phi)
#if(k%%1000==0) print(k)

# Adaptive random walk M-H (see pg. 238-239 in Computational Statistics by Given & Hoeting
).
#This is done because the univariate conditional density is not in closed form
T <- 100
if(k%%T==0){
  accept.rate <- length(which(abs(diff(samples[(T*(k/T-1)+1):(k),1:2]))>0))/T
  beta.tune <- beta.tune*exp(ifelse(accept.rate > 0.44,min(0.01,1/sqrt(k/T)),-min(0.01,1/sqrt(k/
T))))^2
  accept.rate <- length(which(abs(diff(samples[(T*(k/T-1)+1):(k),3]))>0))/T
  sigma2.tune <- sigma2.tune*exp(ifelse(accept.rate > 0.44,min(0.01,1/sqrt(k/T)),-min(0.01,1/s

```

```

qrt(k/T)))^2
  accept.rate <- length(which(abs(diff(samples[(T*(k/T-1)+1):(k,4)])>0))/T
  phi.tune <- phi.tune*exp(ifelse(accept.rate > 0.25,min(0.01,1/sqrt(k/T)), -min(0.01,1/sqrt(k/T
))))^2
  }
}

```

MCMC sampling acceptance rates of Metropolis-Hastings random walks for breakpoint equation parameters. Also trace plots presented to visually check convergence of MCMC sampling of the model.

```

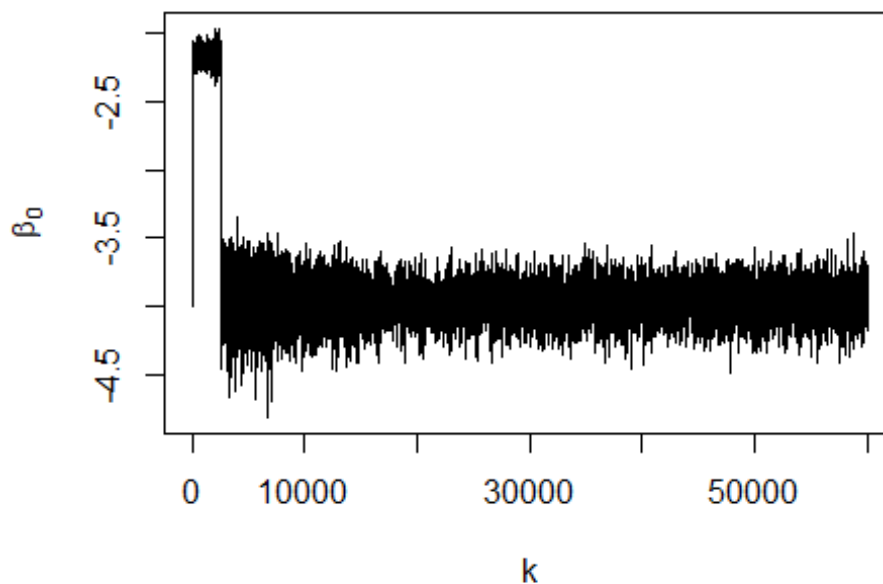
# Acceptance rates for M-H algorithm
length(which(abs(diff(samples[, 1])) > 0))/m.draws # betas
## [1] 0.2544333

length(which(abs(diff(samples[, 3])) > 0))/m.draws # sigma2
## [1] 0.6945667

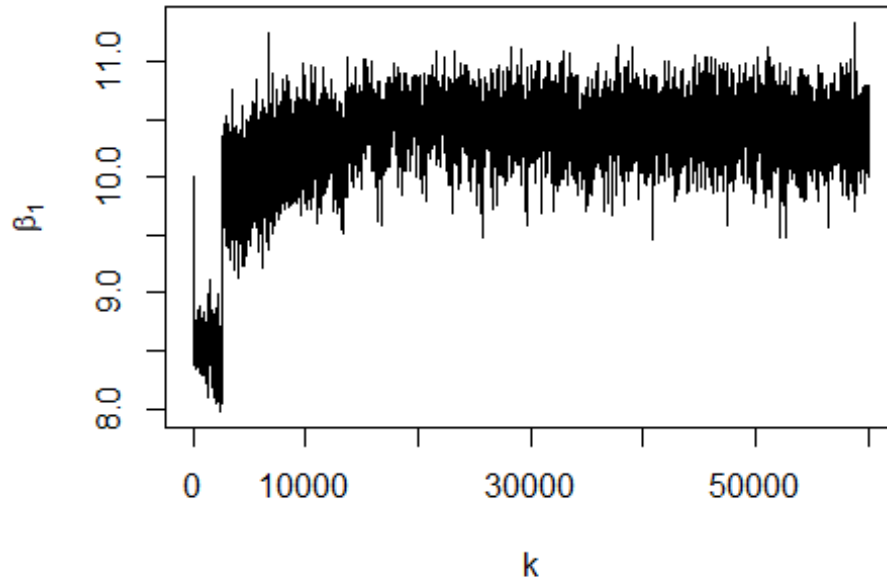
length(which(abs(diff(samples[, 4])) > 0))/m.draws # phi
## [1] 0.4840167

# Trace Plots
plot(samples[, 1], typ = "l", xlab = "k", ylab = expression(beta[0]))

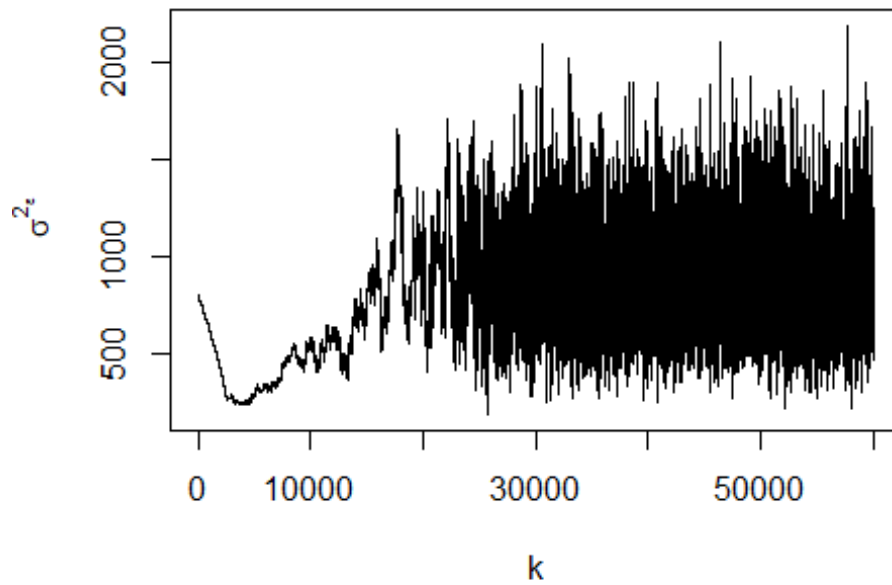
```



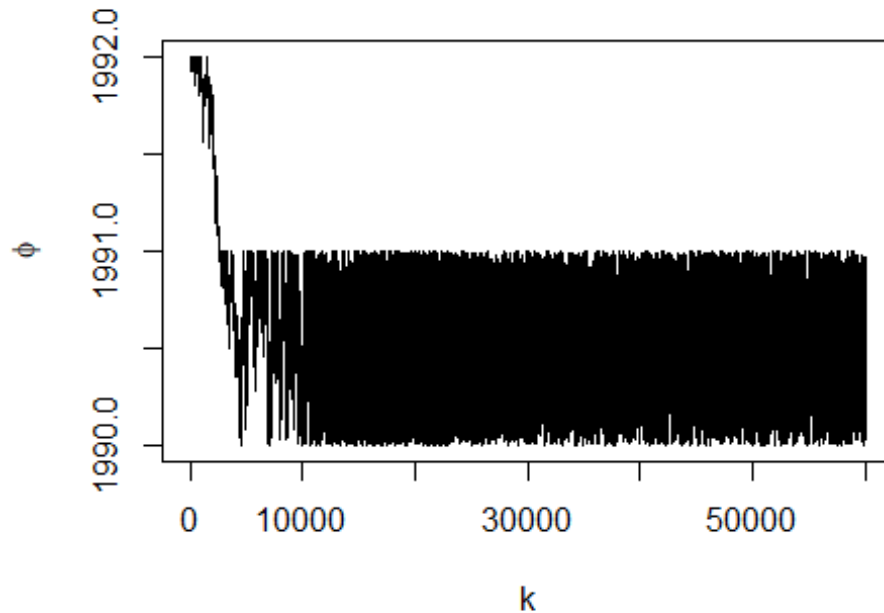
```
plot(samples[, 2], typ = "l", xlab = "k", ylab = expression(beta[1]))
```



```
plot(samples[, 3], typ = "l", xlab = "k", ylab = expression(sigma^2[epsilon]))
```



```
plot(samples[, 4], typ = "l", xlab = "k", ylab = expression(phi))
```



Output of results The mean  $E()$  of  $\beta$ 's and  $\sigma_\epsilon^2$ . Also presented are posterior distributions of each parameter including the breakpoint.

