THE PENNSYLVANIA STATE UNIVERSITY SCHREYER HONORS COLLEGE

DEPARTMENT OF GEOGRAPHY

THE NON-NATIVE GRASS-FIRE CYCLE: THE DYNAMIC AND SPATIOTEMPORAL RELATIONSHIPS BETWEEN GRASS SPECIES AND FIRE REGIMES

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A thesis submitted in partial fulfillment of the requirements for a baccalaureate degree in Geography with honors in Geography

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Abstract

The relationships between grass and fire are complex and dynamic. Considering that fire regimes are dependent on topography, climate, and fuel availability at the site of ignition, changes to the fuel composition and structure of a landscape have the potential to introduce novel fire behavior. Therefore, the flammability of grassy species has global consequences when considering the impact of biological invasions on fuel properties. An increase in non-native grass species invasion encourages fire, which in turn provides opportunities for further colonization of the non-native species. This positive feedback loop has significant implications for global change ecology and fire management decisions. D'Antonio and Vitousek (1992), and Brooks et al. (2004) published foundational papers on the non-native grass-fire cycle. This thesis aims to synthesize the various case studies published on the non-native grass-fire cycle since the publication of Brooks et al. (2004) in order to explore two research questions. 1) What are the mechanisms that drive the non-native grass-fire cycle? 2) How has our understanding of the global distribution of the non-native grass-fire cycle progressed since the publications of D'Antonio and Vitousek (1992) and Brooks et al. (2004)? A review of the literature on the non-native grass-fire cycle revealed that invaded plots, when compared to non-invaded plots, experience a 116% increase in firespread rate, a 560% increase in fire intensity, and a 208% increase in biomass. At fine scales, the interplay between biomass and fire intensity, continuity/cover and fire-spread rate, and composition and fire return interval ensure the continuation of this cycle. At broad scales, pre-existing fire regimes in the Tropical Rainforest and Tropical Savanna terrestrial biomes have been altered, and there has been a complete introduction of fire into some regions in both the Desert and Temperate Broadleaf Forest biomes.

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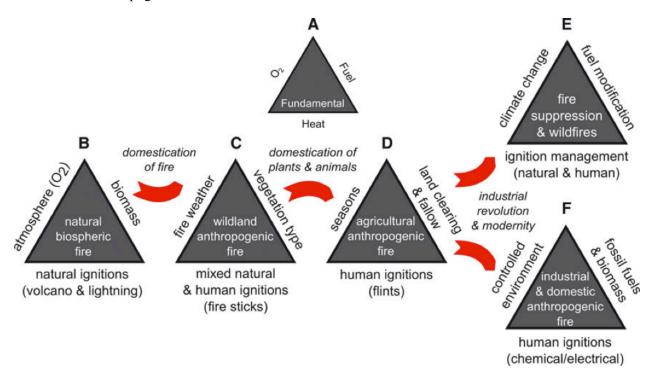
Chapter 1: Introduction

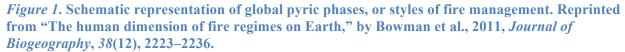
The Grass-Fire Cycle

Landscapes exist in dynamic states, perpetually responding to physical disturbances, defined by the discrete events in time and space that disrupt an ecosystem or community (Turner, Gardner, & O'Neill, 2001, p. 90). Whether anthropogenic or natural, intentional or accidental, physical disturbances have the potential to shape a landscape's physical, biogeochemical, and ecological systems. Disturbance dynamics are integral in the field of landscape ecology, which considers how an ecosystem's spatial and temporal patterns influence and are influenced by its ecological processes (Turner et al., 2001, p. 4). Despite the importance of a broad-scale perspective, disturbance regimes are a multi-scalar phenomenon. Studying the interactions between pattern and process at global, regional, and local levels offers a valuable perspective on how disturbances create and are created by the broad-scale spatial heterogeneity of landscapes (Gergel & Turner, 2002).

Fire is a salient example of a disturbance with implications at multiple scales. Fire regimes are dependent upon topography and climate (broad-scale), and fuel availability at the site of ignition (fine-scale). These abiotic and biotic factors contribute to the frequency, intensity, and extent of fire (Brooks et al., 2004). While some argue for the existence and preservation of 'natural' fire regimes, most agree that the human dimension of fire regimes has been present for centuries and should not be disregarded in discussions about fire (Bowman et al., 2011). In the past century, land-use change (e.g. conversion to agriculture and deforestation) has altered the topography, fuel composition, and fuel structure of landscapes across the globe. Bowman et al. (2011) explain the transition from 'background fire regimes' to 'contemporary human fire regimes' as a variation on the three essential variables of fire ignition and

spread: 1) oxygen, 2) heat, and 3) fuel. Figure 1 illustrates how these variables have evolved over time as a result of anthropogenic influence.





While conversations about naturally occurring and manmade fires typically highlight forest fire events, the picture of global fire distribution and behavior is incomplete without considering the significance of grassland fires. The relationships between grass and fire are complex and dynamic. The woody species and leaf litter typical of a closed-canopy forest floor are often less ignitable than the grassy species associated with open-canopy woodlands and grasslands (D'Antonio & Vitousek, 1992). These grass species produce significant quantities of standing dry biomass that readily burn (D'Antonio & Vitousek, 1992). Grasses are also quicker to recover post-fire than woody species, giving them a competitive resource advantage (D'Antonio & Vitousek, 1992). The fast recolonization sets into motion a grass-fire cycle. The presence of grass species promotes fire, which encourages the further growth of grass species, which then encourages future fire, resulting in a positive feedback loop.

The Social and Ecological Dimensions of Biological Invasions

Flora and fauna exist in their native ranges as a result of geographical boundaries that preclude further migration. Today's global society perpetuates an interconnectedness that allows for the transfer of species out of their natural distributions, across geographical boundaries, and into alien environments. Humans facilitate species introductions from country to country, and continent to continent, as a result of human travel and commerce (Mack et al., 2000). Humans are also perpetuating the spread of invasive species as a result of anthropogenic climate change. Species distributions are expected to shift as a response to changes in temperature and precipitation patterns. Populations are expected to move poleward in latitude and upward in elevation (Lawler et al., 2009). As species distributions shift, non-native populations may have a competitive advantage in adapting to new climates. These conclusions have been drawn using bioclimatic models to compare current geographic ranges with future climate projections (Lawler et al., 2009).

While the term invasion suggests intentionality, non-native species are often introduced accidentally. Whether stowing away in the bilge water of a cargo ship, traveling the world as a sought-after ornamental plant, or hitching a ride on the hull of a motorboat, the transport of these species is facilitated by humans. Once a non-native species reaches a new landscape, it must withstand environmental and ecological changes in order to eventually establish itself as a successful invader. This delay in population establishment is known as the *lag* period of biological invasions (Figure 2) (Mack et al., 2000). Those species that become invasive in the novel ecosystem are competitive with the surrounding resources, allowing for a boom in the population. This is often referred to as the *log* period of biological invasions (Figure 2) (Mack et al., 2000). Once a non-native population is established, there are often cascading effects on the ecosystem.

Invasive species outcompete native species for natural resources, such as water, nutrients, and even light. Other species interfere with native populations through aggression, predation, and hybridization (Mack et al., 2000). The fast-growing populations of invasive plants often result in dense monocultures across entire ecosystems, completely changing the primary productivity, shelter structure, and food availability for entire trophic levels (Mack et al., 2000).

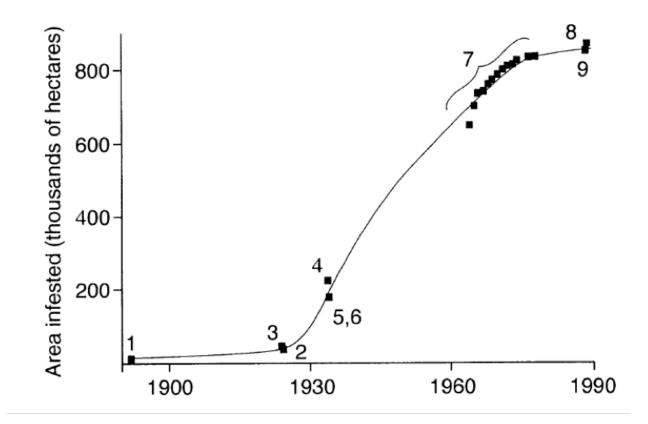


Figure 2. Population spread of *Opuntia rantiaca* in South Africa showing the lag and log phases of proliferation and spread. Reprinted from "Biological control of jointed cactus, Opuntia aurantiaca (Cactaceae), in South Africa" by C. Moran and H.G. Zimmerman, 1991, *Agriculture, Ecosystems, and Environment*, (47), 5-27.

The Non-Native Grass-Fire Cycle

The flammability of grassy species has global implications when considering biological invasions. Landscapes that have been invaded by grasses are likely to experience changes in fire behavior. In regions without previous fire history, the introduction of non-native grasses can result in novel fire regimes (Rahlao, Milton, Esler, Van Wilgen, & Barnard, 2009; van Wilgen & Richardson, 1985). Vegetation mortality in post-fire landscapes opens up physical space and niches for subsequent biological invasion, and the increase in nutrient availability encourages the rapid perpetuation of already established non-native populations (D'Antonio & Vitousek, 1992). For decades now, it has been argued that an increase in non-native grass species invasions encourages fire, which in turn provides opportunities for further colonization of the non-native species (D'Antonio & Vitousek, 1992; Brooks et al., 2004). This positive feedback loop has significant implications for global change ecology and fire management.

In 1992, D'Antonio and Vitousek published "Biological Invasions by Exotic Grasses, the Grass/Fire Cycle, and Global Change," which introduced the concept of a grass-fire cycle. They speculated that the presence of invasive grass species encourages fires of greater frequency, area, and intensity (D'Antonio & Vitousek, 1992). These conclusions were supported by a review of the spatial relationships between biological invasions and instances of fire across the globe. D'Antonio and Vitousek asserted that an increase in the presence of fire and the frequency of grass invasions would have synergistic consequences. They warned that a perpetuation of the grass-fire cycle could trigger ecosystem-level change and play a role in the increasing concentrations of greenhouse gases at a global scale (D'Antonio & Vitousek, 1992).

In the following decades, studies were conducted to empirically test the interactions between fire and non-native grass species. In 2004, Brooks et al. reviewed the case studies and published a paper outlining how fuel properties of invasive grasses alter the intrinsic (e.g. moisture content and tissue flammability) and extrinsic (e.g. fuel load, continuity, and packing ratio) properties of fire regimes. They then proposed an updated graphic model outlining the non-native grass-fire cycle, which was based on the fire regime cycle illustrated in Figure 3.

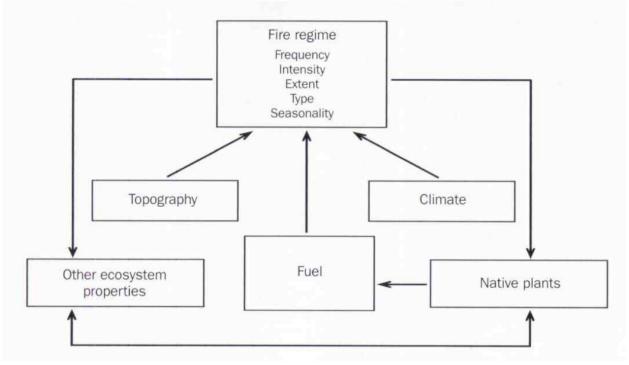


Figure 3. The fire regime cycle. Reprinted from "Effects of invasive alien plants on fire regimes" by Brooks et al., 2004, *BioScience*, 54(7), 677-688.

