AN ABSTRACT OF THE DISSERTATION OF

Janine M. Rice for the degree of Doctor of Philosophy in Geography presented on December 11, 2009.

Title: Forest-Meadow Dynamics in the Central Western Oregon Cascades: Topographic, Biotic, and Environmental Change Effects

Abstract approved:

Julia A. Jones

Montane meadows comprise a small area of the predominantly forested landscape of the Oregon Cascade Range. Tree encroachment in the last century in these areas has threatened a loss of biodiversity and habitat. Climate change in the coming century may accelerate tree encroachment into meadows, and exacerbate biodiversity loss. Multiple environmental factors of topography, biotic interactions, climate, and disturbance, whose interactions and impacts are unclear, influence forest encroachment into meadows. This dissertation examines these complex interactions and factors in two montane meadow ecosystems at Lookout (44° 22′N, 122° 13′W) of the Western Cascade Range and Bunchgrass (44° 17′N, 121° 57′W) of the High Cascade Range of Oregon.

A change detection analysis quantifies how topographic factors and proximity to edge were related to tree encroachment into the two montane meadows of the Cascade Range of Oregon. Areas that have experienced tree encroachment were identified and partitioned by distance to forest edge, aspect, and slope class using historical air photo interpretation over 54 years from 1946, 1967, and 2000 at Lookout and Bunchgrass meadows in the western Cascades of Oregon. Meadow area decreased by more than 1% per year, with a net decrease of 60%, and a net loss of 22 ha at Lookout Meadow and 28 ha at Bunchgrass Meadow from 1946 to 2000. From 72% (Lookout) to 77% (Bunchgrass) of meadow area within 5 m of a forest edge became forest by 2000. Two-thirds to three-quarters of meadow area on south and west aspects at both sites converted to forest from 1946 to 2000. Two-thirds of meadow conversion to forest from 1946 to 2000 occurred on slopes <6° at Bunchgrass Meadow, but meadow conversion to forest was more evenly distributed among slope classes at Lookout Meadow. Restoration efforts may need to focus on westerly or southerly aspects in areas < 5 m from the forest edge.

The effects of biotic interactions and climate on the spatial patterns of two species (Lodgepole pine and Grand fir) were tested at Bunchgrass Meadow, a 37-ha meadow complex in the High Cascades of Oregon. A spatial analysis was used to quantify spatial patterns of more than 900 saplings and trees of these two species that had established since 1916 in a 0.21 ha early tree succession area. The light- and heat-tolerant species, Lodgepole pine, tended to establish initially and at relatively longer distances from other trees; Lodgepole seedlings avoided establishment within 2 m of >35-yr-old Grand fir. In contrast, the shade-tolerant species, Grand fir, tended to establish subsequently at

relatively short distances to other trees, and was closely associated with older trees of both species. Lodgepole pine establishment was associated with warm, dry late summers, while Grand fir establishment was associated with wet springs and cool summers. Tree encroachment was regulated by both climate variability and biotic interactions responding to species' environmental tolerances. Environmental tolerances influenced the rate of tree species establishment in the meadow, but biotic interactions were more important than exogenous factors, such as climate, in controlling the spatial patterns of encroachment dynamics.

The relative contributions of climate change, atmospheric CO_2 concentrations, and fire regimes, and their interacting effects on past and future non-forested areas were investigated with a modeling experiment. A generalized ecosystem model, LPJ-GUESS, was used to disentangle the impacts of environmental drivers (increased temperature, increased atmospheric CO_2 concentrations, and changing fire frequency) on primary production, biomass, and extent of meadow (non-forest area) at a site representing montane meadow and forests of the western Cascades of Oregon. Model projections based on a moderately high future-warming scenario (4 °C increase from 2000 to 2100) indicated that fire disturbance played the largest role in reducing projected forest area and expanding non-forested areas, while fire suppression had the largest opposite effect. Increased temperature altered species composition to higher temperature-tolerant tree species, but it did not have a significant effect on the projected extent of forest or non-forest areas. Increased atmospheric CO_2 concentration increased forest biomass, but it did not significantly change the projected extent of non-forest area. Projected changes in the extent of forest and non-forest areas lagged behind the potential impacts of environmental changes on primary production and biomass. The net effects of potential future environmental factors point to a continued expansion of forests and reduction of non-forested areas if fire suppression is maintained. The use of fire or tree removal may continue to be required to preserve these unique and vital meadow ecosystems of the Oregon Cascades.

Forest-Meadow Dynamics in the Central Western Oregon Cascades: Topographic, Biotic, and Environmental Change Effects

by
Janine M. Rice

A DISSERTATION

Submitted to

Oregon State University

In partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Presented December 11, 2009
Commencement June 2010

Doctor of Philosophy dissertation of Janine M. Rice
presented on December 11, 2009.

APPROVED:

Major Professor, representing Geography

Chair of the Department of Geosciences

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Janine M. Rice, Author

ACKNOWLEDGEMENTS

This work was an interdisciplinary study that was supported by the National Science Foundation's (NSF) Integrated Graduate Education Research Training (IGERT) Fellowship. Thanks to Dr. Julia Jones for her willingness and patient management of the fledgling IGERT program that has now turned into a successful program under her direction. Thanks to the IGERT committee for allowing me this opportunity to partake in this excellent educational training, and put my technical skills to work in ecology.

I offer my gratitude to my advisor Dr. Julia Jones for her mentoring, support and guidance. I am fortunate to have had her guidance through this challenging process. I offer my thanks to my graduate committee, Dr. Julia Jones, Dr. Sarah Shafer, Dr. Gordon Matzke, and Dr. Xiaoli Fern for their support and guidance. I offer a special thanks to Dr. Sarah Shafer who has contributed countless hours, outstanding expertise, and taught me how to be a very thorough, thoughtful scientist.

Thanks to Dr. Sadao Takaoka who introduced me to meadows and inspired this work. I also wish to offer a special thanks to Dr. Charlie Halpern for his wonderful introduction to meadows, ecology, and his guidance and support of my field work and analysis for plot 14. I thank the Bunchgrass crew, Ryan Huago, Nicole Lang, and Jen Leach for vegetation identification training and invaluable dendrochronology assistance. Thanks to Teacher in the Woods field assistants Byron Ball and Lorin Bumbarger for cookie collection at Bunchgrass plot 14.

I especially wish to thank my husband Bob, for all of his love, support, help, conversations, and friendship, and thanks to PY.

CONTRIBUTION OF AUTHORS

Dr. Julia A. Jones helped design, analyze and edit this manuscript. Dr. Julia A. Jones contributed to extending the third chapter, spatial pattern analysis to include correlation analysis as well as providing editing support in preparation for publishing. Dr. Charles Halpern contributed dendrochronology and field assistance and Dr. Joe Antos contributed analytical expertise to the spatial pattern analysis chapter. Dr. Benjamin Smith provided the LPJ-GUESS vegetation model for the modeling analysis chapter and will be a co-author of the published paper. Dr. Julia A. Jones and Dr. Sarah Shafer edited and helped with the design and analysis of the modeling analysis chapter.

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

Page

LISTS OF FIGURES

LIST OF FIGURES (Continued)

LIST OF FIGURES (Continued)

LISTS OF TABLES

LIST OF APPENDICES

Page

LIST OF APPENDIX FIGURES

LIST OF APPENDIX FIGURES (Continued)

LIST OF APPENDIX FIGURES (Continued)

LIST OF APPENDIX FIGURES (Continued)

LIST OF APPENDIX FIGURES (Continued)

LIST OF APPENDIX TABLES

1 INTRODUCTION

Meadows of the Pacific Northwest Cascade Range are dynamic, non-forested areas occurring below the timberline in the montane and subalpine regions. Although they compose a relatively small portion of this extensively forested mountain landscape, they serve important ecological functions (Thompson 2007). Meadows provide habitat and forage for wildlife, and add landscape biodiversity by supporting numerous and sometimes rare bird, mammal, plant, arthropod, microbial and fungi species (Halpern 1984; Debinski et al. 2000; Miller et al. 2003; Mintie et al. 2003). The high biodiversity and species richness of these areas may serve as vital reserves of taxa that are adaptable to the predicted changes in climate over the next century (Whitlock 1992). Additionally, meadow areas provide a visible record of the effects of environmental changes such as climate change and increased atmospheric CO_2 concentration (Romme & Turner 1991; Harte 1995; Mast et al. 1997; Debinski et al. 2000; Cayan et al. 2001).

Since the last glacial period ended at about 16,000 years BP, the western Cascades have experienced numerous contractions and expansions of forest and meadow communities that correspond to shifts in climate and fire disturbance (Whitlock 1992; Gavin & Brubaker 1999). Prior to 13,000 years BP, the tree line was up to 1000 m lower than present, and open meadow with mixed conifer forest *Pinus*, *Picea*, and *Tsuga* species inhabited the upper Cascades. From 11,000 to about 5,000 years BP, a warmer climate caused the tree line to shift above its current position. The more intense summer droughts and higher fire occurrence during this period favored more drought and disturbance adaptive meadow species, such as Bracken Fern (*Pteridium*) and graminoids, to be more common among the mixed forest species *Pseudotsuga, Abies, Pinus* (Sea & Whitlock 1995).

A moister climate has been prevalent for the last 5,000 years, and has caused the distribution of the modern forests we see today. The wetter climate over this time period has seen temperatures fluxuations from warmer, during the Medieval Warm Period (1,200 – 700 years BP), to cooler during the Little Ice age (500 years BP), and back to warmer again at present. Climate fluxuations and fire occurrence are likely to have driven the expansion of meadow areas during warmer, drier periods, and the contraction of meadow areas with conifer infilling during cooler, wetter periods (Sea & Whitlock 1995).

During the last century, meadow habitat has been lost to conifer encroachment (Franklin et al. 1971; Vale 1981; Rochefort & Peterson 1996; Lepofsky et al. 2003; Haugo & Halpern 2006; Dailey 2007; Takaoka & Swanson 2008). Many studies have investigated the causes of this encroachment, and have pointed to multiple environmental factors, such as changes in climate, ecological interactions, topography, fire suppression, and cessation of grazing (Franklin et al. 1971; Magee & Antos 1992; Rochefort & Peterson 1996; Miller & Halpern 1998; Dailey 2007). It is unclear which of these factors is most important, or how they may interact to affect meadows. Natural resource managers have begun investigating methods of prescribed fire and tree removal for meadow restoration and maintenance (Wilson et al. 1999); however, little information exists to guide these efforts. Information is lacking about how topographic gradients would increase or decrease the extent, rate, and timing of tree encroachment. Also, it is unclear how species associations affect the spatial patterns and timing of tree encroachment at early succession stages when restoration efforts are easiest to implement, or how variations in historic and future climate, fire disturbance, and atmospheric CO_2 concentration have impacted and may impact future tree encroachment into meadows.

This dissertation focuses on the causes and effects of forest encroachment into meadows at two topographically diverse dry montane meadow complexes in the central west Cascades of Oregon. The first site, Lookout Mountain meadow, is located in the deeply dissected Western Cascades Range. The second site, Bunchgrass Meadow Special Habitat Area, is in the flatter, rolling topography of the High Cascades Range. Historical forest-meadow changes over topographic gradients are analyzed with an aerial photo change detection analysis in Chapter 2. Tree species spatial and temporal relationships and correlation to variations of climate are characterized with a spatial statistics analysis of early succession tree encroachment in Chapter 3. The relative impacts of climate, atmospheric CO_2 concentrations, and fire regime on forest and non-forest areas are disentangled with a vegetation modeling experiment in Chapter 4.

The objective of the change detection analysis in Chapter 2 is to quantify how topographic factors and proximity to edge are related to tree encroachment into two montane meadows of the Cascade Range of Oregon. This chapter contrasts changes at two topographically diverse sites using aerial photos from 1946 (1:21,333), 1967 (1:15,840), and an orthophoto from 2000 (1:24,000). Areas that have experienced tree encroachment are identified and partitioned by distance to forest edge, aspect, and slope class. This analysis was limited to detecting changes in large trees (areas > 0.1 ha) over two periods (1946-1967 and 1967-2000).

The objective of the spatial analysis in Chapter 3 is to test the effects of biotic interactions and climate on spatial patterns of over 900 saplings and trees of two species (Lodgepole pine and Grand fir) that had established since 1916 in a 0.21 ha area of Bunchgrass Meadow. The ages and locations of all trees in the plot were identified using tree cores and cookies. Individual and inter-species spatial relationships in the context of initial recruitment are characterized for two dominant conifer species. The overall clustered pattern, and strength of relationships between two tree species and two age classes are analyzed with bivariate Ripley's K point pattern method. Spatial patterns of nearest neighbors of each species were examined over time using the J-Summary function at ten-year intervals from 1965 to 1995. A new method is introduced for analyzing establishment distances of two conifer species over time. Initial "pioneer" tree establishment and subsequent infilling establishment distances are quantified over an 88 year dendrochronology record. Tree establishment dates were correlated with monthly temperature and precipitation, snowpack data, and annual cone crop data for Grand fir. These analyses show how differences in individual species environmental tolerances and inter-species interactions influence the spatial patterns and timing of early succession into meadows.

The objective of the modeling experiment in Chapter 4 is to disentangle the individual and combined impacts from climate, atmospheric CO_2 concentrations, and fire regime on forest and non-forested open patch cover. This is accomplished using a generalized ecosystem model, LPJ-GUESS (Smith et al. 2001). A site representing montane meadow and forests of the western Cascades of Oregon is used to model vegetation changes due to historic and potential future climate, atmospheric CO_2 concentrations, and fire regime. These scenarios are used to assess the individual and combined effects of these environmental drivers, determine the presence of lags in vegetation response to changes in environmental drivers. A sensitivity analysis extends this analysis beyond the framework of historic and future scenarios and further explores changes in modeled forest and non-forest trends and thresholds of behavior. This analysis reveals the relative contributions of climate change, atmospheric CO_2 concentrations, and fire regimes, and their interacting effects on past and future non-forested areas in the western Cascades of Oregon.

2 THE EFFECTS OF TOPOGRAPHIC GRADIENTS ON TREE ENCROACHMENT IN TWO MONTANE MEADOWS OF THE WESTERN OREGON CASCADES

Janine Rice

in preparation for journal submission

2.1 Introduction

In the mid and late 20th century, montane meadows in the Pacific Northwest have experienced conifer encroachment (Franklin et al. 1971; Vale 1981; Haugo & Halpern 2007; Dailey 2007; Takaoka & Swanson 2008). Meadows occupy only a few percent of the Cascade mountain landscape, but they contain a rich variety of sometimes rare plant, bird, mammal, arthropod, microbial and fungi species (Franklin & Halpern 1999; Debinski et al. 2000; Miller et al. 2003; Mintie et al. 2003). These high-biodiversity areas may serve as vital reserves of taxa that are potentially adaptable to the predicted changes in climate over the next century (Whitlock 1992). Current efforts to restore and preserve meadows (e.g., Wilson 1999) would be aided by defining areas at high risk of encroachment (Dailey 2007).

Climate change, fire suppression, and shifts in grazing disturbance have been implicated as factors affecting tree encroachment into meadows (Franklin et al. 1971; Vale 1981; Rochefort & Peterson 1996; Mast et al. 1997; Miller & Halpern 1998; Hadley 1999). The implementation of fire suppression and cessation of grazing may have reduced meadow extent in the western Cascade Range of Oregon by about 50% between the mid 1900s and 2000 (Takaoka & Swanson 2008). Most montane meadows occur on south and east facing slopes in the Willamette National Forest (Dailey 2007). During the early 1900s, meadows on north-facing slopes in the subalpine zone (e.g. Three Sisters Wilderness Area, Oregon Cascades) experienced tree encroachment coinciding with regional warming and lower snow pack levels of the early 1900s, but south-facing slopes experienced tree encroachment during the wetter, cooler conditions of the mid 1900s (Miller & Halpern 1998). In contrast, Dailey (2007) found increased tree encroachment in montane meadows of the western Cascade Range of Oregon on south and east aspects during a warmer, wetter period from 1972 to 1995 (U.S. Historical Climate Network 2009). Other factors, such as slope steepness and distance to forest edge may also constrain the rate of tree encroachment (Dailey 2007). It remains unclear how site specific topographic-environmental interactions may influence tree encroachment over time, and studies of a wider range of meadow types and locations are needed to reveal general principles about the effects of environmental factors such as topography, proximity to forest edge, and climate on tree encroachment.

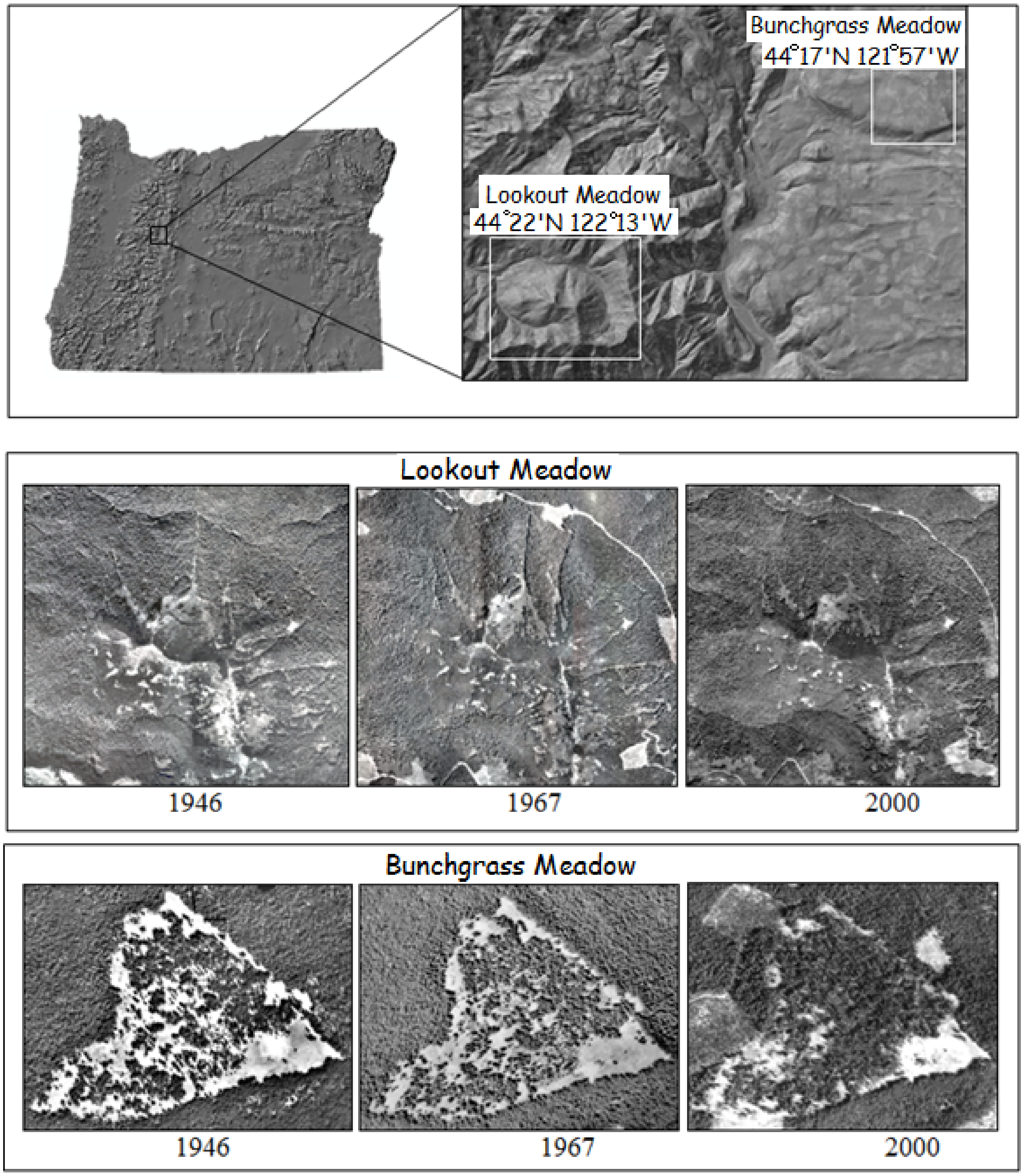
The quantification of spatially variable tree encroachment is scale dependent with potentially greater accuracy and higher encroachment rates at a finer resolution (Weisberg et al. 2007). Therefore, this study quantifies and compares the rates and patterns of tree encroachment into meadows at two contrasting sites, Bunchgrass Meadow in the High Cascade Range, henceforth called Bunchgrass, and Lookout Meadow in the Western Cascade Range, henceforth called Lookout (Figure 2.1). This study uses fine scale (1 m resolution) aerial photography interpretation. The objective of this study is to identify meadow areas that are at risk for tree encroachment by quantifying the rates and extent of forest and meadow change over a 54 year time period (1946 – 2000) using aerial photos from 1946 (1:21,333), 1967 (1:15,840), and 2000 (1:24,000). The analysis was limited to detecting changes in large trees (areas > 0.1 ha) over only two periods (1946-1967, and 1967-2000). The following questions were evaluated:

Question 1: Do topographic factors favor the occurrence of dry montane meadows on dry aspects (e.g. south- and east-facing)?

Question 2: Do trees encroach into meadows by the establishment of shade intolerant trees far from meadow edges, followed by the formation of clusters and subsequent infilling by shade tolerant trees, or do shade tolerant trees encroach into meadows at forest edges?

Question 3: Are tree encroachment rates and amounts higher on relatively flat slopes as compared to steep slopes?

Figure 2.1. Lookout Meadow and Bunchgrass Meadow Study Areas



2.2 Study Sites

2.2.1 Study Area Description

The climate at Lookout and Bunchgrass is characterized by mild temperatures, wet winters and dry summers. Average precipitation at the Upper Lookout meteorological station in the H.J. Andrews Experimental Forest (1994-2008), about 14 km SW of Bunchgrass, and less than 1 km east of Lookout, was 2377 mm, and ranged from 710 mm to 4099 mm. Precipitation occurs mainly as snow from late October to May, and <20% of precipitation occurs from May to October. Snow packs over 2 m deep can occur in late spring, and usually persist to June. The annual average temperature is 6 °C, and can range from 34 °C in the summer to -23 °C in winter.

2.2.2 Lookout Study Area

Meadows at Lookout comprise about 20 ha (in 2000) and extend over an area of about 6.9 km^2 of the Willamette National Forest at 44°22'N, 122°13'W (Figure 2.1). Lookout is in the deeply dissected central west Cascades Range. Slope ranges from flat to over 70°, and elevation ranges from 1000 to 1630 m (3280 to 5348 ft). Forests adjacent to Lookout are dominated by Pacific silver fir (*Abies amabilis)* in closed canopy areas and young Noble fir *(Abies procera)* in more open areas. Dense thickets of Vine maple *(Acer circinatum)* and Sitka alder *(Alnus viridus sinuata)* occur on steep east, north, and west-facing slopes. Meadows are dominated by herbaceous species including

Bear grass (*Xerophyllum tenax)*, Bracken fern *(Pteridium aquilinum)*, and grass (*Festuca* spp.). Meadow area soils are moderately well drained of the Lucky Boy series in the Cryandepts taxonomic class (Dyrness et al. 1962).

Grazing of meadow areas by wildlife (e.g. elk) may have been greatly reduced by the 1880s due to the extirpation of elk, but elk were re-introduced in the 1980s and currently graze these areas (personal observation).

Grazing records at Lookout show 1,500 sheep per year were permitted from 1912 to 1922 (Burke 1979). Burning of meadow areas may have been associated with grazing. Fire records for upper elevation forest near Lookout show a fire return interval of 100-200 years prior to the early 1900s (Cissel et al. 1999), but Native American burning of meadows probably occurred annually up through the early 1800s (Boyd 1999). During the latter half of the 20th century fire has been largely suppressed.

2.2.3 Bunchgrass Study Area

Bunchgrass consists of 20 ha (in 2000) of meadow extending over an area of about 1.7 km^2 in the High Cascade Range in the Willamette National Forest at 44°17'N, 121°57'W (Figure 2.1). Bunchgrass is located on a gently sloping plateau surrounded by landforms of recent shield and composite volcanoes of the High Cascades. Slope ranges from 0 to 44°, and elevation ranges from 1300 to 1375 m (4265 to 4511 ft). Vegetation consists of a mosaic of conifers and dry meadow, and the meadows have experienced significant infilling by conifers over the past 50 years (Halpern et al. in review, Haugo &

Halpern 2007, Lang & Halpern 2007). Forests are dominated by Grand fir *(Abies grandis*) in closed canopy areas and Lodgepole pine *(Pinus contorta*), which commonly occurs in open meadow as young individuals. Meadow vegetation is dominated by grasses (*Festuca spp.* and *Carex pensylvanica*) and forbs (*Phlox spp*. and *Lupinus latifolius*) (Haugo & Halpern 2007). Soils are typically 2 m deep with fine to very-fine-sandy loams derived from andesitic basalt and tephra deposits and contain a large and highly variable component of glacially derived cobbles, stones, and boulders (Haugo & Halpern 2007).

Fire at Bunchgrass has been largely suppressed in the latter half of the 20th century, with limited experimental burning and thinning in 1988. No direct evidence of non-experimental fire disturbance or grazing is evident at Bunchgrass (Haugo & Halpern 2007). Native Americans may have maintained open meadow habitats for hunting, and grazing of sheep by Euro-American settlers with burning of meadow areas is likely to have occurred during the early to mid 20th century (Haugo & Halpern 2007).

2.3 Methods

2.3.1 GIS Change Detection Layers

Vegetation cover was interpreted from black and white aerial photographs from 1946 (1:21,333) and 1967 (1:15,840) and a United States Geological Survey (USGS) black and white digital ortho quadrangle (DOQ) at 1 m resolution (1:24,000) for the year

2000. The 1946 and 1967 photographs were digitally scanned to less than 1 m resolution and rectified using the central portion of photographs to minimize relief displacement. At least 10 control points for each photo were used for each photo. Photos that were not successfully aligned were transformed into orthophotos, were rectified using ArcGIS polynomial rectification (ArcGIS Georeferencing Transformation function) with a root mean square error of less than 2 pixels.

Vegetation in each year was classified as forest, meadow or other using the supervised classification method by ERDAS Imagine image processing software. Forest and shrub (darker and medium tone) and meadow (light tone) vegetation were defined using unique brightness ranges (subsets of pixel grey shade values). Classifications were verified by field surveys and an aerial survey in summer 2005 to correct for misclassification due to differences in tonal signatures of vegetation in each of the photos. Shrubs of medium tonal signature were classified as forest, and were differentiated from meadow areas of lighter tonal signature and distributions were validated by aerial survey. Classified layers were resampled to a 3 m resolution to minimize alignment errors while providing adequate resolution for change detection. Clear cut areas were omitted from this analysis.

Misclassification of meadow area from tree shadows was determined by a comparison between shadow-corrected and shadow uncorrected photos for all years. The range of pixel brightness values for tree shadows that occurred in meadow areas was identified for the 1967 and 2000 photos. Then the identified pixel brightness values were re-classified to meadow. Re-classified shadows were manually verified for correct classification of forest or meadow. This method was not successful at identifying misclassified tree shadows in the 1946 photo, so tree shadows that occurred in meadows were visually identified and manually removed.

Change detection layers for the three time periods (1946 - 1967, 1967 - 2000, and 1946 - 2000) were created by using the operator histogram functions in ERDAS Imagine. Raster histogram values were added together to create change maps with four change criteria (Table 2.1). The change maps were then used to calculate the area for each of the four change criteria to one tenth of a hectare, which may also help to minimize errors.

Table 2.1 Change detection criteria for 1946, 1967, and 2000

Change Code	**Date 1**	**Date 2**
FF	Forested	Forested
FM	Forested	Meadow
MF	Meadow	Forested
MM	Meadow	Meadow

Forest and meadow area change was also analyzed by distance from forest edge, aspect and slope classes. First, forest edge buffer zone, aspect and slope class raster maps were created. Raster maps with edge buffer zones of 0 - 5m, 5 - 10m, 10 - 20m, and >20 m from forest edge were created at 3 m resolution for both sites. Raster maps for aspect and slope classes were derived from a 10 m DEM and resampled to 3 m for consistency. A raster map of four aspect classes was created as north (315-45°), east (45-135°), south (135-225°), and west (225-315°) at both sites. Raster maps of slope classes that evenly distributed meadow area were defined at: 0 - 21°, 21 - 27°, 27 - 31°, and 31 - 75° were created for Lookout, and at: 0 - 5°, 5 - 6°, 6 - 10°, and 10 - 44° for Bunchgrass. The differences between the two-date change detection raster maps and the forest edge buffer zone, aspect, and slope class raster maps were calculated using ERDAS Imagine operator histogram functions. The resulting area change was calculated using ArcGIS.

2.4 Results

2.4.1 Meadow Distribution by Slope, Aspect, and Distance to Forest Edge

In 1946, most meadow area occurred in areas < 5 m from a forest edge (72% at Lookout and 44% at Bunchgrass), and on south and west aspects (72% at Lookout and 86% at Bunchgrass) (Table 2.3 and Table2.4, rows A, H, and O). Meadow area was evenly distributed among slope classes from 0 to 70° at Lookout, but 91% of meadow area was on slopes <10° at Bunchgrass, with slope classes ranging from 0 to 44°. Relatively little meadow occurred > 10 m from the forest edge, on north and east aspects, or on steep slopes, although 19% of Lookout occurred on slopes > 31°. These relationships did not change much from 1946 to 2000 (Table 2.3 and Table 2.4, rows A, H, and O).

The following results used only shadow corrected change layers. Shadows covered less than 3% of meadow area (1 ha) at Lookout, but up to 11% of meadow area (5 ha) at Bunchgrass (Table 2.2). Tree shadows were particularly emphasized at Bunchgrass where slopes are relatively gentle and the air photos were taken with low sun angle (morning sun exposure for the 1946 and 2000 photos, and late afternoon sun exposure for the 1967 photo). Steep topography and noon exposure limited tree shadows at Lookout.

Table 2.2 Meadow cover by aerial photo year with and without shadows

	Meadow Area (ha) No Shadows	**Meadow Area (ha) With Shadows**	**Meadow Shadow Area (ha)**	**Meadow Shadow Area %**
Lookout				
1946	37.5	36.5	1.0	2.7
1967	28.4	28.1	0.3	1.0
2000	15.0	14.7	0.3	2.5
Bunchgrass				
1946	47.8	42.8	5.0	11.4
1967	33.0	30.0	3.0	9.9
2000	20.0	18.6	1.4	6.9

2.4.2 Meadow Area Change

Meadow area declined by about 60% between 1946 and 2000, and experienced a net loss of 22.5 ha at Lookout and 27.8 ha at Bunchgrass (Table 2.3 and Table 2.4, rows R & T). Lookout meadow area decreased from 37.5 ha in 1946 to 28.4 ha in 1967 and to 15.0 ha in 2000 (Table 2.3, rows A, H, and O). Bunchgrass meadow area decreased from 47.8 ha in 1946 to 33.0 ha in 1967 and to 20 ha in 2000 (Table 2.4, rows A, H, and O).

Annual rates of meadow decline were 1.1% at both sites between 1946 and 2000 (Table 2.3 and Table 2.4, row U), or 0.4 ha/year at Lookout, and 0.5 ha/year at Bunchgrass (Table 2.3 and Table 2.4 row S). Lookout annual rates of decline were 1.2% from 1946 to 1967 and 1.4% from 1967 to 2000, or 0.4 ha/year from 1946 to 2000. At Bunchgrass annual rates of meadow decline were 0.7 ha/year from 1946 to 1967 and 0.4 ha/year for 1967 to 2000 (Table 2.3 and Table 2.4).

At both sites the highest rates of meadow decline from 1946 to 2000 occurred < 5 m away from the forest edge and on south and west aspects at Bunchgrass (Table 2.3 and Table 2.4). Rates of meadow loss were higher on low-gradient compared to high-gradient slopes at Bunchgrass, but there were no differences in loss rates among slope classes at Lookout with values rounded to 0.1 ha. Bunchgrass meadow area < 5 m from the forest edge declined by 70% at Lookout and 95% at Bunchgrass, or 0.4 ha/year between 1946 and 2000 (Table 2.3 and Table 2.4, rows R & S). Meadows declined relatively faster on south and west aspects at Lookout (77% or 0.2 ha/year), and on west aspects at Bunchgrass (63% or 0.3 ha/year) (Table 2.3 and Table 2.4, rows R & S). Meadow loss was evenly distributed among slope classes at Lookout (0.1 ha/year or 4.8 to 6.9 ha/yr) from 1946 to 2000 (rows R & S). Meadow loss was concentrated on low-gradient (< 6°) slopes at Bunchgrass 0.2 ha/year from 1946 to 2000 (Table 2.3 and Table 2.4, rows R & S).

Increases in meadow area occurred mostly at Lookout, and they were concentrated near forest edges, on east aspects, and across all slope classes. From 1946 to 1967, Lookout gained 10 ha of meadow within 5 m of a forest edge and nearly half of this was on the east-facing slope. From 1967 to 2000, Lookout gained 3.5 ha of meadow within 5 m of a forest edge and 2 ha of this was on the east-facing slope. Bunchgrass gained 2.6 ha of meadow from 1946 to 1967 and 3.5 ha of meadow from 1967 to 2000.

Table 2.3. Lookout area and two-date change for years 1946 to 1967, 1967 to 2000, 1946 to 2000 showing meadow gain, loss, net change, annual rate of change, and percent change in hectares by distance to forest edge, aspect, and slope.

Lookout		**Distance to forest edge (m)**					**Aspect**				**Slope (degrees)**			
		All	**<5**	**5-10**	**10-20**	**>20**	**N**	**E**	**S**	**W**	**0-21**	**21-27**	**27-31**	**31-75**
A	1946 Meadow area (ha)	37.5	26.9	6.4	3.4	0.8	1.3	9.2	12.2	14.8	9.6	10.6	10.1	7.2
1946-67 Change														
B	Loss (ha)	-19.8	-17.8	-1.6	-0.4	0.0	-0.6	-5.6	-7.1	-6.5	-5.3	-5.7	-4.9	-3.9
C	Gain (ha)	10.7	10.1	0.5	<0.1	<<0.1	1.9	4.8	1.8	2.2	2.8	2.7	2.6	2.6
D	Net (ha)	-9.1	-7.7	-1.1	<-0.4	0.0	1.3	-0.8	-5.3	-4.3	-2.5	-3.0	-2.3	-1.3
E	Annual (ha)	-0.4	-0.4	-0.1	0.0	0.0	0.1	0.0	-0.3	-0.2	-0.1	-0.1	-0.1	-0.1
F	%	-24	-29	-17	-12	0	100	-9	-43	-29	-26	-27	-23	-18
G	Annual %	-1.2	-1.4	-0.8	-0.6	0.0	4.8	-0.4	-2.1	-1.4	-1.2	-1.3	-1.1	-0.9
H	1967 Meadow area (ha)	28.4	22	3.9	1.9	0.6	2.6	8.3	7.1	10.4	6.9	7.7	7.9	5.9
1967-00 change														
I	Loss (ha)	-17.1	-16.1	-0.9	-0.1	0.0	-2.1	-5.9	-4.2	-4.9	-4.2	-4.6	-4.4	-3.9
J	Gain (ha)	3.8	3.5	0.3	<0.1	<<0.1	0.3	2.1	0.8	0.6	1.8	0.9	0.7	0.4
K	Net (ha)	-13.3	-12.6	-0.6	<-0.1	0.0	-1.8	-3.8	-3.4	-4.3	-2.4	-3.7	-3.7	-3.5
L	Annual (ha)	-0.4	-0.4	0.0	0.0	0.0	-0.1	-0.1	-0.1	-0.1	-0.1	-0.1	-0.1	-0.1
M	%	-47	-57	-15	-5	0	-72	-46	-48	-41	-35	-49	-47	-59
N	Annual %	-1.4	-1.7	-0.5	-0.2	0.0	-2.2	-1.4	-1.5	-1.3	-1.1	-1.5	-1.4	-1.8

Table 2.3. Lookout area and two-date change for years 1946 to 1967, 1967 to 2000, 1946 to 2000 showing meadow gain, loss, net change, annual rate of change, and percent change in hectares by distance to forest edge, aspect, and slope. (Continued)

Lookout		**Distance to forest edge (m)**					**Aspect**				**Slope (degrees)**			
		All	**<5**	**5-10**	**10-20**	**>20**	**N**	**E**	**S**	**W**	**0-21**	**21-27**	**27-31**	**31-75**
O	2000 Meadow area (ha)	15.0	7.7	3.7	2.8	0.8	0.7	4.6	3.6	6.1	4.5	3.8	4.2	2.5
1946-2000 change														
P	Loss (ha)	-25.5	-22.2	-2.7	-0.6	0.0	-1.0	-6.3	-9.1	-9.1	-6.6	-7.3	-6.5	-5.1
Q	Gain (ha)	3	2.7	0.2	0.1	0.0	0.4	1.8	0.4	0.4	1.7	0.6	0.4	0.3
R	Net (ha)	-22.5	-19.5	-2.5	-0.5	0.0	-0.6	-4.5	-8.7	-8.7	-4.9	-6.8	-6.1	-4.8
S	Annual (ha)	-0.4	-0.4	0.0	0.0	0.0	0.0	-0.1	-0.2	-0.2	-0.1	-0.1	-0.1	-0.1
T	%	-60	-72	-39	-15	0	-46	-49	-71	-59	-51	-64	-60	-67
U	Annual %	-1.1	-1.3	-0.7	-0.3	0.0	-0.9	-0.9	-1.3	-1.1	-0.9	-1.2	-1.1	-1.2

Table 2.4. Bunchgrass Area and Two-Date Change for Years 1946 to 1967, 1967 to 2000, 1946 to 2000
Showing Meadow Gain, Loss, Net Change, Annual Rate of Change, and Percent Change in Hectares by Distance to Forest Edge, Aspect, and Slope.

Bunchgrass			**Distance to forest edge (m)**				**Aspect**				**Slope (degrees)**			
		All	**<5**	**5-10**	**10-20**	**>20**	**N**	**E**	**S**	**W**	**0-5**	**5-6**	**6-10**	**10-44**
A	1946 Meadow area (ha)	47.8	20.6	10.8	10.1	6.3	5.9	0.6	14.7	26.6	15.6	15.8	12.2	4.2
1946-1967 Change														
B	Loss (ha)	-17.4	-12.8	-3.2	-1.2	-0.2	-2.9	-0.1	-3.8	-10.6	-6.6	-5.9	-3.9	-1.0
C	Gain (ha)	2.6	2.6	<<0.1	<<0.1	0	0.6	0.0	0.4	1.6	0.9	0.8	0.7	0.2
D	Net (ha)	-14.8	-10.2	<-3.3	<-1.2	-0.2	-2.3	-0.1	-3.4	-9.0	-5.7	-5.1	-3.2	-0.8
E	Annual (ha)	-0.7	-0.5	-0.2	-0.1	0.0	-0.1	0.0	-0.2	-0.4	-0.3	-0.2	-0.1	0.0
F	%	-31	-50	-31	-12	-3	-39	-20	-23	-34	-37	-32	-25	-19
G	Annual %	-1.5	-2.4	-1.5	-0.6	-0.2	-1.9	-1.0	-1.1	-1.6	-1.7	-1.5	-1.2	-0.9
H	1967 Meadow area (ha)	33.0	18.4	6.6	5.4	2.6	3.7	0.4	11.3	17.6	9.8	10.8	9.1	3.3
1967-2000 change														
I	Loss (ha)	-16.7	-13.7	-2.4	-0.6	<- 0.1	-2.9	-0.3	-2.4	-11.1	-5.6	-5.9	-4.4	-0.8
J	Gain (ha)	3.5	3.5	<<0.1	0	0	0.3	0.1	1.1	2.0	1.2	1.2	0.8	0.3
K	Net (ha)	-13.2	-10.2	-2.4	-0.6	<-0.1	-2.6	-0.1	-1.3	-9.1	-4.4	-4.7	-3.6	-0.5
L	Annual (ha)	-0.4	-0.3	-0.1	0.0	0.0	-0.1	0.0	0.0	-0.3	-0.1	-0.1	-0.1	0.0

Table 2.4. Bunchgrass area and two-date change for years 1946 to 1967, 1967 to 2000, 1946 to 2000 showing meadow gain, loss, net change, annual rate of change, and percent change in hectares by distance to forest edge, aspect, and slope. (Continued)

Bunchgrass			**Distance to forest edge (m)**				**Aspect**				**Slope (degrees)**			
		All	**<5**	**5-10**	**10-20**	**>20**	**N**	**E**	**S**	**W**	**0-5**	**5-6**	**6-10**	**10-44**
M	%	-40	-55	-36	-11	0	-70	-25	-12	-51	-45	-44	-40	-12
N	Annual %	-1.2	-1.7	-1.1	-0.3	0.0	-2.1	-0.8	-0.3	-1.5	-1.4	-1.3	-1.2	-0.4
O	2000 Meadow area (ha)	20	12.9	3.5	2.8	0.8	1.0	0.3	10.0	8.7	5.5	6.1	5.6	2.8
1946-2000 change														
P	Loss (ha)	-29.6	-17.6	-7.1	-4.2	-0.7	-5.1	-0.3	-5.2	-19.0	-10.7	-10.3	-7.0	-1.6
Q	Gain (ha)	1.8	1.8	0	0	0	0.1	0.1	0.5	1.1	0.6	0.6	0.4	0.2
R	Net (ha)	-27.8	-15.8	-7.1	-4.2	-0.7	-5.0	-0.2	-4.7	-17.9	-10.1	-9.7	-6.6	-1.4
S	Annual (ha)	-0.5	-0.3	-0.1	-0.1	0.0	-0.1	0.0	-0.1	-0.3	-0.2	-0.2	-0.1	0.0
T	%	-58	-77	-66	-42	-11	-85	-33	-32	-67	-65	-61	-54	-33
U	Annual %	-1.1	-1.4	-1.2	-0.8	-0.2	-1.6	-0.6	-0.6	-1.2	-1.2	-1.1	-1.0	-0.6

2.4.3 Maps of Forest-Meadow Change

The two-date change maps show patterns of infilling near forest edges and persistence of meadow areas >10 m from forest edges at Lookout and Bunchgrass (Figure 2.2 – Figure 2.7). For the two time periods, a relatively small amount of forested area converted to meadow (4% between 1946-1967, and 8% between 1967-2000), while 62% between 1946-1967, and 68% between 1967-2000 of meadow areas converted to forest. At Lookout a relatively large area of forest on the north slope converted to meadow, perhaps due to snow avalanching that occurred between 1946 and 1967; this area converted back to forest by 2000 (Figure 2.2 and Figure 2.3).