```
burn.in <- 30000
# E() of beta and sigma2
colMeans(samples[-c(1:burn.in), ])

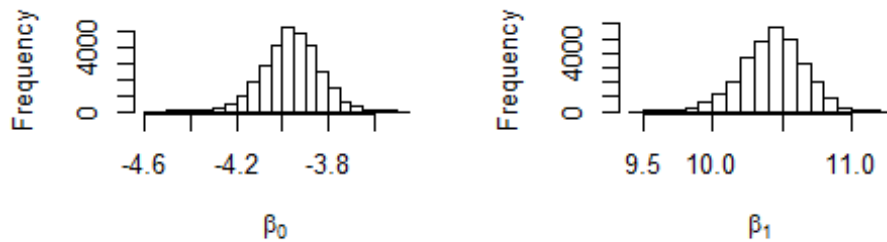
##      (Intercept) woody.20b$RecYear      sigma2      phi
##      -3.961896      10.430219      853.481062      1990.498914

# 95% Equal-tailed CIs
apply(samples[-c(1:burn.in), ], 2, FUN = quantile, prob = c(0.025, 0.975))

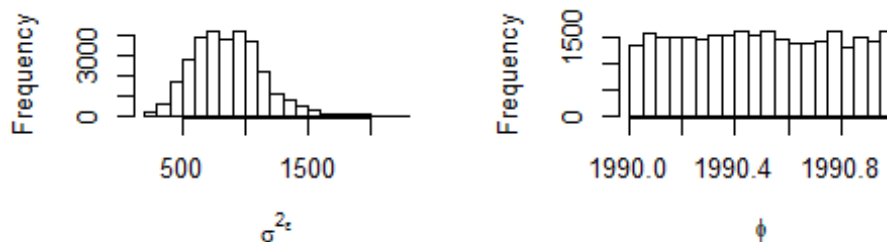
##      (Intercept) woody.20b$RecYear sigma2      phi
## 2.5%      -4.207193      9.963668      402.754      1990.029
## 97.5%      -3.734212      10.845139      1416.111      1990.976

par(mfrow = c(2,2))
hist(samples[-c(1:burn.in),1], xlab = expression(beta[0]))
hist(samples[-c(1:burn.in),2], xlab = expression(beta[1]))
hist(samples[-c(1:burn.in),3], xlab = expression(sigma^2[epsilon]))
hist(samples[-c(1:burn.in),4], xlab = expression(phi))
```

histogram of samples[-c(1:burn.in)] histogram of samples[-c(1:burn.in)]



histogram of samples[-c(1:burn.in)] histogram of samples[-c(1:burn.in)]



Final results of Bayesian hierarchical temporal breakpoint model for the Unburn and ungrazed watershed.

```
# Posterior predictive distribution
burn.in <- 20000
RecYear.pred <- data.frame(RecYear = seq(1986, 2018, by = 1))
n.pred <- dim(RecYear.pred)[1]
y.pred <- matrix(, length(burn.in:m.draws), dim(RecYear.pred)[1])
ev.y.pred <- matrix(, length(burn.in:m.draws), dim(RecYear.pred)[1])

for (k in burn.in:m.draws) {
  beta <- samples[k, 1:2]
  sigma2.e <- samples[k, 3]
  phi <- samples[k, 4]

  x.temp.new <- ifelse(woody.20b$RecYear < phi, "a", "b")
  X.new <- model.matrix(~x.temp.new)
  ev.y.pred[k - burn.in + 1, ] <- ilogit(X.new %*% beta)
  y.pred[k - burn.in + 1, ] <- r.beta(n.pred, ilogit(X.new %*% beta), sigma2.e)
  #if(k%%1000==0) print(k)
}

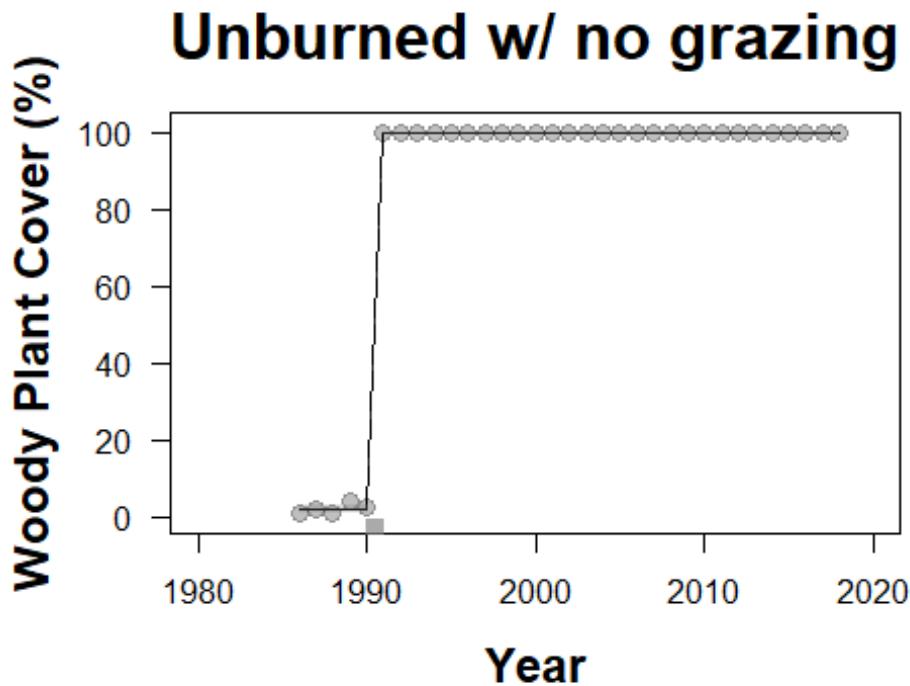
EV.z <- apply(y.pred, 2, mean)
lwr.CI <- apply(y.pred, 2, FUN = quantile, prob = c(0.025))
```

```

upper.CI <- apply(y.pred, 2, FUN = quantile, prob = c(0.975))

#Plot of estimated breakpoint, and prediction
#png("woody20b.png")
par(mfrow = c(1, 1))
plot(woody.20b$RecYear, woody.20b$cover, las = 1,
     xlim=c(1980,2020), ylim = c(0,1.01),
     col = rgb(0,0, 0, 0.25), pch = 19, cex=1.25,
     xlab = "Year", ylab = "Woody Plant Cover (%)", cex.lab=1.5, font.lab=2, yaxt="n",
     main = "Unburned w/ no grazing", cex.main=2, font.main=2)
axis(2, at=pretty(0:1), lab=pretty(0:1) * 100, las=TRUE)
points(RecYear.pred$RecYear, EV.z, typ = "l")
polygon(c(RecYear.pred$RecYear, rev(RecYear.pred$RecYear)),
        c(lwr.CI, rev(upper.CI)), col = rgb(0.5, 0.5, 0.5, 0.3), border = NA)
rug(samples[-c(1:burn.in),4], col=rgb(0.5,0.5,0.5,0.01))

```