In the ten years since Brooks et al. published their findings, scientists have continued to study the dynamic and spatiotemporal relationships between grass species and fire regimes. My research synthesizes these case studies to explore two research questions. 1) What are the mechanisms that drive the non-native grass-fire cycle? 2) How has our understanding of the global distribution of the non-native grass-fire cycle progressed since the publications of D'Antonio and Vitousek (1992) and Brooks et al. (2004)?

Project Outline

Chapter 2 details the methodologies of my collection and analysis of relevant case studies that have been published over the past two decades. I will discuss the qualitative and quantitative frameworks with which I explored the case studies and elaborate on the importance of D'Antonio and Vitousek's 1992 paper and Brooks et al.'s 2004 paper. As a baseline for my review of the dynamic relationships of the non-native grass-fire cycle, I present a figure, modified from Brooks et al. 2004, that expresses the cycle in terms its dynamic relationships (i.e. fire and native vegetation, fire and non-native grasses, native vegetation and non-native grasses, native vegetation and fuel properties, non-native grasses and fuel properties, and fuel properties and fire) and another figure that illustrates the specific mechanisms that drive the cycle. As a baseline for my review of the spatiotemporal relationships of the non-native grassfire cycle, I created a world map showing the geographic locations of the case studies presented in the 1992 and 2004 publications, as well as this thesis.

Chapter 3 is a literature review of the case studies related to the non-native grass-fire cycle over the past decade and a half. I will explore my first research question: What are the mechanisms that drive the non-native grass-fire cycle?

In Chapter 4, I address my second research question: How has our understanding of the global distribution of the non-native grass-fire cycle progressed since the publications of D'Antonio and Vitousek (1992) and Brooks et al. (2004)? This examination of the spatiotemporal relationships of the cycle focuses on the spatial distribution of the state-of-knowledge of the non-native grass-fire cycle across the globe. A cartographic representation comparing the spatial patterns of biological invasions and fire in 1992, 2004 and 2014 highlights the progression of our understanding of the non-native grass-fire cycle through space and time.

Chapter 5 presents a summary of the non-native grass-fire cycle in 2014 by rearticulating the dynamic and spatiotemporal relationships outlined in Chapters 3 and 4. In a discussion of the limitations of this study, I explain how a lack of consistent reporting and methodologies makes it challenging to conduct sufficient meta-analyses. Lastly, I consider potential questions for future research by introducing the human dimension of the non-native grass-fire cycle.

Chapter 2: Research Design and Objectives

The subject of this thesis was established gradually, starting with a general interest in invasive species, and how they are implicated in climate change. The genesis of my project occurred after reading Brooks et al.'s 2004 paper, "Effects of Invasive Alien Plants on Fire Regimes." I was immediately reminded of a 1992 paper by D'Antonio and Vitousek: "Biological Invasions by Exotic Grasses, the Grass-Fire Cycle, and Global Change." The two articles paralleled one another in their underlying theses, while contrasting with one another in methodology. Both explored how non-native vegetation, specifically grass species, interacted with fire regimes and initiated a positive feedback loop between grass and fire. However, where D'Antonio and Vitousek approached the grass-fire cycle from a spatial context, Brooks et al. explored the cycle from a mechanistic and temporal context. By drawing on both papers' conclusions about the grass-fire cycle, I was able to develop a strong foundation on which to base my review of the non-native grass-fire cycle in 2014.

With a 22-year-old paper in one hand, and a 10-year-old paper in another, I was inspired to explore the dynamic and spatiotemporal relationships at play between fire and non-native grasses *today*. Therefore, my intention was to focus my literature review on the past 10 years to explore the research done since Brooks et al.'s most recent review of the grass-fire cycle. My goal was to find peer-reviewed literature that either provided an empirical study of the specific relationships between fire regimes and invasive species, or spoke to the general trends in fire and invasive species over the past decade. I used Thomson Reuters' Web of Science database to collect relevant journal articles. In order to focus my search, I established parameters about the setting of the case studies; in order to focus my review on grass-dominated landscapes, I did not include studies set in heavily forested or primarily coastal landscapes.

I chose to use both qualitative and quantitative frameworks to explore the studies. From the 80 abstracts that I read on the subject of the grass-fire cycle, 40 were appropriate for this research project. The excluded papers typically focused on secondary factors that play a part in the grass-fire cycle (e.g. soil seed banks, root system networks, and soil chemistry). The papers that were considered appropriate were those discussing the primary factors of the grass-fire cycle (e.g. biomass, continuity, and fire behavior properties). Each paper was read carefully and summarized for future consideration. These summaries allowed me to explore the qualitative conclusions offered by the authors. From these, I was able to draw similarities across the case studies, despite the large volume of literature reviewed. In order to explore the quantitative measures in each paper, I developed a database of the studies in an Excel spreadsheet. For each case study, I recorded the authors, publication date, non-native species discussed, native species discussed, geographic location of the case study, methodologies, and any quantitative parameters that were published. The studies published data on biomass, native vs. non-native composition and cover in the study plots, continuity measures, vegetation and soil moisture, and various fire regime dynamics (rates of spread and intensity). Given the diverse methodologies used, the most consistent way to report the data was as a function of percent change between the variable-in-question that was influenced by non-native grasses, and the variable-in-question influenced by native vegetation species (Figure 4).

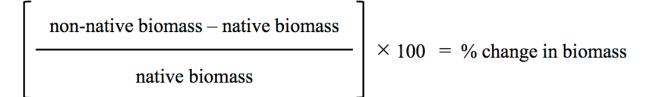


Figure 4. Example of the percent change calculations that will compare invaded and non-invaded plot data

As a baseline for my review of the dynamic relationships of the non-native grass-fire cycle, I revisited Brooks et al.'s fire regime figure (Figures 3 and 5). After a critical review of the graphic version of their model, which I discuss in greater detail in Chapter 3, I developed my own conceptual model and

graphic representation of the non-native grass-fire cycle, modified from Brooks et al. 2004. It addresses the interactions of the cycle (i.e. fire and native vegetation, fire and non-native grasses, native vegetation and non-native grasses, native vegetation and fuel properties, non-native grasses and fuel properties, and fuel properties and fire) and the specific fuel properties and fire behavior characteristics that interact to perpetuate the non-native grass-fire cycle.

As a baseline for my review of the spatiotemporal relationships of the non-native grass-fire cycle, I created a world map showing the geographic locations of the case studies presented in the 1992 and 2004 publications. In 1992, D'Antonio and Vitousek cited cases of the grass-fire cycle in Hawaii, Western North America, tropical America, and Australia (D'Antonio & Vitousek, 1992). By juxtaposing a map of the geographic locations of the documented cases before 2004, and the cases after 2004, I was able to illustrate the spread in the study of the extent and intensity of the grass-fire cycle around the world over the past 25 years. By nature of my case study selection process, it is possible that there have been studies conducted in other locations that are not represented in this distribution of the non-native grassfire cycle.

Chapter 3: Dynamic Relationships of the Non-Native Grass-Fire Cycle

Reevaluating the Conceptual Model

Brooks et al., after exploring how fuel properties are influenced by biological invasions, presented a multiphase conceptual model that outlines the non-native grass-fire cycle. It begins with the introduction of an invasive species into an ecosystem. After the species has naturalized, spread, and impacted the ecosystem, the cycle begins. Brooks et al. outline the interactions between the alien plants, native plants, fuel properties, 'other ecosystem properties', and the 'fire regime' (Figure 5). This foundational paper in the study of invasive grasses and fire, while important in its contribution to the field of fire ecology and biogeography, does not elaborate on the particular mechanisms in which the fuel properties alter the fire behavior.

As a consequence, there are some key questions that are left unanswered. What do they mean by 'other ecosystem processes'? Which fuel property is affecting which property of the fire regime? While many have empirically studied the interactions that Brooks et al. illustrated, the conceptual model remains the same. Without looking critically at Brooks et al.'s representation of the grass-fire cycle, it is difficult to pinpoint the attributes that have the greatest impact on the perpetuation of the cycle. If the most significant interactions in the cycle are identified, the non-native grass-fire cycle conceptual model could be used as a tool for decision-making and mitigation, highlighting critical points of intervention to dampen the positive feedback loop that is created. By critically engaging with Brooks et al.'s conceptual model and considering the current findings on the dynamic relationships between non-native grasses and fire, I create a restructured conceptual model that I believe will be a better tool for identifying these critical points of intervention.

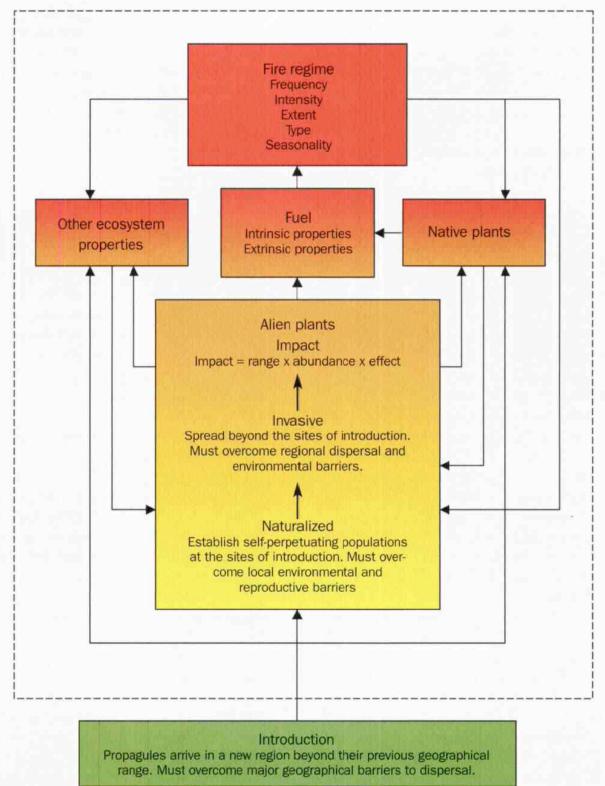


Figure 5. The fire regime cycle after grass invasions. Reprinted from "Effects of invasive alien plants on fire regimes" by Brooks et al., 2004, *BioScience*, 54(7), 677-688.

The Mechanisms of the Non-Native Grass-Fire Cycle

The non-native grass-fire cycle is complex, but it can be simplified dichotomously into fire behavior, and fuel structure and composition. While the conceptual model developed by Brooks et al. in 2004 is comprehensive, it does not explore the specific characteristics of the fire regime and fuel properties that perpetuate the cycle. The literature discussed in this thesis provides insight into these mechanisms. A landscape's non-native grass biomass (weight/area) is closely related to the intensity of the fire that runs through it (Rossiter, Setterfield, Douglas, & Hutley 2003; Rossiter-Rachor, Setterfield, Douglas, Hutley, & Cook, 2008; Rahalo et al., 2009; Saltonstall & Bonnett, 2012). The greater the volumes of fine fuels (grasses) available to burn, the greater the potential for a more intense fire to burn. While fire intensity is dependent on many factors, it is most often correlated with biomass. Non-native grass species composition often relates to the fire return interval (Masocha, Skidmore, Poshiwa, & Prins, 2011; Balch, Bradley, D'Antonio, & Gómez-Dans, 2013). The composition, or proportion of native vegetation to non-native vegetation, varies from season to season, fluctuating with the availability of nutrients, precipitation, and suitable temperature. A greater percentage of non-native grass species across a landscape will decrease the interval at which a fire may reoccur. Cover and continuity of non-native grasses is often associated with the fire-spread rate (Balch et al., 2013; Davies & Nafus, 2013). Patch connectedness increases with more invasive individuals, leading to a significant increase in fire-spread rate.