Figure 2.2. Lookout 1946 to 1967 two-date change detection map

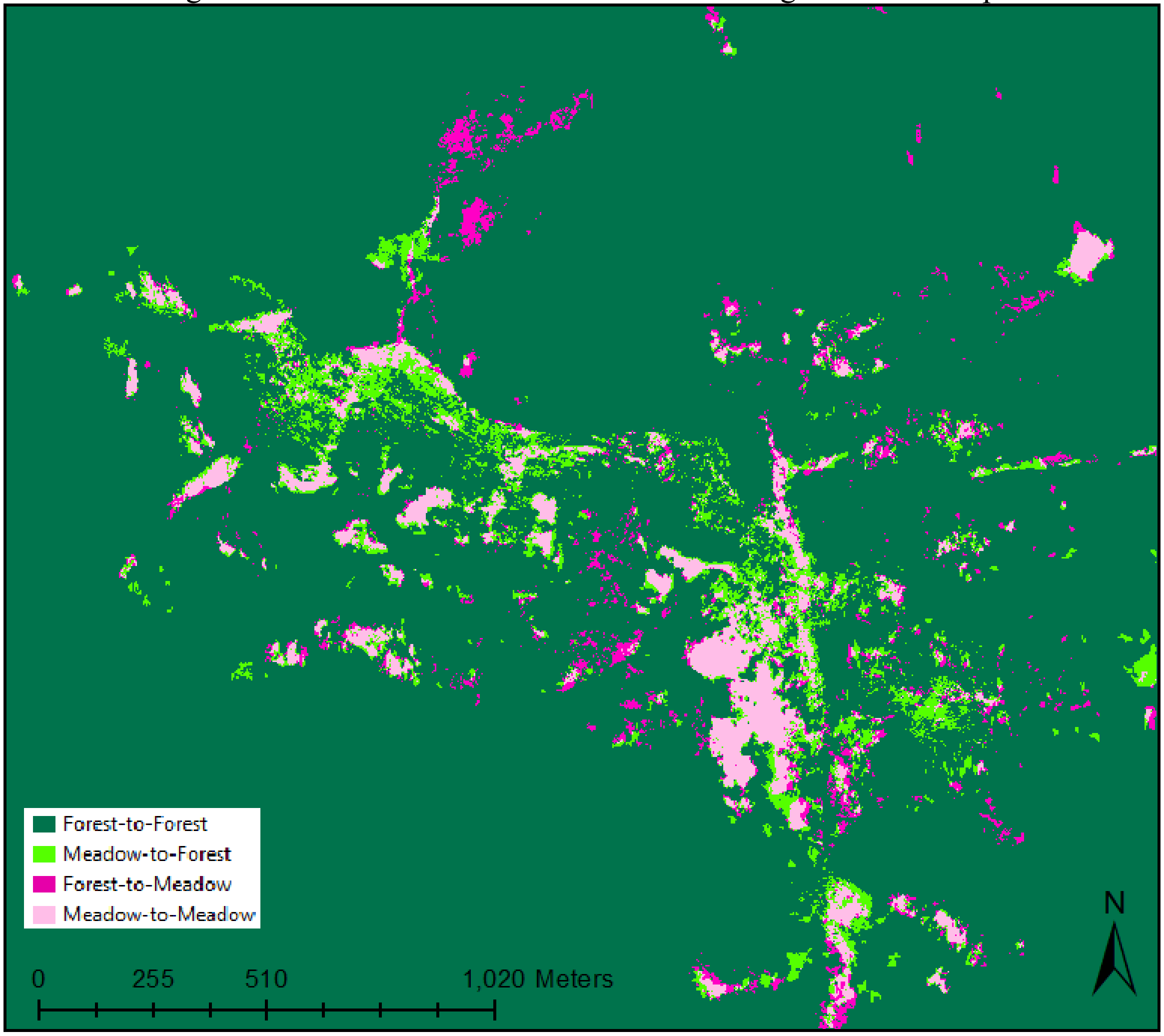


Figure 2.3. Lookout 1967 to 2000 two-date change detection map

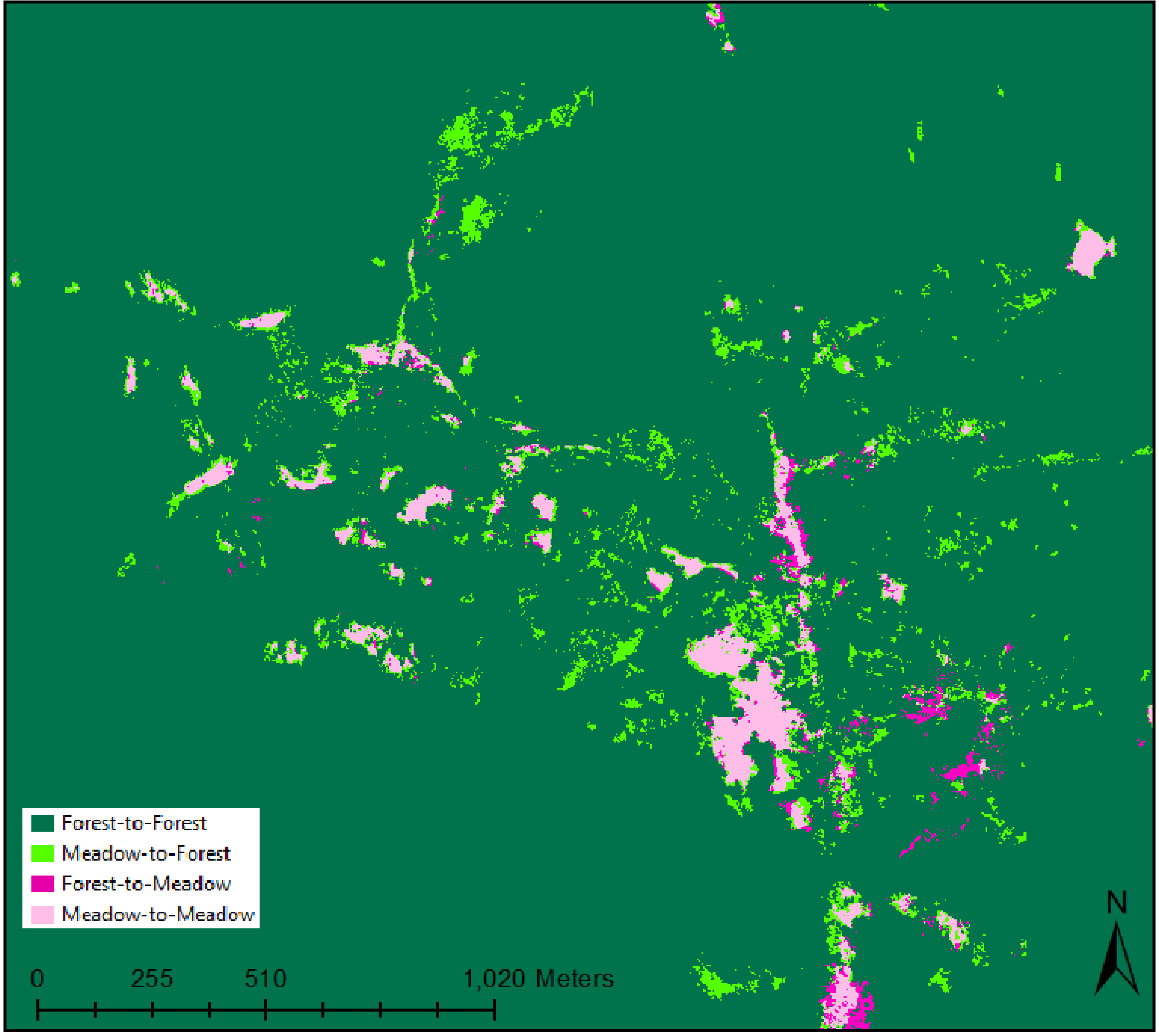


Figure 2.4. Lookout 1946 to 2000 two-date change detection map

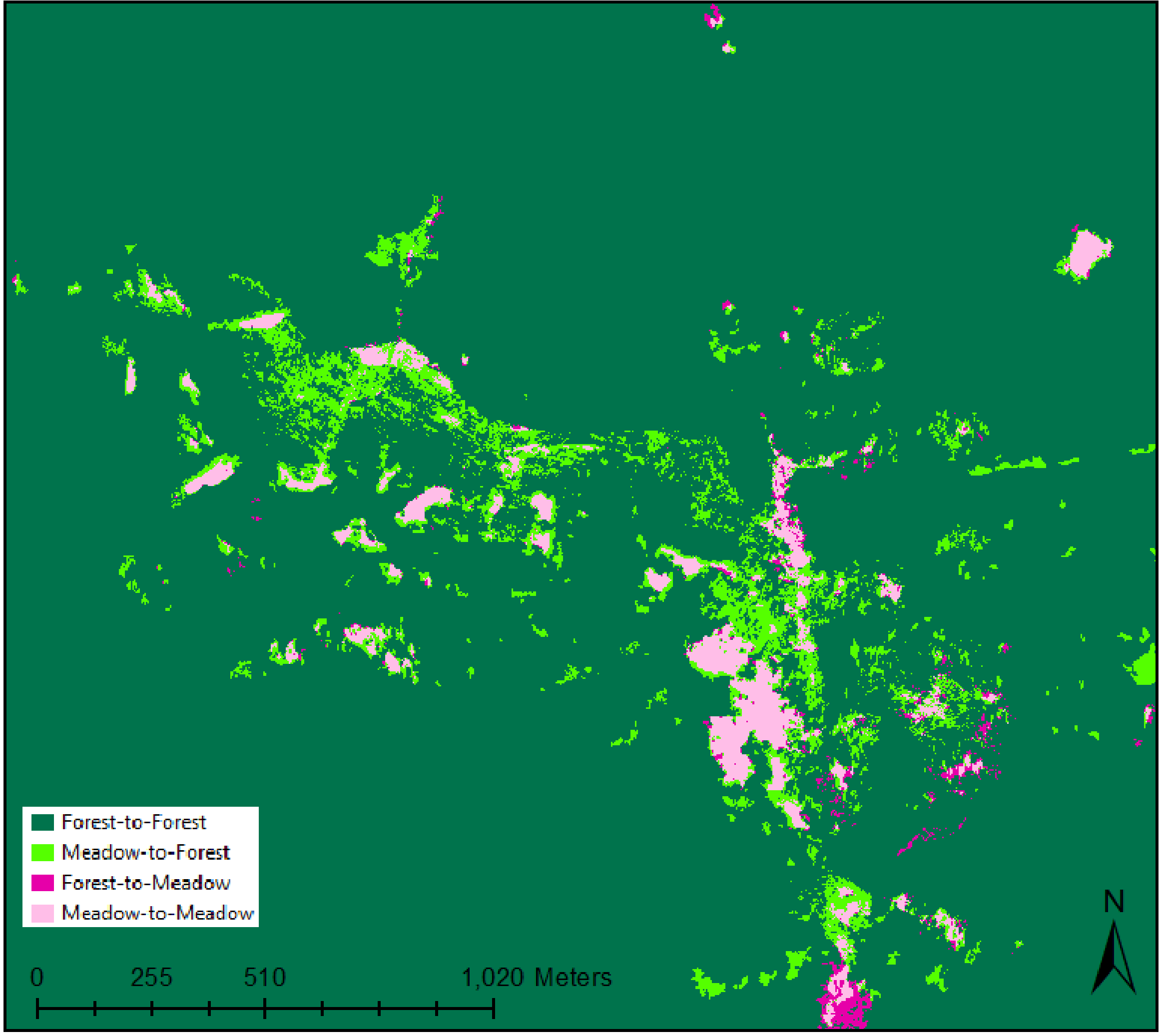


Figure 2.5. Bunchgrass 1946 to 1967 two-date change detection map

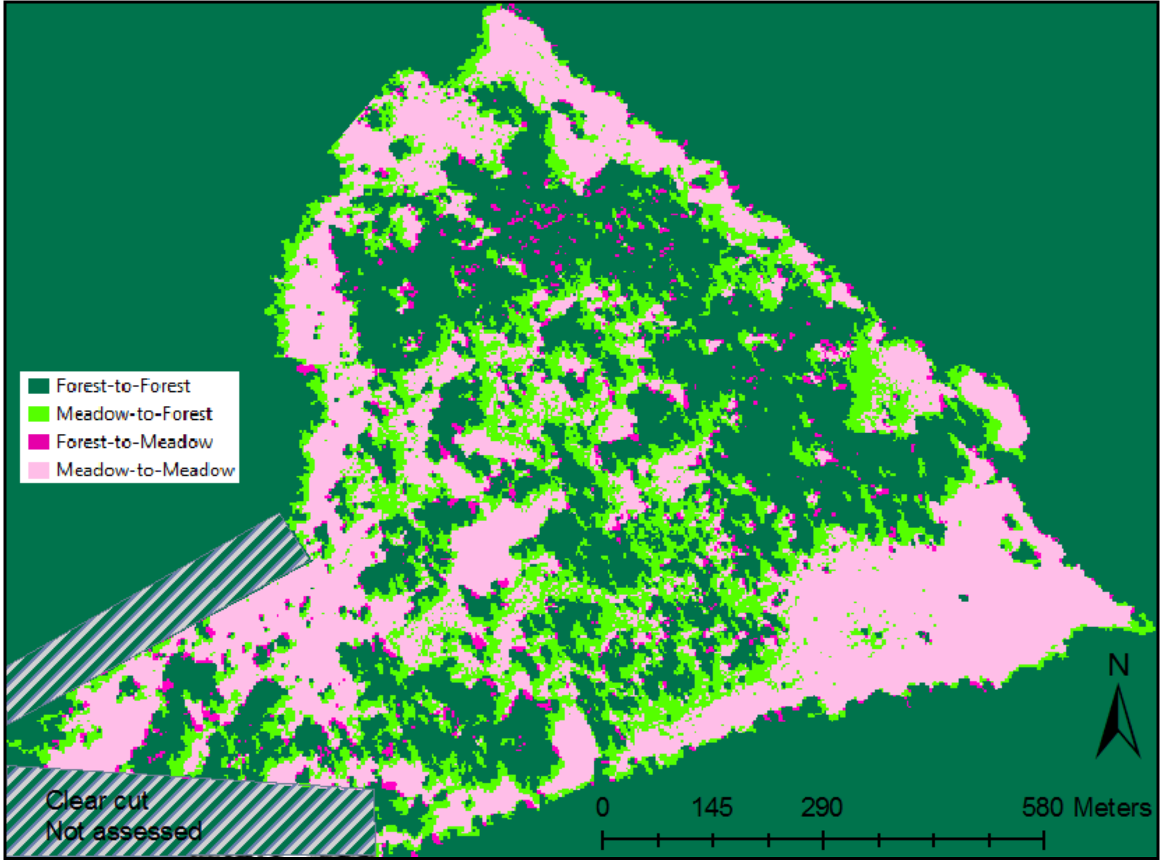


Figure 2.6. Bunchgrass 1967 to 2000 two-date change detection map

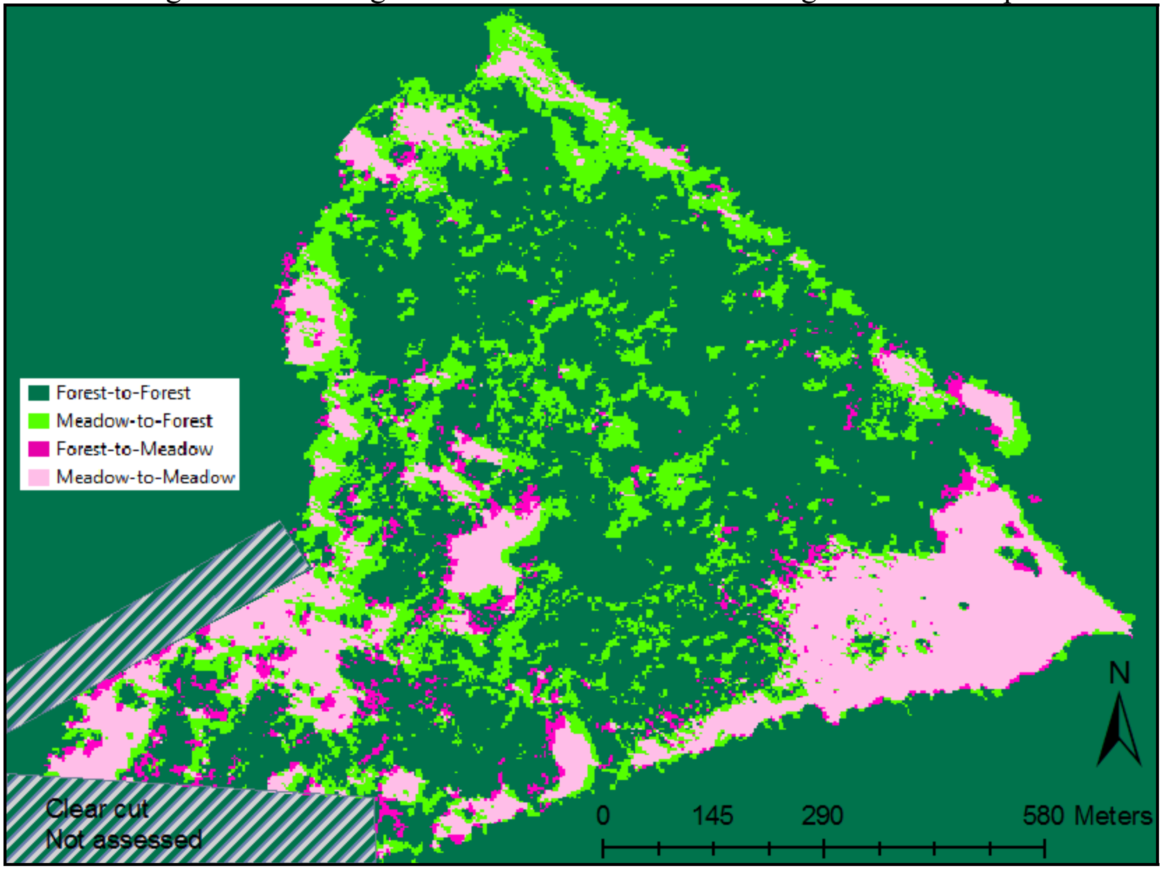
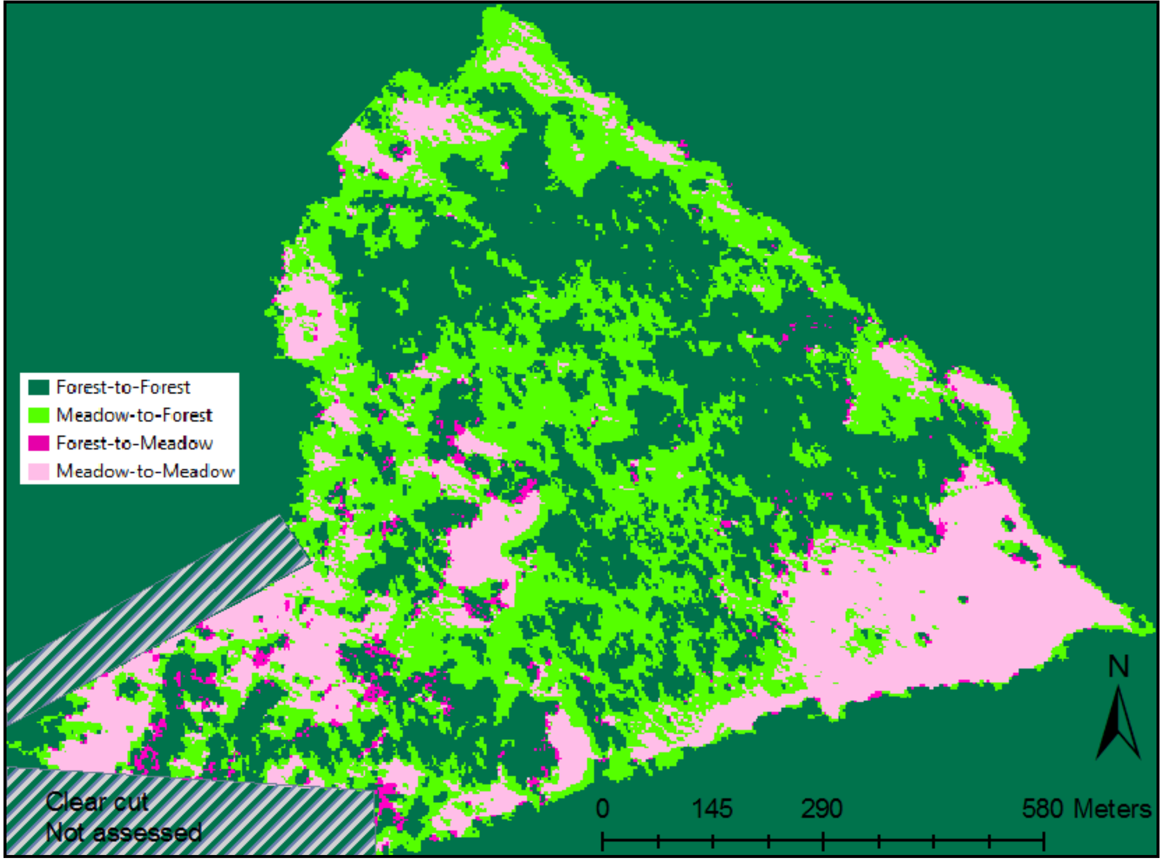


Figure 2.7. Bunchgrass 1946 to 2000 two-date change detection map



2.5 Discussion

2.5.1 Temporal and Aspect Impacts on Meadow Reduction

Meadows in this study were more frequent on south and west-facing slopes. The fastest rates and largest areas of meadow decline occurred on south and west aspects at Lookout, and on the west aspect at Bunchgrass between 1946 and 2000. Yet, Bunchgrass retained the highest amount of meadow area on the south aspect by 2000. These results are not completely consistent with Dailey (2007) findings of more meadow area on south and east slopes in the larger area of the surrounding Willamette National Forest. Meadows or non-forested areas have been observed to occur more frequently on southerly aspects due to higher amounts of drought stress (Romme & Knight, 1981). At Lookout, north aspects are more likely to retain larger amounts of snow as compared to other aspects due to shading. In contrast, meadow prevalence may be attributed to shallow, excessively well drained soils, such as near ridge tops at Lookout (See Appendix A, Figure A.7) (Griffiths 2005). The higher initial amounts of meadow area on westerly aspects at Bunchgrass and southerly and westerly aspects at Lookout provided the largest amount of tree recruitment space on these aspects, and the effect of higher drought stress inhibiting tree encroachment more on southerly aspects seemed to be more of a factor at Bunchgrass than at Lookout.

Loss of montane meadow to tree encroachment was slightly higher from 1946 to 1967 at both Bunchgrass and Lookout, ignoring temporary forest loss due to avalanching at Lookout. The rates of meadow decline may have slowed after 1967, possibly because less meadow area was available as tree canopy closure continued from 1967 to 2000 (Figures 2.2, 2.3, 2.5, and 2.6). It is possible that cooler conditions during the 1946-1967 period (U.S. HCN 2009) may have reduced drought stress and aided tree seedling establishment (Miller & Halpern 1999). As this study is limited to two time periods and does not have a continuous measurement of tree encroachment, it is difficult to determine if cooler conditions from 1946-1967 contributed to increasing the amount and rate of tree encroachment into meadows at Lookout and Bunchgrass. Additionally, the spatial resolution of 3 m may not have detected the presence of smaller trees that would benefit from cooler temperatures.

2.5.2 Slope Gradient Impacts on Meadow Reduction

Flatter meadow areas experienced more tree encroachment at Bunchgrass, but this was not the case at Lookout. Steeper slopes (> 5^{o}) may reduce tree establishment (Weisberg et al. 2007) as disturbance or soil factors may limit tree establishment. Dailey (2007) also noted rapid rates of tree encroachment on steep slopes of montane meadows in the western Cascades at Chucksney Mountain. The finding of this study may signify that disturbance (e.g. mass wasting) or potentially increased drought stress from thinner or rockier soil conditions on steeper slopes at Lookout are not playing a large role in limiting tree establishment, but these conditions may be more of a factor for trees at Bunchgrass. Unlike Bunchgrass, Lookout hosts deciduous tree species Sitka alder (*Alnus* *viridus sinuata*) and Vine maple (*Acer circinatum*) that are adapted to establishing on steep, disturbed slopes (Franklin & Dyrness 1988), and these species as well as conifers were observed to establish on the steep slopes at Lookout (see Appendix A).

2.5.3 Forest Edge Distance Impacts on Meadow Reduction

As expected, the rate and amount of loss of meadow area was highest in areas closest to the forest edge (< 5 m), and meadow loss was consistently decreased with increasing distance from the forest edge. This agrees with the findings of Myster & Picket (1992) that tree stem density decreases with increasing distance to the forest edge. Areas < 5 m away from trees exhibited a rate of tree encroachment at 0.4 ha/year from 1946 to 2000 at both sites, however, Bunchgrass showed a higher rate (0.5 ha/year) from 1946-1967 than from 1967 – 2000 (0.3 ha/year). Bunchgrass also had more meadow loss than Lookout in areas outside 5 m from the forest edge for the period 1946-2000. Meadow loss for Bunchgrass between 5 and 20 m from the forest edge was 35% of the total, while Lookout had only 13% of total meadow loss between 5 and 20 m from the forest edge. This could suggest that shade from forest edges on the westerly, flatter slopes of Bunchgrass may extend further into meadow areas than on the steeper slopes of Lookout, and may help to mitigate higher drought or temperature microclimate conditions. Another factor may be that the shade tolerant Grand fir (*Abies grandis*) and light and drought tolerant Lodgepole pine (*Pinus contorta*) dominating the flatter terrain of Bunchgrass may be better suited to establish at longer distances with higher drought stress and temperatures than the Pacific Silver Fir (*Abies amabilis*) and Noble fir (*Abies procera*) that dominate the steeper slopes at Lookout.

2.6 Conclusions

The area of montane meadows declined dramatically from 1946 to 2000, with about a 60% loss of meadow area at Bunchgrass and Lookout. Meadow declines were higher within 5 m from the forest edge, on west and south aspects, and on flatter slopes at Bunchgrass in the High Cascades, but on steep slopes at Lookout in the West Cascades. At both sites, meadow decline was faster during the period from 1946 to 1967 compared to after 1967. Meadows were more frequent on west and south aspects at both sites. Probable mass movements (avalanches) on steep north and east-facing slopes at Lookout produced temporary increases in meadow. The meadow areas that showed a higher risk of encroachment over the last 54 years may need to be the focus of restoration efforts at Bunchgrass and Lookout Meadows.

3 EARLY STAGES OF TREE ENCROACHMENT IN A MONTANE MEADOW OF THE CASCADES RANGE OREGON: CLIMATE EFFECTS AND BIOTIC INTERACTIONS

Janine Rice, Julia Jones, Charles Halpern, and Joe Antos

In preparation for journal submission

3.1 Introduction

Widespread loss of meadow habitat by coniferous forest encroachment has occurred in the Pacific Northwest during the mid and late 20th century (Franklin et al. 1971; Vale 1981; Rochefort & Peterson 1996; Hadley 1999; Lepofsky et al. 2003; Takaoka & Swanson 2008). Tree encroachment into meadows changes wildlife habitat and associated biodiversity (Franklin & Halpern 1999; Miller et al. 2003; Haugo & Halpern 2007). Because meadows have served as refugia for taxa during climate change (Whitlock 1992), land managers are investigating methods for restoration and preservation of these unique areas in the western Cascades (Wilson 1999). Meadow restoration efforts may be more successful if focused in areas of early tree succession since significant declines in meadow vegetation and soil alteration has been found to rapidly occur after tree establishment (Haugo & Halpern 2007). As little is known about biotic interactions and environmental tolerances that affect trees during the early stages of tree encroachment into meadows, this paper investigates the spatial and temporal patterns of early succession tree encroachment in a dry montane meadow of the Oregon Cascades.

The process of tree encroachment may be spatially patchy and dependent on recruitment space availability, competition, facilitation, climate, and disturbance factors (Veblen 1992). Tree encroachment into grassy areas is often characterized by a slow period with the initial establishment of nuclei patches that serve to facilitate the subsequent growth of persistent species that displace grassland or herbaceous vegetation and eventually coalesce with other patches (Briggs et al. 2002; Seimann & Rogers 2003; Spies 1997). These nuclei patches can serve to facilitate the subsequent establishment of other tree individuals (Callaway 1997) by providing ameliorating shade that reduces seedling heat and drought stress. Competition for light and space can have strong effects on the distribution structure which can vary over space and time (Goldberg 1992). The inter- and intra-species facilitative or competitive relationships may alter the spatial and temporal patterns of early tree succession (Mast et al. 1997; Awada 2005; Fajardo 2006). Additionally, changes in climate can alter the characteristics, timing and spatial patterns of establishment (Taylor 1995; Sykes 1996; Woodward 1995).

This paper addresses how species interactions and environmental tolerances affect the spatial and temporal patterns of early stage tree encroachment in a montane meadow. We focus on a plot that experienced a pulse of tree invasion from 1960-1994 at Bunchgrass meadow in the Western Oregon Cascades (Figure 3.1). Grand fir (*Abies grandis* Dougl.) and Lodgepole pine (*Pinus contorta* Dougl.) are the dominant and subdominant conifers. Lodgepole pine can survive to ages of 400 years and has a wide range of environmental tolerances (Lotan & Critchfield 1990). Lodgepole pine is very shade intolerant, has early rapid growth, and reproduces at 5 to 10 years of age. Cones of Lodgepole pine mature in August to October, with 1- to 3-year intervals between cone crops. Shading and competition inhibit germination and survival, but seedlings are more frost- and drought-resistant than those of Grand fir (Minore 1979; Lotan & Critchfield 1990). Grand fir is much more shade-tolerant than Lodgepole pine. Grand fir reaches maturity at 20 years, when it’s most rapid growth begins. Grand fir seeds are wind-dispersed in September to October, and germinate in the spring following one overwinter period. Germination occurs from late April to early August. Seedlings are sensitive to late summer heat and associated drought. Initial survival is favored by moderate shade (Minore 1979; Foiles et al. 1990). During invasion, Lodgepole pine appears to act as a pioneer tree, facilitating the subsequent establishment of Grand fir, which dominates the later stages of succession (Turner 1985; Garber & Maguire 2004; Halpern et al. in review). Although tree invasion can be associated with warming or reduced drought stress, little is known about specific climate effects on tree establishment success.

This study used a detailed record of establishment of over 900 trees in a 0.2 ha area over the period from 1917-1997 to explore hypotheses that explain spatial and temporal patterns of tree invasion in Bunchgrass meadow:

Hypothesis 1: Tree establishment in the early stages of encroachment into meadows reflects biotic interactions, notably establishment of pioneer Lodgepole pine and Grand fir that facilitate subsequent Grand fir seedling establishment.

Hypothesis 2: Tree establishment reflects interactions between species' life history traits and climate: Lodgepole pine invades during periods of relatively hot, dry summers, whereas Grand fir invades during periods of relatively wet, cool summers.

Hypothesis 3: Tree establishment patterns reflect seed dispersal patterns associated with abundant seed years and large canopies of older trees.

We tested these hypotheses by quantifying spatial relationships among tree establishment locations and temporal relationships among tree establishment dates, precipitation, temperature, snowpack, and cone crop data.

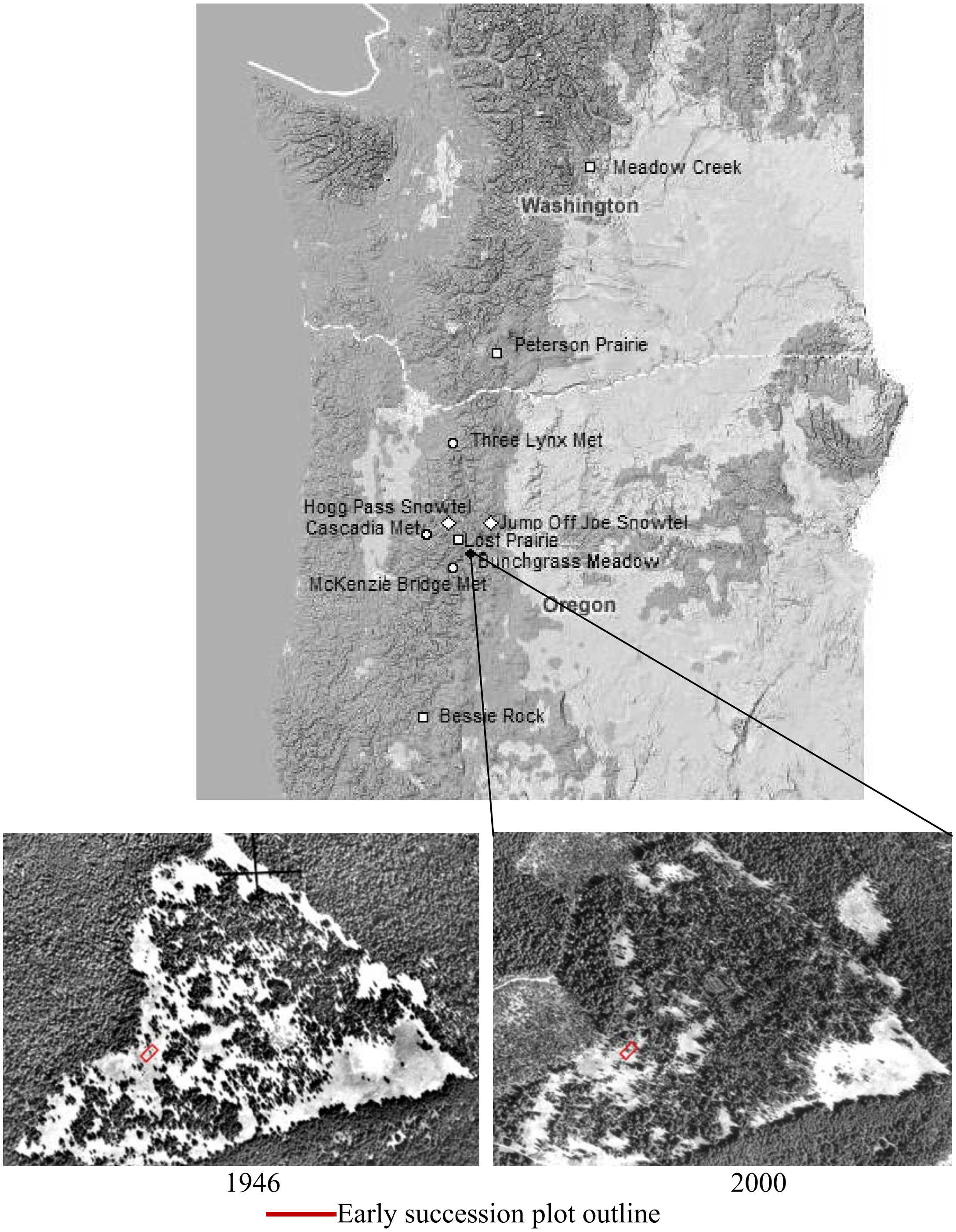
3.2 Study Area

The study was conducted in the Bunchgrass montane meadow designated special habitat area in the central Western Cascade Range in the Willamette National Forest at 44°17'N, 121°57'W (Figure 3.1). The study plot (0.21 ha) experienced initial tree invasion in 1916, and a pulse of tree invasion from 1960 to 1995 (Figure 3.2). This plot is part of a larger series of studies (Lang & Halpern 2007; Haugo & Halpern 2007; Halpern et al., in review).

Vegetation at Bunchgrass meadow consists of a mosaic of conifer and herbaceous meadow species. Meadow vegetation is dominated by grasses (*Festuca idahoensis* and *Carex pensylvanica*) and forbs (*Phlox spp*. and *Lupinus latifolius*). Forests are dominated by Grand fir in closed canopy areas. Lodgepole pine commonly occurs in open meadow as young individuals, but older Lodgepole pine individuals typically occur among patches of established Grand fir. Less common tree species include Douglas-fir (*Pseudotsuga menziesii)*, Pacific silver fir (*Abies amabilis)*, Noble fir (*Abies procera)*, Subalpine fir *(Abies lasiocarpa),* Giant chinquapin (*Castanopsis chrysophylla),* Cascara *(Rhamnus purshiana)*, Western white pine (*Pinus monticola)*, Pacific yew (*Taxus brevifolia),* and Mountain hemlock *(Tsuga mertensiana).*

The climate at Bunchgrass is marine west-coast, characterized by mild temperatures, wet winters and dry summers. The annual average temperature is 7 °C, and can range from 34 °C in the summer to -23 °C in winter. Annual precipitation averages 2400 mm and ranges from 700 to 4100 mm. Precipitation occurs mainly as snow from late October to May, and an occasional summer thunderstorm can occur. Snow packs over 2 m deep can occur in late spring, peaking in April and persisting occasionally into July.

Figure 3.1. Study Area



1946

2000

Bunchgrass meadow is on a gently sloping plateau rising locally above the high Cascade platform composed of lava flows from 3000 m High Cascade volcanoes 10 km to the east. Predominantly southwestern facing slopes have gradients of less than 5%, and elevations range from 1300 to 1375 m (Figure 3.1). Soils are typically 2 m deep, well-drained, fine to very-fine-sandy loams derived from andesitic basalt and tephra deposits (Haugo & Halpern 2007). They grade from Vitric Melanocryands in open meadow to Aquic Vitricryands in older forests (D. Lammers, personal communication).

No direct evidence of fire disturbance or grazing is evident at Bunchgrass meadow. However, it is thought that Native Americans maintained open meadow habitats for hunting (Boyd 1999), and grazing of sheep by Euro-American settlers with burning of meadow areas is likely to have occurred before 1940 (Haugo 2005). Archival records are insufficiently precise to determine the amount or timing of grazing at Bunchgrass (Haugo & Halpern 2007). Fire has been largely suppressed in the later half of the 20th century at Bunchgrass, with limited thinning or experimental burning in areas not associated with this study site.

3.3 Methods

Aerial photographs and field reconnaissance were used to identify a 30 x 70 m (0.21 ha) plot where tree encroachment was in an early stage. The remaining portions of the study area are still meadow, or experienced tree encroachment starting as early as 1916 (Figure 3.1). Based on examination of historical aerial photographs from 1946 and

2000 the 0.21 ha plot was located in an area that was almost treeless in 1946 but invaded by 2000 (Figure 3.1). Plot size was limited to 0.21 ha to capture the early stage of encroachment, and because there was a very high density of tree seedlings.

Within the plot a 10x10 m grid subsystem was surveyed. Within each subplot all live (n = 929) trees and snags (n = 44) > 0.3 m tall were mapped to the nearest 0.1 m. Species and diameter at breast height (dbh) or diameter at tree base (dba) were recorded for all live trees. All live trees were aged from increment cores or basal cross-sections collected in 2003 or 2004. Cores and basal sections were mounted and sanded following standard dendrochronological methods. Annual rings were counted under 10 – 40x magnification. Missing rings from cores without piths were estimated from a series of ring-pattern templates. Ages of trees obtained via cores or disk samples were adjusted for age-to-sample height based on age-height regressions developed from a destructive sample of 30 - 40 seedlings per species (C. Halpern, unpubl. data).

3.3.1 Point Pattern Bivariate Ripley's K Method

We used the bivariate Ripley's K to assess the spatial patterns of all trees by age and species (Lodgepole pine and Grand fir). Young and old age classes for each species were defined for the bivariate test. The young Lodgepole pine age class was defined at less than or equal to 20 years, and the old age class was defined at more than 20 years. The young Grand fir age class was defined at less than or equal to 35 years, and the old age class was defined at more than 35 years. The young and old age class definitions were chosen to provide an adequate sample size and make a distinction between trees establishing prior to and after a major pulse of establishment.