```
#dev.off()
```

## Bayesian hierarchical spatial breakpoint model R Code

Packages needed for analysis

```
knitr::opts_chunk$set(message=FALSE, warning=FALSE, tidy=TRUE, cache=TRUE)
```

```
library(sp)
```

```
library(maps)
```

```
library(maptools)
```

```
library(raster)
```

```
library(MASS)
```

```
library(fields)
```

```
library(mvnmfast)
```

```
library(latex2exp)
```

```
library(gplots)
```

```
library(ggplot2)
```

```
library(reshape2)
```

Data acquisitions

```
url <- "https://www.dropbox.com/s/2qa9u4erwpf0hso/ISIT.txt?dl=1"  
df.ISIT <- read.table(url, header = TRUE)  
pt.ISIT <- SpatialPoints(df.ISIT[, 6:5], proj4string = CRS("+proj=longlat +datum=WGS84 +no  
_defs"))
```

Required functions

The first function is a design matrix ( $\mathbf{X}$ ), followed by the necessary logit and inverse logit functions to transform  $\phi$  and  $\theta$  within mcmc sampling, finally the last function is the density inverse gamma (dIG) in mcmc sampling of  $\sigma_\theta$ .

```
# Makes design matrix (X) for a given breakpoint  
makeX <- function(x, station, phi) {  
  cbind(1, ifelse(x < phi[station], (phi[station] - x), 0), ifelse(x < phi[station],  
    (phi[station] - x)^2, 0))  
}
```

```
# Transformation of theta/phi for mcmc sampling  
logit <- function(x) {  
  5000 * 1/(1 + exp(-x))  
}  
ilogit <- function(x) {
```



```

    log((x/5000)/(1 - x/5000))
  }

# Inverse gamma pdf
dIG <- function(x, q, r) {
  (r^q/gamma(q)) * x^(-(q + 1)) * exp(-r/x)
}

```

MCMC sampling

Setting up the bioluminescent data, model starting values and priors.

```

# Preliminary data steps
y <- log(df.ISIT$Sources + 0.05)
Z <- model.matrix(~as.factor(Station) - 1, data = df.ISIT)
p <- 3 # The number of coefficients(intercept, linear and quadratic)
D <- rdist.earth(df.ISIT[!duplicated(sort(df.ISIT$Station)), 6:5])

# Number of MCMC samples to draw
m.draws <- 40000

# Samples from the posterior that will be saved
samples <- matrix(, m.draws + 1, p + 6)
colnames(samples) <- c(paste("beta", 1:p, sep = ""), "sigma2.e", "sigma2.alpha",
  "rho.alpha", "sigma2.theta", "rho.theta", "mu.theta")
samples.phi <- matrix(, m.draws + 1, length(unique(df.ISIT$Station)))
colnames(samples.phi) <- paste("phi.", unique(df.ISIT$Station), sep = "")
samples.alpha <- matrix(, m.draws + 1, length(unique(df.ISIT$Station)))
colnames(samples.alpha) <- paste("alpha.", unique(df.ISIT$Station), sep = "")

# Starting values
set.seed(2010)
samples.phi[1, ] <- runif(19, 1000, 4000) #Starting values for phi
X <- makeX(x = df.ISIT$SampleDepth, station = df.ISIT$Station, phi = samples.phi[1,
  ])
samples[1, ] <- c(solve(t(X) %*% X) %*% t(X) %*% y, 1, 2, 50, 2, 50, 0) #Starting values
samples.alpha[1, ] <- solve(t(Z) %*% Z) %*% t(Z) %*% y

# Priors
sigma2.beta <- 1000 #Prior variance for beta
q <- 2.1 #Inverse gamma prior with E() = r/(q-1) and Var() = r^2/((q-1)^2(q-2))
r <- 1
u.rho <- 200

# Tuning parameters

```

```

rho.alpha.tune <- 10
theta.tune <- 1/100
sigma2.theta.tune <- 1/5
rho.theta.tune <- 10
mu.theta.tune <- 1/10

# MCMC algorithm
set.seed(4133)
for (k in 1:m.draws) {

  # Sampled paramters
  beta <- samples[k, 1:p]
  sigma2.e <- samples[k, p + 1]
  sigma2.alpha <- samples[k, p + 2]
  rho.alpha <- samples[k, p + 3]
  sigma2.theta <- samples[k, p + 4]
  rho.theta <- samples[k, p + 5]
  mu.theta <- samples[k, p + 6]
  phi <- samples.phi[k, ]
  alpha <- samples.alpha[k, ]

  # Derived paramters
  theta <- ilogit(phi)
  X <- makeX(x = df.ISIT$SampleDepth, station = df.ISIT$Station, phi = phi)
  C.alpha <- exp(-(D/rho.alpha)^2)
  CI.alpha <- solve(C.alpha)
  RI.alpha <- (1/sigma2.alpha) * CI.alpha
  C.theta <- exp(-(D/rho.theta)^2)
  if (k == 1) {
    theta.cov <- diag(1, dim(samples.phi)[2])
  }

  # Sample theta
  theta.star <- rmvn(1, theta, theta.tune * theta.cov) #rmvn: generates multivariate normal deviates from mgcv package
  phi.star <- logit(theta.star)
  X.star <- makeX(x = df.ISIT$SampleDepth, station = df.ISIT$Station, phi = phi.star)
  mh1 <- sum(dnorm(y, X.star %*% beta + Z %*% alpha, sigma2.e, log = TRUE)) +
    dmvn(theta.star, rep(mu.theta, dim(C.theta)[1]), sigma2.theta * C.theta,
      log = TRUE) #dmvn: fast computation multivariate normal density. package: mvnfast
  mh2 <- sum(dnorm(y, X %*% beta + Z %*% alpha, sigma2.e, log = TRUE)) + dmvn(theta,
    rep(mu.theta, dim(C.theta)[1]), sigma2.theta * C.theta, log = TRUE)
  mh <- exp(mh1 - mh2)
  if (mh > runif(1)) {
    phi <- phi.star
    theta <- theta.star
  }
}

```

```

X <- X.star
}

# Sample rho.theta
rho.theta.star <- rnorm(1, rho.theta, rho.theta.tune)
if (rho.theta.star > 0 & rho.theta.star < u.rho) {
  C.theta.star <- exp(-(D/rho.theta.star)^2)
  mh1 <- dmvn(theta, rep(mu.theta, dim(C.theta)[1]), sigma2.theta * C.theta.star,
    log = TRUE)
  mh2 <- dmvn(theta, rep(mu.theta, dim(C.theta)[1]), sigma2.theta * C.theta,
    log = TRUE)
  mh <- exp(mh1 - mh2)
} else {
  mh <- 0
}
if (mh > runif(1)) {
  rho.theta <- rho.theta.star
  C.theta <- C.theta.star
}

# Sample sigma2.theta
sigma2.theta.star <- rnorm(1, sigma2.theta, sigma2.theta.tune)
if (sigma2.theta.star > 0) {
  mh1 <- dmvn(theta, rep(mu.theta, dim(C.theta)[1]), sigma2.theta.star *
    C.theta, log = TRUE) + log(dIG(sigma2.theta.star, q, r))
  mh2 <- dmvn(theta, rep(mu.theta, dim(C.theta)[1]), sigma2.theta * C.theta,
    log = TRUE) + log(dIG(sigma2.theta, q, r))
  mh <- exp(mh1 - mh2)
} else {
  mh <- 0
}
if (mh > runif(1)) {
  sigma2.theta <- sigma2.theta.star
}