Figure 6 is a depiction of the non-native grass-fire cycle, adapted from Brooks et al. (2004). The figure outlines the interactions between fire and native vegetation, fire and non-native grasses, native vegetation and non-native grasses, native vegetation and fuel properties, non-native grasses and fuel properties, and fuel properties and fire. Figure 7 depicts the mechanisms discussed above, within the cycle as a whole. The fire behavior metrics include fire intensity, fire spread-rate, and fire return interval. The fuel property metrics include biomass, cover, continuity, and composition. The two figures are connected by the entities labeled "Fire Regime" and "Fuel Properties."

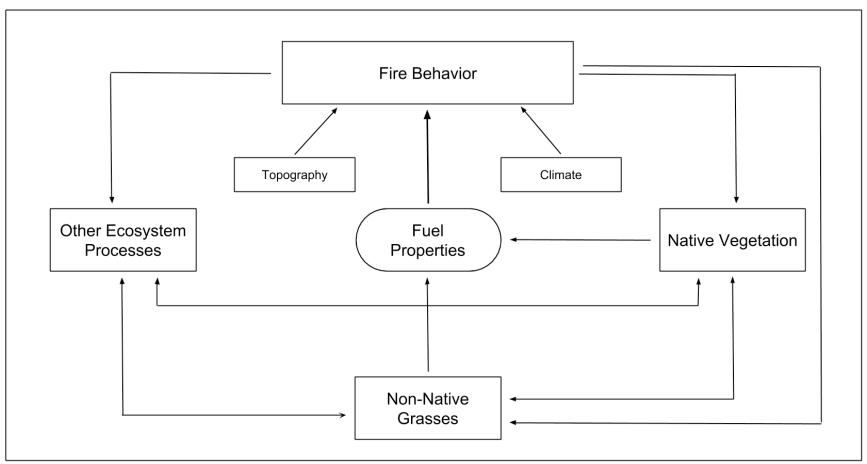


Figure 6. The Non-Native Grass-Fire Cycle in 2014; adapted from Brooks et al. 2004

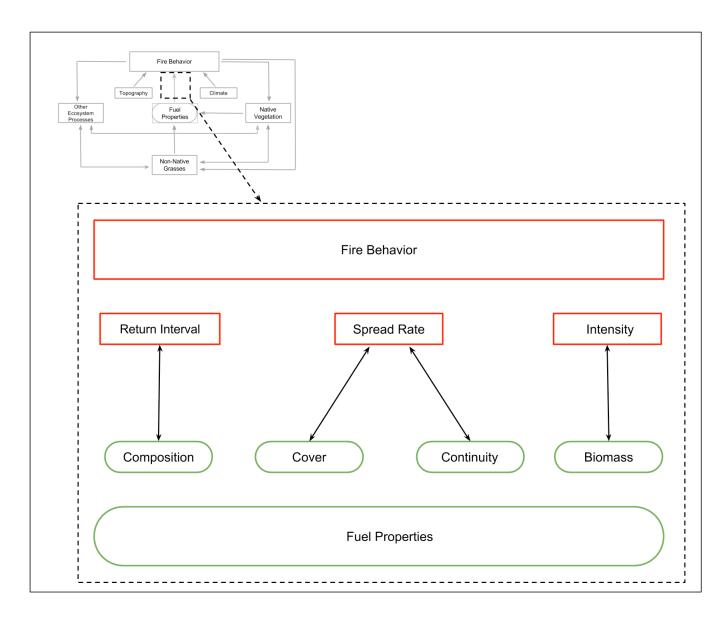


Figure 7. The interactions between fuel properties and the fire regime involved in the non-native grass-fire cycle

In the following literature review, I begin by discussing those studies that approach the cycle from the perspective of fire. These case studies are empirical explorations of how invaded and noninvaded plots experience fire behavior. The authors report on fire intensity, spread rate, and return interval, and how those properties relate to non-native grass species. I then approach the cycle from the other perspective, the non-native grasses. The majority of these case studies present qualitative and quantitative observations on how the presence or absence of fire has influenced the fuel properties of the study site by measuring biomass (Table 3), percent cover (Table 4), composition (Table 5), and continuity. Both sets of case studies provide a comprehensive overview of the relationships between nonnative species and the fuel properties that promote fire behavior (e.g. more continuous fine fuels, greater biomass, lower vegetation and soil moisture).

For a complete database of the studies discussed here, and those discussed on Brooks et al., 2004, and D'Antonio and Vitousek, 1992, see Appendix A.

Fire Behavior

Many studies have explored how particular fuel characteristics associated with non-native grass species influence fire behavior. Rahalo et al., in their 2009 publication on the invasive alien grass *Pennisetum setaceum* in South Africa, explored how fire can be introduced to a fire-free system because of a biological invasion. The Karoo is an ecosystem of typically low primary productivity, and therefore rarely experiences fire because of a lack of fuel for ignition, despite the necessary climate conditions. The introduction of an alien perennial grass, *P. setaceum*, has the potential to drastically change fire patterns. Rahalo et al.'s study took place at the Tierberg Karoo Research Center, where they introduced the invasive grass at low and high fuel loads to delineated plots for burn experiments. The results showed that for higher fuel loads of *P. setaceum*, there was a higher fire intensity and rate of spread (Rahalo et al., 2009). Fire-spread rates were 0.03 and 0.05 m/s for low and high fuel loads, and the respective fire

intensity measurements were 427 and 849 kW/m (Table 1 & Table 2) (Rahalo et al., 2009). The observed changes in the fire characteristics reinforce the idea that the invasion of *P. setaceum* and the subsequent increase in combustible fuels to the Karoo biome would likely introduce fire to the landscape.

In 2003, Rossiter et al. explored how invasions of *Andropogon gayanus* to the savannas of Wildman Reserve and Crater Lake in northern Australia would change fire behavior. While Rahalo et al.'s methodology required that they artificially introduce the invasive population, the landscapes at Wildman Reserve were already heavily invaded with *A. gayanus*. Rossiter et al. conducted fuel reduction burns at the Wildman Reserve and Crater Lake study sites in order to observe how the biological invasions would influence the fire regime. This data was compared with historical fire regime data at Wildman Reserve. The mean rate of fire spread in the invaded plots was 0.72 m/s, while the historical mean rate of spread was 0.37 m/s (Table 1) (Rossiter et al. 2003). The respective fuel loads for the present day and historical mean rates of spread were 10.2 t/ha and 3.2 t/ha, suggesting a relationship between greater fuel loads and increased rates of fire spread (Rossiter et al. 2003). The more heavily invaded plot fire intensity was also eight times higher than the historical fire intensity, with an invaded site fire intensity of 15700 kW/m and a historically (non-invaded) site fire intensity of 2100 kW/m (Table 2) (Rossiter et al., 2003). Rossiter et al. also note that fine-fuel loads are typically four-times greater in landscapes that have been invaded by *A. gayanus*, and these landscapes would therefore experience significant alterations to the fire regime (Rossiter et al. 2003).

Setterfield et al. took a similar approach to Rossiter et al. (2003) in their 2010 publication, "Turning up the heat: the impacts of *Andropogon gayanus* (gamba grass) invasion on fire behavior in northern Australian savannas." They conducted controlled burns in sites with native grasses and sites heavily invaded by *A. gayanus*. The native grass sites experienced lower rates of fire spread and intensity than sites with *A. gayanus* (Setterfield, Rossiter-Rachor, Hutley, Douglas, & Williams, 2010). With biomass measurements at 360 and 1160 grams/m² (native grass and *A. gayanus*), the impact of invasive presence was apparent on the fire intensity, with measures at 3700 and 15700 KW/m, respectively (Table 2) (Setterfield et al., 2010). The fire-spread rate for the invaded plot was 0.6 m/s, and the fire-spread rate for the native grass site was 0.47 m/s (Table 1) (Setterfield et al., 2010).

Authors	Publication Date	Non-Native Grass Species	Invaded Plot Fire-Spread Rate (m/s)	Non-Invaded Plot Fire-Spread Rate (m/s)	Fire Spread Increase (%)
Balch et al.	2013	B. tecotrum	0.009	0.006	38
Rahlao et al.	2009	P. setaceum	0.05	0.03	32
Rossiter et al.	2003	A. gayanus	0.72	0.37	95
Rossiter- Rachor et al.	2008	A. gayanus	0.39	0.08	388
Setterfield et al.	2010	A. gayanus	0.60	0.47	28

Table 1. Experimental fire-spread rates for invaded and non-invaded grasslands plots

Table 2. Experimental fire intensity readings for invaded and non-invaded grassland plots

Authors	PublicationNon-NativeDateGrass Species		Invaded Fire Intensity (kW/m)	Non-Invaded Fire Intensity (kW/m)	Fire Intensity Increase (%)
Grigulis et al.	2005	A. mauritanica	1.599	0.172	830
Rahlao et al.	hlao et al. 2009 P. seta		894	427	109
Rossiter et al.	2003	A. gayanus	15700	2100	648
Rossiter- Rachor et al.	2008	A. gayanus	6408	647	890
Setterfield et al.	2010	A. gayanus	15700	3700	324

Balch et al., in their 2009 paper "Introduced annual grass increases regional fire activity across the arid western USA," explored the relationships between *Bromus tectorum* (an invasive annual grass commonly known as cheatgrass) and fire in the western United States. They analyzed aerial imagery from MODIS and USGS to compare burned areas from historical fires with land cover distribution (i.e. cheatgrass, montane, agriculture, sagebrush, pinyon-juniper, alkali meadow, desert shrub, and nonvegetated) (Balch et al., 2009). The results showed that cheatgrass had the largest proportional area burned when compared to other native vegetation classes (Balch et al., 2009). Cheatgrass experienced the shortest fire return interval, and 39/50 of the largest fire events occurred in areas with significant cheatgrass cover (Balch et al., 2009).

Fuel Structure and Composition

Most of the studies examined fuel characteristics in invaded landscapes and considered the potential for fire, or in some cases, created models and simulations for fire in the future. Grigulis et al. (2005) explored the relationship between fire and *Ampelodesmos mauritanica* in Catalan shrublands in Spain. The large tussock grass had invaded areas in Garraf Natural Park, where this study site was located (Grigulis et al., 2005). In comparing sites with high and low density of *A. mauritanica*, the high-density sites typically contained twice as much aboveground biomass (Table 3) (Grigulis et al., 2005). After estimating plot flammability (as a function of mean inflammation delay and intensity) by performing small-scale burns on different grass and shrub species, Grigulis et al. concluded that plots with a high density of *A. mauritanica* were 40 times more flammable than those with a low density of invasion (Grigulis et al., 2005).

Davies and Nafus' 2013 paper, "Exotic annual grass invasion alters fuel amounts, continuity and moisture content," suggested that exotic annual grasses increase fire frequency because they increase the amount, continuity, and ignitability of fuels. In order to determine the effect that fire has on these fine fuel characteristics, they studied the presence of *Bromus tectorum* in the Northern Great Basin Experimental Range in western United States. Their results showed that fine fuel biomass was 2-3 times greater in invaded communities in 2010 and 2011 (Table 3) (Davies & Nafus, 2013). They also found that fine fuel cover continuity (measured by length of patches of the same cover type separated by <5 cm) was 9-17

times greater in invaded communities, and also that density was greater in invaded communities (Davies & Nafus, 2013). In discussion, Davies and Nafus explained that these factors increase the probability for fire ignition, in that there is a higher chance that fire would come into contact with combustible fuels.