Bivariate Ripley's K (Ripley 1977) L(d) is a cumulative distribution function of all pair-wise distances between points in two samples for an area *A*. This statistic tests whether a point pattern is consistent with complete spatial randomness (based on a Poisson process), or is clustered or regular. The equation is defined as:

$$\hat{L}(d) = \left(\frac{\hat{K}(d)}{\pi} \right)^{1/2}$$

where *K(d)* is:

$$\hat{K}(d) = \frac{A \sum K(i,j)}{N(N-1)} .$$

and *N* is the total number of points, i and j are sample points, and d is a distance between 0 to 10 m at 0.2 m increments. If the distance between i and j is <= d, *K(i,j)* = 1. If the distance between i and j exceeds the distance to one edge of the plot, the following edge correction equation is used:

$$K(i,j) = \left\{ 1 - \left[\cos^{-1}\left(\frac{e_1}{d} \right) \cdot \frac{1}{\pi} \right] / 2\pi \right\}^{-1}$$

where e_1 is the distance to the nearest edge. If the distance between i and j exceeds the distance to both edges of the plot, the following edge correction equation is used:

$$K(i,j)=\left\{1-\left[\cos^{-1}\left(\frac{e_1}{d}\right)+\cos^{-1}\left(\frac{e_2}{d}\right)+\frac{\pi}{2}\right]/\,2\pi\right\}^{-1}$$

where e_1 and e_2 are distances to the nearest two borders.

The Ripley's K function used in this analysis was adapted for S-Plus by Reich & Davis (2005). The results of *L(d)* are plotted every 0.2 m up to a maximum of 10 m and are compared to a confidence bound envelope based on a Monte Carlo procedure involving 100 random perturbations of the data. A result of *L(d)* above the envelope indicates a clustered pattern, a result within the envelope indicates a random pattern, and a result below the envelope indicates a regularly spaced pattern ($p < 0.01$). The bivariate Ripley's K compares two sets of points and uses two Poisson process models. However, large-scale heterogeneity in the spatial point pattern (e.g., when large clusters are present) biases the detection of small-scale pattern using Ripley's K (Wiegand & Moloney 2004; Schiffers et al. 2008).

3.3.2 Point Pattern J Summary Function

We used the J-function (Lieshout & Baddeley 1996) from the R statistical software package to examine spatial pattern of trees at fine spatial scales and changes over time in these patterns. The J-function, *J(d)*, is a ratio of two functions: *G(d),* the nearest neighbor distance distribution function, and $F(d)$, the empty space function. The equation is defined as:

$$J(d) = (1-G(d))/(1-F(d))$$

Where $G(d)$ is the cumulative distribution function of distances between nearest neighbor points (sometimes referred to as the g-function), and $F(d)$ is the cumulative distribution function of distances between randomly selected points and their nearest neighbor points (Thonnes & Lieshout 1999). The estimate of $J(d)$ indicates the type of pattern (clustered when $J(d) < 1$, regular or dispersed when $J(d) > 1$, and a random Poisson point process when $J(d)=1$). The strength of patterns is based on how much the estimate of $J(d)$ differs from 1. When $J(d)$ is plotted against d (distance), it shows the range over which points are clustered or dispersed. We used the J-function for marked points (Lieshout & Baddeley 1996) based on species to examine fine-scale patterns within 4 m of established trees, following guidelines to ensure high power of the test (Thonnes & Lieshout 1999). To correct for edge effects we used only those points >4 m from the nearest edge. The J-function was applied to quantify the degree of clustering in Lodgepole pine and Grand fir on five dates (1965, 1975, 1985, 1995, and 2000) over the early stage of tree establishment in a meadow. The J-function is limited to univariate analysis.

3.3.3 Pioneer Tree Recruitment Analysis

To test how the first trees that invade a meadow facilitate the invasion by subsequent trees, we identified "pioneer trees" and the seedlings that established subsequently within short distances from the pioneer tree. A program was created in Visual Basic to quantify bivariate relationships between the two tree species at fine spatial scales, thus capturing relationships that cannot be quantified using Ripley's K or the J-function. For each year from 1916 to 2004, the program identified the pioneer trees that established more than 5 m away from each other. The cumulative number of trees subsequently establishing within 5 m of the identified pioneer trees, the average distance of subsequent establishment in the 5 m radius around the pioneer trees, and the percent of trees that established in the 5 m radius around each pioneer tree was quantified by species. To characterize differences in species establishment distances over time, the nearest preceding neighbor average distance was also quantified over time by species for the entire plot from 1916 to 2004.

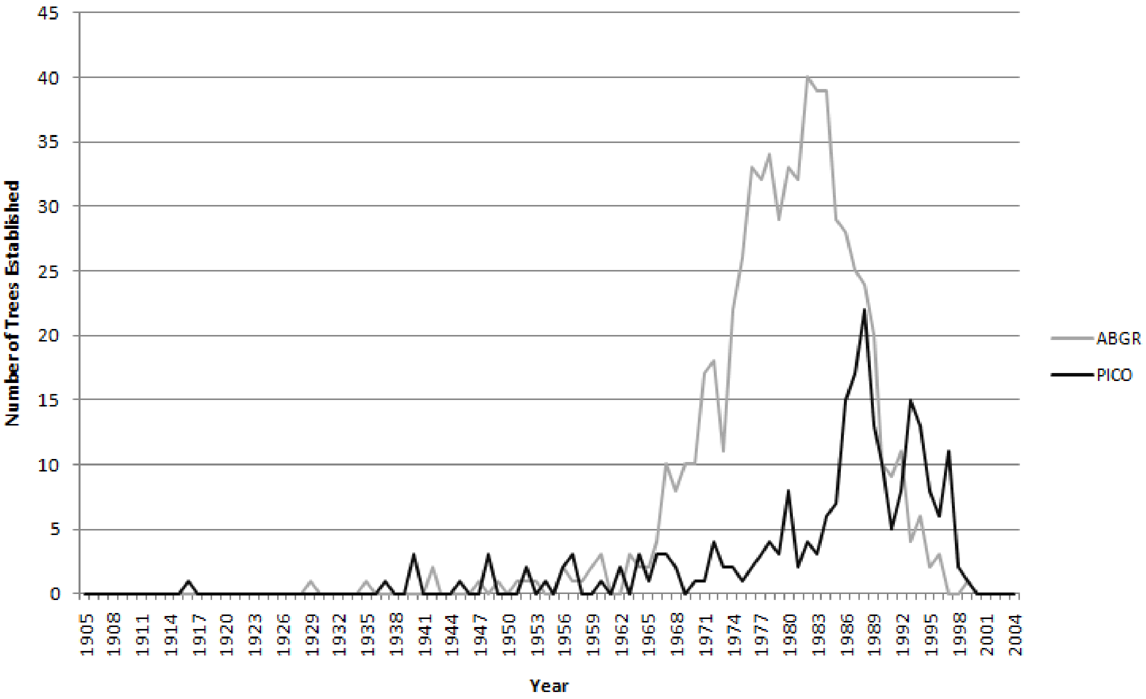
3.3.4 Correlations with Climate Variables and Cone Crop

Records of mean monthly air temperature and total monthly precipitation were obtained for the period 1925 to 2005, and snow data was obtained for the years 1975-1995. Air temperature, precipitation and snow data were obtained from the nearest meteorological stations. Air temperature and precipitation data were from Three Lynx, Cascadia, and McKenzie Bridge stations (U.S. HCN http://cdiac.esd.ornl.gov/r3d/ushcn/statepcp.html#OR), and snow water equivalent data were from Three Meadows Creek, Santiam Pass, McKenzie Bridge, and Hogg Pass SNOTEL sites (NRCS 2009; http://www.wcc.nrcs.usda.gov/snotel/Oregon/oregon.html) (Figure 3.1). The numbers of trees established by year was correlated to the monthly temperature and precipitation, and April snow water equivalent over the period 1964 to 1994. The number of trees established by year was correlated against temperature and precipitation for 36 months in a 3-year window centered on the year of tree establishment to allow for possible errors in tree establishment dates. We report correlations for only the year prior to, the year of, and the year after tree establishment, when correlations were strongest. Year-to-year variation in numbers of Grand fir established were compared with cone-crop years based on analysis of Grand fir cone-crop records from 1963-2003 for four Grand fir plots with $n > 20$ trees that were obtained from J. Franklin, (unpublished. data) (Figure 3.1). No cone crop records were available for Lodgepole pine.

3.4 Results

Tree establishment occurred at low rates from 1916 to 1963 for Grand fir and from 1916 to 1983 for Lodgepole pine followed by a pulse of high rates of establishment (Figure 3.2). In 2004, densities of trees were very high in this plot (3067 Grand fir ha^{-1} and 1100 Lodgepole pine ha^{-1}), and only 7% of sampled Lodgepole pine and 6% of Grand fir in this plot were dead.

Figure 3.2. The Number of established Grand fir (ABGR) and Lodgepole pine (PICO) trees by year



3.4.1 *The process of tree establishment over time in the meadow*

The process of tree establishment in the meadow began with pioneer trees, defined as individuals that established more than 5 m from the nearest preceding tree. Seventeen individual pioneer trees established in the meadow plot between 1916 and 2004; Lodgepole pine was five times more likely than Grand fir to establish 5 or more m away from another tree (14 Lodgepole pine pioneers vs. 3 Grand fir pioneer trees). After pioneer trees were established, seedlings of subsequent trees tended to establish within 5 m of pioneer trees. In the first three decades (1935 to 1965) rates of tree establishment within 5 m of pioneer trees were low for both species (1 to 4 new seedlings ha^{-1} yr^{-1}), but they accelerated from 1971 to 1990 for Grand fir (70 to 170 new seedlings ha^{-1} yr^{-1}) and from 1986 to 1995 for Lodgepole pine (20 to 40 new seedlings ha^{-1} yr^{-1}) (Figure 3.3a). Lodgepole pine established further away from pioneer trees than Grand fir on average, but establishment distances from pioneer trees varied over time, independent of the total density of trees in the plot (Figure 3.3a, b). In two periods (1955 to 1975 and 1991 to 1995), Lodgepole pine and Grand fir established at almost identical average distances from pioneer trees (Figure 3.3b).

Figure 3.3a. Cumulative establishment of Grand fir (ABGR) and Lodgepole pine (PICO) around 5 m pioneer trees over the time period 1935 to 1997

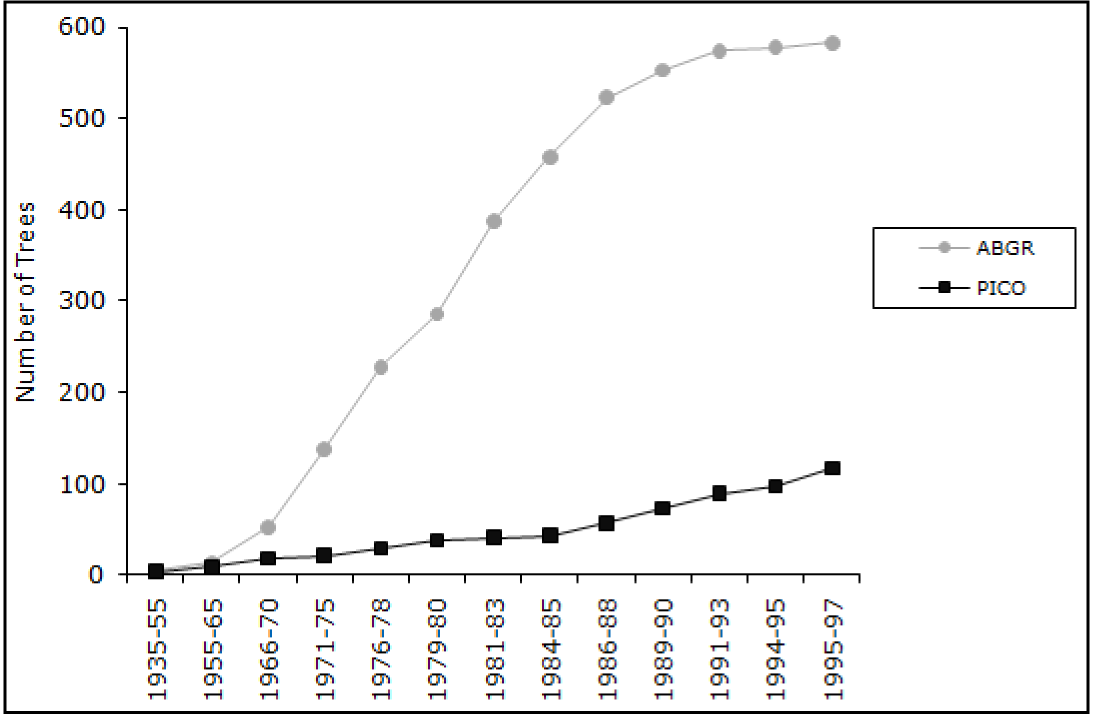
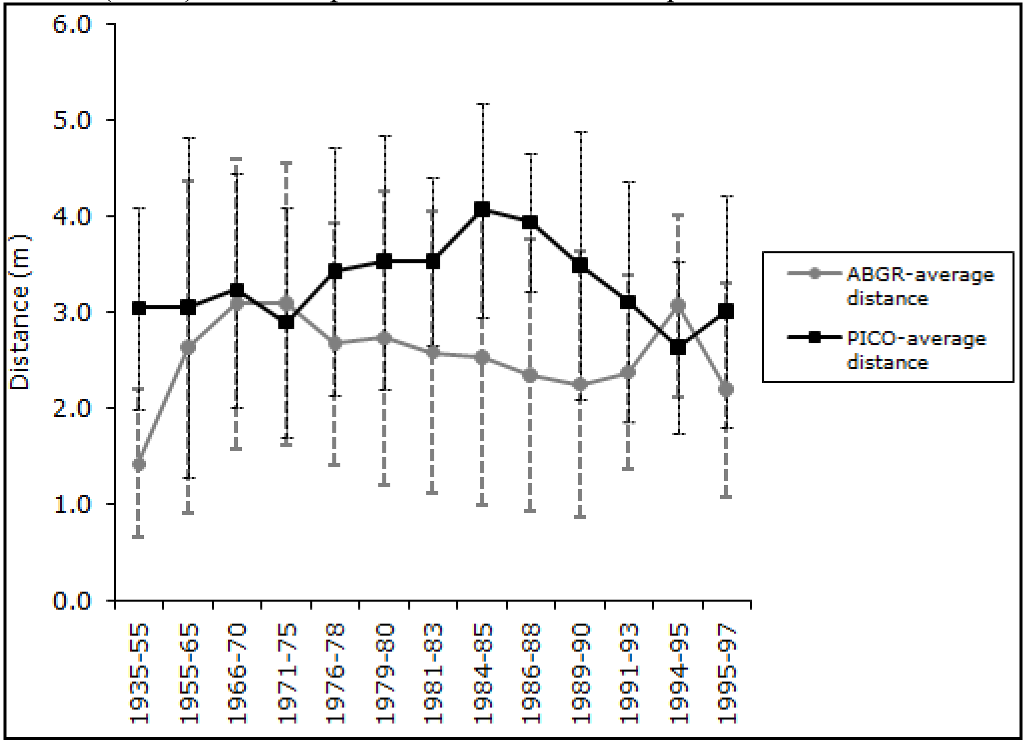
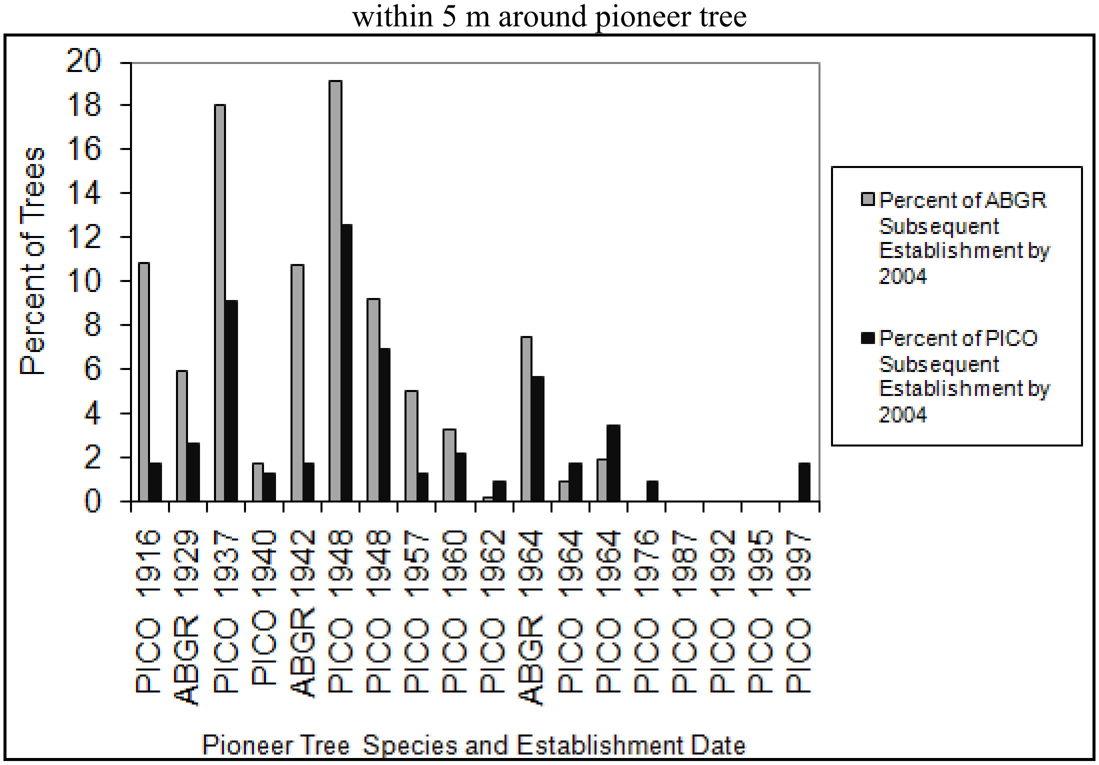


Figure 3.3b. Average establishment distance of Grand fir (ABGR) and Lodgepole pine (PICO) from 5 m pioneer tree over the time period 1935 to 1997



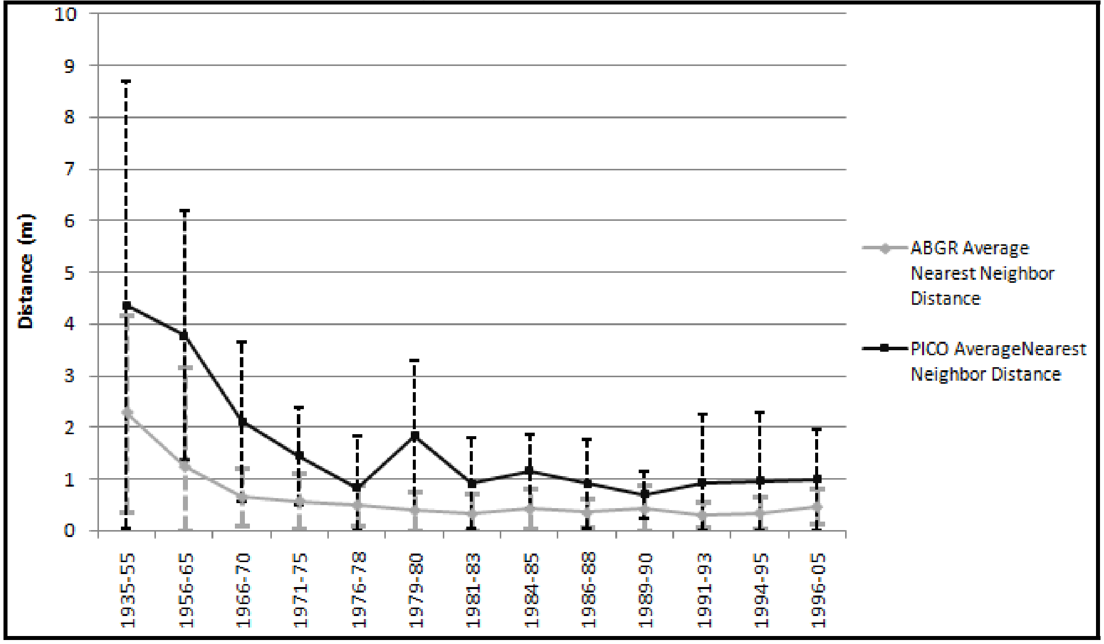
The longer a pioneer tree had been established, the number of seedlings underneath it were generally higher (Figure 3.3c). Overall, Grand fir seedlings were more likely than Lodgepole pine to establish under pioneer trees, independent of whether the pioneer tree was Lodgepole pine or Grand fir, but the relative establishment success of Grand fir and Lodgepole pine changed over time (Figure 3.3c). By 2004, as many as 150 seedlings were found under pioneer trees established before 1950, but very few occurred under pioneer trees established after 1975 (Figure 3.3c). Moreover, the ratio of Grand fir relative to Lodgepole pine establishment near pioneer trees increased over time (Figure 3c). By 2004, a much higher proportion of Grand fir to Lodgepole pine seedlings were found under pioneer trees that had established prior to 1950, whereas roughly equal proportions of Grand fir and Lodgepole pine seedlings occurred under pioneer trees established between 1950 and 1975, and fewer Grand fir than Lodgepole pine seedlings were found under pioneer trees established after 1975 (Figure 3.3c).

Figure 3.3c. Percent of Grand fir (ABGR) and Lodgepole pine (PICO) trees establishing within 5 m around pioneer tree



Seedling establishment distance from the nearest preceding neighbor differed consistently between Lodgepole pine and Grand fir and declined with increasing seedling density (Figure 3.3 d). Lodgepole pine consistently established about two times further away than Grand fir from nearest preceding neighboring seedlings. In the early years of tree establishment prior to 1955, Lodgepole pine established at distances more than 5 m, whereas Grand fir established at distances just over 3 m on average from the nearest preceding neighbor. By the end of the pulse of invasion, after the 1990s, Lodgepole pine was establishing at 1 m and Grand fir was establishing at 0.5 m on average from the nearest preceding neighbor (Figure 3.3d). By 1970, Grand fir was much more likely to occur within 0.5 m of neighboring trees and much less likely to be found beyond 3 m from neighboring trees, compared to Lodgepole pine (Figure 3.3d).

Figure 3.3d. Nearest preceding neighbor average establishment distance of Grand fir (ABGR) and Lodgepole pine (PICO) for all trees in plot



3.4.2 Positive associations between young and adult Lodgepole pine and Grand fir

The process of tree establishment in the meadow produced a strongly clustered spatial pattern of trees in 2004 (Figure 3.4 & Figure 3.5). The most strongly expressed clustering was of young Grand fir (<35-yr-old) relative to old Grand fir (>35-yr-old) and old Lodgepole pine, and old Grand fir relative to old Lodgepole pine (Figure 3.4a); this clustering was strongly expressed at all distances. Young Lodgepole pine was less strongly clustered near old Lodgepole pine and old Grand fir (Figure 3.4b). In contrast, young Lodgepole pine relative to old Grand fir was regularly arranged at distances of 1 m to 2 m (showing repulsion), randomly arranged at of 2 m to 4 m, but clustered at distances beyond 2 m relative to old Grand fir (Figure 3.4b).

Figure 3.4a. Strongly expressed clustering of young and old Grand fir (ABGR) relative to old Lodgepole pine (PICO) and Grand fir in a 0.21 ha plot in Bunchgrass meadow. Bivariate Ripley's K results for old PICO (>20-yr-old) vs. old ABGR (>35-yr-old), old PICO (> 20-yr-old) vs. young ABGR (<=35-yr-old), and young ABGR vs. old ABGR.

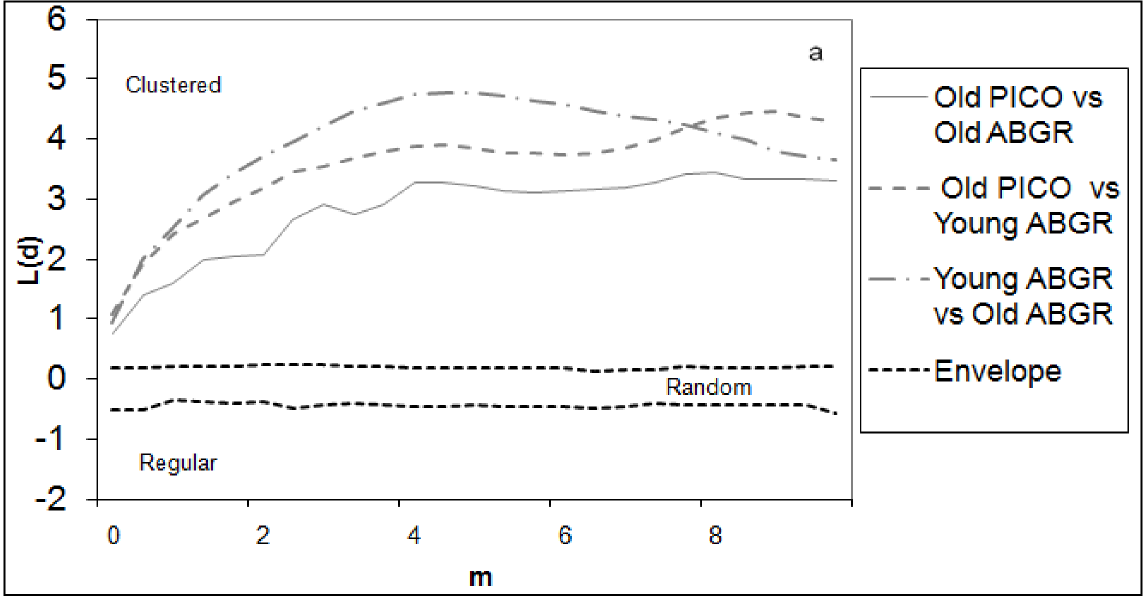
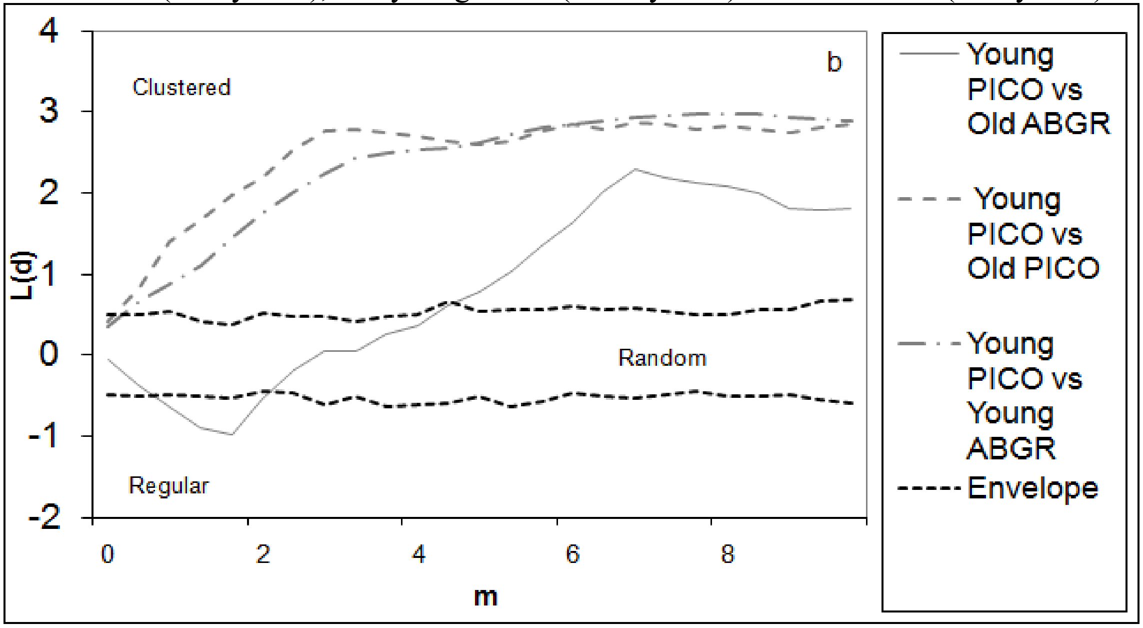


Figure 3.4b. Less strongly expressed clustering of young Lodgepole pine (PICO) relative to young ABGR and old PICO and shorter distance repulsion of young PICO and old Grand fir (ABGR) in a 0.21 ha plot in Bunchgrass meadow. Bivariate Ripley's K results for young PICO (<20-yr-old) vs. old ABGR (>35-yr-old), young PICO (<20-yr-old) vs. old PICO (>20-yr-old), and young PICO (<=35-yr-old) vs. old ABGR (>35-yr-old).



Over short distances (< 5 m), Grand fir was strongly clustered within 0.5 m of other Grand firs, whereas Lodgepole pine was more evenly distributed (Figure 3.5a & b). Grand fir became clustered at much lower densities and much earlier than Lodgepole pine. By 1965, clustering of Grand fir, at a cumulative density of 119 ha^{-1}, was already as strongly expressed as that achieved by Lodgepole pine in 2000, at a cumulative density of 1100 ha^{-1}. The strength of clustering of Grand fir increased dramatically from 1965 to 1975, a decade before its peak rate of establishment, while clustering of Lodgepole pine intensified the most from 1985 to 1995 during its peak rates of establishment (Figure 3.2 & Figure 3.5).

Figure 3.5a. J Summary Function results for Grand fir over the decades 1965, 1975, 1985, 1995, and 2000

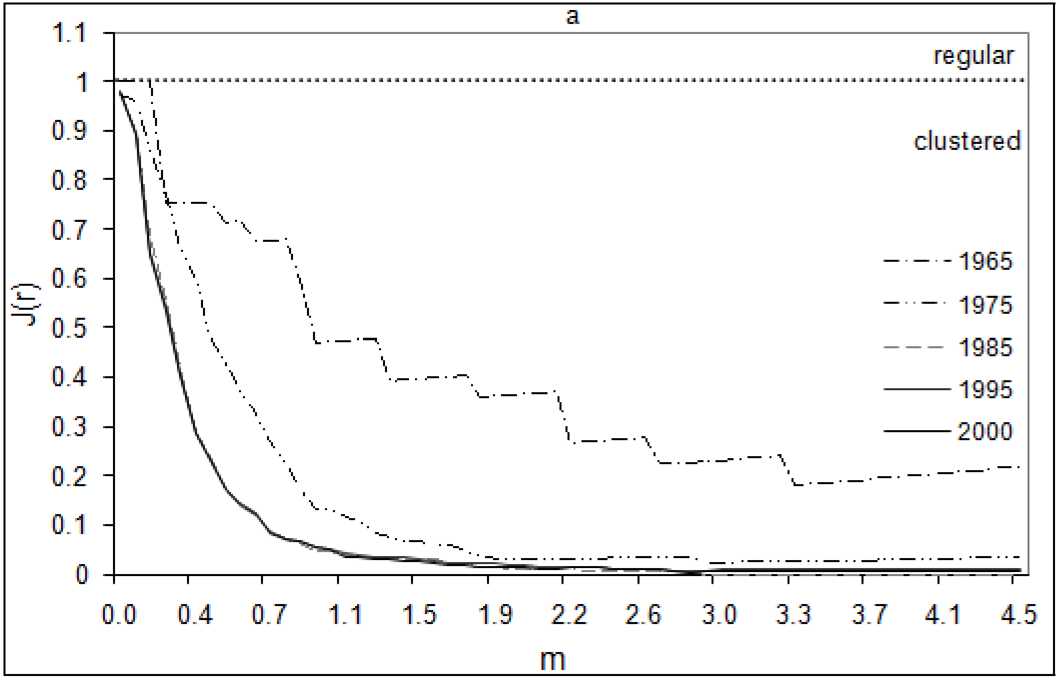
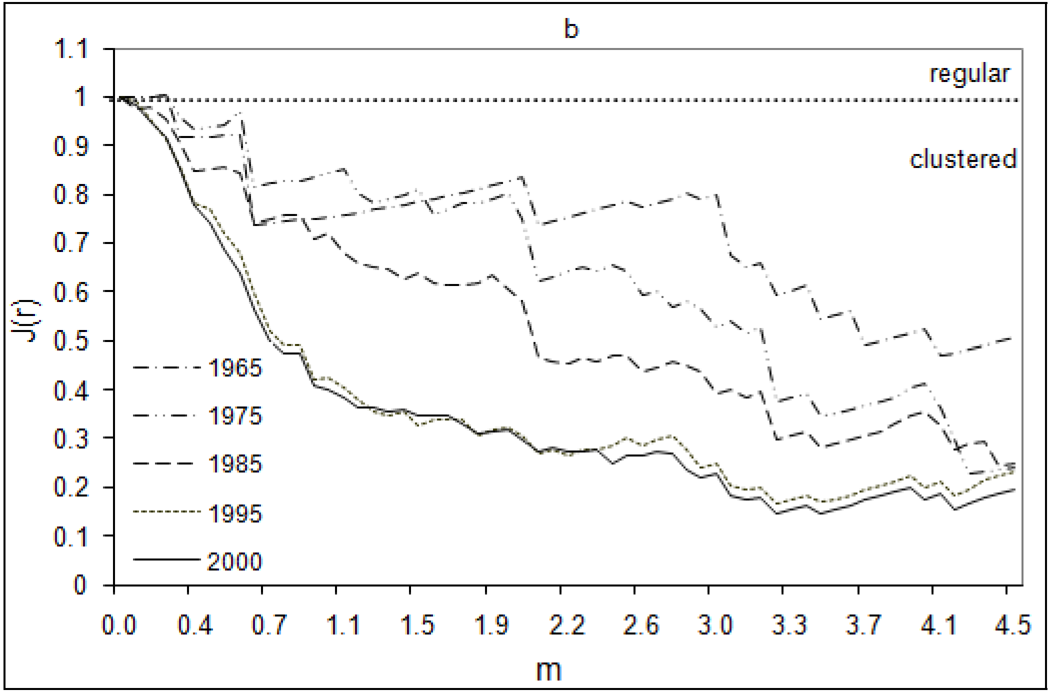


Figure 3.5b. J Summary Function results for Lodgepole pine over the Decades 1965, 1975, 1985, 1995, and 2000



3.4.3 Correlations of tree establishment with climate and cone crops

Establishment rates of Lodgepole pine were positively correlated with air temperatures ($r > 0.4$) in early spring (April) and late summer and early fall (September, October) in the year prior to, the year of, and the year after establishment (Figure 3.6a). In contrast, rates of Grand fir establishment were not strongly correlated with air temperatures in spring, summer, or fall (Figure 3.6b). Establishment rates of Lodgepole pine were not strongly correlated with precipitation ($-0.4 < r < 0.4$) in spring, summer, or fall of the year prior to, the year of, and the year after establishment (Figure 3.6c). In contrast, rates of Grand fir establishment were somewhat ($r > 0.4$) correlated with precipitation in spring and summer of the year prior to, the year of, and the year after establishment (Figure 3.6d). Tree establishment rates were not correlated with April snow packs (data not shown). Grand fir establishment in the early succession plot also experienced small increases in years after Grand fir cone crops, which occur at 2- or 3-year cycles (data not shown).

Figure 3.6a. Correlations of Lodgepole pine (PICO) establishment with monthly temperature in the year prior, year of, and year after establishment for climate stations Cascadia, McKenzie Bridge, and Three Lynx over the years 1964 – 1994.

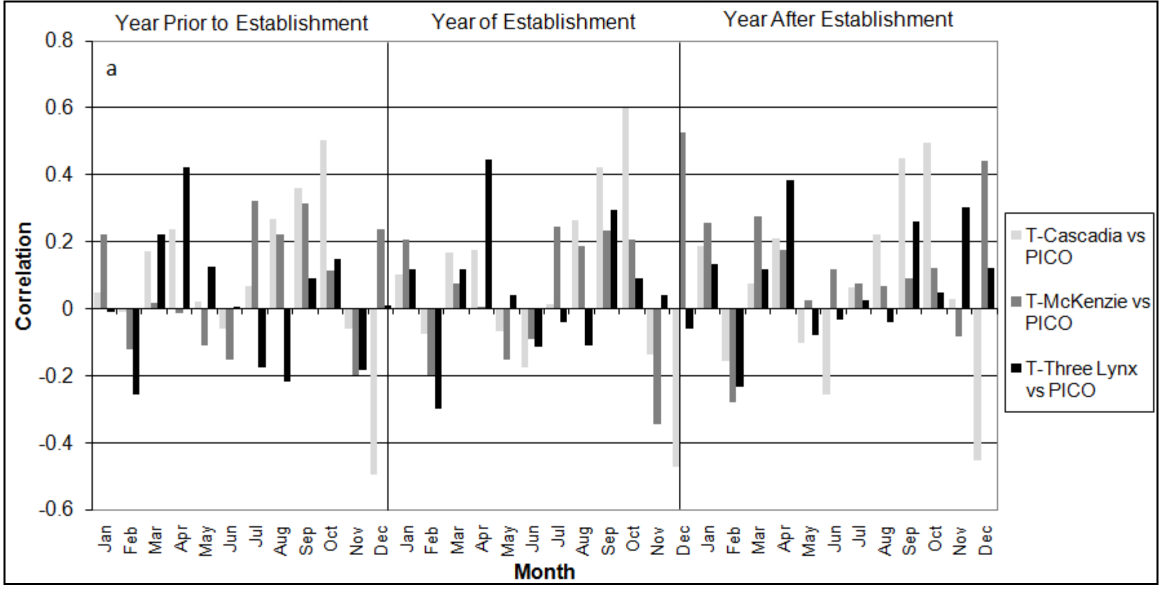


Figure 3.6b. Correlations of Grand fir (ABGR) establishment with monthly temperature in the year prior, year of, and year after establishment for climate stations Cascadia, McKenzie Bridge, and Three Lynx over the years 1964 – 1994.

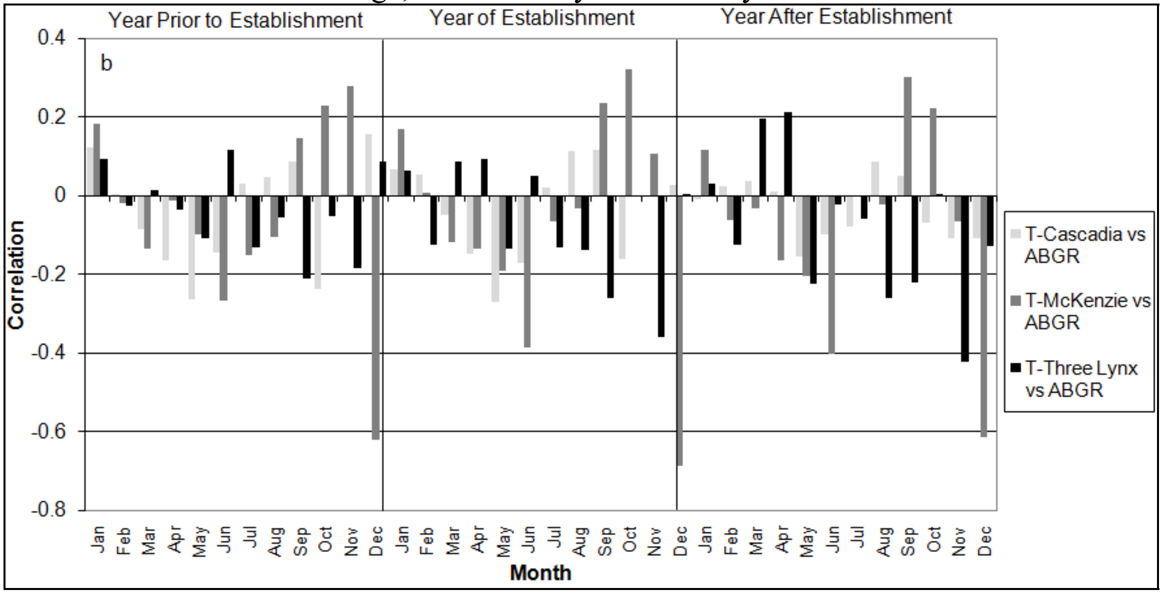


Figure 3.6c. Correlations of Lodgepole pine (PICO) establishment with monthly precipitation in the year prior, year of, and year after establishment for climate stations Cascadia, McKenzie Bridge, and Three Lynx over the years 1964 – 1994.