# Sample mu.theta
mu.theta.star <- rnorm(1, mu.theta, mu.theta.tune)
if (sigma2.theta.star > 0) {
  mh1 <- dmvn(theta, rep(mu.theta.star, dim(C.theta)[1]), sigma2.theta.star *
    C.theta, log = TRUE) + dnorm(mu.theta.star, 0, sqrt(2.25), log = TRUE)
  mh2 <- dmvn(theta, rep(mu.theta, dim(C.theta)[1]), sigma2.theta * C.theta,
    log = TRUE) + dnorm(mu.theta.star, 0, sqrt(2.25), log = TRUE)
  mh <- exp(mh1 - mh2)
} else {
  mh <- 0
}

```

```

if (mh > runif(1)) {
  mu.theta <- mu.theta.star
}

# Sample beta
A <- solve(t(X) %*% X + diag(sigma2.e/sigma2.beta, dim(X)[2]))
b <- t(X) %*% (y - Z %*% alpha)
beta <- t(rmvn(1, A %*% b, sigma2.e * A))

# Sample sigma2.e
sigma2.e <- 1/rgamma(1, q + length(y)/2, r + t(y - X %*% beta - Z %*% alpha) %*%
  (y - X %*% beta - Z %*% alpha)/2)

# Sample alpha
A <- solve((1/sigma2.e) * t(Z) %*% Z + R1.alpha)
b <- (1/sigma2.e) * t(Z) %*% (y - X %*% beta)
alpha <- t(rmvn(1, A %*% b, A))

# Sample sigma2.alpha
sigma2.alpha <- 1/rgamma(1, q + length(alpha)/2, r + t(alpha) %*% C1.alpha %*%
  (alpha)/2)

# Sample rho.alpha
rho.alpha.star <- rnorm(1, rho.alpha, rho.alpha.tune)
if (rho.alpha.star > 0 & rho.alpha.star < u.rho) {
  C.alpha.star <- exp(-(D/rho.alpha.star)^2)
  mh1 <- dmvn(t(alpha), rep(0, dim(C.alpha)[1]), sigma2.alpha * C.alpha.star,
    log = TRUE)
  mh2 <- dmvn(t(alpha), rep(0, dim(C.alpha)[1]), sigma2.alpha * C.alpha,
    log = TRUE)
  mh <- exp(mh1 - mh2)
} else {
  mh <- 0
}
if (mh > runif(1)) {
  rho.alpha <- rho.alpha.star
}

#### Save samples & print iteration number
samples[k + 1, ] <- c(beta, sigma2.e, sigma2.alpha, rho.alpha, sigma2.theta,
  rho.theta, mu.theta)
samples.phi[k + 1, ] <- phi
samples.alpha[k + 1, ] <- alpha
# if(k%%1000==0) print(k)

# Adaptive random walk M-H (see pg. 238-239 in Computational Statistics by

```

```

# Given & Hoeting). This is done because the univariate conditional density
# is not in closed form
T <- 100
if (k%%T == 0) {
  theta.cov <- cov(ilogit(samples.phi[1:k, ])) + diag(1/10^6, dim(samples.phi)[2])
  accept.rate <- length(which(abs(diff(samples.phi[(T * (k/T - 1) + 1):(k),
    1])) > 0))/T
  theta.tune <- theta.tune * exp(ifelse(accept.rate > 0.23, min(0.01,
    1/sqrt(k/T)), -min(0.01, 1/sqrt(k/T))))^2
  accept.rate <- length(which(abs(diff(samples[(T * (k/T - 1) + 1):(k),
    p + 3])) > 0))/T
  rho.alpha.tune <- rho.alpha.tune * exp(ifelse(accept.rate > 0.44, min(0.01,
    1/sqrt(k/T)), -min(0.01, 1/sqrt(k/T))))^2
  accept.rate <- length(which(abs(diff(samples[(T * (k/T - 1) + 1):(k),
    p + 4])) > 0))/T
  sigma2.theta.tune <- sigma2.theta.tune * exp(ifelse(accept.rate > 0.44,
    min(0.01, 1/sqrt(k/T)), -min(0.01, 1/sqrt(k/T))))^2
  accept.rate <- length(which(abs(diff(samples[(T * (k/T - 1) + 1):(k),
    p + 5])) > 0))/T
  rho.theta.tune <- rho.theta.tune * exp(ifelse(accept.rate > 0.44, min(0.01,
    1/sqrt(k/T)), -min(0.01, 1/sqrt(k/T))))^2
  accept.rate <- length(which(abs(diff(samples[(T * (k/T - 1) + 1):(k),
    p + 6])) > 0))/T
  mu.theta.tune <- mu.theta.tune * exp(ifelse(accept.rate > 0.44, min(0.01,
    1/sqrt(k/T)), -min(0.01, 1/sqrt(k/T))))^2
}
}

```

MCMC sampling acceptance rates of Metropolis-Hastings random walks for breakpoint equation parameters. Also trace plots presented to visually check convergence of MCMC sampling of the model.

```

# Acceptance rates for M-H algorithm
length(which(abs(diff(samples.phi[, 1])) > 0))/m.draws # phi
## [1] 0.271

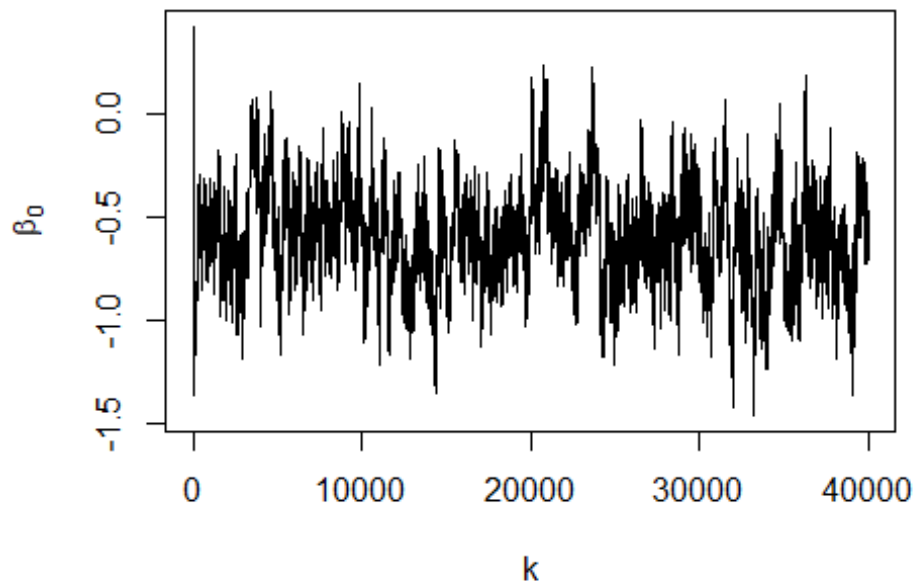
length(which(abs(diff(samples[, p + 3])) > 0))/m.draws #rho.alpha
## [1] 0.429625

length(which(abs(diff(samples[, p + 4])) > 0))/m.draws #sigma2.theta
## [1] 0.46135