The invasion of guinea grass (*Megathyrsus maximus*) on the island of Oahu, Hawaii has been observed to alter the flammability of ecosystems when coupled with anthropogenic ignitions (Ellsworth, Litton, Taylor, & Kauffman, 2013). In 2008, Ellsworth et al., set out to quantify the spatial and temporal variability of fine fuel properties in high fire risk areas on Oahu. Plots dominated by *M. maximus* were selected in which to measure total fine fuel loads (live and dead), fuel composition, and fuel moisture content. Total fine fuel biomass ranged significantly, both spatially and temporally (Table 3). Ellsworth et al. reference D'Antonio and Vitousek's 1992 paper in explaining how these high fuel loads in the areas invaded with *M. maximus* are likely to provide a continuous, flammable fuel source that can perpetuate the non-native grass-fire cycle (Ellsworth et al., 2013).

Brooks and Berry explored the dynamic relationships between invasive species and a multitude of disturbances in the Mojave Desert. In 2006, they published "Dominance and environmental correlates of alien annual plants in the Mojave Desert, USA." There have been many studies conducted in the Mojave to observe how the invasion of non-native plant species is affecting the native and endangered species of the desert. In considering that non-native species richness is positively correlated with high levels of disturbance, Brooks and Berry explored how a variety of disturbances around an area in the southwestern Mojave Desert were impacting non-native species dominance and species richness. They sampled annual plants in 1995, a year of high rainfall, and in 1999, a year of low rainfall. Their findings showed that while non-native species consisted of a small percentage of the composition of species, they contributed a much larger percentage of biomass. In 1995, non-native species comprised 6% of the population and 66% of the total annual plant biomass (Brooks & Berry, 2006). In 1999, non-native species comprised 27% of the population, but 79% of the total annual plant biomass (Brooks & Berry, 2006). After running

the biomass patterns against multiple disturbance types, Brooks and Berry found total alien biomass to be positively correlated with fire in both study years. Fire was also the only variable that *significantly* correlated both years (Brooks & Berry, 2006).

The majority of the studies approached the dynamic relationships between non-native grass species and fire from the perspective of how a historical or present-day presence of fire in a landscape influences non-native and native grass populations and fuel characteristics. Jacquemyn, Brys, and Neubert published, "Fire increases invasive spread of *Molinia* caerulea mainly through changes in demographic parameters" in 2005, which studied how invasions of *Molinia caerulea* in the Kalmthouste Heide have introduced fire into the heathlands of northern Belgium. Their study, running from 1997-2000, compared growth rates and invasion speeds in burned and unburned plots. Through sampling the upper layer of the soil after the fire, Jacquemyn, Brys, and Neubert found that seedling densities were doubled in the burned plots compared to the unburned plots. Permutation tests showed that growth rates were significantly higher in burned plots. Invasion speed (a measure that considers population growth and dispersal) in the burned plots was nearly triple that of the unburned plots. These heathlands are typically of low productivity, but the presence of this perennial tussock grass could increase litter production, and therefore available fuel, which would subsequently increase fire probabilities (Jacquemyn, Brys, & Neubert, 2005).

Saltonstall and Bonnett's 2012 study looked at how fire affects regeneration, growth, and reproductive output of *Saccharum spontaneum* L. The study area consisted of an abandoned agricultural field in central Panama which was cleared of the invasive grass in order to plant native trees. Adjacent to this were large stands dominated by *S. spontaneum*. A high-intensity fire ran through both plots in 2009. In most of the affected areas, the fine fuel biomass was burned completely (Saltonstall & Bonnett, 2012). About a week later, transects were delineated, and intensity of the fire was determined as low, medium, or high, depending on the quality of the culms lefts intact. Plots were then monitored for biomass and seed viability. There was less *S. spontaneum* mortality in the tree plots, suggesting a lower intensity fire

than in grassland plots. In the unburned site, there were 5630 g/m² of the grass (Saltonstall & Bonnett, 2012). The burned area mean biomasses are as follows: Low intensity (1612.7), medium intensity (450.7), and high intensity (6.7) g/m² (Saltonstall & Bonnett, 2012). One week after the fire, 42% of the plots had live sprouts of *S. spontaneum* appearing, and live aboveground non-native biomass recovered within 6 months of the fire (Saltonstall & Bonnett, 2012).

In 2009, Fisher et al. examined the fire history, historical canopy dynamics, and floristic composition of Bold Park, Perth, Australia. The study explored correlations between vegetation condition and composition, fire frequency, and grass invasions. They classified the study plots into three vegetation states: Good Condition, Medium Condition, and Poor Condition (sites invaded with *Ehrharta calycina* or *Pelargonium capitatum*). The Poor Condition sites were the most invaded by *E. calycina* or *P. capitatum*, and Good Condition sites the least invaded. By looking at previous fire records and aerial imagery of Bold Park, Fisher et al. determined that the poor quality sites experienced the greatest number of fires, with the shortest mean fire interval at 4.75 years (Fisher, Loneragan, Dixon, Delaney, & Veneklaas, 2009). The Poor Condition sites also experienced the greatest cover and composition of introduced species compared to native species (Table 4 & Table 5) (Fisher et al., 2009).

In 2011, Gomez-Gonzalez et al. published their study on whether or not anthropogenic fires favored non-native species in the Chilean Coastal Mattoral. The study site, lying on the coastal range in the region of Valparaiso, has experienced human disturbance, but little fire activity. Gomez-Gonzalez et al. observed the soil seedbanks and vegetation establishment patterns in unburned and burned delineated plots. They found that 66% of the annual grasses that established post-fire were alien species, and 51.7% of species in post-fire seedbanks were alien species (Table 5) (Gomez-Gonzalez et al., 2011). Native species also successfully reestablished in the post-fire plots. Gomez-Gonzalez et al. concluded that fire did not favor either the native or non-native species because this landscape, having been previously exposed to fire, is highly resilient to disturbances.

Table 3.	Biomass	measurements	for	invaded	and	non-invaded	plots

Authors	Publication Date	Non-Native Grass Species	Invaded Plot/High Fuel Biomass (g/m^2)	Non-Invaded Plot/Low Fuel Biomass (g/m^2)	Biomass Increase (%)
Brooks & Berry	2006	B. rubens E. cicutarium	100	27	269
Davies & Nafus	2013	B. tectorum	120	35	243
Davies & Nafus	2013	B. tectorum	106	56	89
Elliot et al.	2009	Sarga	136	47	191
Ellsworth et al.	2013	M. maximus	3429	326	952
Grigulis et al.	2005	A. mauritanica	550	250	120
Rahlao et al.	2009	P. setaceum	500	300	67
Rossiter et al.	2003	A. gayanus	1720	250	588
Rossiter- Rachor et al.	2008	A. gayanus	544	125	335
Setterfield et al.	2010	A. gayanus	1160	360	222
Setterfield et al.	2013	A. gayanus	1137	600	90

Authors	Publication Date	Non-Native Grass Species	*Non-Native Cover (%)	*Native Cover (%)
Coffman et al.	2010	Arundo donax L.	65	22
D'Antonio et al.	2000	A. virginicus, S. condensatum, M. minutiflora	49	29
D'Antonio et al.	2000	A. virginicus, S. condensatum, M. minutiflora	57	17
Davies & Nafus	2013	B. tectorum	90	40
Davies & Nafus	2013	B. tectorum	95	45
Fisher et al.	2009	E. calycina, P. capitatum	65	35
Fisher et al.	2009	E. calycina, P. capitatum	77	23
Vila & Lloret	2000	A. mauritanica	40	17
Vila et al.	2001	A. mauritanica	84	16
Vila et al.	2001	A. mauritanica	64	36

Table 4. Percent cover comparison for invaded sites

*Percentages may not add up to 100 if native, non-grass species were included in the study

Authors	Publication Date	Non-Native Grass Species	*Non-Native Composition (%)	**Native Composition (%)
Brooks & Berry	2006	B. rubens E. cicutarium	27	73
Fisher et al.	2009	E. calycina	61	39
Fisher et al.	2009	P. capitatum	42	58
Gomez-Gonzalez et al.	2010	B. hordeaceus, A. caryophyllea, V. myuros, E. peplus, H. glabra, B. minor	98	45
Masocha et al.	A. squamatus, bonariensis D		63	37

Table 5. Species composition comparison for invaded sites

*Non-native composition value representative of species noted in table.

**Native composition value representative of all other grass species present.

By exploring the non-native grass-fire cycle from the perspective of fire behavior, and then fuel structure and composition, I was able to identify the specific mechanistic interactions depicted in Figure 7. Reviewing the literature enabled me to construct a conceptual model of this non-native grass-fire cycle as it stands today. The quantitative data offered by the case studies suggest that, when comparing the fire behavior and fuel property trends between invaded and non-invaded plots, there is consistently higher fire intensity, fire spread-rate, and biomass in invaded plots. *Invaded plots saw a 116.04% increase in fire spread-rate, a 560.4% increase in fire intensity, and a 208.7% increase in biomass.* The studies, despite their variable methodological approaches, consistently support the conclusions and findings of Brooks et al., 2004. This quantitative and qualitative approach in the literature review provides a comprehensive summary of the non-native grass-fire cycle in 2014.

Chapter 4: Spatiotemporal Relationships of the Non-Native Grass-Fire Cycle

The spatial distribution of the non-native grass-fire cycle is a subset of the global distribution of fire. Fire ignition requires certain climatic conditions, topography and fuel availability. The global distribution of fire is illustrated in Figure 8 (Krawchuk, Moritz, Parisien, Van Dorn, & Hayhoe, 2009). Using ArcMap Desktop 10.1, I plotted the coordinates associated with each case study discussed in this thesis, and also those discussed by Brooks et al. (2004), and D'Antonio and Vitousek (1992). This allowed me to explore my second research question: How has our understanding of the global distribution of the non-native grass-fire cycle progressed since the publications of D'Antonio and Vitousek (1992) and Brooks et al. (2004)?

In this chapter, I highlight the biomes implicated in the non-native grass-fire cycle. I then emphasize the most pervasive non-native grass-species that are involved in the cycle. These key players need to be controlled or removed in order to dampen the effects of the positive feedback loop at play in the non-native grass-fire cycle. This simplification can be a useful tool for decision makers in a time of limited resources and tight budgets.

Figure 9 includes the coordinates of the case studies discussed in this paper, those discussed in Brooks et al. (2004), and also in D'Antonio and Vitousek (1992), offering a temporal perspective of the changes in the distribution of studies of the non-native grass-fire cycle. The non-native grass-fire cycle has been studied in North America, South America, Europe, Africa, and Australia (Figure 9 & Figure 10). Few, if any, cases have been documented in Asia, despite having the appropriate climatic and topographical conditions for fire. While Figure 9 offers a perspective on how studies of the phenomenon have progressed through space and time, Figure 10 combines the study site coordinates with a map of terrestrial biomes, offering a geographic and ecological perspective of our understanding of the nonnative grass-fire cycle. It should be noted that there are other case studies that have been conducted on the non-native grass-fire cycle over the past decade that are not portrayed on these maps. As explained in Chapter 2, I set certain parameters for the collected literature that excluded studies focusing on characteristics of the non-native grass-fire cycle that are irrelevant to this thesis (e.g. soil chemistry and soil moisture). It is also important to consider that Figure 9 and Figure 10 illustrate the distribution of our understanding of the non-native grass-fire cycle. The distribution of the phenomenon itself is limited by who is studying the cycle and where they are publishing.