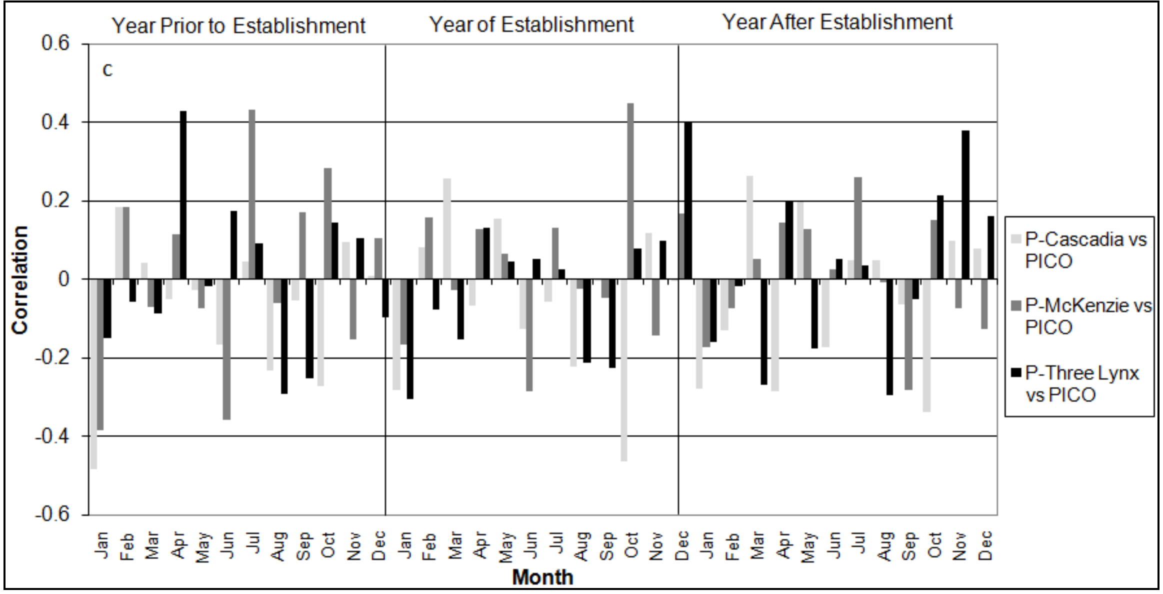
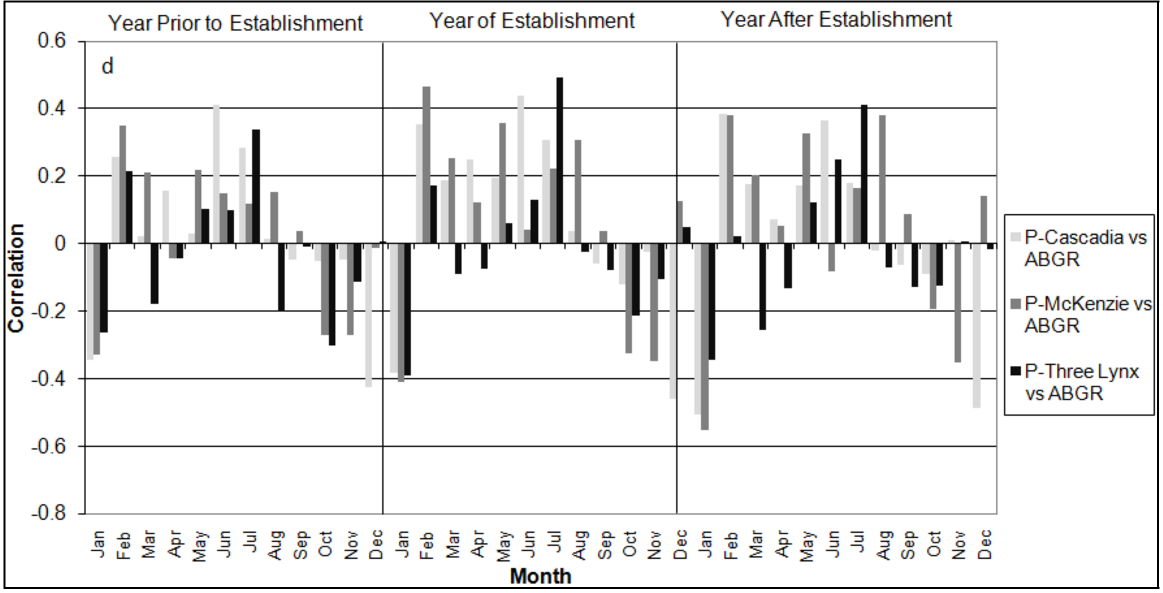


Figure 3.6d. Correlations of Grand fir (ABGR) establishment with monthly precipitation in the year prior, year of, and year after establishment for climate stations Cascadia, McKenzie Bridge, and Three Lynx over the years 1964 – 1994.



3.5 Discussion

Although environmental tolerances influence the rate of tree species' invasion of montane meadows, biotic interactions can be more important than exogenous factors such as climate in controlling invasion dynamics. Grand fir and Lodgepole pine invasion in Bunchgrass meadow is consistent with the environmental tolerances of both species. Spatial patterns of invasion are strongly regulated by biotic interactions, while the temporal patterns also are correlated with climate variables.

Lodgepole pine was a pioneer tree and established further from pre-existing trees, while Grand fir established closer to pre-existing trees. These patterns are consistent with the higher tolerances of Lodgepole pine for light, heat, drought, and frost, and the higher shade tolerance of Grand fir. The very strong association of young Grand fir with older trees of both species, and the increasing frequency of Grand fir relative to Lodgepole pine within 5 m of pioneer trees over time, support the hypothesis that Lodgepole pine act as pioneer trees that facilitate Grand fir invasion more than seedlings of its own species. The fact that in recent years Lodgepole pine has established within 1 m of pre-existing trees, and that young Lodgepole pine were most strongly clustered with young Grand fir, and repulsed at short distances from old Grand fir may indicate that seedlings and saplings of Grand fir do not severely inhibit Lodgepole pine establishment initially.

Lodgepole pine establishment was associated with warm, dry late summers, while Grand fir establishment was associated with wet springs and cool summers. These responses also are consistent with the relatively high tolerances of Lodgepole pine for light, heat, and drought, and the high shade tolerance of Grand fir. Although climate is not a cause of invasion, temperature and moisture regulate the rate of invasion. Because the two tree species have contrasting environmental tolerances, most years from 1925 to 2005 were suitable for establishment of one species or the other.

Seed sources may have limited tree invasion into the meadow complex prior to 1960 (Halpern et al. in review), but since then seed source availability may have reduced the sensitivity of invasion rates to environmental tolerances and biotic interactions. Since 1960 (when cone crop records began) small increases in Grand fir establishment occurred after Grand fir cone crops in western Oregon. Grand firs that had established in the 1940s and 1950s in areas surrounding the plot had matured by the 1970s and may have contributed seed to the pulses of Grand fir invasion in the early succession plot in the 1980s.

3.6 Conclusion

In the absence of fire and grazing since the early 20th century, tree invasion has proceeded rapidly in the Bunchgrass montane meadow complex as revealed by detailed establishment locations and dates for >900 individual trees. The invasion process initially produced sparse nuclei patches of pioneer trees, mostly initiated by Lodgepole pine, followed by establishment of increasingly dominant shade-tolerant Grand fir near pioneer Lodgepole pine trees. Biotic interactions between Grand fir and Lodgepole pine – facilitation of establishment, and ultimately competition for space -- governed the spatial arrangement of invasion, but rates of tree invasion over time were regulated by seed source availability as well as Grand fir and Lodgepole pine's contrasting environmental tolerances to air temperature, precipitation, and snowpack. Without grazing, fire, or harvest, tree invasion in this meadow complex appears irreversible.

4 MODELING THE SENSITIVITY OF OREGON CASCADE FOREST AND NONFOREST VEGETATION TO CHANGES IN CLIMATE, DISTURBANCE AND ATMOSPHERIC CO_2 CONCENTRATIONS

Janine Rice, Sarah Shafer, Julia Jones

In preparation for journal submission

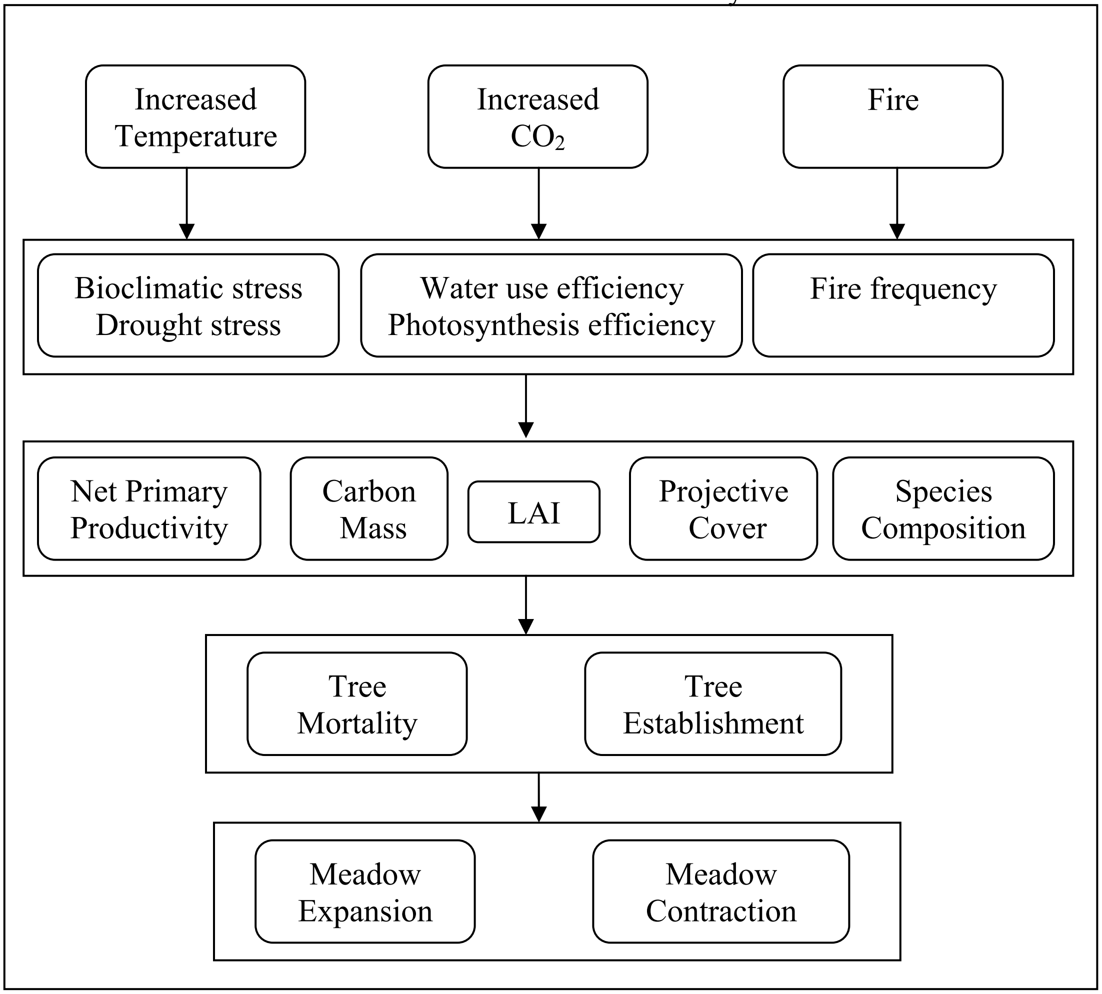
4.1 Introduction

Montane meadows in the western Cascade Range of Oregon are isolated treeless patches dominated by grass and forbs (Hickman 1976; Franklin & Halpern 1999) or mosaics of grass and forb vegetation interspersed with trees (Rice, Chapter 2; Takaoka & Swanson 2008). Montane meadows vary from hundreds of square meters to several hectares, and may persist for at least 50 years (Rice, Chapter 1) to thousands of years (Vale 1981; Highland, dissertation in prep). These small, dynamic features host a rich variety of plant (Hickman, 1976) and animal species that are sometimes rare (Franklin & Halpern 1999; Miller et al. 2003; Debinski et al. 2000; Mintie et al. 2003). Meadows occupy less than 5 percent of the Willamette National Forest and are preferentially located on steep south, east, and west facing slopes (Dailey 2007).

Montane meadows are attributed to many factors, including burning (Vale 1981; Hadley, 1999), grazing (Miller & Halpern 1998; Takaoka & Swanson 2008), climate (Franklin et al. 1971; Rochefort & Peterson 1996; Miller & Halpern 1998), topography and soil conditions (Rochefort & Peterson 1996; Takaoka & Swanson 2008; Dailey 2007), and vegetation competition (Franklin et al. 1971; Magee & Antos 1992; Haugo & Halpern 2007). Widespread loss of meadow habitat by coniferous forest encroachment has occurred in the mid and late 20th century, associated with grazing cessation and fire suppression, and a shift to a cooler, wetter climate (Franklin et al. 1971; Vale 1981; Rochefort & Peterson 1996; Haugo & Halpern 2007; Dailey 2007; Takaoka & Swanson 2008).

Changes in fire, climate, and atmospheric CO_2 concentration may affect meadow expansion and contraction in the Oregon Cascades (Figure 4.1). A shift from the warmer, drier climate of 1920 to 1945, to a cooler, wetter climate after 1945 may have promoted tree encroachment into meadows (Taylor 2000; Rochefort 1996; Miller & Halpern 1998). A cooler climate can reduce drought stress resulting in more tree establishment and meadow contraction. Rising atmospheric CO_2 concentrations may increase plant water use and photosynthetic efficiency (Hickler 2008), as well as establishment and growth of tree and herbaceous vegetation (Bazzaz 1990). Trees have been able to outcompete herbs in the Oregon Cascades; however, the effect of increased water use efficiency from higher CO_2 concentrations may be offset by climate warming and increased summer drought stress (Daly et al. 2000; Neilson & Drapek 1998). Uncertainty still remains about the magnitude of increased plant water use efficiency due to increases in atmospheric CO_2 concentrations (Norby et al. 2007; Bachelet et al. 2001). Natural and anthropogenic fire disturbance before and after Euro-American settlement may have maintained meadow areas by reducing forest cover (Vale 1981; Halpern 1999). Fire suppression began in the early 1900s, but was most effective at limiting the amount of area burned after the mid 1900s (Weisburg & Swanson 2001), approximately when records indicate that trees began to encroach into many meadow areas (Vale 1981; Magee & Antos 1992; Hadley 1999; Halpern 1999).

Figure 4.1. Environmental drivers and associated impacts to forest composition and structure and forest-meadow dynamics.



Several factors specific to the Oregon Cascades may contribute to the decline of montane meadows: (1) a marine west coast climate with a pronounced summer drought, leading to conifer dominance and a paucity of deciduous trees; (2) long-lived conifers with life spans up to 500 or 800 years that can persist for many years once established; (3) elevations spanning near sea level to 3000 m, with a gradient in forest types. Western Hemlock-Douglas-fir forests (*Tsuga heterophylla, Pseudotsuga menziesii*) occur below

1000 m, Pacific Silver Fir (*Abies amabilis*) occurs from 1000 to 1600 m, and Mountain Hemlock (*Tsuga mertensiana*) occurs at 1600 m (Zobel 1976); and (4) a natural disturbance regime dominated by variable-severity fire, with relatively high conifer post-fire survival rates except in rare instances of high-severity fires (Weisberg & Swanson 2003; Weisberg 2004; Hood et al. 2007).

The near-simultaneous timing of fire suppression, climate warming, and increased atmospheric CO_2 concentrations in the 20th century has confounded observational studies aimed at disentangling the environmental factors responsible for forest encroachment into meadows in the Oregon Cascade Range (Franklin et al. 1971; Vale 1981; Rochefort & Peterson 1996; Miller & Halpern 1998; Haugo 2006; Dailey 2007; Takaoka & Swanson 2008). Public land managers are currently investigating the use of fire for restoring and maintaining meadow areas in the Oregon Cascades (Wilson 1999); however, the outcome of ongoing controlled burning experiments (Halpern 1999) will not be evident for many years. The impact and interactions of single or multiple environmental drivers is unclear, making it difficult to assess the effects of potential future changes in these drivers on meadow ecosystems. Therefore, an ecosystem model, LPJ-GUESS, was chosen to test hypotheses about the relative importance of these environmental drivers on forest and meadow expansion or contraction.

LPJ-GUESS (Smith et al. 2001) is a process-based model that simulates vegetation dynamics. It has been applied in Europe (Smith et al. 2001; Badeck et al. 2001; Morales et al. 2005; Koca et al. 2006), the Mediterranean (Gritti et al. 2006), the Great Lakes and eastern United States (Hickler et al. 2004, 2008), Africa (Hely et al. 2006), and Russia

(Wolf et al. 2008). LPJ-GUESS was used for this modeling experiment to assess the relative importance of climate, atmospheric CO_2 concentrations, and fire occurrence on forest-meadow vegetation for a western Oregon Cascades forest-meadow site. This study applied LPJ-GUESS to address the question, "How would the individual and combined historic and projected future climate warming, increased atmospheric CO_2 concentrations, and fire frequency affect the composition and structure of forest vegetation and meadow extent in the Oregon Cascades?"

LPJ-GUESS does not directly simulate montane meadows. Instead, we assess the effects of changes in temperature, atmospheric CO_2 concentrations, and fire frequency on tree productivity, carbon biomass, and foliar projective cover, and on the percent of simulated patches with <=10% tree cover, which we refer to as "open patches." Changes to these variables are used to identify when the interactions of the three environmental drivers simulate conditions more conducive to forest expansion or more conducive to meadow creation and persistence.

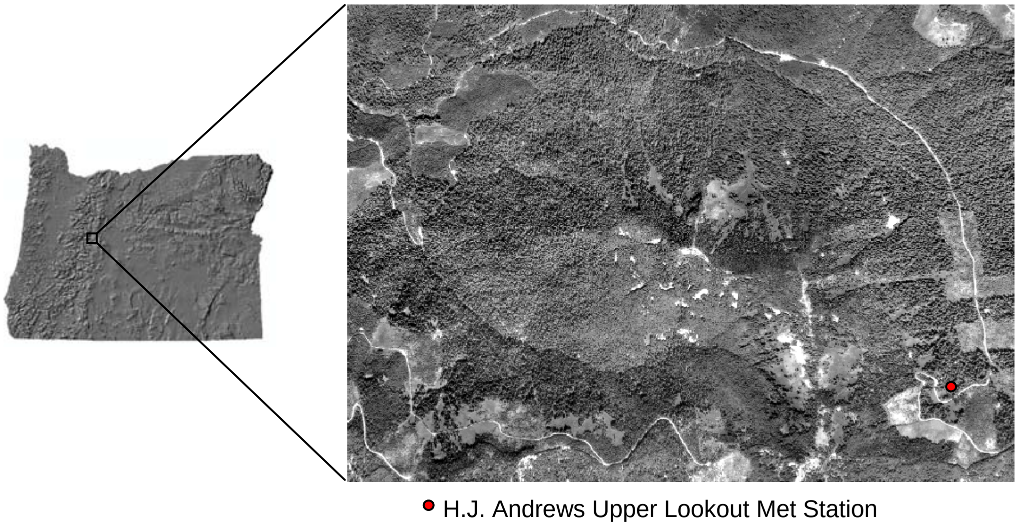
We hypothesize that: 1) The climate of the early 1900s was more conducive to forest than meadow, while recent and potential future climate warming will be less conducive to forests and more conducive to meadow, 2) Rising atmospheric CO_2 concentrations will increase tree photosynthesis rates and water use efficiency enabling forests to expand and reduce meadow extent, 3) Relatively high fire frequency in the 1800s, and potentially in the future, will have the largest impact on reducing forest and increasing meadow cover, and 4) fire suppression will allow other environmental drivers (temperature, CO_2) to dictate vegetation conditions. We explore several hypotheses about the individual and combined vegetation impacts from climate warming, increased atmospheric CO_2 concentrations, and variations in fire occurrence (detailed in Table 4.2 of Section 4.3.5.1).

4.2 Study Site and Associated Model Parameters

4.2.1 Location, Soils, Elevation, Topography, and Associated LPJ-GUESS Parameters

Lookout Mountain of the central west Cascade Range of Oregon is in the Willamette National Forest at 44°22’N, 122°13’W (Figure 4.2), and hosts both forested and meadow sites. Forest and meadow soils are well drained gravelly loams derived from andesitic basalt. Meadow soils are of the Lucky Boy soil series in the Cryandepts taxonomic class and shallow rock outcrops may occur (Dyrness et al. 1962; H. J. Andrews Soil Profile data). Meadow areas at this site range in elevation from 1000 – 1630 m (3300 – 5350 feet), and occur on north, south, east, and west aspects of both gentle (1-10°) and steep slopes (10 - 40°). The LPJ-GUESS soil properties were set to a pre-defined soil type that most closely matched the well drained gravely loam soil properties at the study site, and elevation was set at 1294 m (4245 ft) above sea level.

Figure 4.2 Lookout Mountain Study Area



Source: US Geological Survey 2000

4.2.2 Climate and Associated LPJ-GUESS Input Data

The maritime climate (sampled at the H.J. Andrews Upper Lookout meteorological station on Lookout Mountain ([UPLMET]) is typically characterized by mild temperatures, wet winters, and dry summers (Daly & McKee 2009). Climate records for 1995 to 2007 show the annual average temperature is 7 °C (44° F). The average June – August temperature is 14 °C (63° F), and average December – February temperature is 1 °C (34 °F). Annual precipitation is around 2500 mm (98 inches). The average June – August precipitation is 55 mm (2 inches), and the average December – February precipitation is 360 mm (14 inches). Precipitation occurs mainly as snow from late October to May, and an occasional summer thunderstorm can occur. Spring snow packs may be over 1.5 m (5 feet) deep, and usually persist through June.

The historic climate data used as input for LPJ-GUESS are similar to measured temperature and precipitation. In order to temporally extend climate data beyond short observational records, the model input data were derived from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) data set (Daly et al. 1994) for the years 1900 – 2000, and represented a 2.5 arc minute (~16 km^2) grid cell centered near the peak of Lookout Mountain. PRISM monthly average temperatures compared to UPLMET from 1995 – 2002 had an r^2 of 0.97, but PRISM tended to overestimate temperatures as compared to observed data on average by 1.3° C (Appendix E, Figures E1, E4). PRISM monthly total precipitation compared to UPLMET from 1995 – 2002 had an r^2 of 0.95, but PRISM tended to underestimate precipitation as compared to observed data on average by 20 mm (Appendix E, Figures E2, E3). Modeled snow depths were similar to measured monthly values, and occurred at over 1.5 m depths (Appendix E, Figure E5).

4.2.3 Vegetation and Associated LPJ-GUESS Parameters

Lookout Mountain hosts meadow species at higher elevations and several tree species at all elevations. The lower and mid elevations below 1000 m (3280 feet) are dominated by *Pseudotsuga menziesii* (Douglas-fir) and *Tsuga heterophylla* (Western hemlock) with fewer occurrences of *Taxus brevifolia* (Pacific yew) and *Thuja plicata* (Western red cedar). Elevations above 1000 m (3280 feet) are dominated by *Abies amabilis* (Pacific silver fir), with common *Abies procera* (Noble fir), *Abies grandis*

(Grand fir), *Pinus contorta* (Lodgepole pine), and *Tsuga mertensiana* (Mountain hemlock), uncommon *Chamaecyparis nootkatensis* (Alaska cedar), and *Abies lasiocarpa* (Subalpine fir) may occur. Occasional individuals of *Tsuga heterophylla* (Western hemlock) and *Pseudotsuga menziesii* (Douglas-fir) also occur above 1000 m elevation, although these species are usually restricted to lower elevations (Zobel 1976). On very steep or disturbed slopes, *Acer circinatum* (Vine maple) and *Alnus viridus sinuata* (Sitka alder) occur in dense thickets. Meadow areas from 1000 – 1630 m (3300 – 5350 feet) elevation are dominated by grass species (*Festuca* spp.), and meadow species *Xerophyllum tenax* (Bear grass) and *Pteridium aquilinum* (Bracken fern) (Table 4.1).

Table 4.1 Plant Functional Type code and associated species

Plant Functional Type Code	Plant Functional Type	Species Associated with Plant Functional Type
TBNE	Shade Tolerant Boreal Needleleaved Evergreen	*Abies grandis* (Grand fir), *Abies amabilis* (Pacific silver fir), *Pinus monticola* (Western white pine)
IBNE	Shade Intolerant Boreal Needleleaved Evergreen	*Pinus contorta* (Lodgepole pine), *Abies procera* (Noble fir)
TTNE	Shade Tolerant Temperate Needleleaved Evergreen	*Tsuga heterophylla* (Western hemlock), *Taxus brevifolia* (Pacific Yew)
ITNE	Shade Intolerant Temperate Needleleaved Evergreen	*Pseudotsuga menziesii* (Douglas-Fir)
TBS	Shade Tolerant Broadleaved Summergreen	*Acer circinatum* (Vine maple)
IBS	Shade Intolerant Broadleaved Summergreen	*Alnus viridus sinuata* (Sitka alder)
BE	Shade Tolerant Broadleaved Evergreen	*Quercus chrysolepis* (Canyon live oak), *Arbutus menziesii* (Pacific madrone), *Castanopsis chrysophilia* (Giant chinkpin)
Grass	Grass	C3 grasses, *Carex* spp, Shade intolerant herbaceous meadow species

LPJ-GUESS simulates vegetation dynamics using plant functional types, which represent groups of species with similar characteristics. The plant functional types were parameterized to represent tree and meadow species occurring at Lookout Mountain. Temperate needle leaved evergreen plant functional types were defined to represent lower elevation and shade intolerant *Pseudotsuga menziesii* (Douglas-fir) and shade tolerant *Tsuga heterophylla* (Western hemlock), *Taxus brevifolia* (Pacific yew), and *Thuja plicata* (Western red cedar). Boreal needle leaved evergreen plant functional types were defined to represent upper elevation and shade tolerant *Abies amabilis* (Pacific silver fir), *Abies grandis* (Grand fir), *Chamaecyparis nootkatensis* (Alaska cedar), *Abies lasiocarpa* (Subalpine fir), and *Tsuga mertensiana* (Mountain hemlock); and shade intolerant species *Pinus contorta* (Lodgepole pine) and *Abies procera* (Noble fir). Broad leaved deciduous tree species were represented by a shade tolerant and a shade intolerant plant functional type. Meadow species were represented by a grass plant functional type (Table 4.1).

4.2.4 Disturbance and Land Use History and Associated LPJ-GUESS Parameters

Sheep grazing and fire disturbance have occurred at Lookout Mountain. Grazing records indicate 1,500 sheep per year were permitted from 1912 to 1922 (Burke 1979). Burning of meadow areas may have been associated with grazing (Miller & Halpern 1998). Fire records for upper elevation areas near Lookout Mountain show a fire return interval of 100-200 years prior to the early 1900s (Cissel et al. 1999). During the latter half of the 20th century fire has been largely suppressed. There is also evidence of a small amount of conifer mortality due to insect outbreak in the upper elevations of Lookout Mountain (Takaoka & Swanson 2008).

LPJ-GUESS implemented fire disturbance randomly to mimic historic and potential future fire frequencies. A generic disturbance was randomly implemented every 200 years to represent historic disturbance conditions from other non-fire disturbances, such as insect outbreaks and wind throw (C. Halpern, unpublished data). Figure 4.4 of Section 4.3.4.1 provides more details on the fire frequency values used for model scenarios.

4.3 Methods

4.3.1 Overview of Methodology

A model experiment was designed to test hypotheses about forest vegetation and open patch cover responses to individual and combined changes in climate, atmospheric CO_2 concentrations, and fire regimes that mimic historical and potential future conditions. LPJ-GUESS (version 030124; Smith et al. 2001) was selected for this experiment because it is a process-based model that simulates vegetation dynamics of forest vegetation and open patch cover. The model calculates a variety of variables for each plant functional type, including annual net primary productivity, carbon biomass, and foliar projective cover. LPJ-GUESS provides a flexible framework for simulating vegetation responses to changes in climate, atmospheric CO_2 concentrations, and fire regimes, while representing the effects of these changes on photosynthesis, respiration, and decomposition processes.

Model parameterization, validation, and a sensitivity analysis were conducted before the model experiment was run. Model parameterizations with appropriate values to represent climate, soil, and vegetation conditions at the study site were evaluated by comparing model outputs with empirical measurements (Appendix E). A sensitivity analysis (Appendix F) of the model response to variations in temperature, precipitation, fire return interval, and atmospheric CO_2 concentrations was conducted to test model behavior within and beyond the limits of historic and potential future conditions. This analysis was also used to define the point where environmental driver values produced simulations of increased open patch cover as opposed to forest cover. A detailed description of the sensitivity analysis methods and results are given in Appendix F. Lastly, the model experiment with 11 combinations of single, double, and triple environmental driver impacts from changes in climate, atmospheric CO_2 concentrations, and fire return interval, plus a baseline scenario, was run to test the hypotheses outlined in Table 4.2 (Section 4.3.5.2).

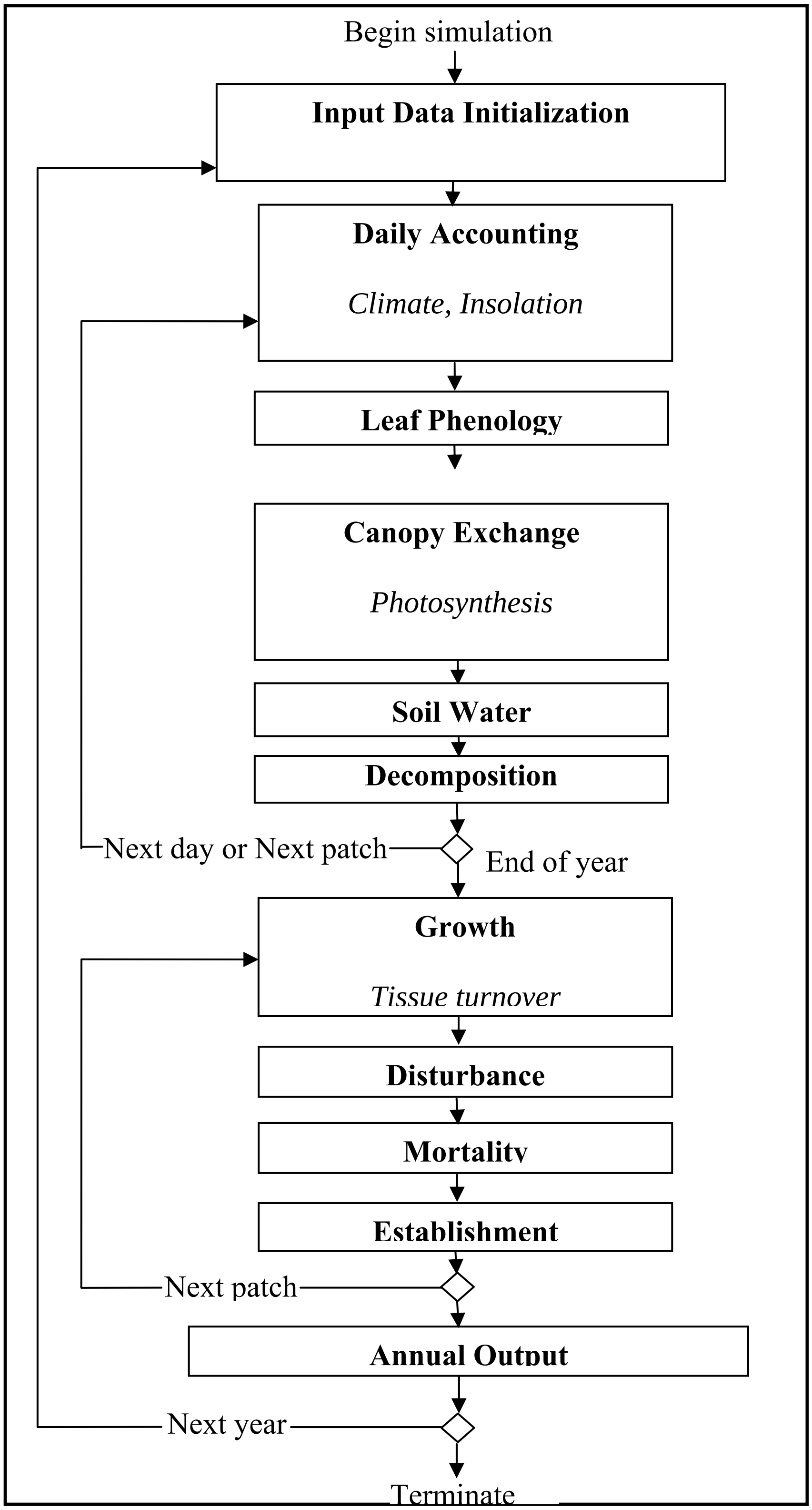
4.3.2 LPJ-GUESS Model Description

The LPJ-GUESS ecosystem model (Smith et al. 2001) is a hybrid model that combines individual-based representations of population dynamics (e.g., competition, establishment, and mortality) derived from FORSKA2 (Prentice et al. 1993) with more generalized representations of plant mechanistic processes (e.g., photosynthesis, respiration, and evapotranspiration) in the dynamic global vegetation model (DGVM) Lund-Potsdam-Jena (LPJ) (Sitch et al. 2003). We ran LPJ-GUESS in cohort mode (i.e., an average individual represents all individuals in a cohort) for 500 duplicate patches and averaged the results. A patch represents the area of influence for one large adult individual tree, defined as 1000 m^2 (~32 m x 32 m). Patches are assumed to be near one another in a landscape with a common propagule pool, but they do not compete for resources.

LPJ-GUESS simulates a variety of ecosystem and physiological processes that are important for simulating forest-meadow dynamics. Vegetation is represented by user-defined plant functional types. The plant functional types represent groups of species with similar characterizations of morphology, phenology, and bioclimatic and fire tolerances that determine light and water competition dynamics (Hickler 2008). The model is driven by input data consisting of mean annual atmospheric CO_2 concentrations, soil texture class, latitude, and monthly total precipitation, mean temperature, mean percent sunshine, and the number of rain days per month. Carbon and water fluxes between the atmosphere, vegetation, and soil layers are simulated with photosynthesis, respiration, decomposition, and hydrology subroutines. Growth increments of net primary productivity (NPP) to leaves, sapwood, and roots are updated annually. Vegetation dynamics of establishment, mortality, disturbance, root turnover, sapwood-to-heartwood conversion, and litter fall for the plant functional types also are updated annually.

The LPJ-GUESS structure (Figure 4.3) involves a set of linked subroutines (see detailed descriptions and equations in Appendix C). Simulations begin by initializing the input data of climate, atmospheric CO_2 concentration, plant functional type parameters, and soil texture class. Daily temperatures are calculated by linear interpolation between consecutive mid-month values. Daily precipitation is calculated by randomly distributing monthly precipitation over the number of days in months when measurable precipitation occurred. Plant functional types are parameterized with bioclimatic limits, root distribution in the soil, and plant physiological characteristics, such as establishment and reproductive potential, photosynthetic and respiration properties, and morphological and allometric characteristics.

Figure 4.3 Flowchart depicting the major subroutines of the LPJ-GUESS model and the order in which they are run.



Accounting updates occur on a daily time step in each patch before leaf phenology and canopy exchange are calculated (Figure 4.3). Temperature, precipitation, snow accumulation and loss, percent sunshine, and day length contribute to calculations of growing degree-days, potential evapotranspiration, and available photosynthetically active radiation (PAR), soil water content in two soil layers, and soil temperature (at 0.25 m) are calculated on a daily time step.

Leaf phenology, canopy exchange, soil water, and decomposition are calculated on a daily time step for each year of the simulations (Figure 4.3). The seasonal state of leaf condition for deciduous trees and grass is first updated to store the fraction of leaf out amount on a given day. The daily net primary productivity (NPP, kg C/m^2) calculation is based on photosynthesis, evapotranspiration, respiration, and a fixed reproduction allocation. Photosynthesis is based on a modified Farquhar system (Haxeltine & Prentice 1996), and is reduced when water stress conditions exist (Monteith 1995). The amount of carbon fixed through photosynthesis is influenced by temperature, atmospheric CO_2 concentrations, photosynthetically active radiation (PAR), and soil water availability. PAR is based on the Lambert-Beer law (Monsi & Saeki 1953), and is calculated at 2 m vertical increments through the canopy. Autotrophic respiration is tracked for sapwood, root, and growth respiration (Lloyd & Taylor 1994; Sprugel et al. 1996). Soil water is estimated using a hydrology routine (Gerten et al. 2004) in two soil layers (0 to 50 cm and 50 to 100 cm depth). Daily decomposition of litter inputs is distributed to the atmosphere and also to slow and fast soil organic matter pools with calculations constrained by soil temperature and soil moisture content (Foley 1995; Meentemeyer 1978).

Growth and population dynamics of trees in each patch are calculated annually based on disturbance, mortality, and establishment. Annual tissue turnover amounts (determined from a parameterized portion of existing carbon mass) are added to soil organic matter pools. New vegetation carbon allocation is distributed to leaves, sapwood, heartwood, roots, and reproduction (Shinozaki 1964; Waring 1982; Huang 1992).

Six sources of mortality occur in the model: 1) Background mortality associated with non-stressed longevity for each plant functional type is stochastically implemented by a random draw from a Normal distribution. 2) Stress mortality occurs when a tree plant functional type's growth efficiency falls below a parameterized value. 3) Stress mortality associated with high temperatures occurs when temperatures exceed a user-specified plant functional type upper temperature tolerance. 4) Mortality of trees and grass can result from fire. The fire subroutine (Thonicke et al. 2001) randomly implements fire on a patch at either a user specified or model specified frequency when fuels are present and flammable. Mortality resulting from fire is determined by a user-specified plant functional type fire resistance parameter that ranges from 0 (little resistance) to 1.0 (high resistance). 5) A generic background disturbance with 100 percent mortality is randomly implemented on a patch based on a user-specified disturbance return interval. The model experiment uses 1 disturbance per 200 years, based on dendrochronology records from Halpern (unpublished data). 6) Mortality occurs when bioclimatic limits, such as cold month temperature limits, are exceeded.

Tree establishment is implemented by a random draw from a Poisson distribution. We parameterized establishment to be possible every year based on information for deciduous and conifer tree species of the Pacific Northwest in Silvics of North America (1990). Establishment only occurs when light availability at the forest floor is higher than a plant functional type's minimum requirement of photosynthetically active radiation required for establishment. The expected frequency of establishment is calculated as the portion of a maximum establishment rate allowed given the amount of forest floor light availability and the amount of reproductive output of existing individuals. This expected frequency is used in the Poisson random draw.

Annual model output variables used were annual net primary productivity (ANPP), carbon biomass (CMass), and foliar projective cover (FPC) for each plant functional type. Annual net primary productivity, carbon biomass, foliar projective cover, and leaf area index calculations are given in Appendix C.

4.3.4 Sensitivity Analysis

A sensitivity analysis was used to evaluate the simulated responses of tree productivity, biomass, and cover, and open patch cover to changes in climate, atmospheric CO_2 concentrations, and fire occurrence beyond the historic and projected future variability of the model experiment scenarios (Appendix F). The analysis involved incrementally varying the input values for: temperature, atmospheric CO_2 concentrations, fire return intervals, precipitation, and temperature and precipitation, while holding other category values to the 1901–1930 average baseline.

4.3.5 Model Experiment

A model experiment was conducted using LPJ-GUESS to test the hypotheses outlined in Table 4.2 and Figure 4.4. Twelve modeling scenarios were used to disentangle the impacts of climate, atmospheric CO_2 concentrations and fire regime on forest vegetation and open patch cover. Combinations of four environmental drivers, climate, atmospheric CO_2 concentrations, future fire suppression, and future fire occurrence (as simulated by LPJ-GUESS) were tested with one baseline comparison scenario, and 4 single driver, 5 double driver, and 2 triple driver scenarios for a total of 12 scenarios.

4.3.5.1 Modeling Protocol

The model experiment setup for LPJ-GUESS included two consecutive phases for each scenario simulation: 1) A spin-up phase of 850 years that allowed the simulated vegetation to reach equilibrium conditions assumed to represent the pre-industrial era. The spin up consisted of repeating the first 30 years of climate data from 1901 – 1930 and holding atmospheric CO_2 concentrations constant at 280 ppm. Fire occurrence was allowed during the spin-up only for scenarios that tested fire effects (see Table 4.2). 2) Different combinations of historic and future data spanning the years 1700 to 2100

(Figure 4.4) were introduced after the spin-up as defined for each scenario. A representative grid cell located at 44.21° latitude, -122.12° longitude at 1,294 m elevation was used for all scenario simulations.

4.3.5.1.1 Climate Data

Monthly temperature and precipitation data for 1900-2000 were obtained from the PRISM data set (Daly et al. 1994). Monthly rain day values (used to represent the number of days with precipitation in a month), and monthly percent sunshine or cloudiness values (used to calculate the percent of mean monthly sunshine) for 1901-2002 were downscaled from the CRU TS 2.1 global gridded data set (Mitchell & Jones 2005; S. Shafer, unpublished data). Input climate data for the years 1700 – 1900 were represented by continuously repeating the years 1901-1930 of the PRISM climate data set (Figure 4.4e, f). For the years 1900 to 2000, gridded observed monthly precipitation and temperature data from the PRISM data set and gridded observed monthly rain day and percent sunshine from the CRU TS 2.1 data set were used (Figure 4.4g).

Future mean monthly temperature data for the years 2001-2100 were obtained from the ECHAM5 global coupled atmosphere-ocean general circulation model simulations produced using the SRES A2 greenhouse gases emissions scenario (IPCC 2007; SRES, Nakićenović et al. 2000). These data were downscaled to 1/8 of a degree by the Climate Impacts Group (2008). The ECHAM5 simulations projected a temperature increase of about 5 °C in 2100 from the historic 1901-1930 PRISM average. The A2 scenario represents a mid-high greenhouse gas emissions scenario that assumes high population growth and less concern for rapid economic development, and projects a 4-5 °C increase in global mean temperature by the year 2100 (IPCC 2007). Precipitation, cloudiness, and rain days for the years 2001-2100 were held at the 1971-2000 PRISM monthly values by continuously repeating these years. The 1971-2000 PRISM precipitation values were used since future precipitation changes are not expected to exceed 20% (Mote et al. 2005; IPCC 2007) and simulated responses to this amount of precipitation change were relatively small (Appendix F). Cloudiness and rain day values for the missing year of 1900 were estimated by linear regression of cloudiness vs. precipitation and rain day vs. precipitation data in the existing record.