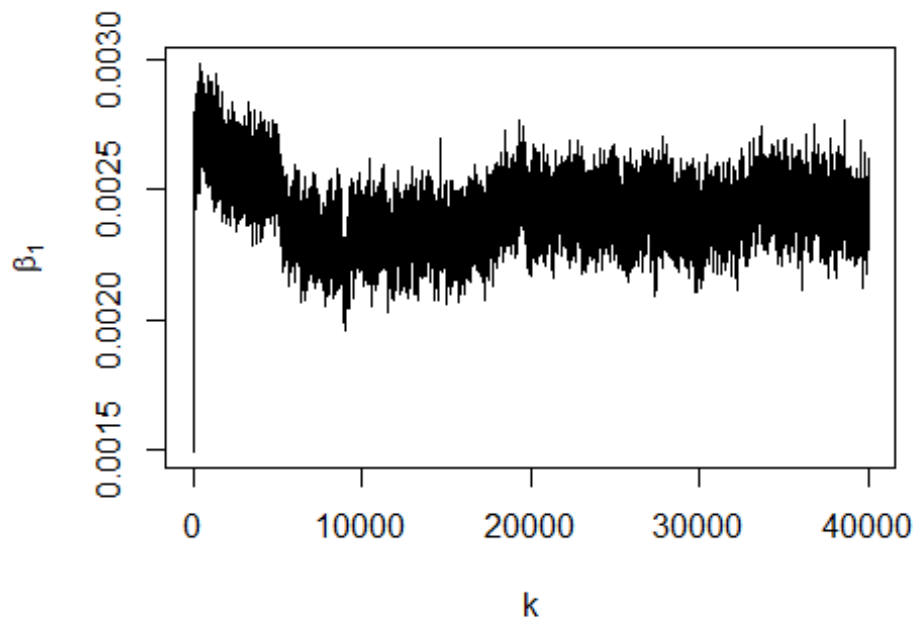
length(which(abs(diff(samples[, p + 5])) > 0))/m.draws #rho.theta
## [1] 0.439575

```

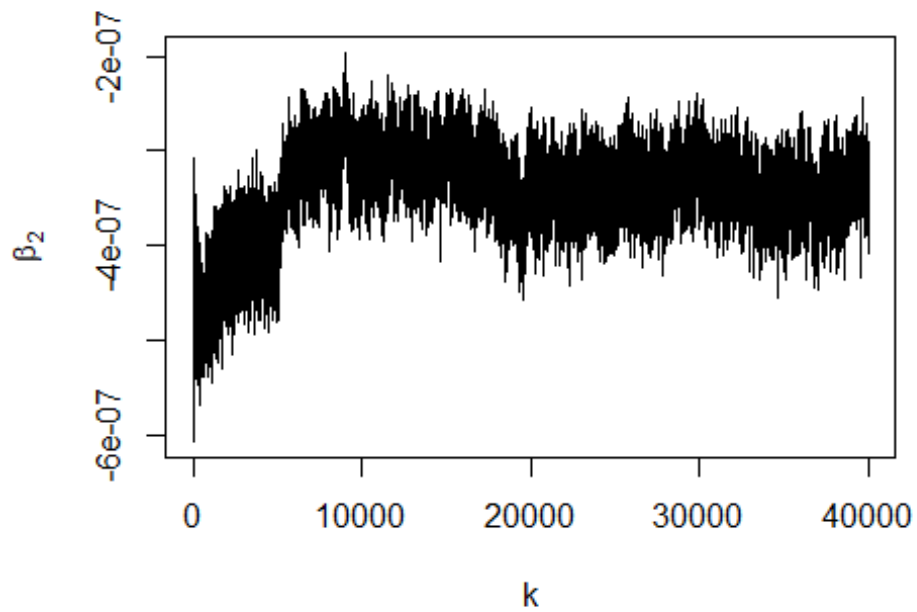
```
length(which(abs(diff(samples[, p + 6])) > 0))/m.draws #mu.theta
## [1] 0.458
# Trace plots
par(mfrow = c(1, 1))
plot(samples[, 1], typ = "l", xlab = "k", ylab = expression(beta[0]))
```



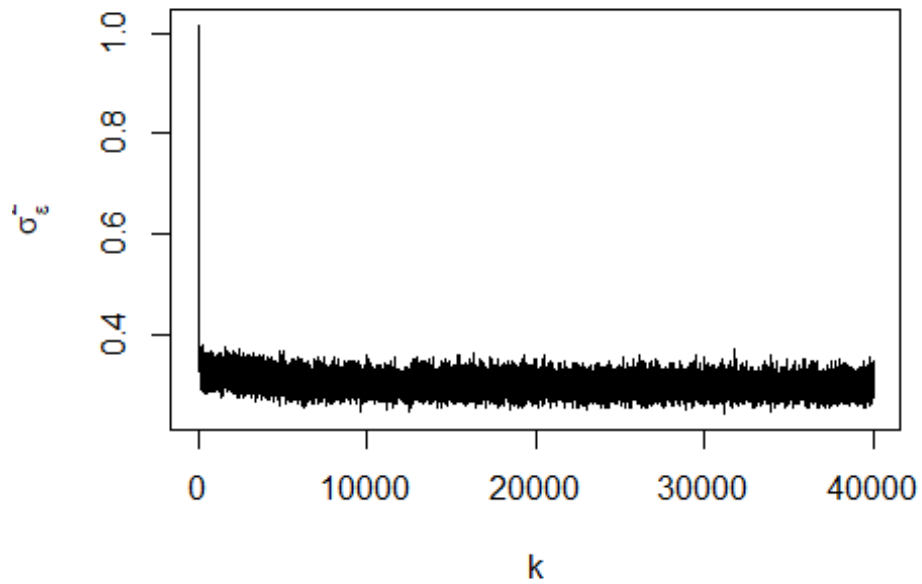
```
plot(samples[, 2], typ = "l", xlab = "k", ylab = expression(beta[1]))
```



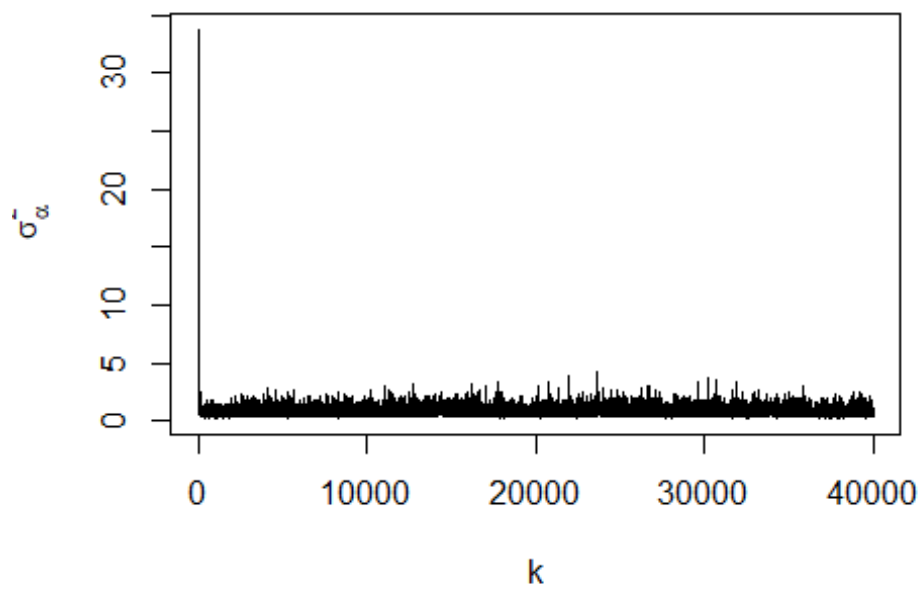
```
plot(samples[, 3], typ = "l", xlab = "k", ylab = expression(beta[2]))
```



```
plot(samples[, p + 1], typ = "l", xlab = "k", ylab = expression(sigma[epsilon]^2))
```

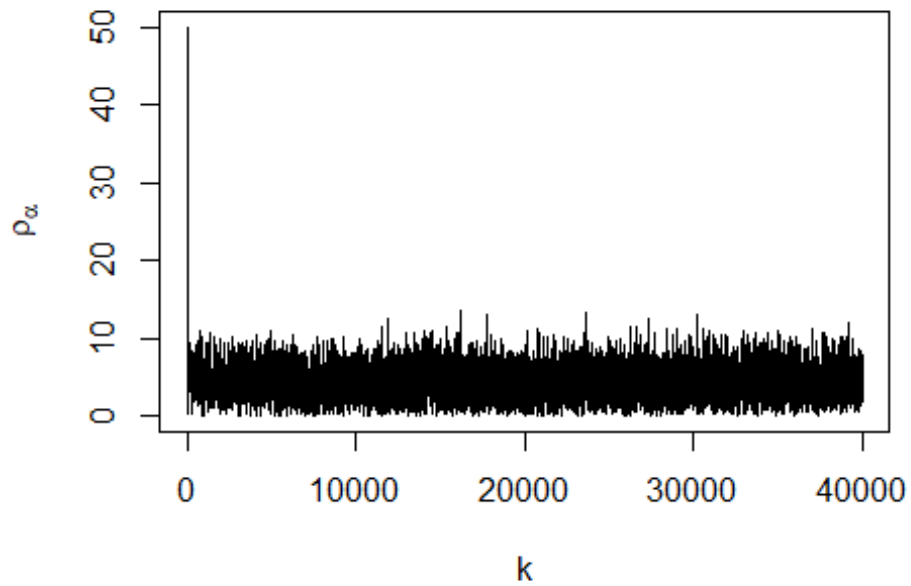