Most of the case studies (Figure 9) are located in North America and Central America, with only a few in Europe and Africa. As previously stated, many of the locations of these case studies are prone to fire. Certain study sites, namely those in Africa and Europe, originally lacked the fuel availability for fire ignition despite having the appropriate climate and topographical conditions. However, the biological invasions discussed in the case studies resulted in an increase in biomass and continuity of fuel, introducing fire into the landscapes. For the most part, the non-native grass-fire cycle has been recorded in fire-prone biomes. These regions have sufficient primary productivity (vegetative presence) and the appropriate climate conditions (e.g. seasonality, wind events, low moisture levels, and ignition sources) for fire to burn (Krawchuk et al., 2009). Study sites that were already exposed to fire typically reported an increase in fire intensity or a decrease in return interval. Even in landscapes that already experienced fire, biological invasions and novel fire regimes have had significant impacts on the native community. The increased vegetation mortality associated with fire can have cascading impacts on the ecosystem's delicate, interconnected web of energy.

Fifteen of the studies considered in this thesis were conducted in the western United States, focusing on just under 20 invasive grass species. The most prevalent non-native grass in this region is Cheatgrass (*B*. tecotrum). Most of the study sites were concentrated in the Great Basin region of the United States. The studies spread across three biomes: grassland, desert, and chaparral, or Mediterranean (Appendix C; Figure 18). The grasslands and chaparral landscapes have the necessary climatic conditions and fuel availability for fire, so that the non-native grass-fire cycle is altering pre-existing fire regimes. However, in the desert biome, the increase of biomass and continuity as a result of species invasions has allowed for sufficient fuel sources to create novel fire regimes.

There have been two publications and a dozen studies on the non-native grass-fire cycle in Hawaii. As an island, Hawaii is more susceptible to biological invasions than locations on the mainland. Hawaii is in the tropical rainforest biome, and is therefore potentially vulnerable to fire because of its climate and topography (Appendix C; Figure 19) (Christopherson & Birkeland, 2013). The Theory of Island Biogeography explains that as a result of the state's isolation from the mainland, Hawaii has many endemic, unique species, but lacks the proper predatory population to ward off invasions. Invasive species can easily fill niches that are left empty as a result of the isolation of the island (Convention on Biological Diversity, 2002). Once the population has been established, invasive grass species have a greater impact on Hawaii, as an island, because of its delicate and unique species composition (Convention on Biological Diversity, 2002).

Four publications on the non-native grass-fire cycle considered in this paper were conducted in Latin America. They highlighted five different species implicated in the non-native grass-fire cycle. The biomes where we see case studies on the non-native grass-fire cycle in Latin America typically experience fire. In the tropical rainforest, tropical dry broadleaf forest, and desert biomes, there have been a number of studies (Appendix C; Figure 20) (Christopherson & Birkeland, 2013). The non-native grassfire cycle in many of these cases was accentuated by human activity, both through intentional biological invasions and anthropogenic fire ignition.

While Western Europe is not densely populated with studies on the non-native grass-fire cycle, there has been an increase in our understanding of its presence over the past 10 years. Four of the studies considered in this thesis have been published here, with a focus on the Mauritania vine reed in Spain. Thus far, the phenomenon has been documented in Spain and Belgium, located in the Mediterranean and heathland (shrub-like habitat) biomes respectively (Appendix C; Figure 21) (Christopherson & Birkeland, 2013). While the Mediterranean biome is already exposed to fire, the heathlands of Belgium previously lacked fire activity until the introduction of *Molinia caerulea* (Jacquemyn, Brys, & Neubert, 2005).

Southern Africa has fewer studies than those in the Americas, with only two studies over the past decade. The research on the non-native grass-fire cycle has focused on seven species suspected of being involved in the non-native grass-fire cycle. Despite the lower density of studies, this region is important because fire has been introduced into a fire-free region. While some of the older case studies in this region can be found in a Mediterranean biome (near Cape Town, South Africa), others are located in the Karoo biome (Appendix C; Figure 22) (Christopherson & Birkeland, 2013). This biome is known for its dry climate and sparse vegetation (Rahalo et al., 2009). However, biological invasions into the Karoo have led to an increase in fuel availability and an introduction of fire (Rahalo et al., 2009).

Australia is the most likely of all seven continents to experience fire (Bradstock 2010). Fire is a natural part of the Australian landscape, but with the invasion of certain species, it is more likely to occur. Seven of the studies discussed in this thesis were conducted in Australia. Gamba grass has been the species most often cited as being implicated in the non-native grass-fire cycle. The case studies involved in this feedback loop are located along the periphery of the continent, in the tropical and savanna biomes of Australia (Appendix C; Figure 23) (Christopherson & Birkeland, 2013). Few, if any, studies have been conducted in the central desert biome of Australia.



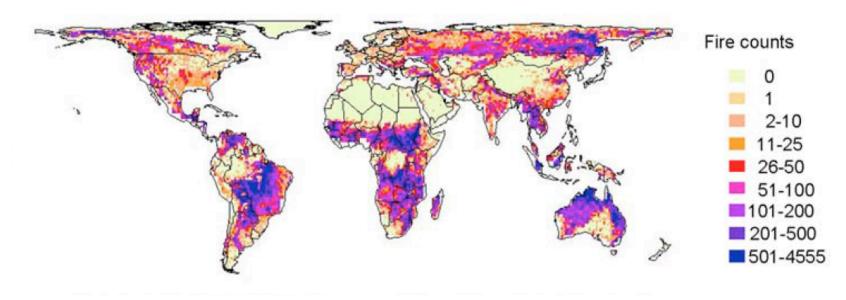
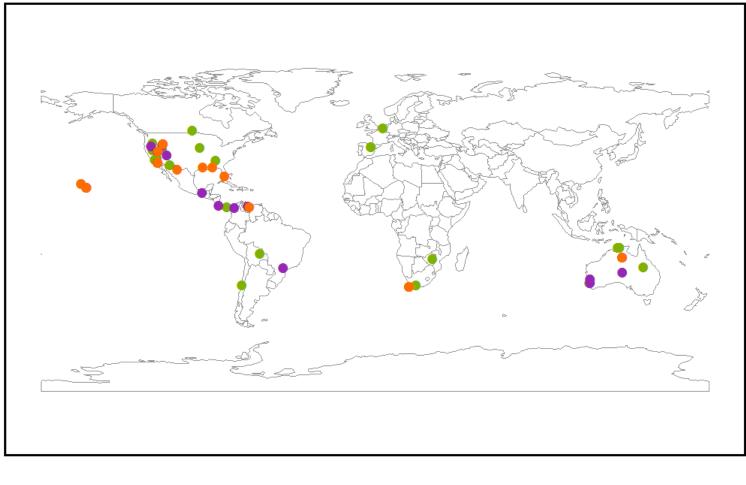


Figure 8. Global distribution of fire. Reprinted from "Global Pyrogeography: the Current and Future Distribution of Wildfire" by M.A. Krawchuk et al., 2009, PLoS ONE, 4(4), e5102. doi:10.1371/journal.pone.0005102



The Progression of our Understanding of the Non-Native Grass-Fire Cycle's Distribution through Time



D'Antonio & Vitousek 1992 Case Studies 🗧 Brooks et al. 2004 Case Studies 🗧 Munin 2014 Case Studies

Figure 9. A map of the locations of the study sites discussed in D'Antonio and Vitousek (1992), Brooks et al. (2004), and this thesis

The Biomes Implicated in the Non-Native Grass-Fire Cycle

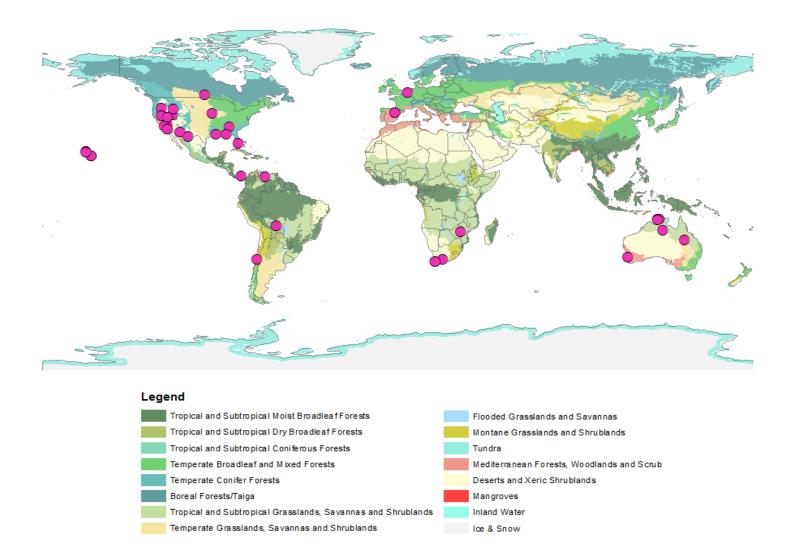


Figure 10. A map of the biomes in which the non-native grass-fire cycle has been studied

Biomes of the Non-Native Grass-Fire-Cycle

A fire regime is defined and controlled by fuel, climate, and topography. Until now, I have focused on how fuel composition and structure influence the fire regime. Now, having illustrated in Figure 10 the geographical relationship between terrestrial biomes and the non-native grass-fire cycle, I can offer insight into how climate has shaped our understanding of the distribution of the phenomenon. Terrestrial biomes are large ecosystems defined by the dominant vegetation found there (Christopherson & Birkeland, 2013). There are six biomes where the majority of case studies occur. They include 1) Mediterranean Forest, Woodland, and Scrub, 2) Desert and Xeric Shrubland, 3) Tropical and Subtropical Grassland, Savanna, and Shrubland, 4) Tropical and Subtropical Moist Broadleaf Forest, 5) Tropical and Subtropical Dry Broadleaf Forest, and 6) Temperate Broadleaf and Mixed Forest,

Mediterranean Forest, Woodland, and Scrub

The Mediterranean Biome is defined by its short, grassy woodlands and drought-adapted vegetation. The climate is typically dry, with only 25-65 centimeters of rain annually (Christopherson & Birkeland, 2013). Much of the rain is seen during the winter months, so areas in this biome experience little precipitation during the summer. Seven studies discussed in this thesis were conducted in the Mediterranean Forest, Woodland, and Scrub Biome (van Wilgen & Richardson, 1985; Vilà & Lloret, 2000; Vilà et al., 2001; Grigulis et al., 2005; Fisher et al., 2009; Coffman et al., 2010; Gómez-González et al., 2011). The studies spanned five continents and explored the impacts of 6 different species on the non-native grass-fire cycle, namely perennial veldtgrass and rose geranium. These regions are fire-adapted, so while they did not experience an introduction of fire, pre-existing fire regimes were significantly altered throughout this terrestrial biome (Christopherson & Birkeland, 2013).