4.3.5.1.2 Atmospheric CO_2 Concentrations

Pre-industrial mean annual atmospheric CO_2 concentrations were set at 280 ppm (Figure 4.4i) and increased from 280 ppm to 288 ppm for the period 1700-1960 according to annual CO_2 concentrations obtained from ice core data (Etheridge et al. 1998) (Figure 4.4j). From 1961 to 2000 (Figure 4.4k), annual CO_2 concentrations were obtained from Mauna Loa observatory measurements (Keeling et al. 2001). For 2001-2100 annual CO_2 concentrations (Figure 4.4l) were taken from the IPCC Fourth Assessment Report (2007) A2 scenario CO_2 projections.

4.3.5.1.3 Fire Occurrence

Prior to 1800, the fire return interval was set at 200 years for scenarios involving fire (Table 4.2 Scenarios 4, 5, 7-12). This return interval represents the fire frequency associated with the cooler climatic conditions from the mid 1600s - 1800 (Weisberg & Swanson 2003; Figure 4.4a). From 1801-1920, the fire return interval was set at 100 years for scenarios involving fire (Table 4.2, Scenarios 4, 5, 7-12). This value reflects increased fire frequencies associated with Euro-American settlement in the region (Weisberg & Swanson 2003; Figure 4.4b). From 1921-2000, the fire return interval was set at 1000 years to reflect fire suppression for scenarios involving fire (Table 4.2, Scenarios 4, 5, 7-12) (Figure 4.4c). From 2001-2100, two different fire regimes were simulated: (1) from 2001 – 2100, the fire interval was set at 1000 years for scenarios suppressing future fire (Table 4.2, Scenarios 4, 7, 9, and 11, Figure 4.4d), and (2) the fire interval was model determined in scenarios involving future fire (Table 4.2, Scenarios 5, 8, 10, and 12, Figure 4.4d). The fire return intervals specified for each scenario represent the upper limits for fire occurrence. Regardless of the fire return interval, no fires were simulated in the absence of flammable fuels.

4.3.5.1.4 Model Output

The model outputs for each scenario were analyzed to determine the impacts from changes in environmental drivers on tree net primary productivity, carbon biomass, foliar projective cover, and open patch cover. Each scenario used the average of 500 replicate patches for each plant functional type's annual net primary productivity (ANPP) in kg C/m^2, carbon mass (CMASS) defined as total above and below ground biomass (kg C/m^2), and percent foliar projective cover (FPC) defined as the spatial fraction of the modeled grid cell occupied by a particular plant functional type. Percent of open patches was defined as the percentage of the 500 replicate patches with <= 10% tree cover. To distinguish between "background" variation caused by model processes with random components (i.e. establishment, mortality, and generic disturbance) from actual changes in output introduced by the different scenarios, a confidence interval was used. The 30 year mean of the model years 1771-1800, 1871-1900, 1971-2000 and 2071-2100 and two standard deviations for a 95% confidence interval were calculated. Significant differences between scenario outputs were defined as only the scenarios with differences outside the confidence interval.

4.3.5.2 Model Experiment Scenarios and Hypotheses

We used twelve modeling scenarios to disentangle the effects of climate, atmospheric CO_2 concentrations, and fire regimes on forest-meadow vegetation dynamics and to test the hypotheses outlined in Table 4.2 and Figure 4.4.

Scenario 1 (Table 4.2) established a baseline of tree net primary productivity, carbon biomass, foliar projective cover, and of open patch cover. For this scenario, fire did not occur, climate was represented by continuously repeating 1901 to 1930 climate values, and atmospheric CO_2 concentrations were held at 280 ppm. This scenario is compared with the other 11 scenarios (Table 4.2).

The single environmental driver scenarios (Table 4.2 Scenarios 2, 3, 4, and 5) test the influence of individual drivers on tree net primary productivity, carbon biomass, foliar projective cover, and on open patch cover over the period 1700 to 2100. The climate scenario (Table 4.2 Scenario 2) tests if tree productivity and cover decrease, open patch cover increases, and vegetation composition shifts to species more tolerant of increased temperature and drought stress caused by temperature increases of 5°C from 1900-2100, while atmospheric CO_2 is maintained at pre-Industrial levels (280 ppm) and fire is completely suppressed. The CO_2 scenario (Table 4.2 Scenario 3) tests if tree productivity and cover increase and open patch cover decreases as a result of atmospheric CO_2 rising from 280 to 856 ppm over the period 1700-2100, while air temperatures are held at 1901-1930 levels and fire is completely suppressed. The future fire suppression scenario (Table 4.2 Scenario 4) tests if tree productivity and cover increase and open patch cover decreases in response to fire suppression from 1920 through 2100 (~1000 year fire return interval), while holding air temperatures at 1901-1930 levels and atmospheric CO_2 at pre-Industrial levels (280 ppm). The future fire scenario (Table 4.2 Scenario 5) tests if tree productivity and cover decrease and open patch cover increases when a historic fire regime is followed until 2000, and model-simulated fire occurrence is allowed from 2000-2100, while holding air temperatures at 1901-1930 levels and atmospheric CO_2 at pre-Industrial levels (280 ppm).

The double environmental driver scenarios (Table 4.2 Scenarios 6, 7, 8, 9, and 10) test the influence of combining two environmental drivers on tree net primary productivity, carbon biomass, fractional projective cover, and on open patch cover over the period 1700 to 2100. The climate-CO_2 scenario (Table 4.2 Scenario 6) tests if tree productivity and cover increase and open patch cover decreases due to the effect of increased productivity and water use efficiency associated with increasing atmospheric CO_2 concentrations from 280 to 856 ppm offsetting increased temperature and drought stress associated with a temperature increase of 5°C, while fire is suppressed. The climate-future fire suppression scenario (Table 4.2 Scenario 7) tests whether tree productivity and cover decrease and open patch cover increases as a result of increased temperature and drought stress associated with a temperature increase of 5°C and fire suppression from 1920-2100, while holding atmospheric CO_2 to 280 ppm. The climate-future fire scenario (Table 4.2 Scenario 8) tests whether tree productivity and cover decrease and open patch cover increases due to the effect of increased temperature and drought stress caused by a temperature increase of 5°C that is further enhanced by an increase of fire frequency after following a historic fire regime prior to 2000, while holding atmospheric CO_2 to 280 ppm. The CO_2-future fire suppression scenario (Table 4.2 Scenario 9) tests whether tree productivity and cover increase and open patch cover decreases due to the effects of increased productivity and water use efficiency associated with increasing atmospheric CO_2 concentrations from 280 to 856 ppm that is further enhanced by future fire suppression after following a historic fire regime until 2000, while holding air temperatures at 1901-1930 levels. The CO_2-future fire scenario (Table

4.2 Scenario 10) tests whether an increase in tree productivity and cover and a decrease in open patch cover occurs due to the effects of an increased fire return interval following a historic fire regime prior to 2000, which offsets the increased productivity and water use efficiency associated with increasing atmospheric CO_2 concentrations from 280 to 856 ppm, while holding air temperatures at 1901-1930 levels.

The triple environmental driver scenarios (Table 4.2 Scenarios 11 and 12) test the influence of combining three environmental drivers on tree net primary productivity, carbon biomass, foliar projective cover, and open patch cover over the period 1700 to 2100. The climate-CO_2-future fire suppression scenario (Table 4.2 Scenario 11) tests whether tree productivity and cover increase and open patch cover decreases with increased temperature and drought stress associated with a temperature increase of 5°C, increasing atmospheric CO_2 concentrations from 280 to 856 ppm, and fire suppression after following a historic fire regime prior to 2000. The climate-CO_2-future fire scenario (Table 4.2 Scenario 12) tests whether tree productivity and cover decrease and open patch cover increases due to the effects of increased temperature and drought stress associated with a temperature increase of 5 °C and future fire occurrence after following a historic fire regime before 2000, which offsets the effects of increased productivity and water use efficiency associated with increasing atmospheric CO_2 concentrations from 280 to 856 ppm.

Table 4.2. Model scenarios testing hypotheses for combinations of historic and future climate, CO_2 and fire regime (letters in parentheses refer to Figure 4.4 scenarios a – l)

#	Scenario Name	Fire	Climate	CO_2	Hypothesis
1	Baseline	Turned off	Pre 1800 (e)	280 ppm (i)	
2	Climate	Turned off	Variable (e-h)	280 ppm (i)	Historic climate was conducive to tree plant functional types, and future climate warming will be less conducive to existing tree plant functional types reducing tree productivity, biomass, and cover, and increasing open patch cover. Future climate warming will foster the establishment and growth of plant functional types with higher temperature tolerances resulting in the replacement of high elevation (boreal) tree by low-elevation (temperate) tree plant functional types.
3	CO_2	Turned off	Pre 1800 (e)	Variable (i-l)	Increased atmospheric CO_2 concentrations will positively impact tree plant functional types by increasing productivity, resulting in increased tree growth, biomass, and cover that outcompetes and reduces open patch cover.
4	Fire with Future Fire Suppression	Variable (a-d)	Pre 1800 (e)	280 ppm (i)	Increased fire frequency occurring prior to the early 1900s, and potentially in the future will contribute to a reduction of tree plant functional type's productivity, biomass, and cover, and increased open patch cover, while fire suppression will allow a transition to higher tree productivity, biomass and cover that eventually reduces open patch cover.

Table 4.2 Model scenarios testing hypotheses for combinations of historic and future climate, CO_2 and fire regime (letters in parentheses refer to Figure 4.4 scenarios a – l) (Continued)

#	Scenario Name	Fire	Climate	CO_2	Hypothesis
5	Fire with Future Fire	Variable (a-d)	Pre 1800 (e)	280 ppm (i)	Increased fire frequency occurring prior to the early 1900s, and potentially in the future will contribute to a reduction of tree plant functional type’s productivity, biomass, and cover, and increased open patch cover.
6	Climate and CO_2	Turned off	Variable (e-h)	Variable (i-l)	Increased atmospheric CO_2 and consequent increased water use efficiency will offset the impact of future climate warming and drought stress on existing tree plant functional types, resulting in an increase of tree productivity, biomass and cover, and reduction of open patch cover.
7	Climate and Fire with Future Fire Suppression	Pre-1800 (a)	Variable (e-h)	280 ppm (i)	Historic climate was conducive to existing tree plant functional types, and the historic higher fire occurrence offsets the climate effects, expanding open patch cover. Future climate will be less conducive to existing tree plant functional types, and fire suppression will not impact the effects of a warming climate resulting in a reduction of tree productivity, biomass and cover, and increase open patch cover.
8	Climate and Fire with Future Fire	Pre-1800 (a)	Variable (e-h)	280 ppm (i)	Historic climate was conducive to existing tree plant functional types, and the higher fire occurrence of this period offset climate effects expanding open patch cover. Future climate will be less conducive to existing tree plant functional types, and future fire will exasperate the negative effects of future climate warming reducing tree productivity, biomass, and cover, and further expanding open

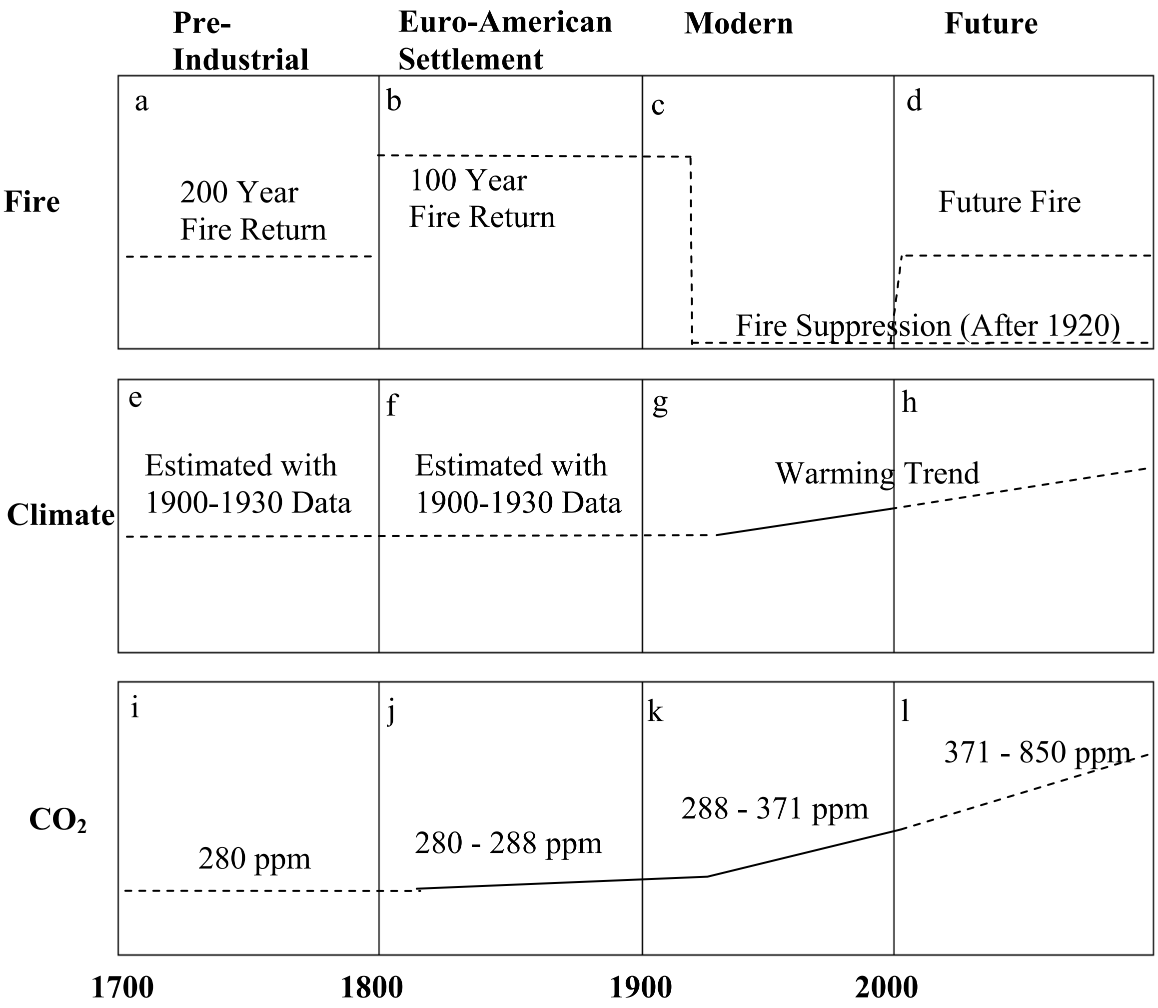
Table 4.2 Model scenarios testing hypotheses for combinations of historic and future climate, CO_2 and fire regime (letters in parentheses refer to Figure 4.4 scenarios a – l) (Continued)

#	Scenario Name	Fire	Climate	CO_2	Hypothesis
					patch cover.
9	CO_2 and Fire with Future Fire Suppression	Pre-1800 (a)	Pre 1800 (e)	Variable (i-l)	Increased atmospheric CO_2 concentrations increase tree plant functional type's productivity but historic fire will negate this positive effect. Recent and future fire suppression will not impact the positive effect of rising atmospheric CO_2 resulting in an overall increase in future tree productivity, biomass, and cover and decreased open patch cover.
10	CO_2 and Fire with Future Fire	Pre-1800 (a)	Pre 1800 (e)	Variable (i-l)	Higher atmospheric CO_2 concentrations increase tree plant functional type's productivity and the higher historic fire frequency will negate this effect. Increased future fire occurrence will negate the effect of even higher atmospheric CO_2 resulting in an overall reduction of tree productivity, biomass, and cover and increased open patch cover.
11	Climate, CO_2, and Fire with Future Fire Suppression	Variable (a-d)	Variable (e-h)	Variable (i-l)	Historic climate and atmospheric CO_2 concentrations were conducive to existing tree plant functional types, and the higher fire frequencies of the historic fire regime negated this effect reducing tree cover and expanding open patch cover. Future climate warming will not be conducive to existing tree plant functional types, but increased atmospheric CO_2 concentrations and fire suppression will be conducive to tree plant functional types, resulting in an overall increase of tree productivity, biomass, and cover, and reduction of open patch cover.

Table 4.2 Model scenarios testing hypotheses for combinations of historic and future climate, CO_2 and fire regime (letters in parentheses refer to Figure 4.4 scenarios a – l) (Continued)

#	Scenario Name	Fire	Climate	CO_2	Hypothesis
#	Scenario Name	Fire	Climate	CO_2	Hypothesis
12	Climate, CO_2, and Fire with Future Fire	Variable (a-d)	Variable (e-h)	Variable (i-l)	Historic climate and atmospheric CO_2 concentrations were conducive to existing tree plant functional types, and the historic fire regime negated this effect reducing tree cover and expanding open patch cover. Future climate warming and increased fire occurrence will not be conducive to existing tree plant functional types, and will offset the effects of increased atmospheric CO_2 concentrations, resulting in an overall decrease of tree productivity, biomass, and cover, and an increase of open patch cover.

Figure 4.4 Climate, atmospheric CO_2 concentration, and fire return interval used in historic and future scenarios (dashed line signifies estimates, solid line signifies observed data)



4.3.5.3 Extended Model Simulations

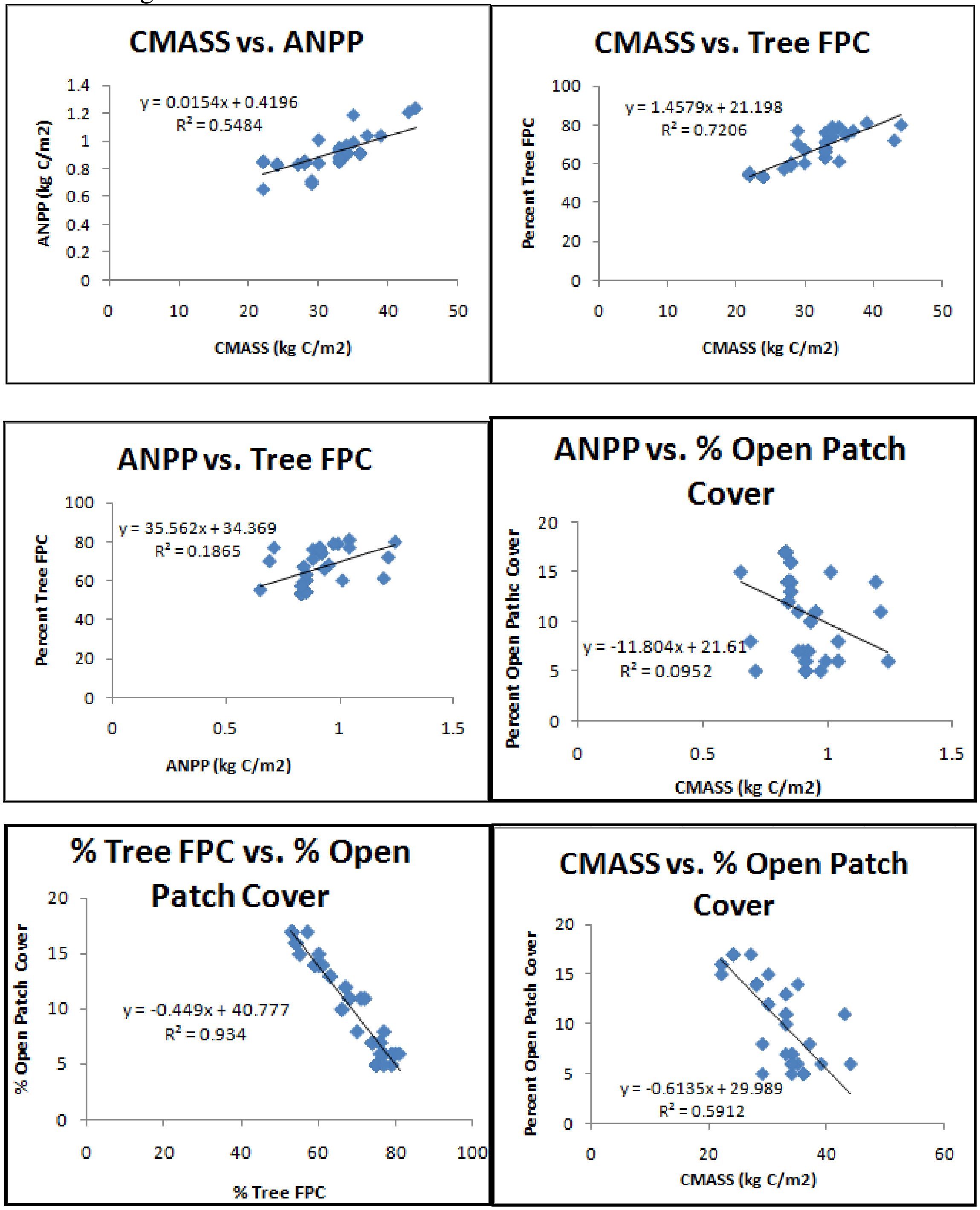
The simulated response for each scenario (Table 4.2) was compared with a simulation from extended model runs that repeated the 1971 – 2000 or 2071 – 2100 climate, CO_2, and fire regime values unique to each scenario for 2000 years. The outputs for the average of the last 1000 years with a 95% confidence interval of the extended model run were compared with the averages and 95% confidence intervals of the last 30 years of each century between 1700 – 2100 scenario simulations. This allowed an assessment of whether the simulated vegetation in the scenarios had a delay in response to changes of modern and future environmental inputs.

4.4 Results

4.4.1 Overview of results

All scenarios over the period 1700 – 2100 resulted in tree productivity ranging from 0.65 to 1.24 kg C/m^2, tree carbon biomass ranging from 22 to 44 kg C/m2, tree cover ranging from 53% to 81%, and open patch cover ranging from 5% to 17% (Figure 4.6, Table 4.3). Some, but not all, model outputs were correlated (Figure 4.5). Tree productivity, carbon biomass, and cover were positively correlated. Tree carbon biomass and tree cover ($r^2 = 0.72$) and tree carbon biomass and tree productivity ($r^2 = 0.55$) were strongly correlated. Tree productivity and tree cover were weakly related ($r^2 = 0.19$). Tree productivity, carbon biomass, and cover were all negatively related to open patch cover. Tree cover and open patch cover ($r^2 = 0.93$) and tree carbon biomass and open patch cover ($r^2 = 0.59$) were strongly negatively related, and tree productivity was not related to open patch cover ($r^2 = 0.09$).

Figure 4.5. Scatter plots showing the range of the 12 scenarios 30-year means for the years (1771-1871, 1871-1900, 1971-2000,and 2071-2100, and relationship between two model output variables: Tree Annual Net Primary Productivity (ANPP), Tree Carbon Biomass (CMASS), Tree Foliar Projective Cover (FPC), and Percent Open Patch Cover with fitted regression line and r^2 value.

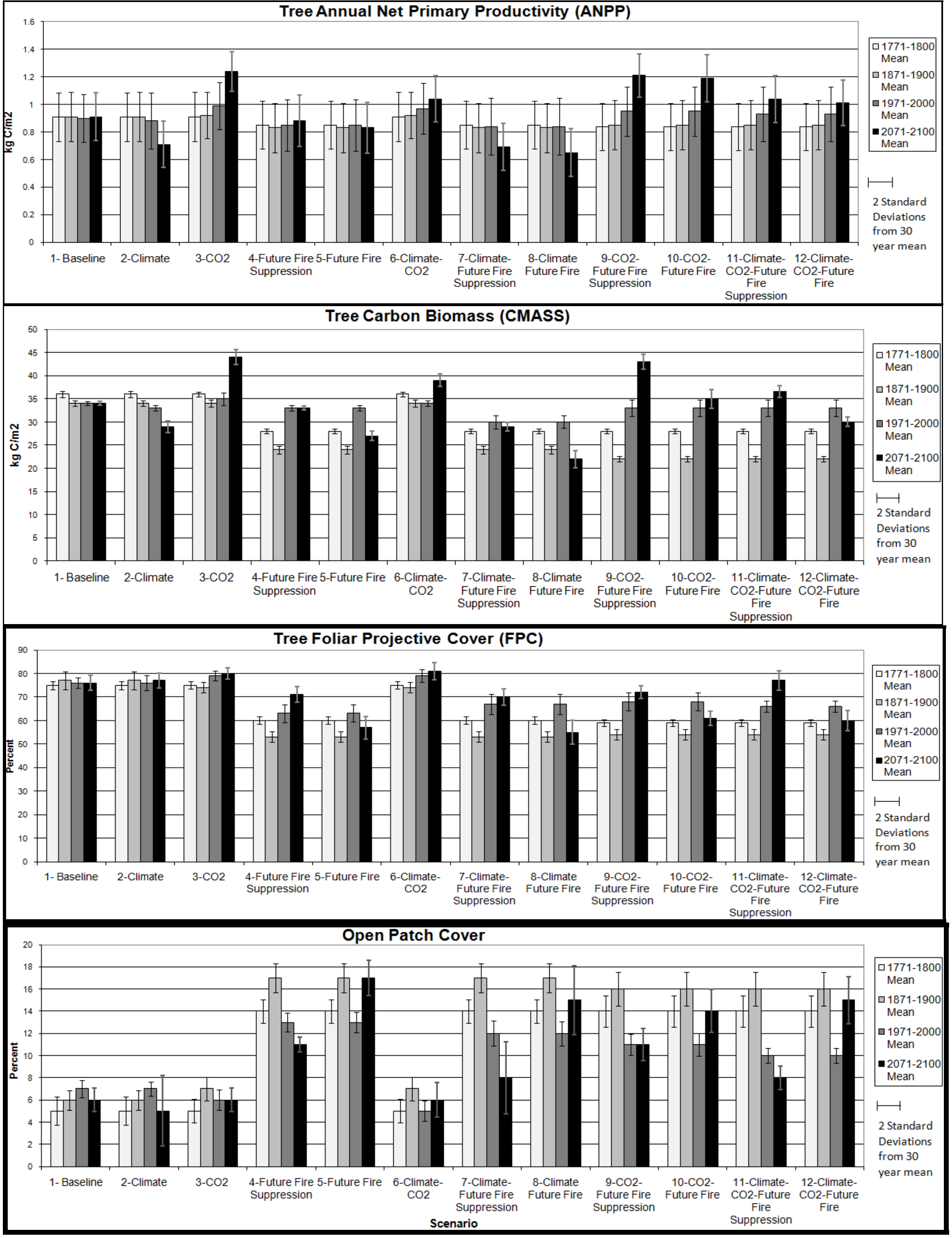


Scenario results with varying assumptions showed how meadow and tree productivity, carbon biomass, and cover may have varied over the time period 1700–2100 (Table 4.3, Figure 4.6). Prior to 2000, the highest values of open patch cover and lowest tree productivity, carbon biomass, and cover occurred during the late 1800s in scenarios with fire (Scenario 4, 5, 7, and 8). The highest values of tree productivity, carbon biomass, and cover and the lowest open patch cover occurred during the late 1900s in scenarios with no fire, increased atmospheric CO_2, and increased temperatures (Scenario 1, 2, 3, and 6). Model outputs differed much more among scenarios after 2000 than before (Table 4.3, Figure 4.6). After 2100, the highest values of open patch cover and lowest tree productivity, carbon biomass, and cover occurred in scenarios with fire (Scenarios 5 and 8), while the highest values of tree productivity, carbon biomass, and cover and lowest open patch cover occurred in scenarios with fire turned off (Scenarios 1, 2, 3, and 6) or with fire suppression (Scenarios 7 and 11). The potential future scenario for 2071-2100 (warming, increased fire, and increased CO_2, Scenario 12) led to almost as much open patch cover in the late 2000s as in the late 1800s, and higher open patch cover than in all other scenarios for the late 2000s, except for increased fire with no temperature or CO_2 changes (Scenario 5) (Table 4.3, Figure 4.6). (Details of model runs for selected individual years are in Appendix G).

Table 4.3. LPJ-GUESS scenario results for tree Annual Net Primary Productivity (ANPP), tree Carbon biomass (CMASS), tree Foliar Projective Cover (FPC), and Open Patch Cover averaging the output of the last 30 years for each century.

		Single Environmental Driver Scenarios				Double Environmental Driver Scenarios					Triple Driver Scenarios	
Average	1 Baseline	2 Climate	3 CO_2	4 Future Fire Suppression	5 Future Fire	6 Climate-CO_2	7 Climate-Future Fire Suppression	8 Climate Future Fire	9 CO_2-Future Fire Suppression	10 CO_2-Future Fire	11 Climate-CO_2-Future Fire Suppression	12 Climate-CO_2-Future Fire
Tree ANPP kg C/m^2												
1771-1800	0.91±0.18	0.91±0.18	0.91±0.18	0.85±0.17	0.85±0.17	0.91±0.18	0.85±0.17	0.85±0.17	0.85±0.17	0.85±0.17	0.85±0.17	0.85±0.17
1871-1900	0.91±0.18	0.91±0.18	0.92±0.17	0.83±0.18	0.83±0.18	0.92±0.17	0.83±0.18	0.83±0.18	0.85±0.18	0.85±0.18	0.85±0.18	0.85±0.18
1971-2000	0.90±0.17	0.88±0.20	0.99±0.17	0.85±0.19	0.85±0.19	0.97±0.19	0.84±0.21	0.84±0.21	0.95±0.18	0.95±0.18	0.93±0.20	0.93±0.20
2071-2100	0.91±0.17	0.71±0.17	1.24±0.14	0.88±0.19	0.83±0.19	1.04±0.17	0.69±0.17	0.65±0.18	1.21±0.16	1.19±0.17	1.04±0.17	1.01±0.17
Tree CMASS kg C/m^2												
1771-1800	36±0.7	36±0.7	36±0.5	28±0.6	28±0.6	36±0.6	28±0.5	28±0.6	28±0.6	28±0.6	28±0.6	28±0.6
1871-1900	34±0.6	34±0.6	34±0.7	24±0.8	24±0.8	34±0.7	24±0.8	24±0.8	22±0.6	22±0.6	22±0.6	22±0.6
1971-2000	34±0.5	33±0.6	35±1.3	33±0.6	33±0.6	34±0.6	30±1.4	30±1.4	33±1.8	33±1.8	33±1.8	33±1.8
2071-2100	34±0.5	29±1.3	44±1.6	33±0.4	27±1.0	39±1.3	29±1.0	22±1.8	43±1.6	35±2.0	37±1.3	30±1.0
Tree FPC (%)												
1771-1800	75±1.8	75±1.8	75±1.6	60±1.6	60±1.6	75±1.6	60±1.6	60±1.6	59±1.5	59±1.5	59±1.5	59±1.5
1871-1900	77±3.9	77±3.9	74±2.3	53±2.3	53±2.3	74±2.3	53±2.3	53±2.3	54±2.3	54±2.3	54±2.3	54±2.3
1971-2000	76±2.1	76±3.2	79±1.9	63±3.7	63±3.7	79±2.6	67±4.3	67±4.3	68±3.8	68±3.8	66±2.4	66±2.4
2071-2100	76±3.2	77±3.2	80±2.4	71±3.3	57±4.8	81±3.6	70±3.5	55±5.1	72±2.7	61±3.0	77±4.2	60±4.3
Open patch cover (%)												
1771-1800	5±1.3	5±1.3	5±1.1	14±1.0	14±1.0	5±1.1	14±1.0	14±1.0	14±1.4	14±1.4	14±1.4	14±1.4
1871-1900	6±0.9	6±0.9	7±1.0	17±1.3	17±1.3	7±1.0	17±1.3	17±1.3	16±1.5	16±1.5	16±1.5	16±1.5
1971-2000	7±0.7	7±0.7	6±0.9	13±0.9	13±0.9	5±0.9	12±1.1	12±1.1	11±1.0	11±1.0	10±0.7	10±0.7
2071-2100	6±1.1	5±3.2	6±1.1	11±0.7	17±1.6	6±1.5	8±3.3	15±3.1	11±1.5	14±1.9	8±1.1	15±2.1

Figure 4.6. LPJ-GUESS scenario results and standard deviation for tree Annual Net Primary Productivity, tree Carbon Biomass, tree % of Foliar Projective Cover, and % of Open Patch Cover averaging the output of the last 30 years for each century 1700-2100.



More than 200 years were required for simulated tree vegetation to achieve equilibrium with input environmental conditions; scenarios (30-year average) and extended scenario (1000-year) simulations produced different outputs during both modern and future time periods (Table 4.4, Figure 4.7 and 4.8). In almost all cases involving 1971-2000 simulations, the 1000-yr simulations led to significantly higher tree carbon biomass, and only scenarios involving fire suppression or future fire had significantly higher tree cover, and less open patch cover than the 30-year average scenario simulations (Figure 4.7). However, the 1000 year extended scenario simulations for 2071-2100 had varying effects compared to 30-year average scenario simulations: some combinations of factors led to significantly higher tree carbon biomass and cover, and less open patch cover, while others had the opposite effect (Figure 4.8). The 1000-yr extended simulation using 2071-2100 values for increased CO_2 and future fire produced the highest and only significant differences for open patch cover of any scenario in any century (27%), but not the lowest carbon biomass (Figure 4.8). The 1000-year extended simulation for 2071-2100 involving increased CO_2 and fire suppression produced the highest and largest significant difference for tree carbon biomass, while tree cover was most significantly increased in extended simulations involving temperature warming, CO_2 increase and fire suppression. Extended simulations involving future temperature warming produced a consistent significant decrease in tree carbon biomass as compared to the 30-year simulations. Tree productivity produced no significant differences between the 30-year and 1000-year extended simulations for either 1971-2000 or 2071-2100 (Figure 4.7 & 4.8).

Table 4.4. LPJ-GUESS Results of scenarios for tree Annual Net Primary Productivity (ANPP), tree Carbon biomass (CMASS), of tree Foliar Projective Cover (FPC), and Open Patch Cover comparing 1971-2000, 2071-2100 average scenario output with average extended scenario model output.

	1	2	3	4	5	6	7	8	9	10	11	12
Average	Baseline	Climate	CO$_2$	Future Fire Suppression	Future Fire	Climate-CO$_2$	Climate-Future Fire Suppression	Climate Future Fire	CO$_2$- Future Fire Suppression	CO$_2$- Future Fire	Climate-CO$_2$-Future Fire Suppression	Climate-CO$_2$-Future Fire
Tree ANPP kg C/m^2												
1971-2000 Scenario	0.90±0.17	0.88±0.20	0.99±0.17	0.85±0.19	0.85±0.19	0.97±0.19	0.84±0.21	0.84±0.21	0.95±0.18	0.95±0.18	0.93±0.20	0.93±0.20
1971-2000 Extended	0.91±0.1	0.87±0.1	1.05±0.04	0.91±0.1	0.91±0.1	0.96±0.09	0.87±0.1	0.87±0.1	1.05±0.04	1.05±0.04	0.96±0.09	0.96±0.09
2071-2100 Scenario	0.91±0.17	0.71±0.17	1.24±0.14	0.88±0.19	0.83±0.19	1.04±0.17	0.69±0.17	0.65±0.18	1.21±0.16	1.19±0.17	1.04±0.17	1.01±0.17
2071-2100 Extended	0.91±0.1	0.64±0.09	1.30±0.04	0.91±0.1	0.86±0.03	0.95±0.09	0.64±0.09	0.59±0.08	1.30±0.04	1.20±0.05	0.95±0.09	0.83±0.1
Tree CMASS kg C/m^2												
1971-2000 Scenario	34±0.5	33±0.6	35±1.3	33±0.6	33±0.6	34±0.6	30±1.4	30±1.4	33±1.8	33±1.8	33±1.8	33±1.8
1971-2000 Extended	34±1.0	33±0.7	42±0.7	34±1.0	34±1.0	37±1.4	33±0.7	33±0.7	42±0.7	42±0.7	37±1.4	37±1.4
2071-2100 Scenario	34±0.5	29±1.3	44±1.6	33±0.4	27±1.0	39±1.3	29±1.0	22±1.8	43±1.6	35±2.0	37±1.3	30±1.0
2071-2100 Extended	34±1.0	21±0.7	53±1.6	34±1.0	26±0.9	32±0.5	21±0.7	18±0.5	53±1.6	41±1.1	32±0.5	24±1.1
Tree FPC (%)												
1971-2000 Scenario	76±2.1	76±3.2	79±1.9	63±3.7	63±3.7	79±2.6	67±4.3	67±4.3	68±3.8	68±3.8	66±2.4	66±2.4
1971-2000 Extended	76±4.0	77±1.6	79±1.4	76±4.0	76±4.0	80±2.0	77±1.6	77±1.6	79±1.4	79±1.4	80±2.0	80±2.0
2071-2100 Scenario	76±3.2	77±3.2	80±2.4	71±3.3	57±4.8	81±3.6	70±3.5	55±5.1	72±2.7	61±3.0	77±4.2	60±4.3
2071-2100 Extended	76±4.0	76±2.5	82±2.4	76±4.0	53±2.2	89±2.7	76±2.5	60±2.1	82±2.4	52±2.3	89±2.7	59±3.0
Open Patch Cover (%)												
1971-2000 Scenario	7±0.7	7±0.7	6±0.9	13±0.9	13±0.9	5±0.9	12±1.1	12±1.1	11±1.0	11±1.0	10±0.7	10±0.7
1971-2000 Extended	7±3.0	6±1.0	7±1.0	7±3.0	7±3.0	6±1.3	6±1.0	6±1.0	7±1.0	7±1.0	6±1.3	6±1.3
2071-2100 Scenario	6±1.1	5±3.2	6±1.1	11±0.7	17±1.6	6±1.5	8±3.3	15±3.1	11±1.5	14±1.9	8±1.1	15±2.1
2071-2100 Extended	7±3.0	5±1.0	6±0.7	7±3.0	20±2.0	6±0.9	5±0.9	14±1.5	6±0.7	25±1.9	6±0.9	27±1.6

Figure 4.7. LPJ-GUESS results and standard deviation comparing 1971-2000 average scenario output with average extended model output.