```
plot(samples[, p + 2], typ = "l", xlab = "k", ylab = expression(sigma[alpha]^2))
```

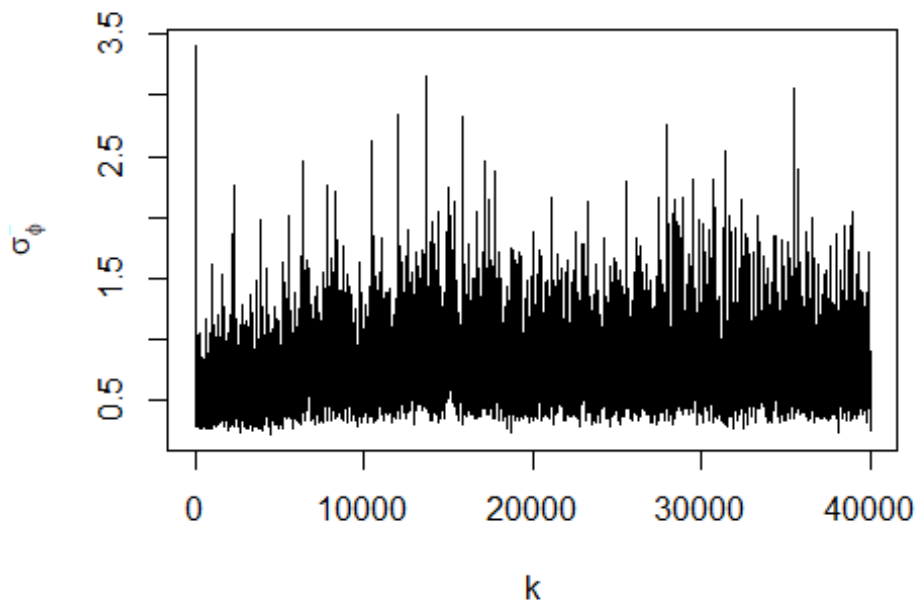


```
plot(samples[, p + 3], typ = "l", xlab = "k", ylab = expression(rho[alpha]))
```

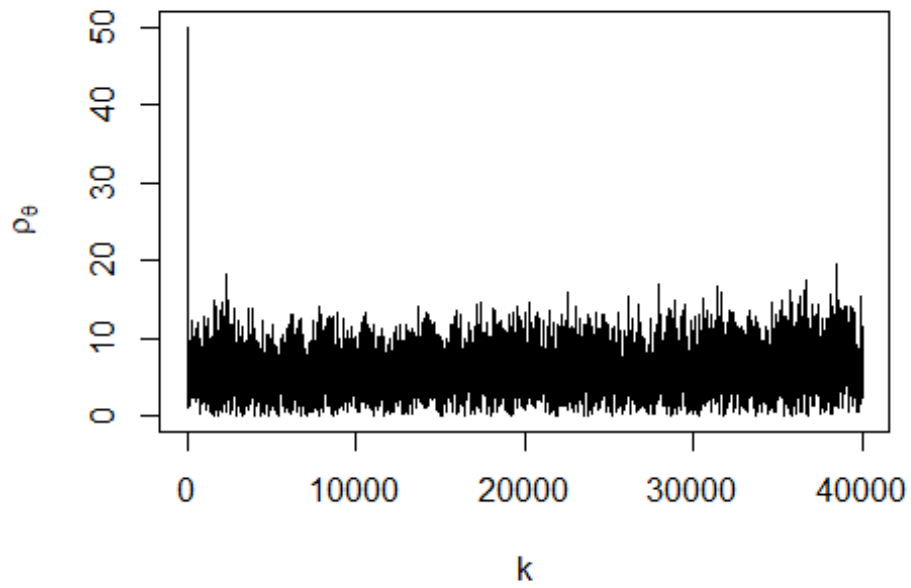




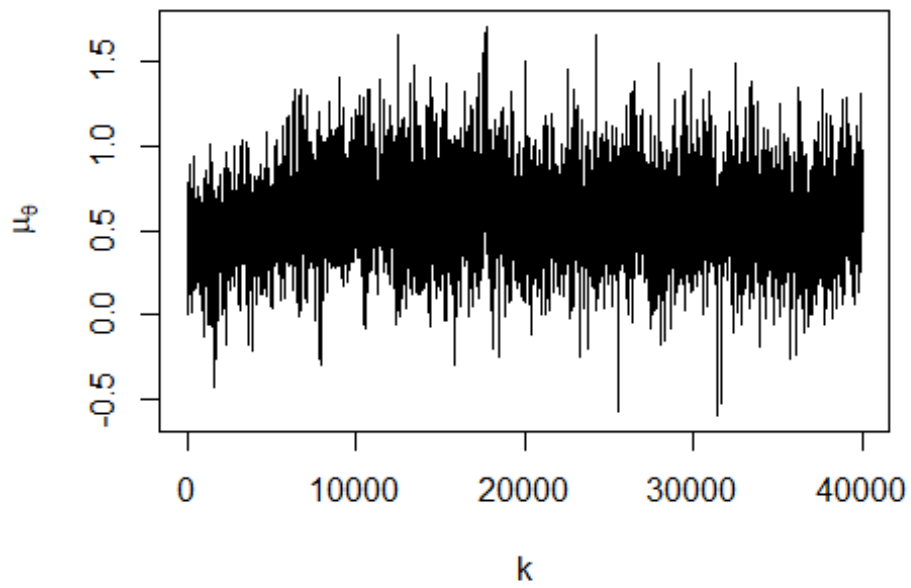
```
plot(samples[, p + 4], typ = "l", xlab = "k", ylab = expression(sigma[phi]^2))
```



```
plot(samples[, p + 5], typ = "l", xlab = "k", ylab = expression(rho[theta]))
```



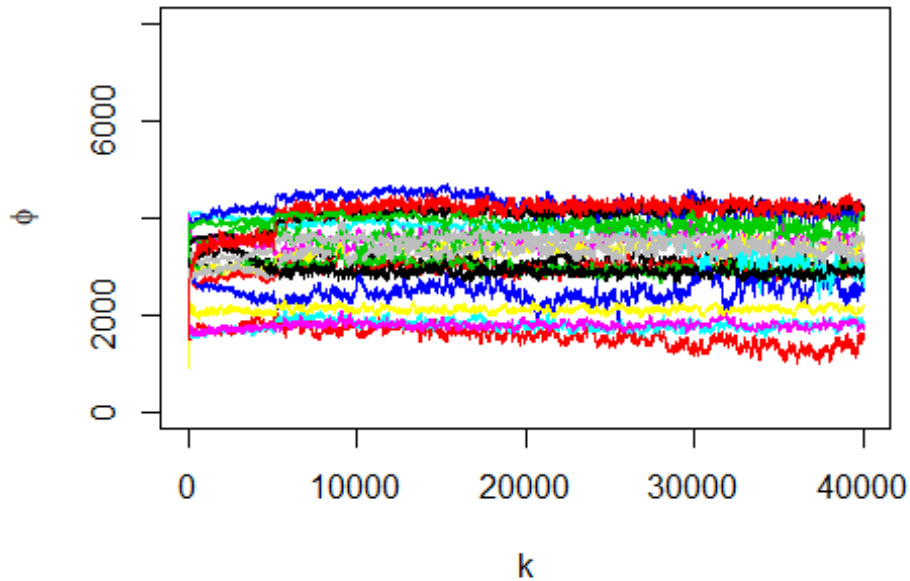
```
plot(samples[, p + 6], typ = "l", xlab = "k", ylab = expression(mu[theta]))
```