Desert and Xeric Shrubland

The Desert and Xeric Shrubland Biome is most commonly defined by its lack of precipitation. Warm Desert Biomes receive less than 2 centimeters of rain per year, causing chronic precipitation deficits (Christopherson & Birkeland, 2013). Vegetation common to this biome is mostly limited to xerophytic plants that can withstand the low levels of precipitation. This biome, because of its characteristically sparse vegetation, has seen an introduction of fire as result of biological invasions. One of the studies discussed in this thesis can be found in the Warm Deserts of this biome (Brooks & Berry, 2006). However, in Cold Desert ecosystems, there is typically sufficient precipitation to support a layer of vegetation on the ground. These deserts, found in the western United States, have pre-existing fire regimes that were altered by the introduction of invasive grasses. Many of the studies discussed in this thesis can be found in the Desert and Xeric Shrubland Biome. They have focused on the impacts of cheatgrass (e.g. Rahlao et al., 2009; Balch et al., 2013; Davies & Nafus, 2013)

Tropical and Subtropical Grassland, Savanna, and Shrubland

Precipitation in the Tropical and Subtropical Grassland, Savanna, and Shrubland Biome is seasonal, ranging from 9-150 centimeters annually (Christopherson & Birkeland, 2013). Typically, precipitation levels are in deficit. This, coupled with high temperatures, makes this biome prone to fire events. The typical vegetation of the Tropical Savanna Biome includes sparse grass, bush thickets, and trees with flattened crowns (Christopherson & Birkeland, 2013). Six of the studies discussed in this thesis are found in the Tropical and Subtropical Grassland, Savanna, and Shrubland Biome (Rossiter et al., 2003; Rossiter-Rachor et al., 2008; Elliott et al., 2009; Setterfield et al., 2010; Masocha et al., 2011; Setterfield et al., 2013) Just as with the studies found in the Mediterranean Biome, pre-existing fire regimes have been altered due to the introduction of invasive grasses. The species most studied in this biome is gamba grass.

Tropical and Subtropical Moist and Dry Broadleaf Forest

These two biomes are often clumped together as the Tropical Rain Forest Biome. Tropical Rain Forests are often characterized by their thick canopy of trees and the epiphytes that grow along the forest floor and tree trunks (Christopherson & Birkeland, 2013). Precipitation is in surplus all year, with annual averages ranging from 180-400 centimeters (Christopherson & Birkeland, 2013). Many of the studies discussed in this thesis can be found in the Tropical and Subtropical Moist or Dry Broadleaf Forest Biomes (e.g. D'Antonio et al., 2000; Saltonstall & Bonnett, 2012; Ellsworth et al., 2013). These studies followed ten invasive grasses and how their presence was altering pre-existing fire regimes throughout the biome.

Temperate Broadleaf and Mixed Forest

The Temperate Broadleaf and Mixed Forest Biome is characterized by its mixed conifer and deciduous tree species and seasonal pattern of precipitation (Christopherson & Birkeland). These regions typically experience 75-150 centimeters of rain annually (Christopherson & Birkeland). While some species in this biome are fire-prone, most regions in the Temperate Broadleaf and Mixed Forest Biome do not usually experience fire. However, in the case of the Kalmthouste Heide heathlands in Belgium, the introduction of *M. caerulea* introduced novel fire regimes into a previously unburnable biome (Jacquemyn, Brys, & Neubert, 2005).

The Key Players

Gamba Grass

Gamba grass (*Andropogon gayanus*) is a perennial grass that originated from tropical Africa. From the family Poaceae, this grassy species can grow up to 4 meters tall (Cook et al., 2005). With an extensive root system and hairy leaves, this grass is able to extract water easily, making it resilient in dry climates (Figure 11). Gamba grass is prevalent throughout tropical America, and since its introduction, it has become naturalized in Brazil (Cook et al., 2005). This invasive species is also found in northern Australia (Cook et al., 2005). It was likely introduced into Central and South America for grazing purposes.



Figure 11. Gamba grass (A. gayanus); photograph from Cook et al., 2005

Cheatgrass

Cheatgrass (*Bromus tectorum*), also known as the downy brome, is an annual grass with a fine, fibrous root system. With hairy leaves and dense stems, cheatgrass has been shown to injure livestock as a result of consumption (Figure 12) (Pokorny, 2007). Originating from southern Europe and southwest Asia, this grass has invaded Russia and the Great Basin of the United States (Pokorny, 2007). The impacts of the invasion are more severe in North America because of its involvement in the promotion of fire (Pokorny, 2007).



Figure 12. Cheatgrass (B. tectorum); photograph from Texas Invasives, 2007

Perennial Veldtgrass

The perennial veldtgrass (*Ehrharta calycina*) is a member of the Poaceae family, native to Namibia, Lesotho, and South Africa (Figure 13) (University of Queensland, 2011). It is now naturalized in southern Australia, but considered invasive in western Australia and Victoria, where it outcompetes for resources with the native vegetation and increases fire hazard and frequency (University of Queensland, 2011). On Kangaroo Island, Australia, *E. calycina* is one of the top five weeds threatening biodiversity (University of Queensland, 2011).



Figure 13. Perennial veldtgrass (E. calycina); photograph from Queensland Government

Guinea Grass

Guinea grass (*Megathyrsus maximus*) is a member of the Poaceae family originating from Africa. This grass, found in a variety of habitats (e.g. orchards, vineyards, roadsides, railways, and riparian areas) has been naturalized throughout Australia (Figure 14) (University of Queensland, 2011b). There is a major effort in Queensland to manage the spread of guinea grass, but it is not legally declared a noxious weed (University of Queensland, 2011b).



Figure 14. Guinea grass (M. maximus); photograph from Queensland Government

Rose Geranium

Rose geranium (*Pelargonium capitatum*) is a perennial shrub originating from South Africa ("Rose Geranium," 2005). It was originally brought from Africa for ornamental and medicinal reasons. The plant, which grows up to 1 meter in height, is know for its pink flowers that are thought to have healing, homeopathic properties (Figure 15) ("Rose Geranium," 2005). Rose geranium is distributed throughout Australia and is best controlled through mechanical management techniques ("Rose Geranium," 2005).



Figure 15. Rose geranium (P. capitatum); photograph from Albert and Brown Supply Co.

Fountain Grass

Fountain grass (*Pennisetum setaceum*) is a perennial grass native to Africa and Southeast Asia, likely brought to South Africa as an ornamental plant ("Pennisetum setaceum Rubrum, n.d.). Its leaves can grow up to 3 meters tall, with its flowers reaching another meter above (Figure 16). Fountain grass has a rapid growth rate and requires warm temperature to thrive ("Pennisetum setaceum Rubrum, n.d.).



Figure 16. Fountain grass (P. setaceum); photography from Missouri Botanical Garden

Considering the Origins of Invasive Species

As seen in Figure 9 and Figure 10, there have been few publications on the non-native grass-fire cycle in Africa, and none in Asia. It is possible that this absence is a result of a publication bias or a lack of research on the phenomenon on these continents. However, it is interesting to consider the origin of the species involved in the non-native grass-fire cycle. Many of the invasive grasses throughout the world are native to and originated from Asia as a result of ornamental plant trading or accidental transport (D'Antonio & Vitousek, 1992). Some examples include *Bromus tectorum, Pennisetum setaceum, and Saccharum spontaneum* ("Bromus Tectorum," 2007; "Pennisetum setaceum 'Rubrum," n.d.; Germplasm Resources Information Network, n.d.). A great number of the biological invasions in South America originated from Africa through an effort by Europeans to support grazing (e.g. *Andropogon gayanus, Megathyrsus maximus, Ehrharta calycina, Pelargonium capitatum, and Ampelodesmos mauritanica*) (Hardion, Verlaque, Saltonstall, Leriche, & Vila, 2014 "Green panic, Megathyrsus maximus var. pubiglumis," 2011; "Perennial veldtgrass, Ehrharta calycina," 2011; D'Antonio & Vitousek, 1992; "Andropogon gayanus," n.d.; "Rose Geranium (Pelargonium capitatum x radens)," n.d.).

The non-native grass-fire cycle has proven to be a multi-scalar phenomenon. As seen in Chapter 3, the cycle alters fuel properties at the fine-scale. However, stepping back to look at the global picture, we can see that, as our understanding of its distribution increase, the non-native grass fire cycle has influenced entire landscapes and regions at the broad-scale.

Chapter 5: The Non-Native Grass-Fire Cycle in 2014

In 1992, D'Antonio and Vitousek introduced the non-native grass-fire cycle to the research community. Brooks et al. responded with confirmation and elaboration on the phenomenon in 2004, offering a conceptual model on the dynamic relationships within the non-native grass-fire cycle. Stepping into the world of academia in 2014, I was unsettled by the absence of a response to Brooks et al.'s conceptual model. I was unable to find a paper published after Brooks et al., 2004 that offered an extension, elaboration, or criticism of the model. Having studied and contemplated how anthropogenic climate change is likely to influence global fire distribution and species (native and non-native) distribution, I was surprised that the interaction between the two was understudied. Unsatisfied with the explanations offered by D'Antonio and Vitousek (1992) and Brooks et al. (2004), and the volume and depth of the research on distribution projects for fire and non-native grass-fire cycle? 2) How has our understanding of the global distribution of the non-native grass-fire cycle progressed since the publications of D'Antonio and Vitousek (1992) and Brooks et al. (2004)?

In Chapter 1, I provided an introduction to the concept of fire as a multi-scalar phenomenon, with influences at fine scales (fuel availability, composition, and structure) and broad-scales (landscape pattern and process interactions). After providing a discussion on the impact of biological invasions on a community, I brought the two topics of fire and invasive species together with a brief history of the non-native grass-fire cycle by introducing the two foundational papers considered for this thesis: D'Antonio and Vitousek (1992) and Brooks et al. (2004). In Chapter 2, I presented the frameworks through which I conducted my literature collection, review, and analysis. Chapters 3 and 4 offered a dynamic and spatiotemporal discussion of the non-native grass-fire cycle in 2014. Reviewing the case studies that were published on the phenomenon over the past decade, it became clear that the dynamic relationships

identified by Brooks et al. (2004) have been widely accepted. I was able to identify the mechanisms that drive the relationships between particular fuel properties and fire regime characteristics (Figure 7), and produce two maps using the geographical coordinates of the study sites in order to depict any spatiotemporal relationships of the non-native grass-fire cycle (Figures 9 & 10).

The non-native grass-fire cycle is a dynamic global phenomenon that appears to be increasing in spatial extent and severity over the past two decades. As the cycle propagates at fine scales, fine fuel biomass, continuity, cover, and composition are increasing. Subsequently at broader scales, fire intensity and spread rates are increasing, while fire return interval is decreasing. Certain mechanisms interact within the positive feedback loop of the non-native grass-fire cycle, (literally) adding 'fuel to the fire'. *Invaded plots saw a 116% increase in fire-spread rate, a 560% increase in fire intensity, and a 208% increase in biomass* (Figure 17). The complex interactions between biomass and fire intensity, continuity/cover and fire-spread rate, and composition and fire return interval ensure the continuation of this cycle.