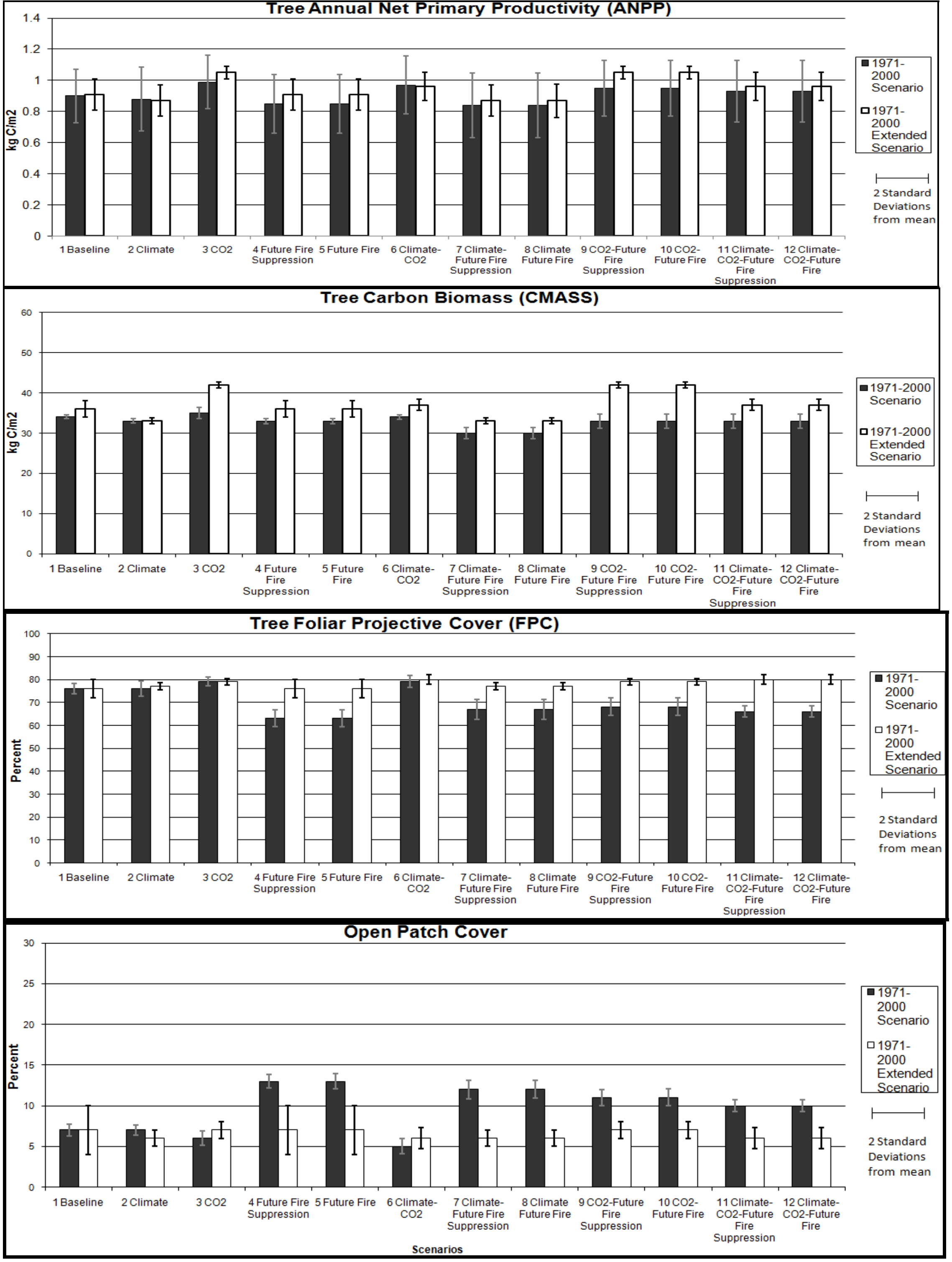
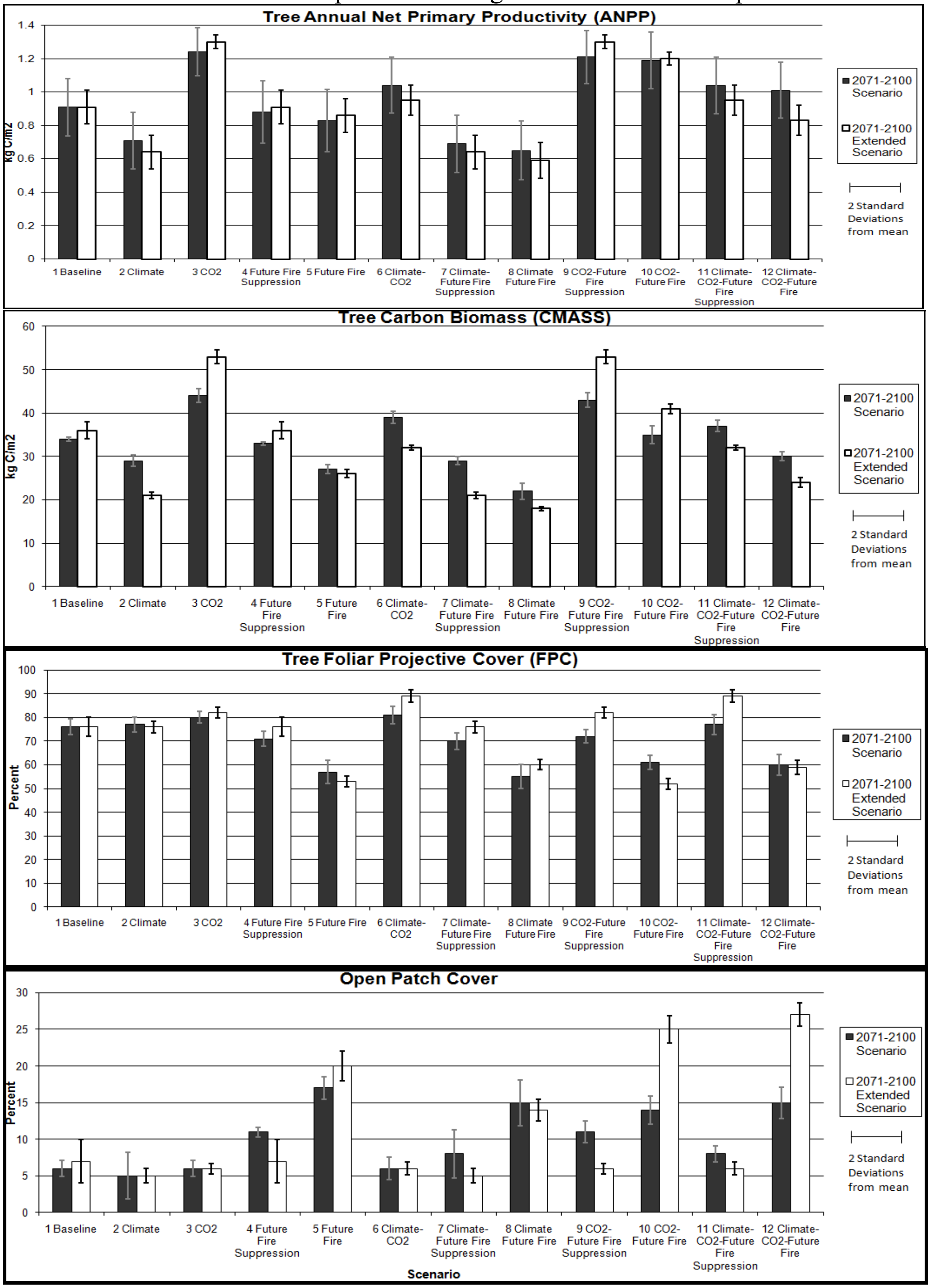


Figure 4.8. LPJ-GUESS results and standard deviation comparing 2071-2100 average scenario output with average extended model output.



The model sensitivity analysis (Appendix F) showed that historic and future changes in temperature, precipitation, atmospheric CO_2 concentrations, and fire had relatively little effect on the number of open patches. Very frequent fire (less than 100 year return) and large reductions in precipitation (>90%) were necessary to decrease tree cover. A tripling or more of average annual temperature and atmospheric CO_2 concentrations had relatively little impact on tree cover, but a 12 ºC temperature increase from pre-industrial levels shifted tree species composition from upper elevation (boreal) conifers to lower elevation (temperate) conifer species and then to deciduous species. The model simulations generally matched vegetation conditions in areas of similar temperature and precipitation amounts spanning from eastern to western Oregon.

4.4.2 Details of historic and future simulations

Open patch cover and tree productivity, carbon biomass, and cover varied little among centuries in the baseline (Scenario 1, Table 4.3 and Figure 4.6), but changes in single drivers (temperature, atmospheric CO_2, and fire) had a range of effects on open patch cover and tree productivity, carbon biomass, and cover. Temperature warming from the late 1800s to 2100 (Scenario 2) led to no significant decline in tree productivity (0.91 to 0.71 kg C/m^2), a significant decline in tree carbon biomass (36 to 29 kg C/m^2), and no significant change in tree cover or the number of open patches (Table 4.3, Figure 4.6). Increases in atmospheric CO_2 from the late 1800s to the late 2000s (Scenario 3) led to no significant increase in tree productivity (0.91 to 1.24 kg C/m^2), but a significant increase in tree carbon biomass (36 to 44 kg C/m^2), and no significant increase in tree cover (75% to 80%), or open patch cover. Fire suppression from the early 1900s to 2100 after fire occurrence during the 1800s (Scenario 4) led to no significant increase in tree productivity (0.85 to 0.88 kg C/m^2), but a significant increase of tree carbon biomass (24 to 33 kg C/m^2), tree cover (53% to 71%), and a significant reduction in open patch cover (from 17% to 11%). Future fire (Scenario 5) reversed these trends, producing no significant reduction in tree productivity (0.85 to 0.83 kg C/m^2), but a significant decrease in tree carbon biomass from the late 1900s to 2100 (33 to 27 kg C/m^2) and tree cover (63% to 57%), and a significant increase in the number of open patches (13% to 17%) when fire occurrence increased during the 1800s and after 2000.

Changes in combinations of two drivers had a range of effects on open patch cover and tree productivity, carbon biomass, and cover such that centuries with fire favored increased numbers of open patches, while those with increased atmospheric CO_2 or fire suppression favored forests (Table 4.3, Figure 4.6). The combination of increased air temperature and increasing atmospheric CO_2 from the late 1800s to the late 2000s (Scenario 6) led to no significant increase in tree productivity (0.91 to 1.04 kg C/m^2), a significant increase in tree carbon biomass (36 to 39 kg C/m^2), and tree cover (75% to 81%), but no significant change in the percent of open patches. The combination of increased air temperature and fire suppression from the late 1800s to the late 2000s (Scenario 7) led to no significant decrease in tree productivity (0.85 to 0.69 kg C/m^2), a significant increase in tree carbon biomass (24 to 29 kg C/m^2) and tree cover (53% to 70%), and a significant halving of the percent of open patches (from 17% to 8%). The combination of increased air temperature and future fire from the late 1900s to the late 2000s (Scenario 8) led to no significant decline in tree productivity (0.84 to 0.65 kg C/m^2), and significant reductions in tree carbon biomass (24 in the late 1800s to 30 in the late 1900s to 22 kg C/m^2 in the late 2000s), tree cover (53% in the late 1800s to 67% in the late 1900s to 55% in the late 2000s), and significant increases in open patch cover (from 17% in the late 1800s to 12% in the late 1900s to 15% in the late 2000s) when fire occurrence increased during the 1800s and after 2000. The combination of increased atmospheric CO_2 after the late 1800s and fire suppression from the early 1900s to 2100 (Scenario 9) led to no significant increases in tree productivity (0.85 to 1.21 kg C/m^2), a significant doubling of tree carbon biomass (22 to 43 kg C/m^2), a significant increase in tree cover (54% to 72%), and a significant decrease in open patch cover (from 16% to 11%). The combination of increased atmospheric CO_2 after the late 1800s and fire suppression in the 1900s followed by increased fire after 2000 (Scenario 10) led to no significant increase in tree productivity (0.85 to 1.19 kg C/m^2), an unexpected significant increase in tree carbon biomass (22 to 35 kg C/m^2), tree fractional projective cover (54% to 61%), and a slight decrease in open patch cover (from 16% to 14%) (Table 4.3, Figure 4.6).

Changes in combinations of three drivers produced intermediate effects on open patch cover and tree productivity, carbon biomass, and cover reflecting the offsetting effects of fire and increased atmospheric CO_2 on meadows and forests (Table 4.3, Figure 4.6). The combination of increased air temperature and increasing atmospheric CO_2 after the late 1800s, and fire suppression after the early 1900s to 2100 (Scenario 11) led to no significant increase in tree productivity (0.84 to 1.04 kg C/m^2, a significant increase in tree carbon biomass (28 to 37 kg C/m^2) and tree cover (59% to 77%), and a significant halving of open patch cover (from 16% to 8%). The combination of increased air temperature, increasing atmospheric CO_2, and fire occurrence during the 1800s, and fire suppression in the1900s followed by fire occurrence from 2000 to 2100 led to no significant increase in tree productivity (0.85 to 1.01 kg C/m^2), a significant increase in tree carbon biomass (22 in the late 1800s to 33 in the late 1900s to 30 kg C/m^2 in the late 2000s) and tree cover (54% in the late 1800s to 60% in the late 2000s), and a recovery of open patch cover to near late 1800s high levels (15% in the late 2100s compared to 16% in the late 1800s) after significant reduction in the late 1900s (down to 10%).

4.4.3 Unexpected Results

The single driver (2 and 3) and double driver (6, 7, 8, and 10) scenario results did not completely support hypothesis assertions about future changes in open patch cover and tree cover. Tree productivity was not changed more than 2 standard deviations from the mean in all scenarios, and could not be used to determine significant changes for any scenario (Figure 4.6).

The climate and CO_2 increase scenarios (2, 3, 6, and 7) resulted in an unexpected decrease or no change in open patch cover and sometimes an increase of tree cover (Figure 4.6). Temperature warming alone (Scenario 2) led to a decline in tree carbon biomass (36 to 29 kg C/m^2), but tree cover and open patch cover did not significantly change. Increasing CO_2 alone (Scenario 3) led to a significant increase in tree carbon biomass (36 to 44 kg C/m^2), but no significant increase of tree cover or open patch cover. Open patch cover may have already achieved a minimum value (6% ±1.1): the minimum average value for open patch cover in the baseline scenario was 5%. Increasing temperature and CO_2 (Scenario 6) led to a significant increase in tree carbon biomass (36 to 39 kg C/m^2), and tree cover (75% to 81%), but the percent of open patch cover was not significantly reduced (6%±1.5) as it may have achieved a minimum value. Temperature warming and future fire suppression (Scenario 7) led to no significant decrease in tree carbon biomass (30 to 29 kg C/m^2), and an unexpected significant increase in tree cover from the late 1800s (60% to 70%), and a significant decrease in open patch cover (17% to 8%). This increase in tree cover may have been the result of temperature warming leading to an expansion of tree cover by temperate tree plant functional types that replaced boreal plant functional types whose cover was decreasing (Appendix G, Table G3).

The double and triple driver temperature warming, CO_2 increase combined with future fire (Scenarios 8, 10, and 12) resulted in no consistent significant reduction in future values of tree carbon biomass or cover compared to levels in the late 1700s and late 1800s, and no significant increases in open patch cover (Figure 4.6). Temperature warming and future fire (Scenario 8) led to a significant decrease in tree carbon biomass (28 to 22 kg C/m^2), but no significant decrease of tree cover or increase of open patch cover from levels in the late 1700s. The consistent tree and open patch cover may also have been the result of temperature warming leading to an expansion of tree cover by temperate tree plant functional types that replaced boreal plant functional types whose cover was decreasing (Appendix G, Table G3). Increases of CO_2 and future fire occurrence (Scenario 10) led to an unexpected significant increase in tree carbon mass (28 to 37 kg C/m^2), and no significant overall decrease of tree cover or increase of open patch cover.

Temperature warming with increased CO_2 and fire in the 21st century (Scenario 12) did not produce a significant decrease in tree carbon biomass (28 in the late 1700s to 30 kg C/m^2 in the late 2000s) or tree cover (59% in the late 1700s to 60% in the late 2000s), or a significant increase in open patch cover (14% to 15%) from late 1700s or 1800s levels (Figure 4.6). Fire in the 21st century combined with warmer temperatures reduced the productivity of boreal plant functional types, and these factors, combined with increasing CO_2, led to a corresponding increase in productivity and carbon biomass of temperate needle leaved evergreen, broadleaved deciduous and broadleaved evergreen plant functional types.

4.5 Discussion

This study applies an individualized process based model to assess the sensitivity of plant functional type productivity, carbon mass, and cover to single and multiple factor changes of environmental drivers at a montane meadow site in the western Cascades of Oregon. Simulations using LPJ-GUESS (Smith 2001) with climate data simulated under the SRES A2 greenhouse gas emissions scenario for future climate (IPCC 2007; Nakićenović et al. 2000) indicated that forest was the dominant vegetation cover historically and in the future. Shade-tolerant, fire-intolerant high-elevation tree species (e.g. Pacific silver fir) dominated in all scenarios throughout the past three centuries, and through the year 2100, though at reduced levels by the end of the 21st century.

Meadows have been observed to exist as isolated treeless patches or mosaics of trees and herbaceous vegetation comprising hundreds of square meters to several square hectares and persisting for 50 to 1000s of years (Rice, Chapter 2; Takaoka & Swanson 2008; Vale 1981). In this study, modeled open patch cover was defined as non-forested areas with no or few trees present (the portion of simulated patches with <=10% tree cover), regardless of whether the grass plant functional type was simulated to cover the entire patch or only a portion of the patch. Open patches were not necessarily equivalent to meadows because trees were able to establish in these patches, and they reverted to forest on average in 6 years, and ranged from one year to over 150 years (Baseline Scenario, Appendix E).

Fire played a key role in controlling tree carbon biomass, cover, and open patch cover, consistent with ecological studies showing that meadows are fire maintained (Vale 1981; Hadley 1999). Fire was turned off for Scenarios 1, 2, 3, and 6, which resulted in lower percentages of open patch cover and higher tree carbon biomass and cover as compared to scenarios including fire occurrence (Scenarios 4, 5, 7-12) (see Appendix G, Figures G1-G3). To model actual historic conditions, fire was suppressed from 1925 to 2000 in all scenarios, and also suppressed from 2000-2100 in scenarios 4, 7, 9, and 11. This resulted in many cases of decreased open patch cover and increased tree carbon biomass and cover as compared to pre-1800s output.

4.5.1 Single and Multiple Environmental Driver Effects

The scenarios with single or double environmental drivers had the largest effects on tree carbon mass, and cover, with CO_2 increases causing the largest increases, and fire causing the largest decreases. The triple environmental driver scenarios were less affected, although future tree carbon biomass and cover increased from late 1800s levels. The single and multiple factor results were consistent with Luo et al.'s (2008) findings that single and double environmental drivers can have more substantial affects on model output than triple environmental drivers, and suggest that the consideration of single and multi-factor ecosystem responses can be critical for predicting impacts due to global change. Model projections combining temperature warming, increased CO_2, and fire regime changes were generally in agreement with other modeling studies and field experiments. Tree vegetation was most reduced when fire was frequent, while fire suppression resulted in forest expansion and increases in productivity and carbon mass, consistent with Lenihan et al. (2008). The expansion of conifer species tolerant of higher temperatures and the resulting reduction of boreal conifer species by the end of 2100 was consistent with other regional modeling studies simulating future climate warming (Bachelet et al. 2001; Diffenbaugh et al. 2003; Busing et al. 2007). However, in this study, boreal conifer species still dominated the study site as a result of simulated vegetation not being in equilibrium with environmental conditions. The conifer expansion that has been observed in field studies (Haugo & Halpern 2007) was simulated with a delay in the potential impact from current and future temperature, CO_2, and fire suppression or fire occurrence. Other modeling studies have found that simulated forest vegetation responded 150-200 years after warming began in simulations of climate change effects on boreal and tropical regions by Jones et al. (2009), Plattner et al. (2009), and Chapin & Starfield (1997). The potential lag of vegetation response emphasizes the importance of using models with transient vegetation responses to predict long term trends since vegetation may be in the process of a change that cannot be observed in field experiments (Rustad 2006).

The single environmental driver scenarios showed that interactions between temperature increase, higher atmospheric CO_2 concentrations, and fire frequency had additive effects when combined in the double and triple driver scenarios. The double and triple driver scenarios compared with the additive effects of single driver scenarios had no significant difference in productivity, carbon biomass and cover. An apparently additive effect for net primary productivity and biomass was noted in other modeling studies and field experiments of wetter forested sites (Luo et al. 2008; Norby et al. 2007). Non-additive effects or feedbacks, such as elevated CO_2 enhancing a plant's ability to withstand drought stress caused by warmer temperatures have been empirically noted at drier sites (Morgan et al. 2004). However, in this study, it is likely that the relatively high amount of future precipitation did not allow a large or long enough increase in drought stress conditions to produce a noticeable feedback of increased atmospheric CO_2 causing an increase in water use efficiency. Another potential feedback is the alleged increased fire occurrence attributed to temperature warming in the western U.S. (Westerling et. al 2006). The potential for a climate warming induced increase of fire frequency has been incorporated into LPJ-GUESS (Thonicke et al. 2001); however it was not observed in this study. A potential indirect feedback may result from increased atmospheric CO_2 causing increased growth and biomass, which as a result of increased fuel loads, an increase of fire frequency occurs (Bazzaz 1990). The delay of vegetation response to temperature warming, increased atmospheric CO_2, or fire frequency change, or relatively wet precipitation conditions throughout all scenarios may have constrained the occurrence of a feedback in the simulations reported here.

4.5.1 Model Uncertainty

Although the LPJ-GUESS model validation (Appendix E) and sensitivity analysis (Appendix F) found that the model simulated realistic vegetation representations of plant functional types, there are several sources of uncertainty due to simplifications or unclear representations in model structure, parameterization, and input data. Model structure uncertainty affecting meadow persistence may be due to: 1) Unclear definitions of the spatial scale and temporal persistence of treeless cover or meadows, 2) A simple soil module that may not correctly capture soil moisture conditions and may be more conducive to forest persistence (see Appendix E, Figure E9), and 3) an accelerated forest succession process resulting from newly established tree individuals simulated as saplings at 1.2 m in height instead of seedlings (Smith et al. 2001).

The spatial scale of simulated open patches is unclear as some patches classified as forest also contained grass cover. These sub-patch grass areas could represent additional meadow habitat, but since LPJ-GUESS does not simulate the spatial distribution of plant functional types within a patch, grass cover within forest patches could also represent grass existing in forest canopy gaps and thus grass cover from forest patches was not included in estimated open patch cover. This study could be improved by spatially distinguishing between grass both inside and outside the projective cover of trees.

The simulated persistence of an individual open patch with <= 10% tree cover (out of the 500) was found to occur from 1 to 150 years (average of 6 years) in simulations (Appendix E). Montane meadows in the western Cascades of Oregon are observed to persist for several or thousands of years when site conditions inhibit or eliminate tree establishment (Rice Chapter 2, Takaoka and Swanson 2007). The open patches simulated by LPJ-GUESS were created by fire or a generic disturbance randomly implemented throughout the simulation. Simulations of individual open patch persistence (Baseline Scenario) did not exceed 150 years; however, the average number of open patches throughout the simulations showed an average persistence of more than 1000 years could occur. The temporal persistence of an individual patch may be interpreted as representing open patch persistence; however, this study used the average of all patches to represent open patch persistence.

This study would also be improved by enhancements to the LPJ-GUESS model that incorporate: 1) a more detailed soil module that allows a better representation of soil properties and associated soil moisture conditions, and 2) a young tree (i.e., seedling) simulation module to improve the representation of the timing of forest succession during its earliest stages and help mitigate the issue of a potentially accelerated forest succession process in recently disturbed or bare patches.

Model parameterization may also contribute uncertainty to simulations of meadow persistence, and may be due to: 1) a possible underestimation of precipitation and overestimation of temperature, 2) uncertain mortality and generic disturbance parameterization, and 3) uncertain parameterization of plant functional type establishment and bioclimatic definitions.

Although PRISM precipitation and temperature data were highly correlated with actual measurements from a nearby meteorological station ($r^2 = 0.95$ and $r^2 = 0.97$), precipitation tended to be underestimated during the fall and winter (averaging -20 mm), and temperatures tended to be overestimated during the spring, summer and fall (averaging +1.3ºC) (Appendix E, Figures E1-E4). The sensitivity analysis results (Appendix F, Figure F1a-e) showed that a potential underestimation of precipitation may slightly reduce tree productivity and carbon biomass, but tree cover and open patch cover would remain relatively consistent. The sensitivity analysis also showed (Appendix F, Figure F2a-e) the potential overestimation of temperature may reduce tree productivity and carbon biomass, but tree and open patch cover would also remain relatively consistent. Even with the potential underestimation of tree productivity and carbon biomass caused by possible precipitation and temperature inaccuracies, modeled productivity and carbon biomass were within empirical measurement ranges (Appendix E, Figures E12 & E13).

Empirical measurements of tree mortality show a wide range (2-25%) of potential mortality rates (Appendix E, Table E6). Modeled mortality rates tended to be less than 10%, and may be under or overestimated (Appendix E, Figure E14). However, a sensitivity analysis by Wramneby et al. (2008) showed a low impact on productivity and biomass from background mortality parameter scaling. Another source of mortality uncertainty may be attributed to the parameterization of a generic disturbance with 100% mortality (e.g. insect outbreaks, ice storms, or wind throw). This study used a random occurrence of every 200 years, and may or may not represent actual mortality from these disturbance events for which empirical measurements are limited. The 200 year generic disturbance setting resulted in a simulated average tree age of 131 years with 2 x the standard error at 60 years. This age distribution closely matched dendrochronology records from mature stands of a nearby forest and meadow complex (C. Halpern, unpublished data).

The plant functional type establishment parameter was set to allow the possibility of establishment every year, so as not to limit deciduous or conifer species establishment (Silvics of North America, 1990). This may overestimate the establishment occurrence of some plant functional types, however a test with a lower establishment rate of every 5 years was found not to impact output results.

Bioclimatic definitions of plant functional types determine survival temperatures and photosynthetic temperature limits. The parameter definitions for boreal, deciduous, broadleaved evergreen, and grass plant functional types have been extensively validated to correctly simulate plant functional type distributions in other modeling studies for

Europe and the eastern United States (Smith et al. 2001; Hickler 2008; Wolf 2008). This study added two new temperate needleleaved plant functional types to represent shade tolerant (e.g. Western hemlock) and shade intolerant (e.g. Douglas-fir) species. The climate that these species occur in (at 500 ft elevation in the west Cascades) was tested in the model and the plant functional type output corresponded with the observed occurrence of these temperate needleleaved evergreens. However, the modeled presence of these new temperate plant functional types may or may not exactly correspond to actual distributions of these species (below 1000 m, Zobel 1976).

Uncertainty from these issues could be lowered by more testing of model parameterizations and gathering species specific empirical information to be used to improve the accuracy of parameter definitions for LPJ-GUESS. Although model uncertainties are substantial, potential errors from all of the above mentioned uncertainties may have been mitigated in this study by using confidence intervals and considering directional trends and differences between 30-year average outputs. Additionally, the sensitivity analysis conducted in this study, and the modeling experiments of numerous other LPJ-GUESS studies (Smith et al. 2001; Thonicke et al. 2001; Gritti et al. 2006; Koca et al. 2006; Hickler et al. 2004 & 2008) have produced accurate representations of vegetation change due to climate, CO_2, and fire impacts. Wramneby et al. (2008) found LPJ-GUESS had relatively low impacts on model projections under varying model parameterizations. See Appendix E for further discussion on model uncertainty.

4.5.3 Implications for management

The results of this study point to a continued need of fire or other disturbance as a means to maintain montane meadows, since tree cover was most reduced in scenarios with more frequent fire. This sensitivity analysis of different fire return intervals in Appendix F supports the conclusions and practices of ongoing meadow restoration projects (e.g. Chucksney Mountain Meadow Restoration) that recommend the implementation of prescribed fire every 5 to 20 years to maintain meadow habitats. A 10-year fire return intervals produced relatively large areas of grass cover in the sensitivity analyses (Appendix F). The future results of the model experiment pointed out three issues: 1) if atmospheric CO_2 concentrations continue to increase to 856 ppm, tree carbon biomass and tree cover will increase if fire suppression continues, and 2) if future temperatures increase by 4-5 ºC, upper elevation conifer mortality is likely to increase, and lower elevation temperate conifer species will eventually dominate these sites. 3) There may be time lags in vegetation response to the impacts of climate warming, fire suppression, and increased CO_2, which may result in continued forest expansion even if temperatures and CO_2 do not rise beyond current levels. A continued conifer presence and potential increases of future forest biomass point to a continued need of frequent prescribed fire to maintain meadow areas in the future.

4.5.2 Future work

This study could be improved by more validation and testing of input data and parameterizations, and incorporating enhancements to the LPJ-GUESS model. Model runs incorporating other IPCC SRES future warming scenarios with lower and higher temperature and atmospheric CO_2 increases would show other possible projections for meadow or forest persistence and forecast potential differences in timings of structural and compositional changes. Forest and open patch cover values and reactions to future warming and CO_2 increases could be compared with observational information (yet to occur), and may provide important guidance for parameterization. Enhancing LPJ-GUESS to distinguish between meadow vegetation that occurs inside and outside of the tree canopy would allow explicit representations of forest versus meadow vegetation, and could be spatially validated with aerial photo interpretation. Further sensitivity analyses and testing of parameterizations defined by better empirical information for mortality, establishment, and bioclimatic limits of plant functional types may improve model projections. Model performance could also be improved by better definitions of soil parameterizations (expanding the 9 major soil type definitions) and/or incorporating a more detailed soil module that allows improved representation of soil properties and associated soil moisture conditions. As drought stress conditions may have been underestimated in model runs (Appendix E, Figure E9), this would allow meadow and forest persistence to be more accurately represented.

4.6 Conclusions

The model experiment in this study showed that individual environmental drivers exhibited the largest influence on forests and open patches while multiple environmental drivers displayed the positive or negative additive effects of the individual drivers. Fire disturbance played the largest role in maintaining and expanding meadow areas historically and will likely continue to do so under the potentially warmer future climate. Recent and potential future increases of atmospheric CO_2 concentrations as forecasted by the SRES A2 scenario (IPCC, 2007) were projected to contribute the most to the current trend of forest expansion and open patch reduction unless fire frequency or disturbance frequency increases. Temperature warming of 5 ºC from early 1900s levels as simulated by ECHAM5 under the IPCC SRES A2 emissions scenario was projected to cause a change in species composition to temperate conifers, and increase the presence of deciduous species, but did not impact forest or open patch cover. The impacts from the combination of increased temperature, atmospheric CO_2, and fire regime changes lagged behind the potential impacts of recent and future environmental changes, suggesting that consideration of the timing of multiple environmental factors can be critical for extrapolating conclusions about the impacts of environmental change on vegetation. Multiple environmental driver model projections resulted in forecasts of continued forest dominance under a moderately high impact climate change scenario (SRES A2), and point to a need of frequent prescribed fire or tree removal to maintain meadow areas in the future.

5 CONCLUSIONS

Topography, biotic interactions, climate, and disturbance affected the extent and persistence of montane meadows at Lookout (western Cascade Range) and Bunchgrass (Cascade Range) of Oregon. The overriding impacts from multiple factors of facilitative tree interactions, climate, and especially fire suppression in areas that are topographically conducive to tree establishment have recently caused these meadows to experience large contractions due to forest encroachment.

Tree encroachment into meadow areas varied over the varying topography of Bunchgrass and Lookout, and showed areas of higher and lower risk for tree encroachment. Aerial photo change detection of the two topographically different meadow complexes for three time periods: 1946, 1967, and 2000 found an annual meadow loss rate of 1% and an overall reduction of about 60% in meadow area from 1946–2000. The distribution of meadow areas tended to be highest on west or south aspects but more limited on east or north aspects at both sites. A higher level of meadow creating disturbance occurred at the steeper Lookout site resulting in more interrupted tree establishment on north and east aspects. Tree encroachment varied over the topographic classes as higher amounts and rates of meadow loss tended to be on west and south aspects, within 5 m away from the forest edge, and on flatter slopes at Bunchgrass in the High Cascades, but on steep slopes at Lookout Mountain in the West Cascades. The meadow areas of higher risk for tree encroachment over the last 54 years may need to be the focus of restoration efforts at Bunchgrass and Lookout meadows.

Spatiotemporal patterns and climate correlation analysis of early stage tree encroachment revealed how species interactions and environmental tolerances influence the location and timing of early tree establishment into a meadow that was dominated by two tree species, Grand fir *(Abies grandis* Dougl.) and Lodgepole pine *(Pinus contorta* Dougl.).

Spatial analysis of early tree establishment showed that biotic interactions are more important than climate in controlling invasion pattern dynamics. Clustering of Grand fir developed early in the invasion period (1965), whereas clustering of Lodgepole pine developed much later (1985). Grand fir seedlings were strongly clustered around Lodgepole pine or previously established Grand fir trees, especially at distances less than 4 m. In contrast, Lodgepole pine was five times more likely than Grand fir to establish 5 or more m away from another tree, and young Lodgepole pine was repulsed from older Grand fir trees at distances < 2 m. Average distances of establishment from the nearest prior seedling were consistently twice as high for Lodgepole pine as for Grand fir throughout the pulse of invasion. This showed a tendency of Lodgepole pine to establish in more open meadow areas first and facilitate the subsequent establishment of Grand fir.

Differing species environmental tolerances to climate influenced invasion during the early stages of tree encroachment at Bunchgrass meadow. Establishment rates of Lodgepole pine were positively correlated with late summer air temperature (September) and negatively correlated with summer precipitation (August). In contrast, establishment rates of Grand fir were positively correlated with late spring precipitation (May) and negatively correlated with late summer air temperature (August). Grand fir cones were produced at 2-3 year cycles, and Grand fir establishment from 1960 to 2003 was higher in years after high cone production in the previous fall. Thus, tree invasion was regulated both by climate variability and biotic interactions responding to species' tolerances for light, heat, and moisture. The contrasting environmental tolerances and facilitative interactions of the two tree species enhanced the tree encroachment process by encouraging the establishment of one species or the other during the drier-warmer and cooler-wetter climate fluctuations over the last century.

Model simulations using LPJ-GUESS disentangled the individual and combined impacts from historic and potential future changes of temperature, atmospheric CO_2, and fire regime. Though there is uncertainty associated with the model projections, this modeling analysis enabled the extension of hypothesis testing about environmental driver impacts on vegetation that is not feasible with empirical experiments. Scenario projections with a future 5 ºC temperature increase and a tripling of atmospheric CO_2 concentration showed that the current trend of forest persistence and expansion would likely continue if fire suppression is maintained. The interactions between different environmental drivers had both positive and negative additive effects. Single and double environmental drivers produced the highest impacts on increasing or decreasing future tree biomass, while combining three drivers had a lower impact. However, increased fire occurrence had the largest impact on reducing forest cover and increasing meadow cover in all scenarios, while fire suppression had the largest opposite effect. Increased atmospheric CO_2 concentrations played a large role in expanding forest biomass and cover, but did not significantly reduce meadow cover. Future temperature warming resulted in a delayed shift in existing forest composition to higher temperature tolerant species. The current trend of forest expansion and meadow reduction was projected to continue and lag behind the potential impacts of environmental changes. The preservation of meadow areas may continue to require frequent fire or tree removal, and temperature increases may cause a change in the forest species that encroach into meadow areas.

The multiple factors investigated had positive and negative variable effects on meadows at Lookout Mountain and Bunchgrass. Fire occurrence played the largest role of increasing and maintaining meadow extent in agreement with Vale (1981) and Hadley (1999). The factors that contributed to decreasing historic and future meadow extent and persistence include: flatter, southerly and westerly slopes in areas near forest edges, tree species facilitation interactions and tolerance to fluxuations in climate, and most importantly fire suppression. Land managers will likely continue to need to use fire or tree removal to preserve these meadow habitats of remarkable biodiversity in the western Cascade landscape.

Bibliography

Awada, T., Henebry, G. M., Redmann, R. E., Sulistiyowati, H. 2005. *Picea glauca* Dynamics and spatial patterns of seedlings regeneration along a chronosequence in the mixedwood section of the boreal forest. *Ann. For. Sci* 61:789 - 794.

Bachelet, D., Neilson, R. P., Lenihan, J. M., Drapek, R. J. 2001. Climate Change Effects on Vegetation Distribution and Carbon Budget in the United States. *Ecosystems* 4:164-185.

Badeck, F.W., Lischke, H., Bugmann, H., Hickler, T., Hönninger, K., Lasch, P., Lexer, M.J., Mouillot, F., Schaber, J., Smith, B. 2001. Tree species composition in European pristing forests: Comparison of stand data to model predictions. *Climatic Change* 51:307-347.

Bazzaz, F. A. 1990. The Response of Natural Ecosystems to the Rising Global CO_2 Levels. *Annual Review of Ecology and Systematics* 21:167-196.

Boyd, R. (Editor). 1999. Indians, fire and the land in the Pacific Northwest. Oregon State Press, Corvallis, OR.

Bragg, T. B., Hubert, L. C. 1976. Woody plant invasion of unburned Kansas Bluestem Prairie. *Journal of Range Management* 29:19 - 24.

Briggs, J. M., Hoch, G. A., Johnson, L. C. 2002. Assessing the rate, mechanisms and consequences of the conversion of Tallgrass prarie to *Juniperus virginiana* forest. *Ecosystems* 5:578 - 586.

Burke, C. 1979. Historic fire in the Central Western Cascades, Oregon. Masters Thesis, Oregon State University, Corvallis, OR.

Busing, R. T., Solomon, A. M., McKane, R. B, Burdick, C. A. 2007. Forest dynamics in Oregon landscapes: Evaluation and application of an individual-based model. *Ecological Applications* 17(7):1967–1981.

Callaway, R. and Walker, L. 1997. Competition and Facilitation: A Synthetic Approach to Interactions in Plant Communities. Ecology 78(7):1958-1967.

Cayan, D. R., S. A. Kammrediener, M. D. Dettinger, J., M. Caprio, D. H. Peterson. 2001. Changes in the onset of spring in the western United States. *Bulletin of the American Meteorological Society* 82:399 – 415.

Chapin, F. S., Starfield, A., M., 1997. Time lags and novel ecosystems in response to transient climatic change in arctic Alaska. *Climatic Change* 35:449–461.

Chucksney Mountain Meadow Restoration Project: Using the tool of prescribed fire. U. S. Forest Service. http://www.reo.gov/ecoshare/ccamp/pdf/chucksney.pdf.

Cissel, J. H., Swanson, F. J., Weisberg, P. J. 1999. Land management using historical fire regimes: Blue River, Oregon. *Ecological Applications* 9(4):1217 - 1231.

Climate Impacts Group. 2009. ECHAM SRES A2 Scenario. Downscaled 1/8 degree Temperature and Precipitation data. Center for Science in the Earth System University of Washington http://cses.washington.edu/data/ipccar4/.

Dailey, M. 2007. Meadow classification in the Willamette National Forest and conifer encroachment patterns in the Chucksney-Grasshopper meadow complex, Western Cascade Range, Oregon. Masters Thesis, Oregon State University, Corvallis, OR.

Daly, C., Neilson, R. P., and Phillips, D.L. 1994. A Statistical-Topographic Model for Mapping Climatological Precipitation over Mountanious Terrain. *Journal of Applied Meteorology* 33:140-158.

Daly, C., Bachelet, D., Lenihan, J. M., Neilson, R.P., Parton, W., Ojima, D. 2000. Dynamic simulations of tree-grass interactions for global change studies. *Ecological Applications* 10(2):449-469.

Daly, C. & Levno, A. 2009. Snow depth and snow water equivalent measurements along a road course in the Andrews Experimental Forest. Long-Term Ecological Research. Forest Science Data Bank, Corvallis, OR. [Database]. Available: http://andrewsforest.oregonstate.edu/data/abstract.cfm?dbcode=MS007 (22 November 2009).

Daly, C. & McKee, W. 2009. Meteorological data from benchmark stations at the Andrews Experimental Forest. Long-Term Ecological Research. Forest Science Data Bank, Corvallis, OR. [Database]. Available: http://andrewsforest.oregonstate.edu/data/abstract.cfm?dbcode=MS001

Debinski, D. M., Jakubauskas, M. E., Kindscher, K. 2000. Montane Meadows as Indicators of Environmental Change. *Environmental Monitoring and Assessment* 64:213 – 225.

Diffenbaugh, N. S., Sloan, L. C., Snyder, M. A., Bell, J. L., Kaplan, J, Shafer, S. L., Bartlein, P. J. 2003. Vegetation sensitivity to global anthropogenic carbon dioxide emissions in a topographically complex region. *Global Biogeochemical Cycles* 17(2):1067

Dyrness, C.T., Norgren, J., Sollins, P., Vance-Borland, K. 1962-1996. Soil descriptions and data for soil profiles in the Andrews Experimental Forest, selected reference stands, Research Natural Areas, and National Parks http://www.fsl.orst.edu/lter/data/abstract.cfm?dbcode=SP001&topnav=135.

Etheridge, D. M., Steele, L. P., Langenfelds, R. L., Fancey, R. J., Barnola, J. M., Morgan, V. I. 1998. Historical CO_2 record from the Law Dome DE08, DE08-2, and DSS ice cores http://cdiac.ornl.gov/trends/co2/lawdome-data.html

Fajardo, A., Goodburn, J. M., Graham, J. 2006. Spatial patterns of regeneration in managed uneven-aged Ponderosa pine/Douglas-fir forests of Western Montana, USA. *Forest Ecology and Management* 223:255 - 266.

Foiles, M., Graham, R., and Olson, D. Jr.1990. *Abies grandis* (Grand fir). in Silvics of North America. USDA Forest Service Agricultural Handbook 654. US Department of Agriculture, Washington, DC, USA. http://www.na.fs.fed.us/spfo/pubs/silvics_manual/table_of_contents.htm

Foley, J. A. 1995 An equilibrium model of the terrestrial carbon budget Tellus (1995), 47B, 310-319.

Franklin, J. F., Moir W. H., Douglas G. W., and Wiberg, C. 1971. Invasion of subalpine meadows by trees in the Cascade Range, Washington and Oregon. *Arctic and Alpine Research* 3:215 – 224.

Franklin, J. F. and C.T. Dyrness. 1988. Natural vegetation of Oregon and Washington. Corvallis, OR: Oregon State Univerity Press.

Franklin, J. F. & Halpern. C.B. 1999. Pacific Northwest forests. in: Barbour, M.G. & Billings, W.D. (eds.) *North American terrestrial vegetation* (*2nd ed*), pp. 123 - 159. Cambridge University Press, New York, NY, US.

Gavin, D., Brubaker, L., Lertzman, K. 2003. Holocene Fire History of a Coastal Temperate Rain Forest Based on Soil Charcoal Radiocarbon Dates. Ecology 84(1):186-201.

Gerten, D., Schaphoff, S. Haberlandt, U., Lucht, W., Sitch, S. 2004. Terrestrial vegetation and water balance – hydrological evaluation of a dynamic global vegetation model. *Journal of Hydrology* 286:249 – 270.

Garber, S. M., Maguire, D. A. 2004. Stand productivity and development in two mixed-species spacing trials in the Central Oregon Cascades. *Forest Science* 50(1):92 - 105.

Goldberg, D. & Barton, M.1992. Patterns and Consequences of Interspecific Competition in Natural Communities: A Review of Field Experiments with Plants. *The American Naturalist* 139(4):771-801.

Griffiths, R., Madritch, M., Swanson, A. 2005. Conifer invasion of forest meadows transforms soil characteristics in the Pacific Northwest. *Forest Ecology and Management* 208:347-358.