```

plot(samples.phi[, 1], typ = "l", xlab = "k", ylab = expression(phi), ylim = c(0,
  8000))
for (i in 2:19) {
  points(samples.phi[, i], typ = "l", col = i)
}

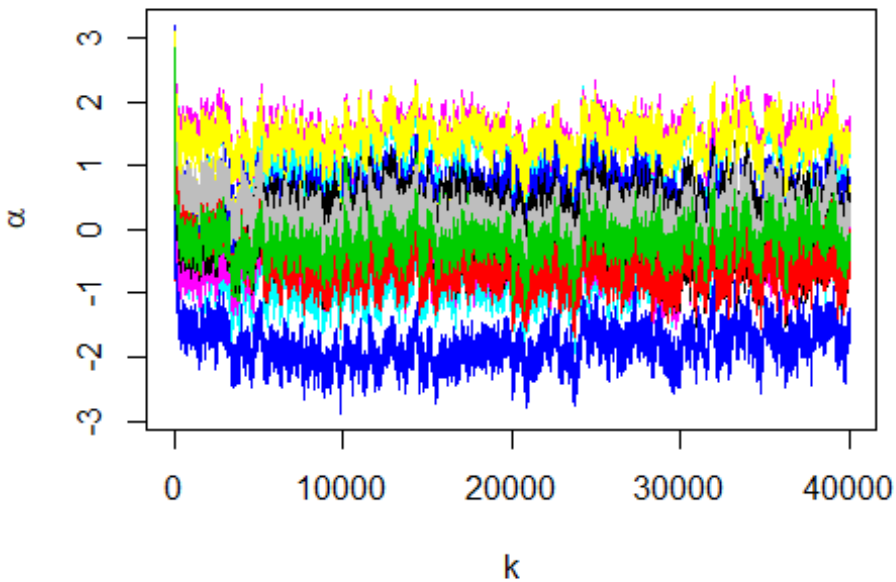
```



```

plot(samples.alpha[, 1], typ = "l", xlab = "k", ylab = expression(alpha), ylim = range(samples.alpha))
for (i in 2:19) {
  points(samples.alpha[, i], typ = "l", col = i)
}

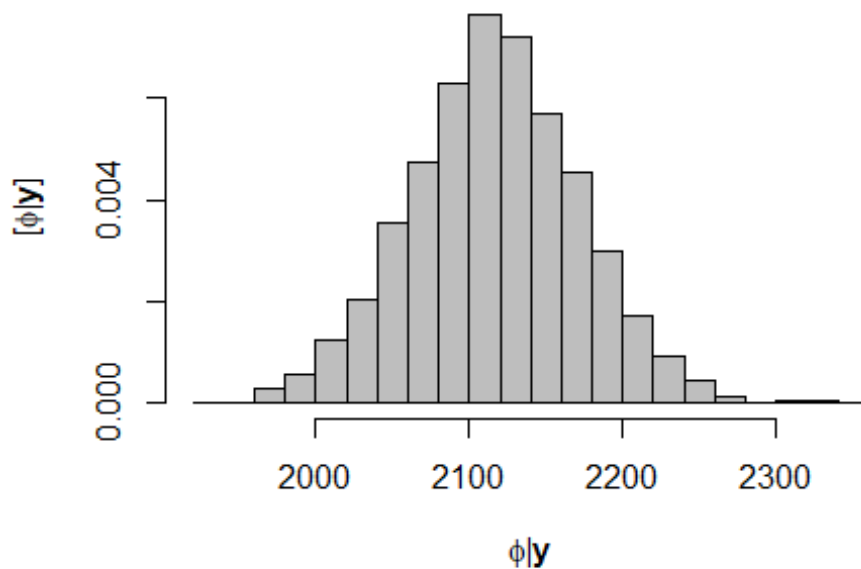
```



#### Output of results

This first result is for an individual sampling station. (Where it says ‘*station*’, any of the station numbers (1-19) can be input. For our purposes we chose station number 15.) This code also gives  $E()$  of  $\beta$ 's and  $\sigma^2$  and their 95% credible intervals (CI).

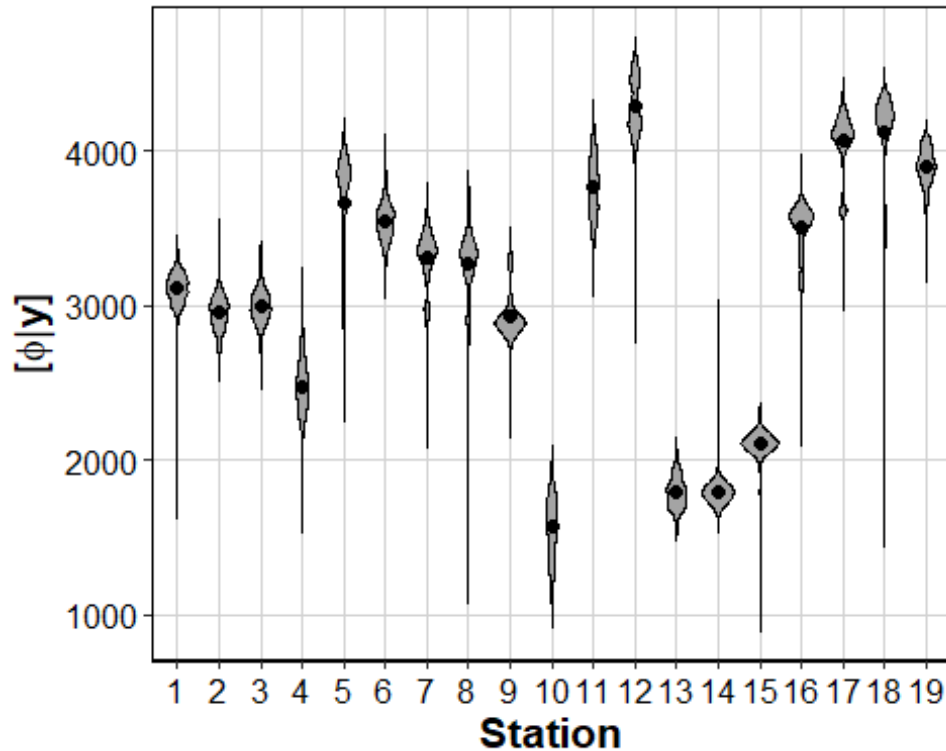
```
# Posterior of breakpoint for single station
station <- 15
burn.in <- 10000
hist(samples.phi[-c(1:burn.in), station], col = "grey", freq = FALSE, main = "",
      xlab = TeX(" $\phi$  |  $\mathbf{y}$ "), ylab = TeX(" $\lbrack\phi$  |  $\mathbf{y}\rbrack$ "))
```



This next code chunk gives the mean for each station's breakpoint and plots them all together as a violin plot.

```
# Posterior mean and 95% CI of breakpoint for all stations
burn.in <- 10000

# organizes the data for input into ggplot
long.phi <- melt(samples.phi)
# Creation of violin plot with ggplot
phi.plot <- ggplot(long.phi, aes(x = Var2, y = value)) + geom_violin(trim = FALSE,
  fill = "#A4A4A4", color = "black") + stat_summary(fun.y = mean, geom = "point",
  size = 2, color = "black") + scale_x_discrete(labels = c(1:19)) + ylab(TeX("$\\lbrack\\phi | \\mathbf{y}\\rbrack$")) +
  xlab("Station") + theme(axis.title.y = element_text(face = "bold", size = 16,
  color = "black"), axis.text.y = element_text(size = 12, color = "black"),
  axis.title.x = element_text(face = "bold", size = 16, color = "black"),
  axis.text.x = element_text(size = 12, color = "black"), panel.background = element_blank(),
  panel.grid.major = element_line(color = "lightgrey", size = 0.25), panel.border = element_rect(
  colour = "black",
  fill = NA, size = 1))
phi.plot
```



The posterior predictive distribution and breakpoint with uncertainties for a single station plotted. Once again to stay consistent with our example we are using station number 15.