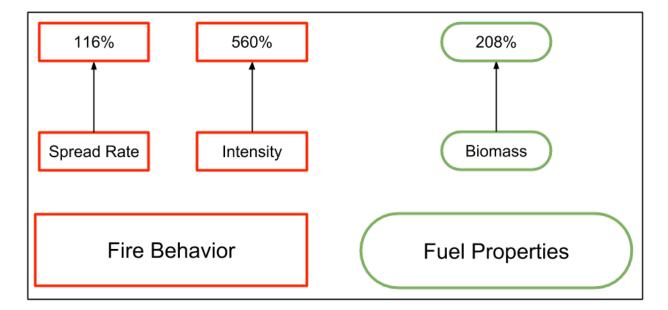


Figure 17. Percent increase in fire behavior and fuel property metrics

With multidimensional interactions between fire regimes, vegetation, and fuel properties, the non-native grass-fire cycle has been entering into and producing a positive feedback loop on five continents and at least 15 countries. The greatest density of case studies can be observed in North America, primarily west of the Mississippi River and in Hawaii. While it is true that these locations are prone to fire and have experienced extensive biological invasions over the past few centuries, the density also suggests that North America is the nucleus of research on the non-native grass-fire cycle. The biomes that are implicated in the non-native grass-fire cycle include 1) Mediterranean Forest, Woodland, and Scrub, 2) Desert and Xeric Shrubland, 3) Tropical and Subtropical Grassland, Savanna, and Shrubland, 4) Tropical and Subtropical Moist Broadleaf Forest, 5) Tropical and Subtropical Dry Broadleaf Forest, and 6) Temperate Broadleaf and Mixed Forest. The Desert and Xeric Shrubland and Temperate Broadleaf and Mixed Forest. The Desert and Xeric Shrubland and Temperate Broadleaf and Mixed Forest Biomes exhibited novel fire regimes, while the others experienced an alteration in pre-existing fire regimes as a result of biological invasions.

Limitations

The calculated average percent increases in biomass and fire intensity support the claim that these two mechanisms interact in a positive feedback loop to perpetuate the non-native grass-fire cycle. While a calculated average percent increase in fire spread-rate was obtained, there was not enough data reported on continuity (the metric closely associated with fire spread-rate in the cycle) to produce a similar percent increase value. The lack of quantitative data on continuity limits the ability to link this fuel property and fire spread-rate with as much confidence as intensity and biomass. Increasing the empirical studies on how continuity parameters influence the non-native grass-fire cycle would be a valuable contribution to the field, since there has already been significant study on fire spread-rates. There was also insufficient reporting on cover and composition to calculate average percent change.

In my exploration of the mechanisms that drive the non-native grass-fire cycle, my analysis was limited by the highly varied methodological approaches taken in different case studies. The authors of these studies opted for a variety of study site delineations, experimental methods, and reporting measures. While some approached the phenomenon by experimentally burning a delineated patch in a landscape, others observed landscapes that had experienced past fires. Other case studies consisted of observational measurements of areas historically exposed to fire, or landscapes with pro-fire climates that have been recently invaded by a non-native grass species. In regards to reporting measures, biomass comparisons were problematic with measurements published as either grams per square meter (fine-scale) or tons per hectare (broad-scale); the differences in scale offer uncertainty with conversions, especially when extrapolating grams per square meter to tons per hectare. Perhaps the most significant limitation in regards to methodologies is the difference in study site delineations. Some authors investigated sites that were invaded, comparing their characteristics with adjacent, non-invaded sites. Others looked at single plots, distinguishing between the individual species within that plot as native or non-native. In light of this, comparing reports of biomass and composition became problematic. Naturally, the biomass in an invaded site vs. a non-invaded site is much different than the difference between biomass of the invasive individuals and the native individuals in a single site. While there is merit in varying the methodology with which to study a phenomenon, it poses challenges to meta-analysis. Regardless, the case studies produced consistent conclusions despite their different approaches.

Looking Towards the Future

The human dimension of the non-native grass-fire cycle is both vast and vastly overlooked. Humans have driven the presence of current fire regimes and patterns of biological invasions, and the future of the non-native grass-fire cycle is in our hands. Global climate change, as we know it today, is a consequence of anthropogenic disturbance dating back to the Industrial Revolution. As human activity, on both a local and global scale, continues to deplete the quantity and quality of Earth's resources, the planet is thrown out of its natural equilibrium. Global climate change has affected all facets of nature (both biotic and abiotic), and has the potential to challenge the well being of society. As anthropogenic global change persists, species distributions are expected to shift poleward and upward in altitude (Lawler et al., 2009). This shift includes the non-native species as well, which is likely to introduce completely new populations to ecosystems on a global scale. Warming temperatures and variable precipitation patterns are likely to increase and alter the global distribution of fire in the future (Krawchuk et al., 2009). To what extent climate change will influence the already intricate cycle is a question for future research.

The synergism that is likely to be conceived from global change and non-native grass-fire cycle could have serious implications for society. As these fires and invasions move closer to residential and developed areas, the risk of property damage or loss of life increases dramatically. With these risks to society in mind, it is important now more than ever for politicians and decision makers to consider the implications of the non-native grass-fire cycle in order to intervene. By using the conceptual model produced in this thesis as a tool for defining critical points of intervention within the cycle, policy makers can ensure that their limited resources (time, finances, etc.) are put to efficient and effective use.

Appendix A: Non-Native Grass-Fire Cycle Case Study Database

Authors	Publication Date	Country	Latitude	Longitude	Non-Native Grass Species	Native Species
Balch et al.	2013	USA	38.9113	-116.8466	B. tectorum	Various native land cover classes
Davies & Nafus	2013	USA	43.4833	-119.7167	B. tectorum	A. tridentata, E. elymoides, F. idahoensis, K. macrantha, P. spicata
Ellsworth et al.	2013	Hawaii	21.5615	-158.0733	M. maximus	-
Fensham et al.	2013	Australia	-23.4578	144.6312	C. ciliaris	A. jerichoensis, B. ewarthiana, C. fallax
McGranahan et al.	2013	USA	40.7463	-94.2501	S. phoenix	-
Setterfield et al.	2013	Australia	-13.0417	130.8973	A. gayanus	A. semialata, H. contortus, S. intrans

Table 6. Case studies of the non-native grass-fire cycle from 1946-2013

						49
Saltonstall & Bonnett	2012	Panama	9.1017	-79.6128	S. spontaneum	-
Abatzoglou & Kolden	2011	USA	39.9297	-114.3857	B. tectorum, B. rubens, P. ciliare	-
Brooks & Chambers	2011	USA	-	-	B. madritensis ssp. rubens, B. tectorum, T. caput-medusa	J. occidentalis, P. monophylla
Lindsay et al.	2011	USA	31.5078	-110.2991	E. lehmanniana	A. palmeri
Masocha et al.	2011	Zimbabwe	-19.0833	31.2500	A. squamatus, B. pilosa, C. bonariensis, D. uncinatum, S. cordifolia, T. minuta	H. contortus, H. fîlipendula, M. minutiflora
Bradley et al.	2010	USA	33.8737	-85.6894	I. cylindrica, L. sinense, L. vulgare, P. lobata,	-
Coffman et al.	2010	USA	34.3679	-118.5336	A. donax L.	P. balsamifera, P. fremontii, S. laevigata
Gomez- Gonzalez et al.	2010	Chile	-33.0469	-71.6034	A. caryophyllea, B. hordeaceus, B. minor, E. peplus, H. glabra, V. myuros	B. berteroanus, D. humifusa, O. micrantha, P. lineraris, P. firma

		1				50
Setterfield et al.	2010	Australia	-13.0920	132.3937	A. gayanus	A. semialata, H. contortus, S. intrans
Elliot et al.	2009	Australia	-12.7500	130.8333	Sarga	E. miniata
Fisher et al.	2009	Australia	-31.9434	115.7723	E. calycina, P. capitatum	B. attenuata, B. menziesii, E. gomphocephala
Rahlao et al.	2009	South Africa	-33.1500	22.2667	P. setaceum	G. krebsiana, R. spinosa, T. sinuata
Veldman et al.	2009	Bolivia	-16.2500	-61.6667	U. maxima	D. insularis, L. virgata
Rossiter- Rachor et al.	2008	Australia	-12.7167	131.8167	A. gayanus	A. semialata, E. miniata, E. tetrodonta, E. triseta
Brooks & Berry	2006	USA	35.1783	-117.0451	B. rubens, E. cicutarium, S. barbatus, S. arabicus	-
Prater & DeLucia	2006	USA	39.8500	-119.8167	B. tectorum	Native sagebrush vegetation

		1		1		51
Grigulis et al.	2005	Spain	41.2943	-1.8516	A. mauritanica	E. multiflora, P. halepensis
Jacquemyn et al.	2005	Belgium	51.4010	4.4074	M. caerulea	C. vulgaris, E. tetralix
Keeley et al.	2005	USA	32.9360	-116.7559	B. diandru, C. melitensis, V. myuros, H. incana	-
Keeley et al.	2003	USA	36.4867	-118.5658	B. tectorum	A. californica, Q. douglasii
Rossiter et al.	2003	Australia	-12.7167	131.8167	A. gayanus	A. semialata, E. miniata, E. tetrodonta, E. triseta
Brooks and Pyke	2001	USA	38.9113	-116.8466	-	-
Drewa et al.	2001	Mexico	29.1688	-106.2520	B. eriopod	-
Keeley	2001	USA	32.9360	-116.7559	-	-

	1	1	1	1		52
Vila et al.	2001	Spain	41.2943	-1.8516	A. mauritanica	B. retusum, Q. coccifera, R. officinalis
Lippincott	2000	USA	30.4048	-87.1503	I. cylindrica	-
D'Antonio et al.	2000	USA	19.4571	-155.2865	-	-
Vila & Lloret	2000	Spain	41.2943	-1.8516	A. mauritanica	E. multiflora, G. alypun, R. officinalis, P. halepensis
Bell	1998	USA	32.9360	-116.7559	A. donax	-
Grace	1998	USA	30.3390	-92.4922	T. sebifera	-
Freifelder et al.	1998	USA	19.4571	-155.2865	-	-
Richardson et al.	1997	South Africa	-34.0693	18.4662	-	-

						53
Bilbao	1995	Venezuela	8.9477	-67.4230	-	-
Londsdale and Miller	1993	Australia	-18.2620	133.4558	M. pigra	-
Smith & Tunison	1992	USA	19.4571	-155.2865	_	-
Hughes et al.	1991	USA	19.4571	-155.2865	-	-
Bilbao & Medina	1990	Venezuela	9.4425	-68.3410	-	-
Billings	1990	USA	38.9113	-116.8466	B. tectorum	-
National Park Service	1990	USA	19.4571	-155.2865	-	-
Pellant	1990	USA	38.9113	-116.8466	B. tectorum	-

						54
Whisenant	1990	USA	43.0505	-113.8772	-	-
Doren and Whiteaker	1990	USA	25.6061	-80.8803	S. terebinthifolius	-
Whisenant	1990	USA	43.0505	-113.8772	-	-
Christenson & Abbott	1989	Australia	-30.0447	116.1720	-	E. miniata
Schmid & Rogers	1988	USA	36.7642	-111.8689	-	-
Mack	1986	USA	38.9113	-116.8466	B. tectorum	-
Nadkarni & Odion	1986	USA	32.9360	-116.7559	L. multiflorum	-
Baruch et al.	1985	Venezuela	8.9477	-67.4230	-	-

						55
Smith	1985	USA	19.4571	-155.2865	-	-
vanWilgen & Richardson	1985	South Africa	-34.0693	18.4662	-	-
Thompson & Shay	1985	Canada	50.2020	-98.2042	P. australis	-
Pohl	1983	Costa Rica	9.8484	-84.1394	H. rufa	-
Zedler et al.	1983	USA	32.5958	-116.8438	-	-
Coutinho	1982	Brazil	-23.7168	-49.2208	-	-
Gill et al.	1981	Australia	-18.2620	133.4558	-	-
Mack	1981	USA	38.9113	-116.8466	B. tectorum	-