Gritti, E. S., Smith, B., Sykes, M. T. 2006. Vulnerability of Mediterranean Basin ecosystems to climate change and invasion by exotic plant species. *Journal of Biogeography* 33: 145-157.

Harte, J., Shaw, R. 1995. Shifting dominance within a montane vegetation community: results of a climate warming experiment. *Science* 267(5199):876 – 880.

Hadley, K. S. 1999. Forest history and meadow invasion at the rigdon meadows archaeological site, Western Cascades, Oregon. *Physical Geography* 20(2):116 – 133.

Haugo, R. 2005. Fire and restoration of an encroached meadow in the Western Cascades, Oregon, University of Washington, Seattle, WA. (Unpublished).

Haugo, R., Halpern, C. 2007. Vegetation responses to conifer encroachment in a Western Cascades meadow: a chronosequence approach. *Canadian Journal of Botany* 85:285 - 298.

Halpern, C., Smith, B., Franklin, J. 1984. Composition, Structure, and Distribution of the Ecosystems of the Three Sisters Biosphere Reserve/Wilderness Area. U.S.D.A. Final Report.

Halpern, C.B. 1999. Effects of prescribed burning at Bunchgrass Meadow: an establishment report and baseline data (submitted to the McKenzie Ranger District, Willamette National Forest). Web report: http://www.fsl.orst.edu/lter/pubs/webdocs/reports/bg.cfm?topnav=55.

Halpern, C., Antos, J., Rice, J., Haugo, R., Lang, N. 2009. Tree invasion of a montane meadow complex: temporal trends, spatial patterns, and biotic interactions. *Journal of Vegetation Science* (in review).

Harmon, M., Bible, K., Ryan, M.G.,Shaw, D. C., Chen, H.,Klopatek, J.,Li, X. 2004. Production, Respiration, and Overall Carbon Balance in an Old-growth *Pseudotsuga- Tsuga* Forest Ecosystem. *Ecosystems* 7(5): 498-512

Haxeltine, A. & Prentice, I. C. 1996. A general model for the light-use efficiency of primary production. *Functional Ecology*, 10:551-561.

Hely, C., Bremond, L., Alleume, S., Smith, B., Sykes, M. T., Guiot, J. 2006. Sensitivity of African biomes to changes in precipitation regime. *Global Ecology and Biogeography* 15:258-270.

Hessl, A, Milesi, C., Keane, R. Peterson, D. 2004.Ecophysiological Parameterization Database for Pacific Northwest Trees or Forests. http://sain.utk.edu/apps/pnwin/ecophys/ecophys.php

Hickler, T., Smith, B., Sykes, M. T., Davis, M. B.,Sugita, S., Walker, K. 2004. Using a generalized Vegetation Model to Simulate Vegetation Dynamics in Northeastern USA. *Ecology* 85(2):519-530.

Hickler, T., Smith, B., Prentice, C., Mjofors, K., Miller, P., Arneth, A., Sykes, M. 2008. CO2 fertilization in temperate FACE experiments not representative of boreal and tropical forests. *Global Change Biology* 14:1-12.

Hickman, C. 1976. Non-Forest Vegetation of the Central Western Cascade Mountains of Oregon. *Northwest Science* 50(3):145-155.

Highland, S. Dissertation in progress. Oregon State University.

Hood, S. M., McHugh, C. W., Ryan, K. C., Reinhardt, E., Smith, S. L. 2007. Evaluation of a post-fire tree mortality model for western USA conifers. *International Journal of Wildland Fire*, 16:679-689.

Huang, S., Titus, S. J., Wiens, D. P. 1992. Comparison of nonlinear height-diameter functions for major Alberta tree species. *Canadian Journal of Forest Research* 22:1297-1304.

IPCC 4th Assessment Report. 2007. SRES A2 Scenario CO_2 data. http://www.ipcc-data.org/ancilliary/tar-isam.txt

IPCC, 2007: Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 996 pp.

Jones, C., Lowe, J. Liddicoat, S, Betts, R. 2009. Committed terrestrial ecosystem changes due to climate change. *Nature Geosciences* 2:484-486.

Keeling, C. D., Piper, S. C., Bacastow, R. B., Wahlen, M., Whorf, T. P., Heimann, M., Meijer, H. A. 2001. Exchanges of atmospheric CO_2 and $13CO_2$ with the terrestrial biosphere and oceans from 1978 to 2000. I. Global aspects, SIO Reference Series, No. 01-06, Scripps Institution of Oceanography, San Diego, 88 pages, 2001. http://scrippsco2.ucsd.edu/data/mlo.html

Koca, D., Smith, B., Sykes, M. T. 2006. Modelling regional climate change effects on potential natural ecosystems in Sweden. *Climatic Change* 78:381-406.

Lang, N., Halpern C. B. 2007. The soil seed bank of a montane meadow: consequences of conifer encroachment and implications for restoration. *Canadian Journal of Botany* 85:557 - 569.

Lepofsky, D., Heyerdahl, E.K., Lertzman, K., Schaepe, D., Mierendorf, B. 2003. Historical Meadow Dynamics in Southwest British Columbia: A Multidisciplinary Analysis. *Conservation Ecology* 7(3):5. http://www.consecol.org/vol7/iss3/art5.

Lieshout, M.N.M. Van & Baddeley, A.J. 1996. A nonparametric measure of spatial interaction in point patterns. *Statistica Neerlandica* 3:344 - 361.

Lloyd, J. & Taylor J.A. 1994. On the temperature dependence of soil respiration. *Functional Ecology* 8: 315-323.

Lotan, J. E.; Critchfield, W. B. 1990. Pinus contorta Dougl. ex. Loud.—Lodgepole pine. In: Burns, R.M.; Honkola, B. H., Tech. coordinators. Silvics of North America: Vol. 1, Conifer. Agric. Handbook 654, Washington, D.C.: U.S. Dept. of Agriculture pp. 302 - 315.

Lenihan, J. M., Bachelet, D., Neilson, R. P., Drapek, R. 2008. Simulated response of conterminous United States ecosystems to climate change at different levels of fire suppression, CO2 emission rate, and growth response to CO2. *Global and Planetary Change* 64:16–25

Luo, Y., Gerten, D, Le Maire, G.,*, Parton, W. J., Weng, E., Zhou, X., Keough, C. Beier, C., Ciais, P., Cramer, W., Dukes, J, Emmett, B, Hanson, P. J., Knapp, A., Linder, S., Nepstad, D, Seyrustad, L. 2008. Modeled interactive effects of precipitation, temperature, and [CO2] on ecosystem carbon and water dynamics in different climatic zones. *Global Change Biology* 14:1–14.

Magee, T.K., and J.A. Antos. 1992. Tree invasion into a mountain-top meadow in the Oregon Coast Range, USA. *Journal of Vegetation Science* 3: 485-494.

Mast, J. N., Veblen, T. T., Hodgson, M. E. 1997. Tree invasion within a pine/grassland ecotone: an approach with historic aerial photography and GIS modeling. *Forest Ecology and Management* 93:181 - 194.

Meentemeyer, V. 1978. Macroclimate and lignin control of litter decomposition rates. *Ecology* 59: 465-472.

Miller, E. A., and C. B. Halpern. 1998. Effects of environment and grazing disturbance on tree establishment in meadows of the Western Cascade Range, Oregon, USA. *Journal of Vegetation Science* 9:265 - 282.

Miller, J. C., Hammond, P. C., Ross, D. N. 2003. Distribution and functional roles of rare and uncommon moths (*Lepidoptera: Noctuidae: Plusiinae*) across a coniferous forest landscape. *Annals of the Entomological Society of America* 96(6):847 – 855.

Minore, D., 1979. Comparative autecological characteristics of northwestern tree species: a literature review. USDA General Technical Report PNW-87.

Mintie, A. T., Heichen, R. S., Cromack, K., Myrold, D. D., Bottomley, P. J. 2003 Ammonia-oxidizing bacteria along forest to meadow transects in the Oregon Cascade Mountains. *Applied & Environmental Microbiology* 69(6):3129 – 3136.

Mitchell, T., and P. Jones. 2005. An improved method of constructing a database of monthly climate observations and associated high-resolution grids. *International Journal of Climate Policy* 25: 693-712.

Monsi, M. & Saeki, T. 1953. Japanese Journal of Botany 14: 22-52.

Monteith, J.L., 1995. Accomodation between transpiring vegetation and the convective boundary layer. *Journal of Hydrology* 166: 251-263.

Morales, P., Sykes, M.T., Prentice, I.C., Smith, P., Smith, B., Bugmann, H., Zierl, B., Friedlingstein, P., Viovy, N., Sabaté, S., Sánchez, A., Pla, E., Gracia, C.A., Sitch, S., Arneth, A., Ogee, J. 2005. Comparing and evaluating process-based ecosystem model predictions of carbon and water fluxes in major European forest biomes. *Global Change Biology* 11(12):2211 - 2233.

Morgan, J. A., Pataki, D. E., Körner, C., Clark, H., Del Grosso, S. J., Grünzweig, J. M., Knapp, A. K., Mosier, A. R., Newton, P. C. D., Niklaus, P. A., Nippert, J. B., Nowak, R. S., Parton,W. J., Polley, H. , Shaw M. R. 2004. Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO2. 2004. *Oecologia* 140:11-25.

Mote, P., E. Salathé, and C. Peacock. 2005. Scenarios of future climate for the Pacific Northwest. Report prepared for King County, WA by the Climate Impacts Group, University of Washington, Seattle, WA, USA.

Myster, R. P., Pickett, S. T. A. 1992. Effects of palatability and dispersal mode on spatial patterns of trees in old fields. *Bulletin of the Torrey Botanical Club* 119(2):145-151.

Nakićenović N., Swart, R. (eds.) (2000) Special report on emissions scenarios. A special report of working group III of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 599 pp.

Natural Resource Conservation Service (NRCS). 2009. Hogg Pass, McKenzie Bridge, Three meadows Creek, Santiam Pass SNOTEL data http://www.wcc.nrcs.usda.gov/snotel/Oregon/oregon.html

Neilson, R. P., Drapek, R. 1998. Potentially complex biosphere responses to transient global warming. Global Change Biology 4:505-521.

Norby, R., J., Rustad, L. E., Dukes, J. S., Ojima, D. S., Parton, W. J., Del Grosso, S. J., McMurtrie, R. E., Pepper, D. E. 2007. Ecosystem Responses to Warming and Interacting Global Change Factors in Canadell JG, Pataki D, Pitelka L (eds) (2007) Terrestrial Ecosystems in a Changing World. The IGBP Series, Springer-Verlag, Berlin Heidelberg.

Plattner, G. K., 2009. Terrestrial ecosystem inertia. *Nature Geosciences* 2:467-469.

Prentice, I.C., Sykes, M. T. & Cramer, W. 1993. A simulation model for the transient effects of climate change on forest landscapes. *Ecological Modelling* 6:51-71.

Reich, R. and Davis, R. 2005. On-line spatial analysis library and documentation for S-Plus.

Ripley, B.D. 1977. Statistical inference for spatial processes. Cambridge University Press.

Rochefort, R.M. and D.L. Peterson. 1996. Temporal and spatial distribution of trees in subalpine meadows of Mount Rainier National Park. *Arctic and Alpine Research* 28:52 - 59.

Romme, W. H., and Turner, M. G. 1991. Implications of global climate change for biodiversity in the Greater Yellowstone Ecosystem. *Conservation Biology* 5: 373 – 386.

Romme, W. H., and Knight, D. H., 1981. Fire frequency and subalpine forest succession alont a topographic gradient in Wyoming. *Ecology* 62(2):319-326.

Rustad, L. E. 2006. From transient to steady-state response of ecosystems to atmospheric CO2-enrichment and global climate change: conceptual challenges and need for an integrated approach. *Plant Ecology*182:43 –62

Schiffers, K., Schurr, F., Tielborger, K., Carsten Urbach, C., Moloney, K., Jeltsch, F. 2008. Dealing with virtual aggregation - a new index for analysing heterogeneous point patterns. *Ecography* 31: 545-555

Sea, D.S. and Whitlock, C. 1995. Postglacial vegetation and climate of the Cascade Range, Central Oregon *Quaternary Research* 43(3): *370 – 381.*

Seimann, E. & Rogers, W.E. 2003. Changes in light and nitrogen availability under pioneer trees may indirectly facilitate tree invasion of grasslands. *Journal of Ecology* 91:923 - 931.

Shinozaki, K., Yoda, K., Hozumi, K., Kira, T. 1964. A quantitative analysis of plant form - the pipe model theory. I. basic analyses. *Japanese Journal of Ecology* 14: 97-105.

Shinozaki, K., Yoda, K., Hozumi, K., Kira, T. 1964. A quantitative analysis of plant form - the pipe model theory. II. further evidence of the theory and its application in forest ecology. *Japanese Journal of Ecology* 14: 133-139.

Silvics of North America USDA Forest Service Agricultural Handbook 654. US Department of Agriculture, Washington, DC, USA. 1990. http://www.na.fs.fed.us/spfo/pubs/silvics_manual/table_of_contents.htm

Sitch, et al. 2003. Evaluation of ecosystem, plant geography and global carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology* 9: 161-185.

Smith, B., Prentice, I. C., Sykes, M. T. 2001. Representation of vegetation dynamics in the modeling of terrestrial ecosystems: comparing two contrasting approaches within European climate space. *Global Ecology and Biogeography* 10:621-637.

Spies, T. 1997. Forest Stand Structure, Composition and Function. In *Creating a Forestry for the 21st Century: The Science of Ecosystem Management*. K. K. Kolm, J. F. Franklin. D C: Island Press

Sprugel, D.G., Ryan M.G., Renee Brooks, J., Vogt, K.A., Martin, T.A. 1996. Respiration from the organ level to the stand. In: Smith, WK & Hinckley, TM (eds), Physiological Ecology of Coniferous Forests.

Swanson, F., Halpern, C., Cissell, J. 2007. Restoration of dry, montane meadows through prescribed fire, vegetation and fuels management: A program of research and adaptive management in western Oregon. Project 01C-3-3-10 Final Report to the Joint Fire Science Program. 29 September 2007.

Sykes, M. T., Prentice, I. C. 1996. Climate change, tree species distributions and forest dynamics: A case study in the mixed conifer/northern hardwoods zone of northern Europe. *Climatic Change* 34(2):1480-1573.

Takaoka, S. and Swanson, F. 2008. Changes in the extent of meadows and shrub fields in the Central Western Cascade Range, U. S. A. *Professional Geographer,* Publish Pending.

Taylor, A. H. 1995. Forest expansion and climate change in the Mountain hemlock (Tsuga mertensiana) zone, Lassen Volcanic National Park, California, U.S.A. *Arctic and Alpine Research* 23(3):207 - 216.

Taylor, A. H. 2000. Fire regimes and forest changes in mid and upper montane forests of the Southern Cascades, Lassen Volcanic National Park, California, U.S.A. *Journal of Biogeography* 27:87 - 104.

Thompson, J. 2007. Mountain meadows — here today, gone tomorrow? Meadow science and restoration. Science Findings Issue 94. PNW Research Station, Portland, OR.

Thompson, R. S., Anderson, K. H., Bartlein, P. J. 1999. Atlas of Relations Between Climatic Parameters and Distributions of Important Trees and Shrubs in North America U.S. Geological Survey. Professional Paper 1650 A&B http://pubs.usgs.gov/pp/p1650-a/

Thonicke, K., Venevsky, S., Sitch, S. 2001. The role of fire disturbance for global vegetation dynamics: coupling fire into a Dynamic Global Vegetation Model. *Global Ecology & Biogeography* 10:661-677.

Thonnes, E. & Lieshout, M.C. Van. 1999. A comparative study on the power of van Lieshout and Baddeley’s J-Function. *Biometrical Journal* 41(6):721 – 734.

Timber Resource Statistics for Western Oregon, 1997, Resource Bulletin PNW-RB-237

Turner, D. P. 1985. Successional relationships and a comparison of biological characteristics among six Northwestern conifers. *Torrey Botanical Club* 112(4):421 - 428.

U.S. HCN temperature and precipitation data for Three Lynx, McKenzie Bridge, and Cascadia Met stations http://cdiac.esd.ornl.gov/r3d/ushcn/statepcp.html#OR

Vale, T.R. 1981. Tree invasion of montane meadows in Oregon. *American Midland Naturalist* 105: 61 - 69.

Veblen, T. T., 1992. Regeneration Dynamics In *Plant Succession: Theory and Prediction* ed. D. C. Glen-Lewin, R. K. Peet, and T. T. Veblen. New York: Chapman and Hall

Waring, R.H., Schroeder, P.E.,Oren, R. 1982. Application of the pipe model theory to predict canopy leaf area. *Canadian Journal of Forest Research* 12:556-560.

Waring, R. H.,Law, B., and Bond, B. 1999. NPP Temperate Forest: OTTER Project Sites, Oregon, U.S.A., 1989-1991. Data set. Available on-line [http://www.daac.ornl.gov] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, U.S.A.

Weisberg, P. J., Swanson, F. J. 2003. Regional synchroneity in fire regimes of the western Oregon and Washington, USA. *Forest Ecology and Management* 172:17-28.

Weisberg, P. J. 2004. Importance of Non-Stand-Replacing Fire for Development of Forest Structure in the Pacific Northwest, USA. *Forest Science* 50(2):245-258.

Weisberg, P. J., Lingua, E., Pillai R. 2007. Spatial Patterns of Pinon-Juniper Woodland Expansion in Central Nevada. *Rangeland Ecol Management* 60:115-124.

Westerling, A. L., Hidalgo, H. G., Cayan, D. R., Swetnam, T. W. 2006. Warming and Earlier Spring Increase Western U.S. Forest Wildfire Activity. Science 313:940:943.

Wiegand, T. & Moloney, K. 2004. Rings, circles, and null-models for point pattern analysis in ecology. Oikos 104(2):209-229 http://www.thorsten-wiegand.de/pdf/Oikos12497.pdf

Whitlock, C., 1992. Vegetational and climatic history of the Pacific Northwest during the last 20,000 years: implications for understanding present-day biodiversity. *The Northwest Environmental Journal* 8:5 - 28.

Wilson, N., Bergland, E., Ford, P., Kamrath. S. & Phillips, J. 1999. *Bunchgrass Meadow special habitat area management plan.* U.S. Department of Agriculture Forest Service McKenzie River Ranger District, Willamette National Forest, OR, US.

Wolf, A., Blyth, E. Harding, R, Jacob, D., Keup-Thiel, E., Goettel, H., Callaghan, T. 2008. Sensitivity of an ecosystem model to hydrology and temperature. *Climatic Change* 87:75-89.

Woodward, A., Schreiner, E.G., Silsbee D.G. 1995. Climate, geography, and tree establishment in subalpine meadows of the Olympic Mountains, Washington, U.S.A. *Arctic and Alpine Research* 27(3):217 - 225.

Wramneby, A., Smith, B., Zaehle, S., Sykes, M. 2008. Parameter uncertainties in the Modeling of vegetation dynamics – Effects on tree community structure and ecosystem functioning in European forest biomes. *Ecological Modelling* 216:277-290.

Zobel, D.B., McKee, A., Hawk, G. M., Dyrness C. T. 1976. Relationships of Environment to Composition, Structure, and Diversity of Forest Communities of the Central Western Cascades of Oregon. *Ecological Monographs* 46(2):135-156.

APPENDICES

APPENDIX A

Figure A.1 Lookout Meadow and reclassified meadow shadow area 1946 map

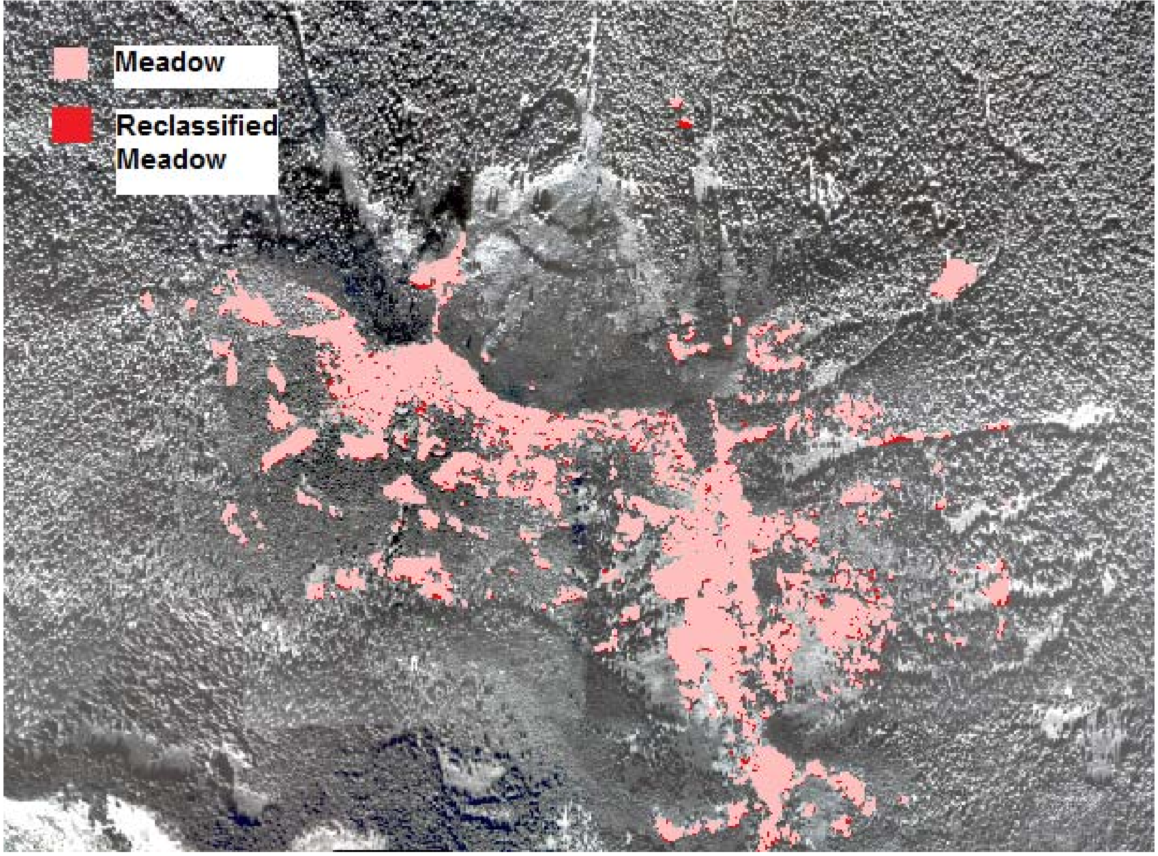


Figure A.2 Lookout Meadow and reclassified meadow shadow area 1967 map

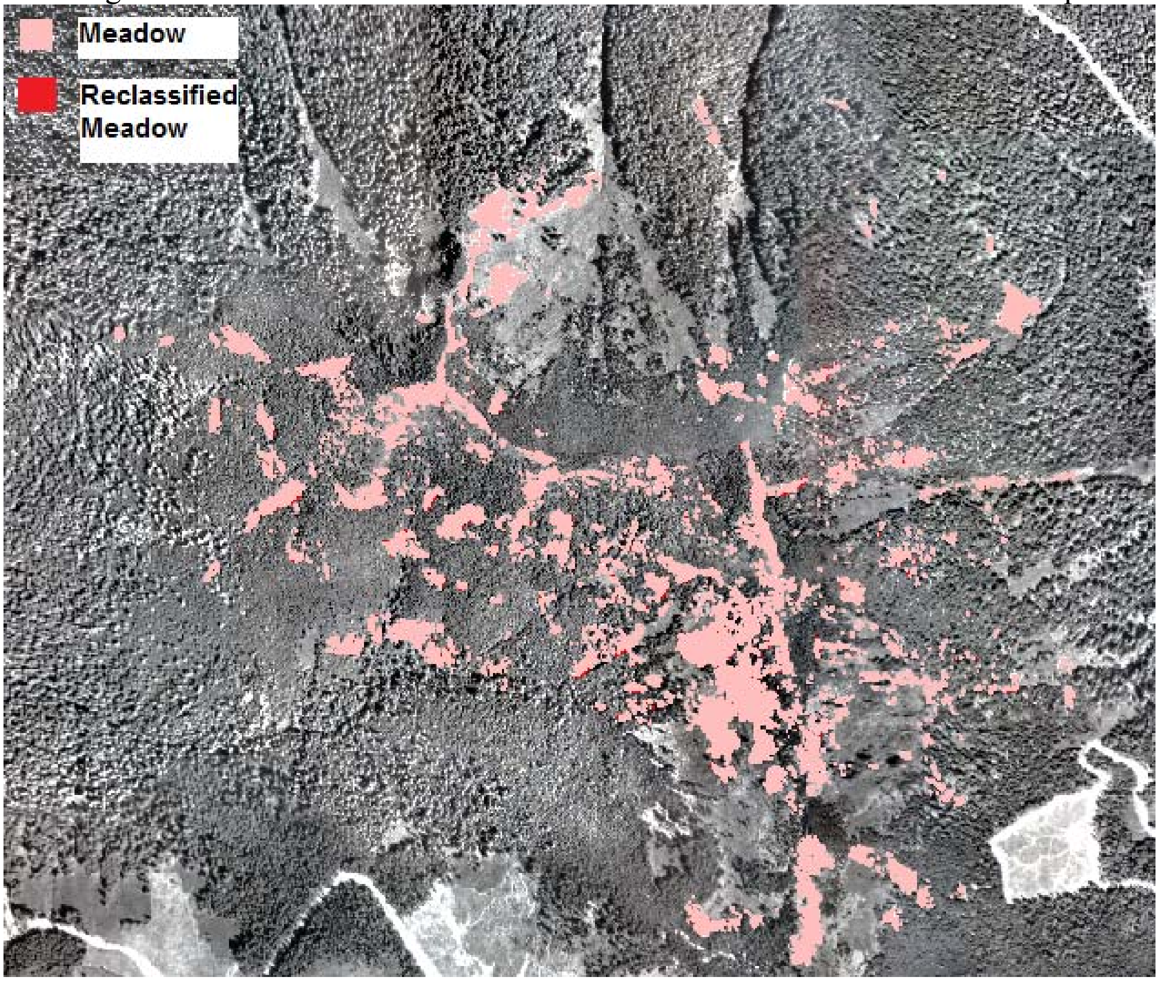


Figure A.3 Lookout Meadow and reclassified meadow shadow area 2000 map

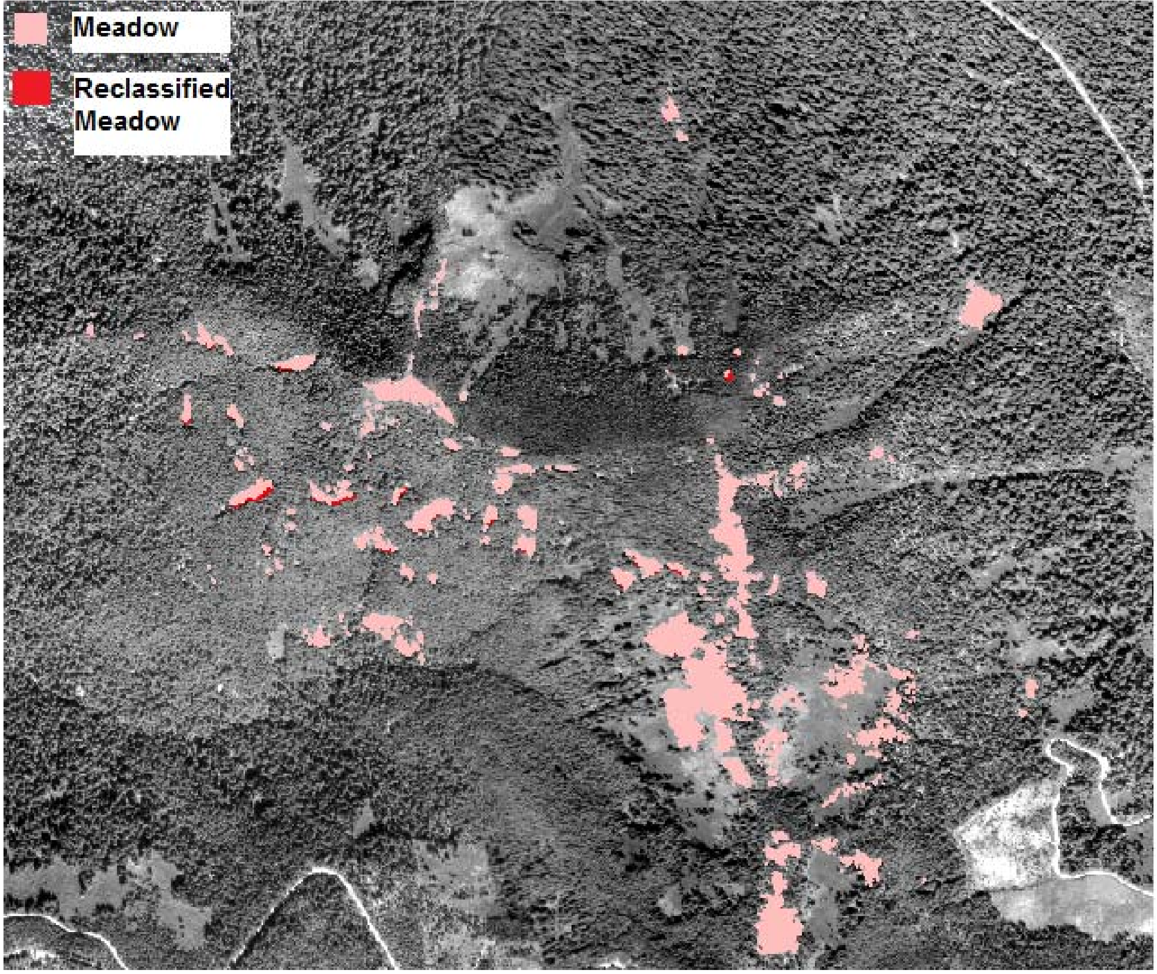


Figure A.4 Bunchgrass Meadow and reclassified meadow shadow area 1946 map

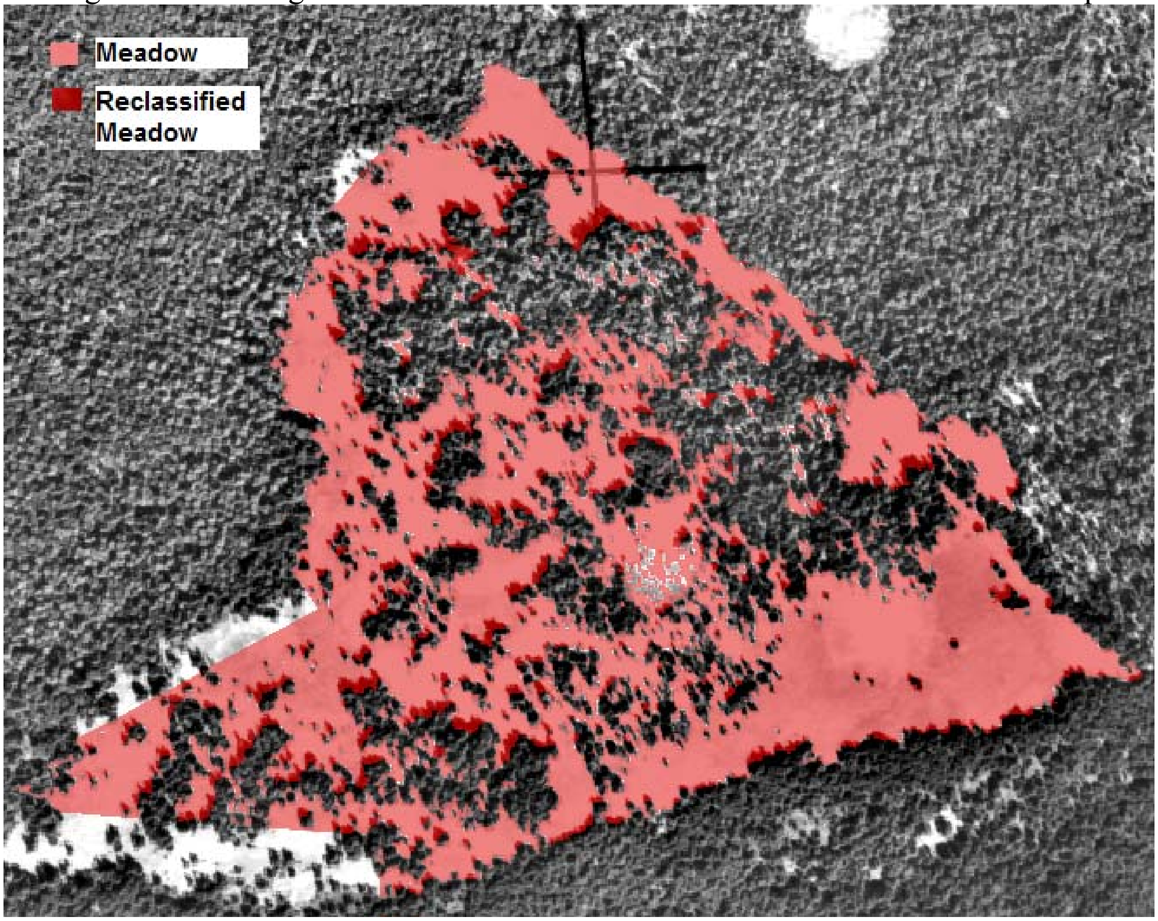


Figure A.5 Bunchgrass Meadow and reclassified meadow shadow area 1967 map

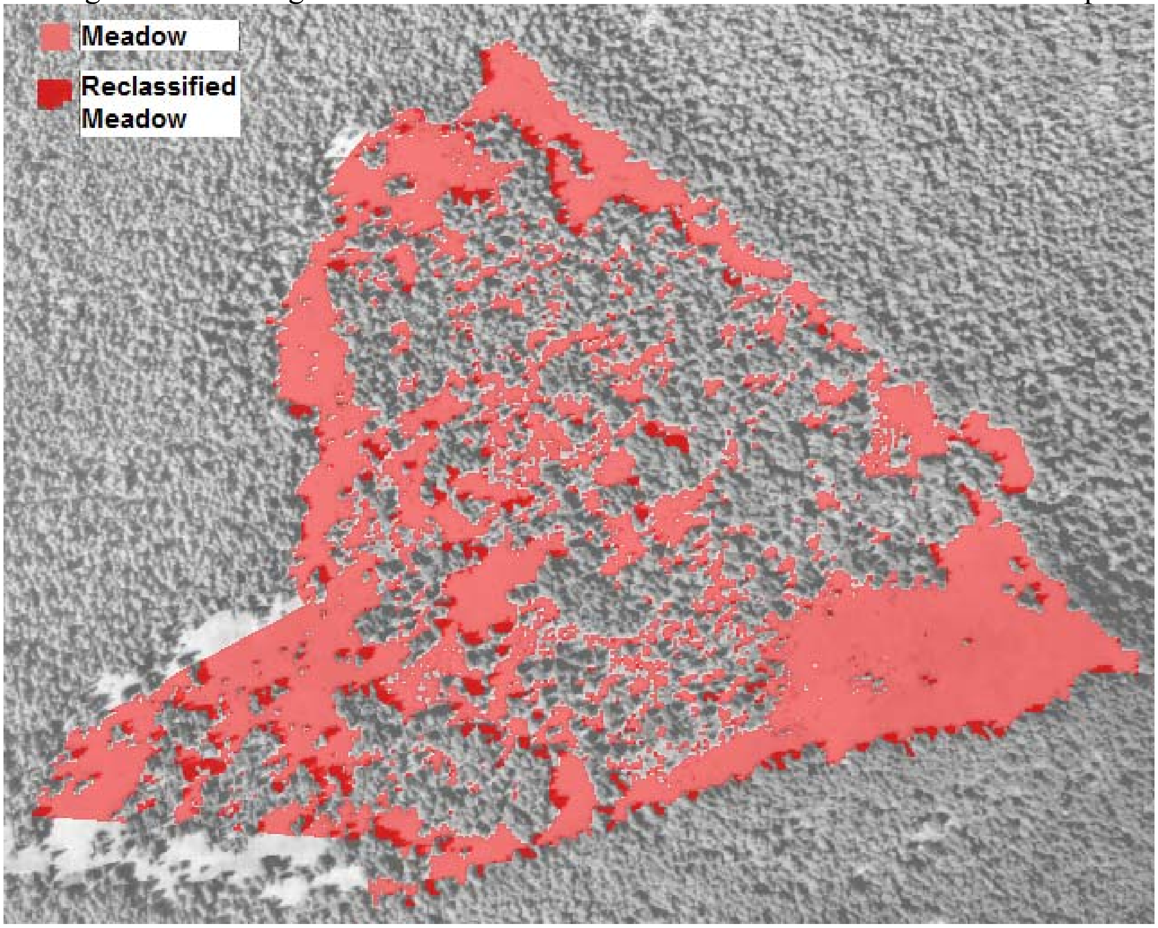


Figure A.6 Bunchgrass Meadow and reclassified meadow shadow area 2000 map

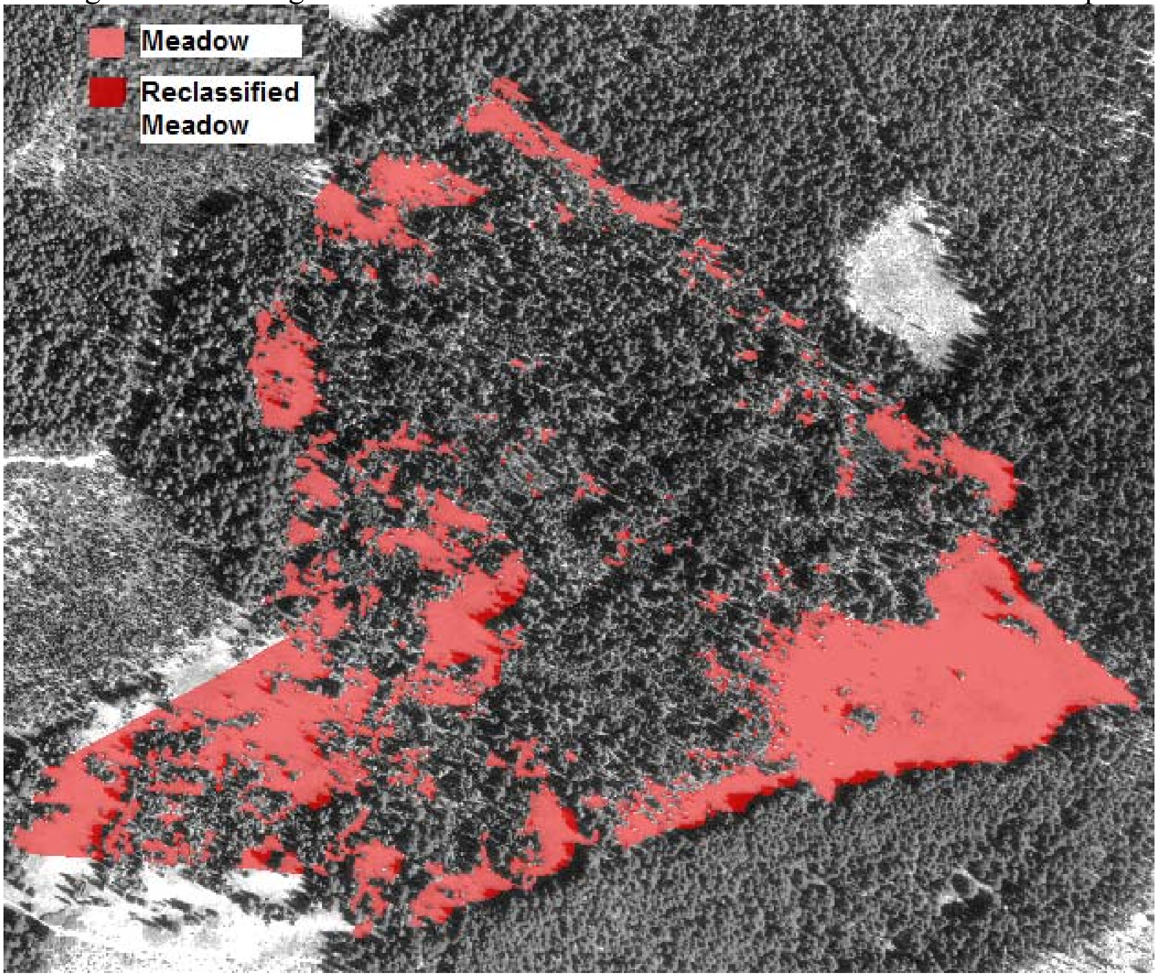


Table A1. Lookout area by aspect

Lookout		
	m^2	**% of Study Area**
N	2,284,653	41.6
E	1,226,022	22.3
S	943,116	17.2
W	1,042,531	19.0