```
# Posterior predictive distribution for single station
station <- 15
burn.in <- 10000
SampleDepth.pred <- data.frame(SampleDepth = seq(500, 5000, by = 10))
n.pred <- dim(SampleDepth.pred)[1]
y.pred <- matrix(, length(burn.in:m.draws), dim(SampleDepth.pred)[1])
ev.y.pred <- matrix(, length(burn.in:m.draws), dim(SampleDepth.pred)[1])

for (k in burn.in:m.draws) {
  beta <- samples[k, 1:p]
  sigma2.e <- samples[k, p + 1]
  sigma2.alpha <- samples[k, p + 2]
  rho.alpha <- samples[k, p + 3]
  phi <- samples.phi[k, ]
  alpha <- samples.alpha[k, station]

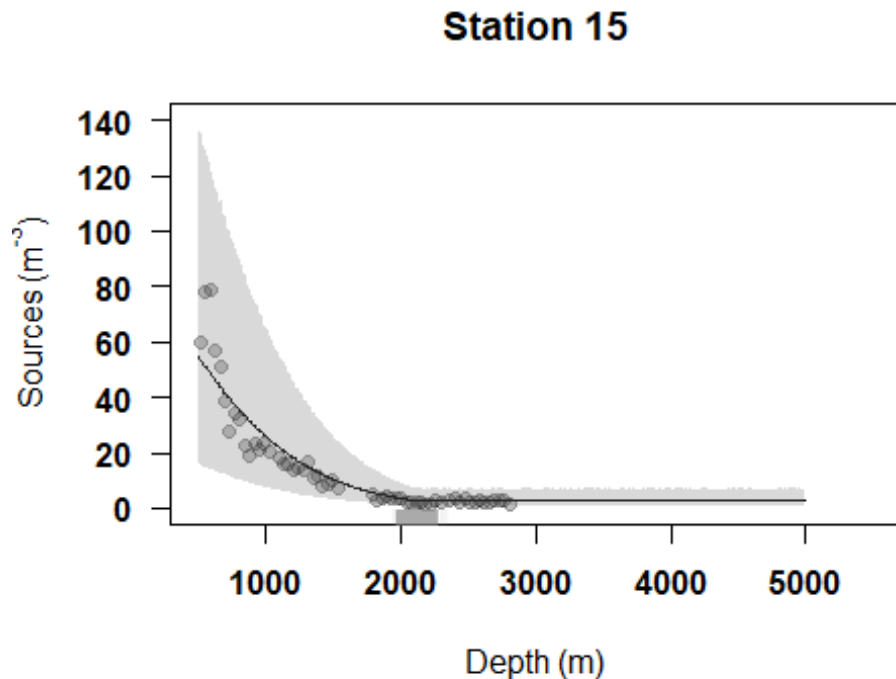
  X.new <- makeX(x = SampleDepth.pred$SampleDepth, station = station, phi = phi)
  ev.y.pred[k - burn.in + 1, ] <- exp(X.new %*% beta + alpha)
  y.pred[k - burn.in + 1, ] <- exp(rnorm(n.pred, X.new %*% beta + alpha, sqrt(sigma2.e)))
  # if(k%%1000==0) print(k)
}
```

```

EV.y <- apply(y.pred, 2, mean)
lwr.CI <- apply(y.pred, 2, FUN = quantile, prob = c(0.025))
upper.CI <- apply(y.pred, 2, FUN = quantile, prob = c(0.975))

# Plot of estimated breakpoint, and prediction of an individual station
par(mfrow = c(1, 1))
plot(df.ISIT[df.ISIT$Station == station, 1], df.ISIT[df.ISIT$Station == station,
  2], las = 1, xlim = c(500, 5500), ylim = c(0, max(upper.CI)), col = rgb(0,
  0, 0, 0.25), pch = 19, font = 2, xlab = "Depth (m)", ylab = TeX("Sources (m^{-3})"),
  main = "Station 15")
points(SampleDepth.pred$SampleDepth, EV.y, typ = "l")
polygon(c(SampleDepth.pred$SampleDepth, rev(SampleDepth.pred$SampleDepth)),
  c(lwr.CI, rev(upper.CI)), col = rgb(0.5, 0.5, 0.5, 0.3), border = NA)
rug(samples.phi[-c(1:burn.in), station], col = rgb(0.5, 0.5, 0.5, 0.01))

```



Results of Bayesian hierarchical spatial breakpoint model. A spatially interpolated breakpoint map.

```

# Map showing expected value of breakpoint
burn.in <- 10000
rl.phi.ev <- raster(crs = proj4string(pt.ISIT), resolution = 1/20, xmn = -17,
  xmx = -10, ymn = 48, ymx = 50.5)
D <- rdist.earth(df.ISIT[!duplicated(sort(df.ISIT$Station)), 6:5])

```

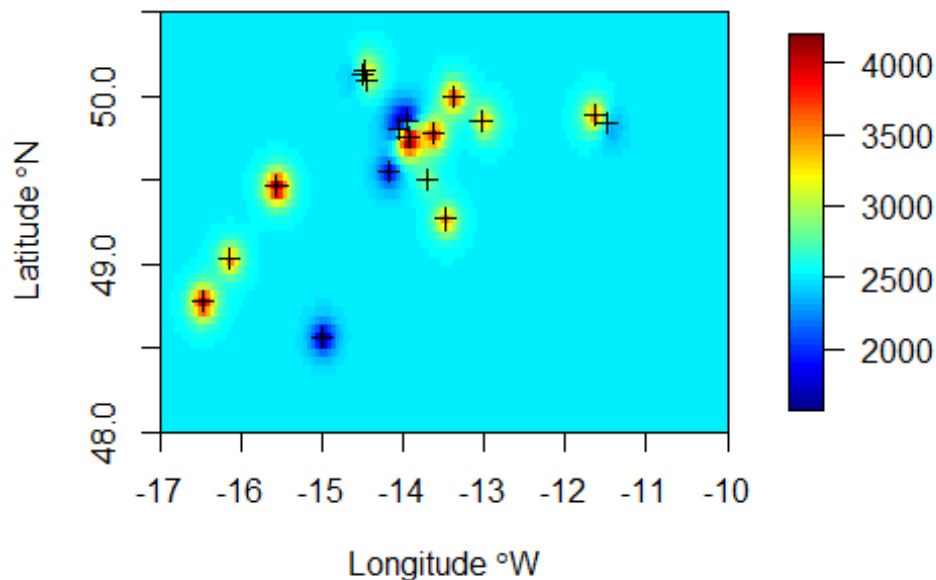
```

D.cross <- rdist.earth(x1 = rasterToPoints(rl.phi.ev)[, -3], x2 = df.ISIT[!duplicated(sort(df.ISIT$Station)),
  6:5])
phi.pred <- matrix(, length(burn.in:m.draws), prod(dim(rl.phi.ev)))

for (k in burn.in:m.draws) {
  phi <- samples.phi[k, ]
  theta <- ilogit(phi)
  sigma2.theta <- samples[k, p + 4]
  rho.theta <- samples[k, p + 5]
  C.theta <- exp(-(D/rho.theta)^2)
  C.theta.cross <- exp(-(D.cross/rho.theta)^2)
  theta.pred <- C.theta.cross %*% solve(C.theta) %*% theta
  phi.pred[k - burn.in + 1, ] <- logit(theta.pred)
  # if(k%%1000==0) print(k)
}

rl.phi.ev[] <- colMeans(phi.pred)
image.plot(rl.phi.ev, zlim = range(rl.phi.ev[]), xlab = TeX("Longitude $\degree$W"),
  ylab = TeX("Latitude $\degree$N"))
plot(pt.ISIT, add = TRUE, col = "black")

```





All breakpoint plots for stations 1-19, except station 15 which was used in the chapter.