						56
Stocker & Mott	1981	Australia	-18.2620	133.4558	-	-
Campbell et al.	1980	South Africa	-34.0013	18.5523	-	-
Bradbury	1978	USA	32.9360	-116.7559	-	_
Baird	1977	Australia	-31.9606	115.8322	-	-
Humphries et al.	1972	Australia	-26.3439	133.3679	-	-
Young & Evans	1972	USA	41.4881	-120.5448	T. caput-medusa	-
Blydenstein	1967	Colombia	8.5183	-75.6270	-	-
Wright & Klemmedson	1965	USA	43.0505	-113.8772	B. tectorum	S. hystrix, S. thurberiana

Klemmendson & Smith	1964	USA	38.9113	-116.8466	B. tectorum	-
Stewart & Hull	1949	USA	42.2730	-114.3402	B. tectorum	-
Platt & Jackman	1946	USA	38.9113	-116.8466	B. tectorum	-

Appendix B: Non-Native Grass Species Profiles

Common Name	Scientific Name	Family	Origin	Identification
Gamba Grass	Andropogon gayanus	Poaceae	Tropical Africa	
Cheatgrass, Downy Brome	Bromus tectorum	Poaceae	Southern Europe and Southwest Asia	
Perennial Veldtgrass	Ehrharta calycina	Poaceae	Southern Africa	Environmenta al Wited &
Guinea Grass	Megathyrsus maximus	Poaceae	Africa	
Rose Geranium	Pelargonium capitatum	Geraniaceae	South Africa	
Fountain Grass	Pennisetum setaceum	Poaceae	Africa	

Table 7. Pervasive non-native species involved in the non-native grass-fire cycle

Appendix C: Biomes of the Non-Native Grass-Fire Cycle by Geographic Region

The Non-Native Grass-Fire Cycle in the United States

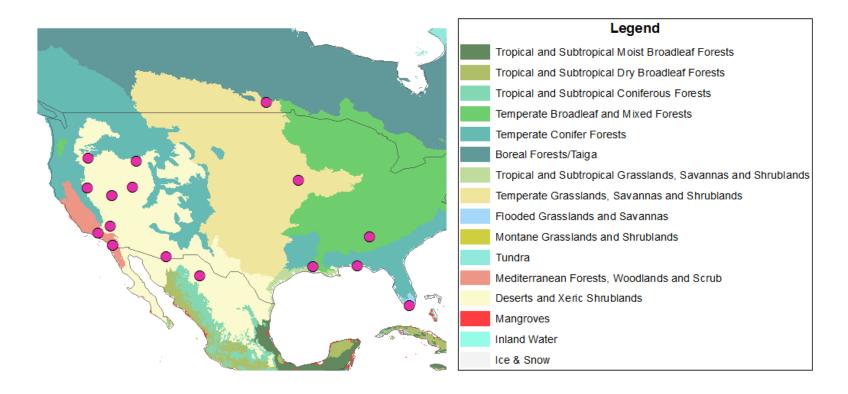


Figure 18. The biomes implicated in the non-native grass-fire cycle in the United States

The Non-Native Grass-Fire Cycle in Hawaii

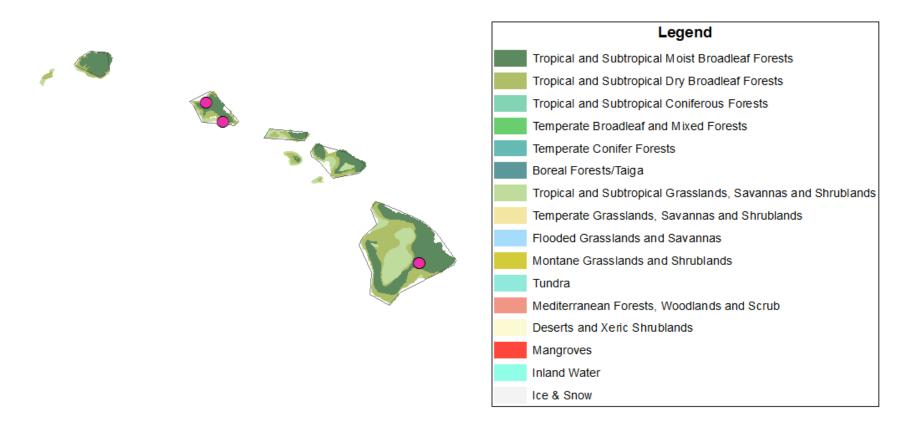
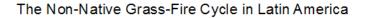


Figure 19. The biomes implicated in the non-native grass-fire cycle in Hawaii, USA



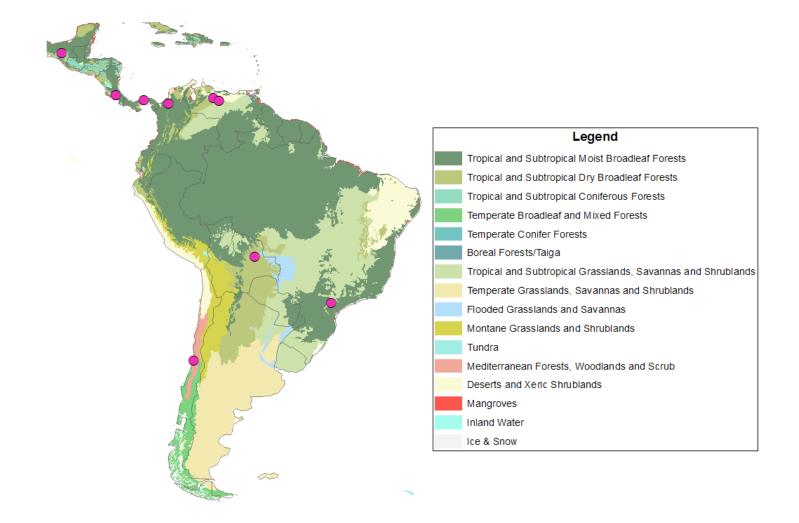


Figure 20. The biomes implicated in the non-native grass-fire cycle in Latin America

The Non-Native Grass-Fire Cycle in Western Europe

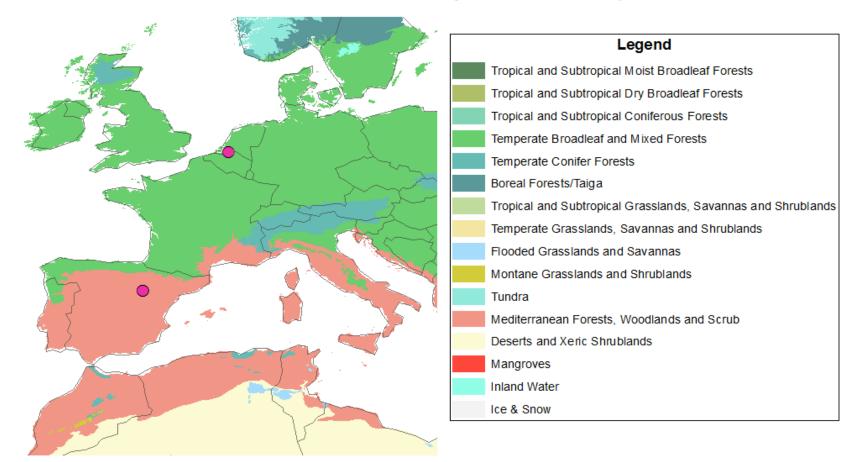
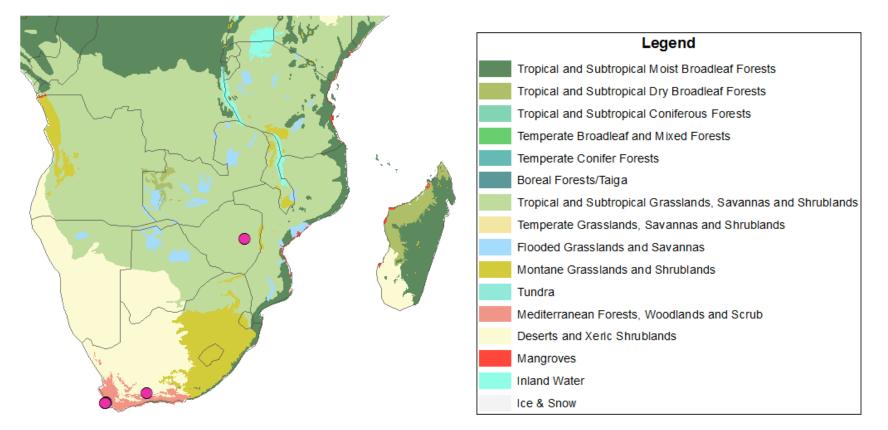


Figure 21. The biomes implicated in the non-native grass-fire cycle in Western Europe



The Non-Native Grass-Fire Cycle in Southern Africa

Figure 22. The biomes implicated in the non-native grass-fire cycle in Southern Africa

The Non-Native Grass-Fire Cycle in Australia

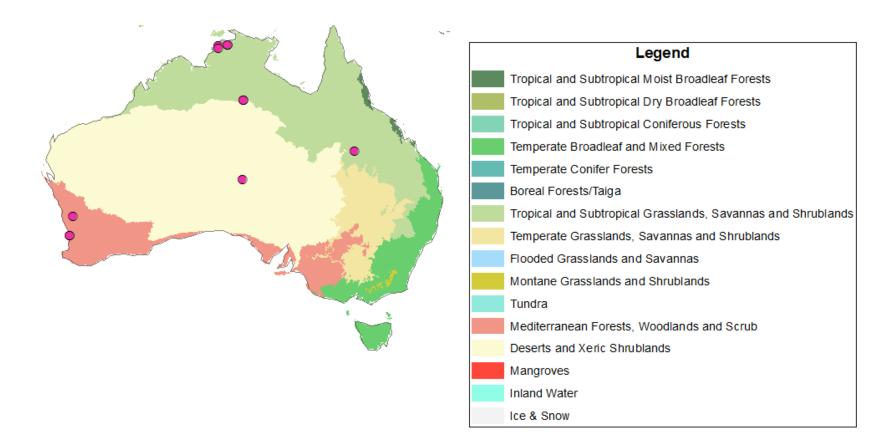


Figure 23. The biomes implicated in the non-native grass-fire cycle in Australia

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Academic Vita

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Education

The Pennsylvania State University, University Park, PA Bachelor of Arts in Geography The Schreyer Honors College

Experience

Research Assistant, The Pennsylvania State University

- Assisted M.S. candidate in performing digital imagery analysis of specimens, culminating in the completion of a thesis paper and pending publication
- Currently assisting Ph.D. candidate in qualitative field research on the elderly's vulnerability to ٠ hurricanes in coastal communities

Office Manager, Geospatial Data Analysis Corporation

Acted as interim office manager; contributed to a data collection effort involving international crop statistics for the corporation's agricultural intelligence products

Leadership

President, Schreyer Honors College Student Council

Presided over all meetings of the council and executive board; acted as ex-officio member ٠ of all committees, including the college's Scholar Alumni Society Board; served as official representative of the Schreyer Honors College Student Council

Honors

G. D. Richardson and Kathy LaSauce Undergraduate Scholarship; 2014 Quentin and Louise Wood Honors Scholar Award; 2013

Association Memberships

Alpha Phi Omega National Service Fraternity

As a brother of the Alpha Beta chapter of Alpha Phi Omega, I am committed to developing leadership, promoting friendship, and providing service to our fraternity, campus, community, and nation.

April 2013 – April 2014

August 2011 – December 2014

December 2013 - August 2014

Summer 2013

Spring 2014 - present