Figure A.7. Map of Lookout aspect classes

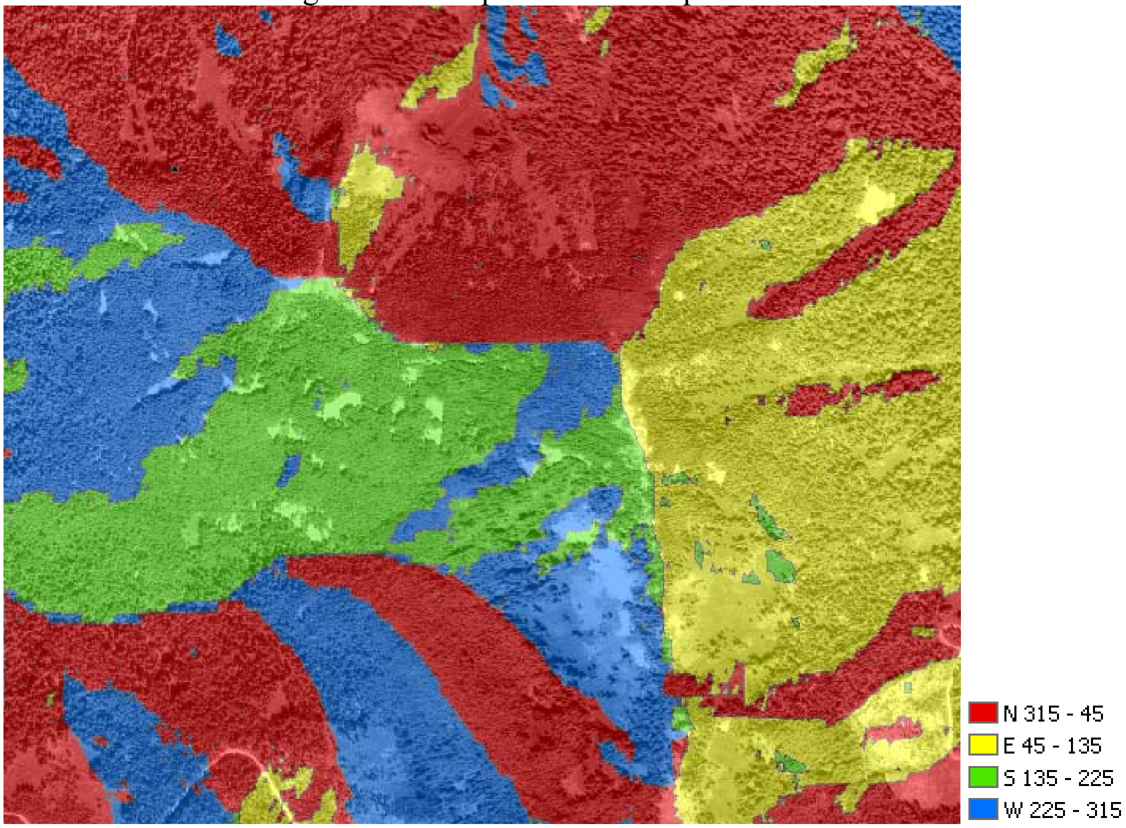


Table A2. Lookout area by slope

Lookout Area by Slope		
° Slope	**m^2**	**% of Area**
0-21	1,675,642	27
21-27	1,810,367	29
27-31	1,483,691	24
31-75	1,188,892	19

Figure A.8. Map of Lookout slope classes (degrees)

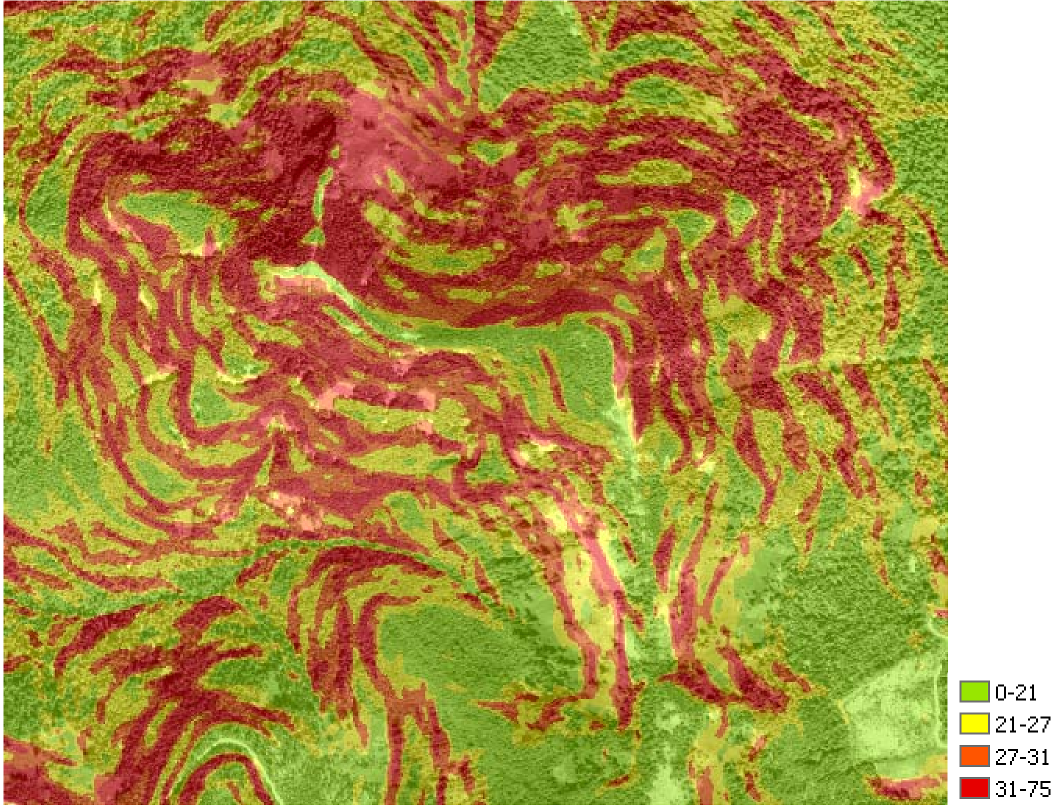


Table A3. Area by aspect

Bunchgrass		
	m^2	**% of Area**
N	313,517	22.2%
E	127,716	9.0%
S	376,599	26.6%
W	597,578	42.2%

Figure A.9. Map of Bunchgrass aspect classes

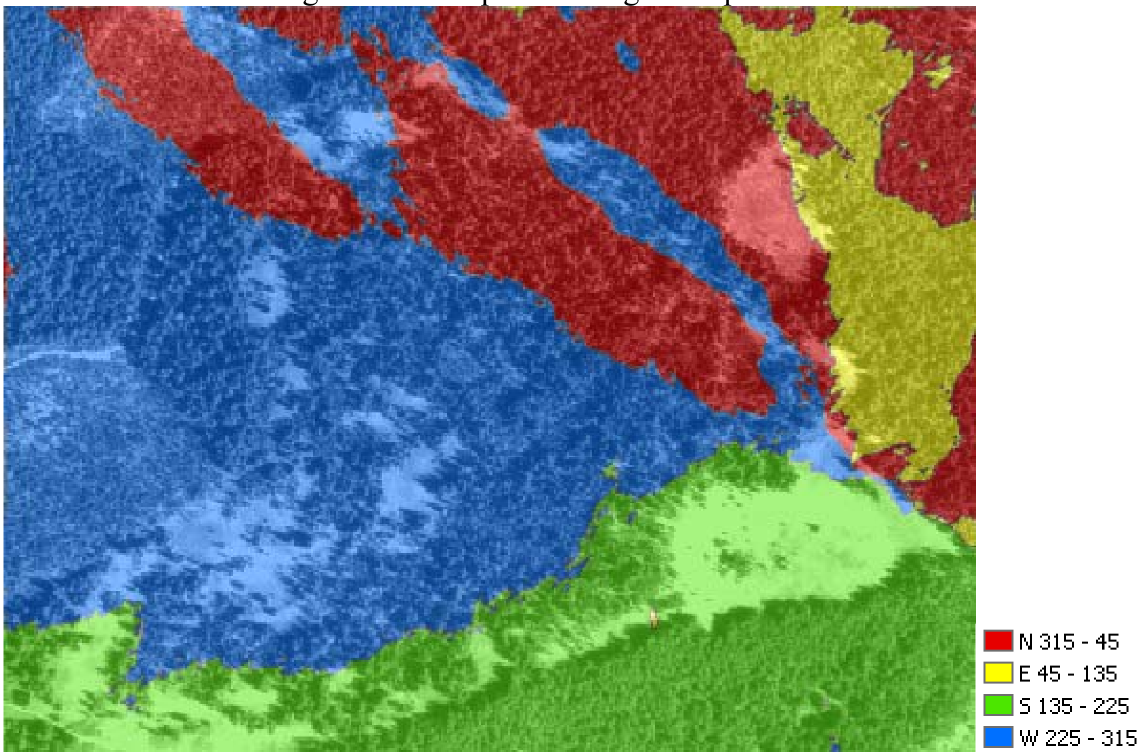
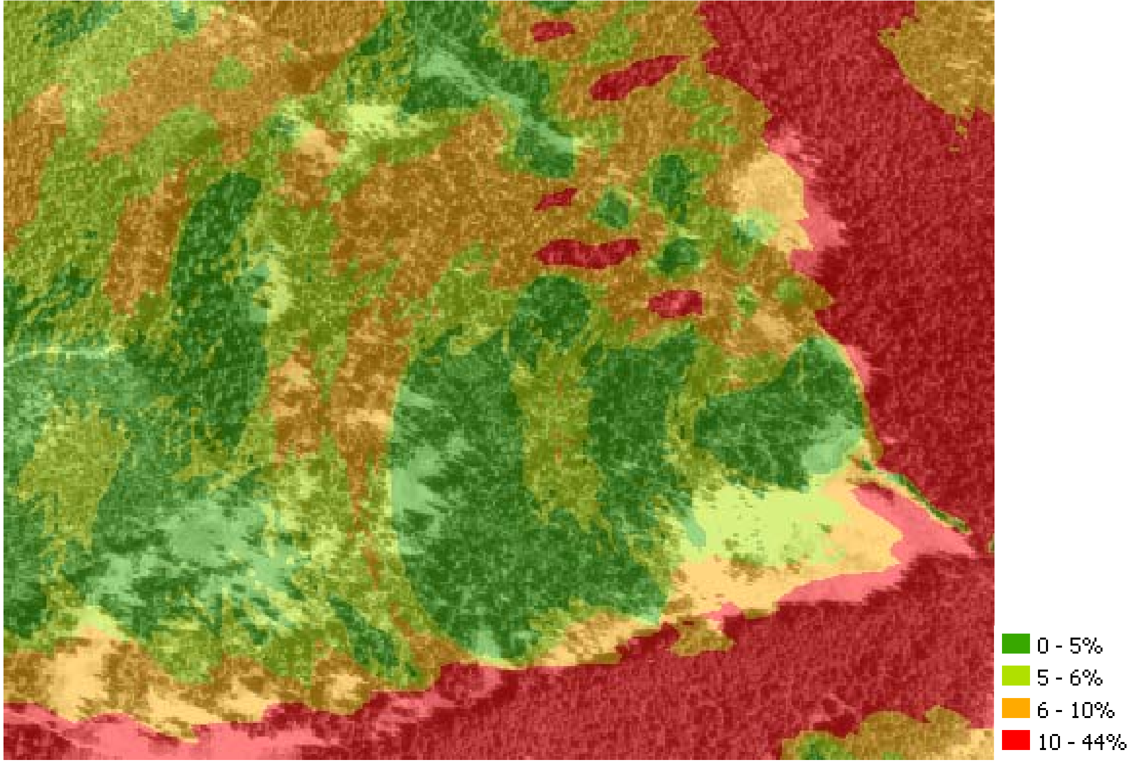


Table A4. Bunchgrass area by slope

Bunchgrass Area by Slope		
° Slope	**m^2**	**%**
0-5	420867	25
5-6	432180	25
6-10	422205	25
10-44	421212	25

Figure A.10. Map of Bunchgrass slope classes



APPENDIX B

Figure B.1. Bunchgrass Tree location map 2004

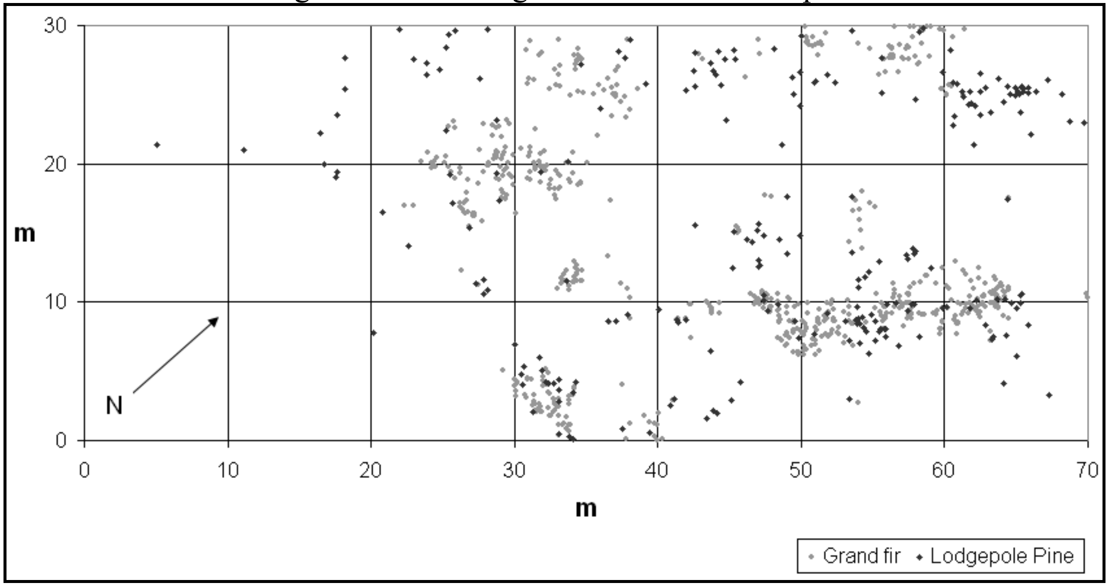


Figure B.2. Bunchgrass Age class map 2004

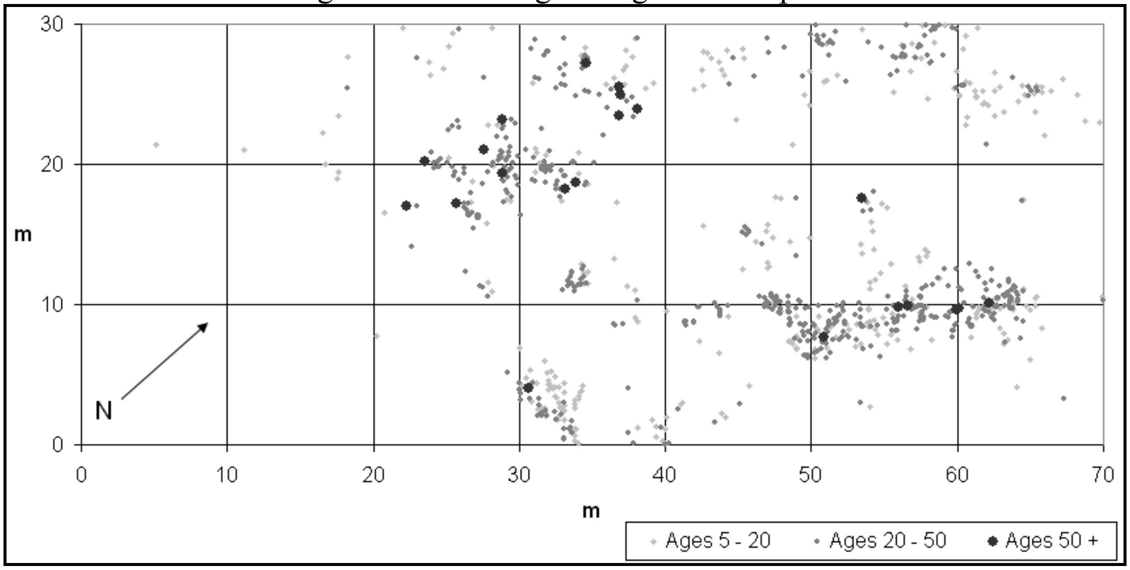


Figure B.3. Bunchgrass establishment map 1935

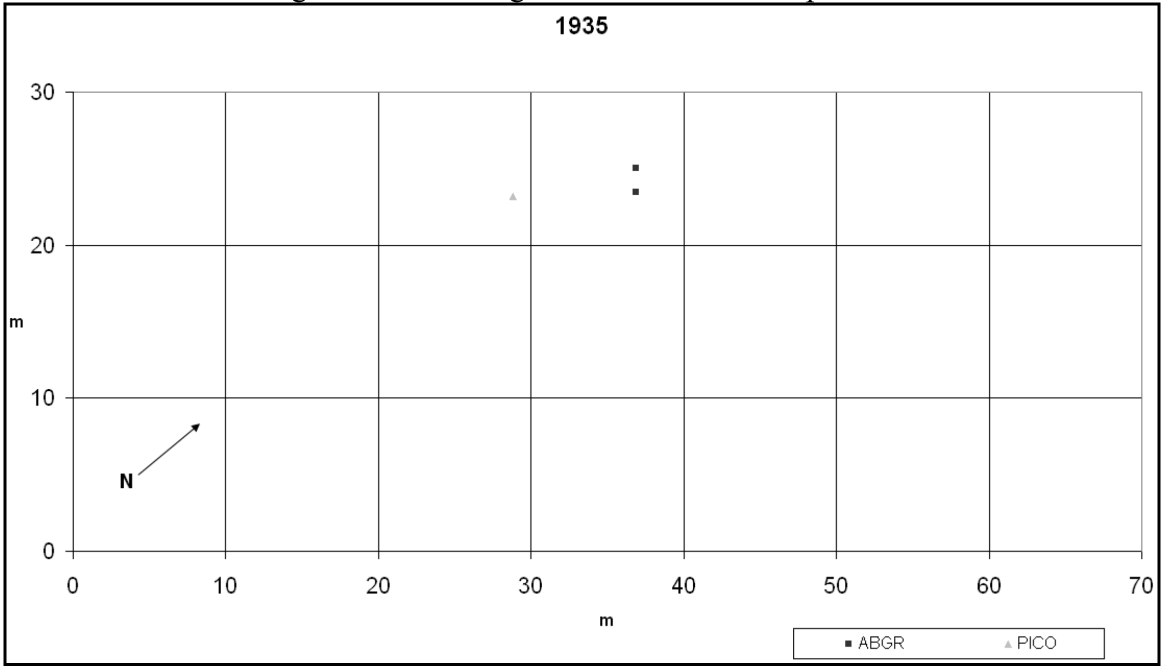


Figure B.4. Bunchgrass establishment map 1945

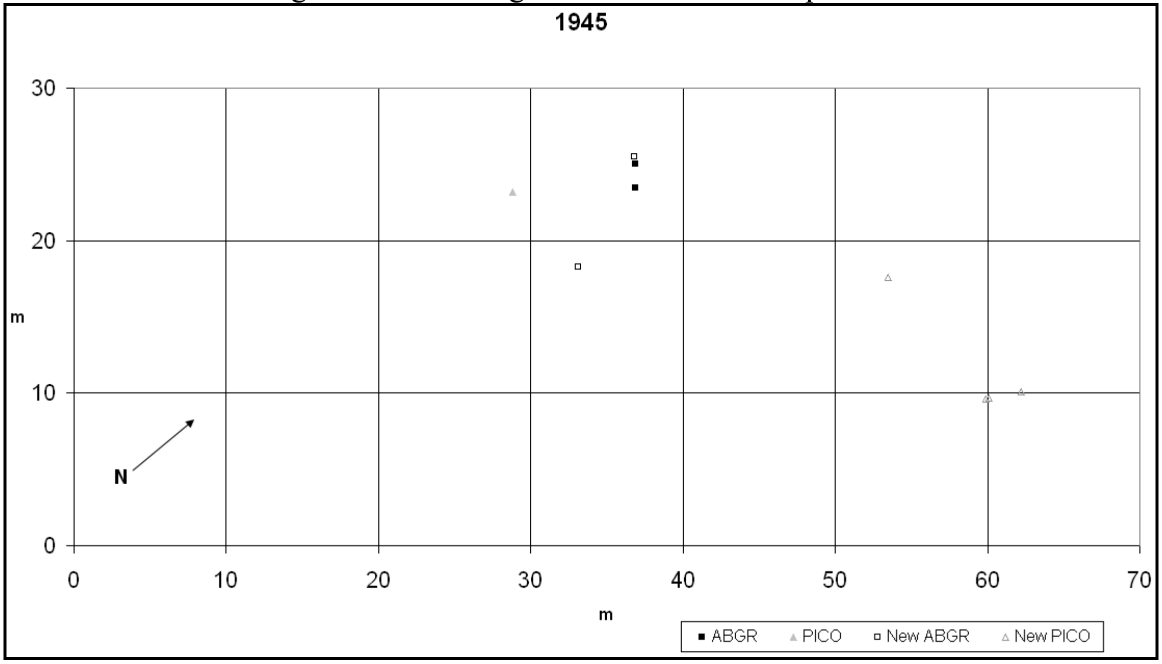


Figure B.5. Bunchgrass establishment map 1955

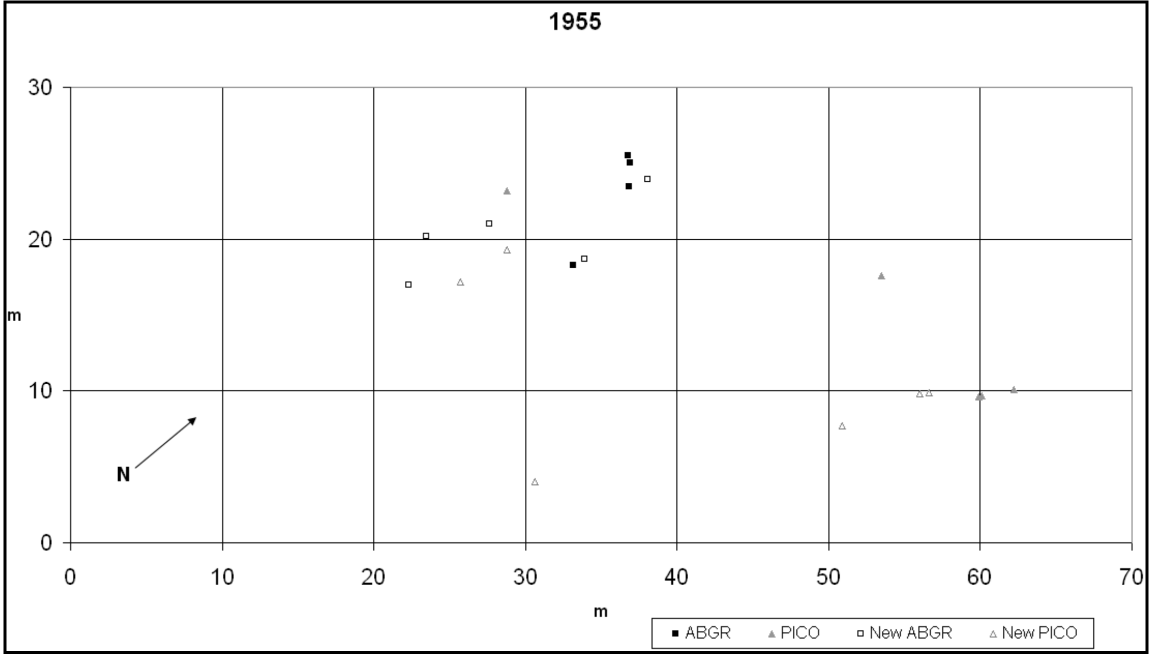


Figure B.6. Bunchgrass establishment map 1965

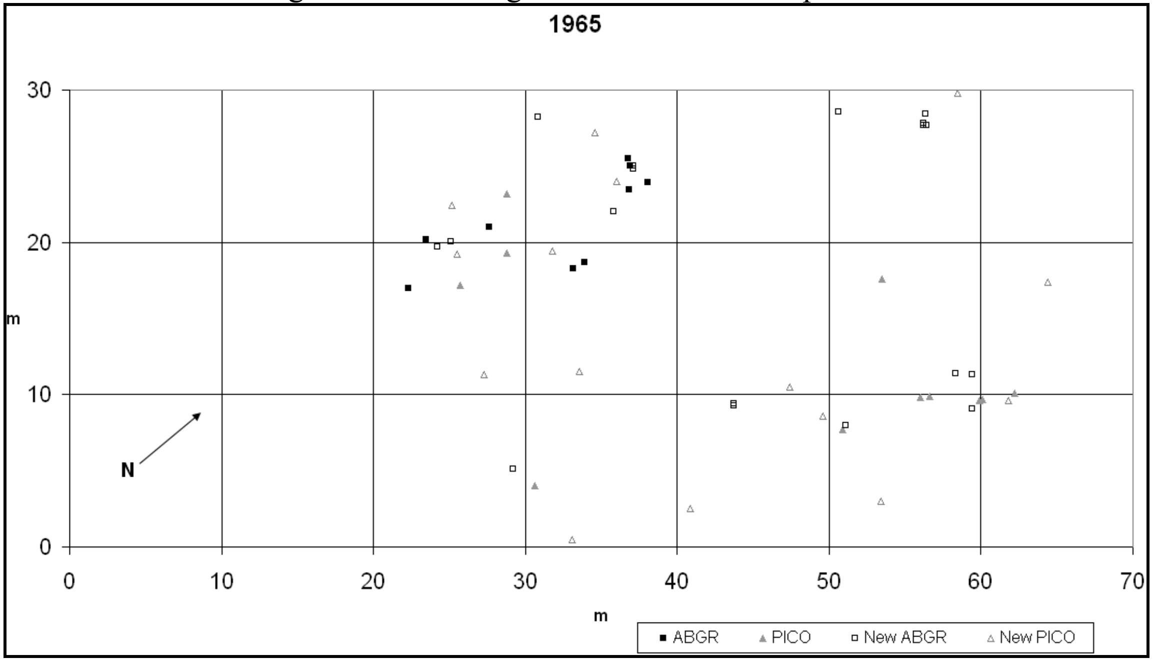


Figure B.7. Bunchgrass establishment map 1975

Figure B.8. Establishment map 1985

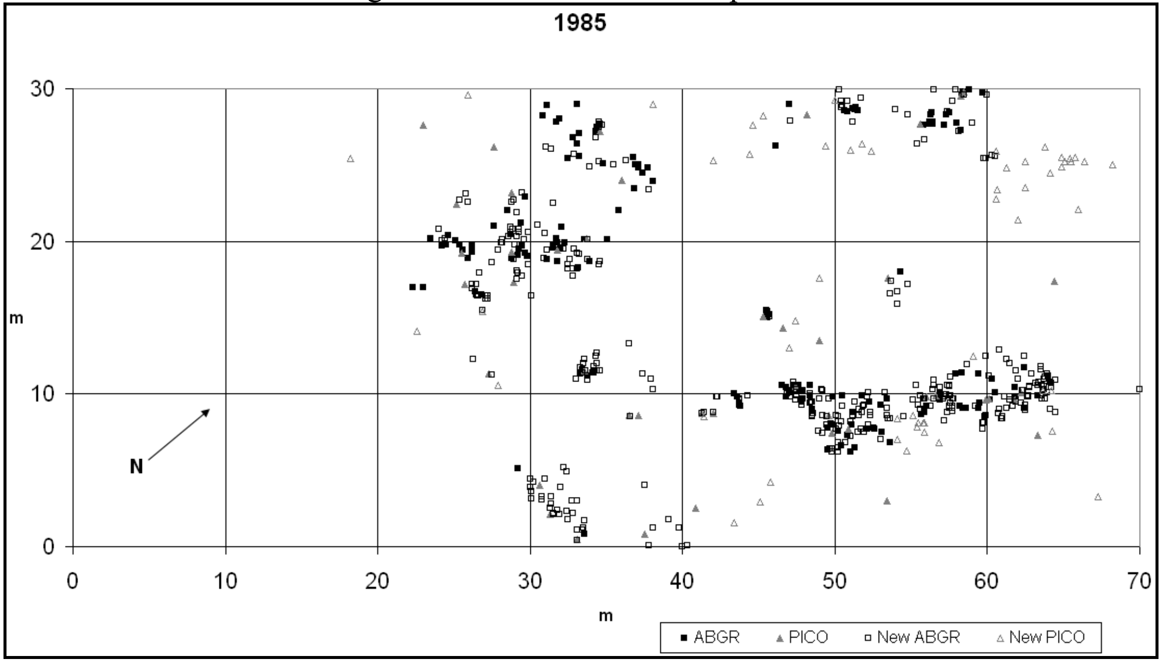


Figure B.9. Bunchgrass establishment map 1995

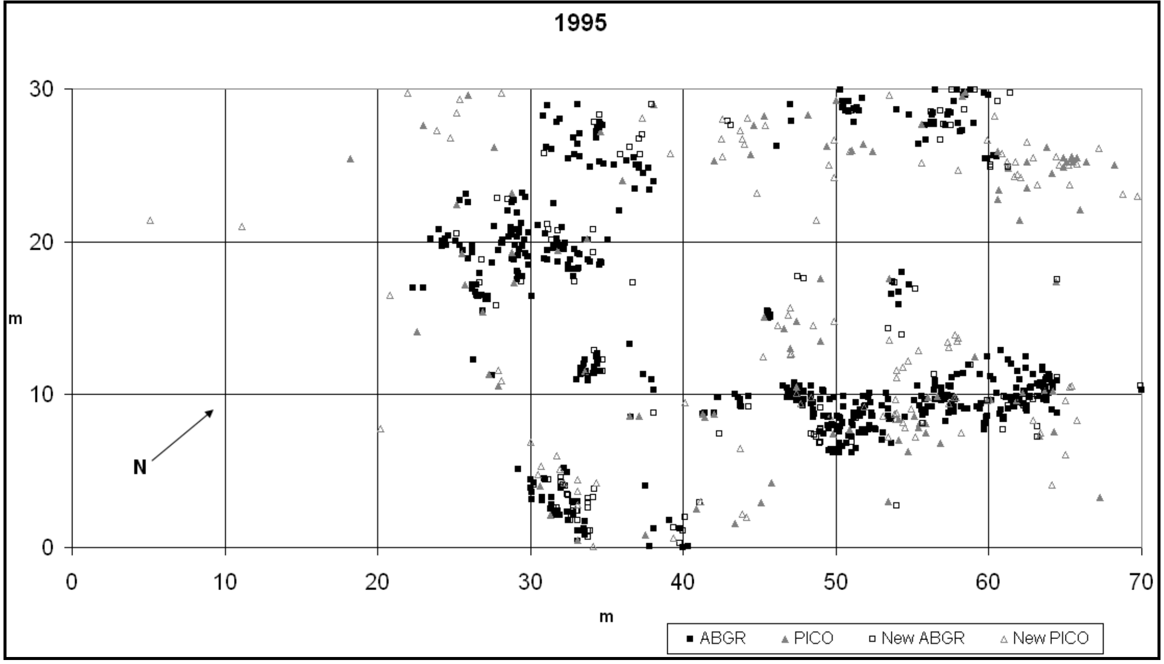
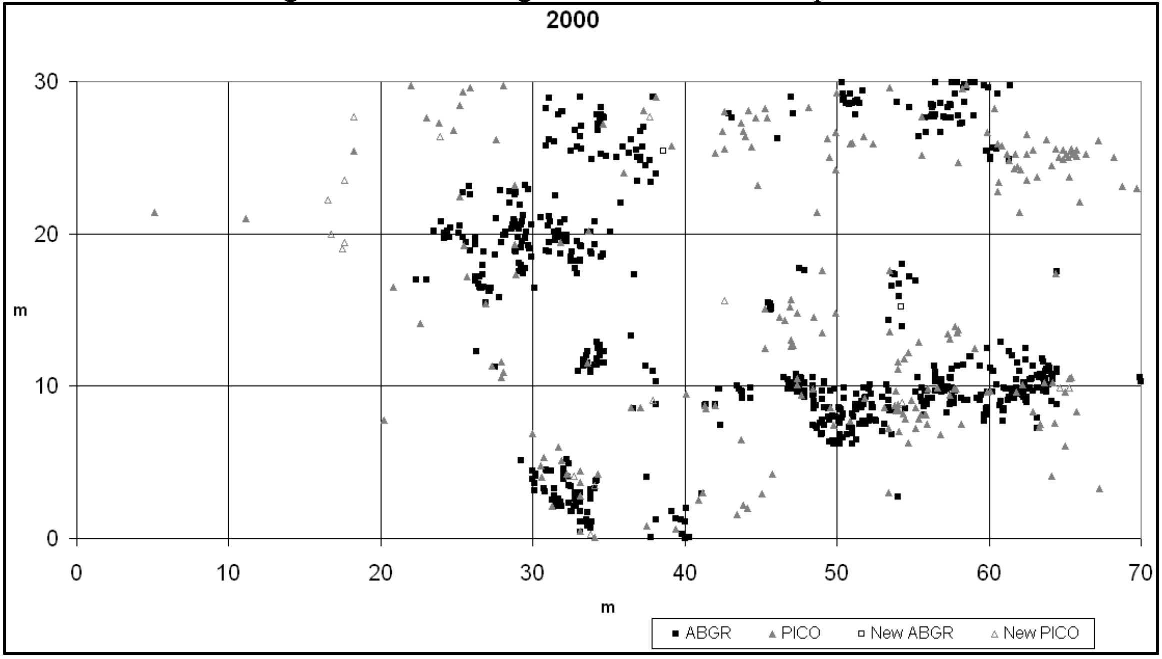


Figure B.10. Bunchgrass establishment map 2000



APPENDIX C

The detailed descriptions for components of the LPJ-GUESS model are listed below.

Daily Precipitation Interpolation

The probability of rain (1) is calculated where:

(1) Probability of rain = 0.25 + (0.75 * rain days/number of days in month)

If a randomly generated fraction is <= Probability of rain, then a daily precipitation (2) amount is assigned based on an exponential distribution:

(2) Daily precipitation = (-log(random fraction)) $^{1.2}$ * monthly precipitation

The daily precipitation amount (3) is normalized by multiplying:

(3) Daily precipitation * (Cumulative monthly precipitation before day being considered/Total monthly precipitation)

Leaf Phenology

The fraction of full leaf out cover for deciduous plant functional type's and grass is calculated as:

Full leaf out cover = minimum of:

$$\left\{ \begin{array}{l} 1.0 \qquad \text{or} \\ \\ \dfrac{\text{(accumulated number of days above } 5\,^{\circ}\text{C} - \text{cumulated chilling days} <= 0\,^{\circ}\text{C)}}{\text{Growing degree days above } 5\,^{\circ}\text{C to attain full leaf cover}} \end{array} \right.$$

Where growing degree days above 5 °C is:

200 for shade tolerant deciduous trees

150 for shade intolerant deciduous trees

50 for grass

Canopy Exchange – Photosynthesis and Water Exchange

Photosynthesis is based on Haxeltine and Prentice (1996), and is calculated by integrating daily gross daily photosynthesis minus respiration at 1 m vertical increments through the tree canopy. The Lambert-Beer law (Monsi & Saeki 1953) is used to calculate the fraction of photosynthetically active radiation (APAR) captured by the tree canopy at a single vertical depth. Gross daily photosynthesis, *A*, is constrained by the amount of leaf area, air temperature, CO_2 partial pressure, and available APAR, and is given by:

(4) A = Net Photosynthesis + Leaf Respiration

Canopy Exchange - Evapotranspiration

Actual evapotranspiration, AET, is constrained by soil moisture and based on a Monteith parameterization given by:

(5) $AET = \min(E_{supply}, E_{demand})$

Where, E_{supply} = Maximum ET rate * root weighted soil moisture availability

Maximum ET rate = 5 mm/day

And, $E_{demand} = eet*\alpha_m*gc/ (gc + GM)$

eet = equilibrium evapotranspiration rate based on latitude, temperature, and fraction of sunshine hours.

gc = non water stressed canopy conductance calculated by photosynthesis routine (above)

α_m = 1.391 and GM = 3.26 are empirical parameters from Monteith 1995

Canopy Exchange - Respiration

Autotrophic respiration, R, is calculated daily for sapwood, root, and growth, and is based on a modified Arrhenius dependence on temperature g(T) (Lloyd & Taylor, 1994, Haxeltine & Prentice, 1996):

(6) $R = R_{sap} + R_{root} + R_{growth}$

Where, R_{sap} = respcoeff* k * c_mass / cton * g(T_{air})

R_{root} = respcoeff * k * c_mass / cton * g(T_{soil})

R_{growth}= (assimilation - R_{sap}- R_{growth}) *0.25

respcoeff = plant functional type respiration coefficient

k = 0.0548, respiration constant

c_mass = carbon biomass (kgC/m^2)

cton = carbon-nitrogen mass ratio of tissue constant

g(T) = EXP [308.56 * (1 / 56.02 - 1 / (T - 227.13))]

T = absolute temperature in K

assimilation = daily net assimilation (GPP-leaf respiration) kgC/m^2/day

Canopy Exchange - Net primary productivity

Net annual primary productivity (NPP, kgC m^{-2}) is given by:

(7) $NPP = GPP-(R_m - R_g)$

where *GPP* is net assimilated NPP from photosynthesis – maintenance respiration R_m is total maintenance and R_g is the growth respiration.

Soil Water

Updates soil water in two 0.5 meter deep soil layers, adding rain and snow melt inputs to the first layer, losses to and base flow losses from the second layer, while subtracting evaporation from the soil surface, and evapotranspiration and interception by vegetation.

Decomposition

Daily organic matter decomposition rates are first calculated:

*(8) decay rate = e(-klitter*gtemp_soil*moist_response/365.0)*

Where, *klitter* is a decay constant

gtemp_soil is a daily respiration response at 0.25 m soil depth

moist_response is 0.25 + (0.75 * soil water content)

Decomposition of leaf, root, wood, and allocation to reproduction is then distributed as carbon flux to the atmosphere, and slow and fast organic matter pools.

Growth - Carbon Allocation

Carbon (8) is initialized into four tissue pools and annual increments to each pool occur for each live plant functional type. The annual net primary productivity less the fraction used for reproduction is allocated to the four tree carbon tissue pools if growth conditions permit. Grasses have only leaf and root tissue pools.

(9) $C = C_{leaf} + C_{root} + C_{sapwood} + C_{heartwood}$

Where, $C_{leaf\_inc} = ltor * C_{root}$

$C_{root\ \_inc} = (C_{leaf\_inc} + C_{leaf})/ltor - C_{root}$

$C_{sapwood\_inc} = bminc - C_{leaf\_inc} - C_{root\ \_inc}$

$C_{heartwood\_ind} = - C_{sapwood\_inc}$

ltor= leaf to root mass ratio

bminc = individual biomass increment of cmass_leaf_inc + cmass_root_inc + cmass_sap_inc

Growth - Plant Allometry

Tree height (10) is used to determine the vertical distribution of photosynthetically active radiation, and crown area (11) is used to calculate foliar projective cover and is given by:

$$(10)\ \text{Height} = k_{\text{allom2}} \cdot D^{k_{\text{allom3}}}$$

$$(11)\ \text{CA} = \min\left(k_{\text{allom1}} \cdot D^{krp}, CA_{\max}\right)$$

Where, k_{allom1}, k_{allom2}, k_{allom3} and k_{rp} are constants

D= mean stem diameter, and

$CA_{\max}$ = maximum crown area (m).

LAI (12) (m^2 leaf / m^2 area) is given by:

$$(12)\ LAI = C_{\text{leaf}} * SLA/CA$$

C_{leaf} is leaf carbon mass,

SLA is the specific leaf area in kg C/m^2,

CA is the crown area

Growth - Tissue Turnover

A portion of leaf, root and sapwood tissue is lost as living tissue each year and is reallocated by:

$$(13)\ C_{\text{t,new}} = C_{\text{t,old}} * (1 - turn_{\text{t}})$$

Where, $turn_t$ is the turnover rate (year^{-1}) for tissue t (C_{tleaf}, C_{troot}, C_{tsapwood})

C_{tleaf} is kg C/m^2 transferred to the litter pool

C_{troot} is kg C/m^2 transferred to the litter pool

$C_{tsapwood}$ is kg C/m^2 converted to heartwood biomass

Fire Mortality

Mortality due to fire disturbance is based on Thonicke et al. 2001 fire routine and uses a calculated fire probability. Fire is stochastically implemented in a patch if a random fraction falls below the calculated fire probability that is defined by fuel load availability, and upper soil layer moisture conditions given in:

(14) Fire probability = $s * e^{((s-1)/ (k1(s-1)3 + k2(s-1)2 + k3(s-1)))}$

Where s = annual mean daily fire probability (n/365); k1, k2, and k3 are constants, and

n = SUM ($e^{(-\Pi*(\text{daily upper soil } H_2O)/\text{mean litter moisture flammability threshold})2)}$)

Above ground biomass is transferred to the atmosphere, and below ground biomass is transferred to the litter pool. Each individual is stochastically killed in a patch if a random fraction falls above a specified plant functional type fire resistance parameter.

Generic Disturbance Mortality

Mortality from a generic disturbance, such as, wind throw, ice, land movement, and insect outbreak is implemented when a random draw from a normal distribution falls below a specified probability of disturbance return. All plant functional type's are removed from the patch when a generic disturbance in implemented. This study uses 1 disturbance per 200 years.

Mortality

Mortality is randomly implemented annually for each patch before establishment, and can be caused by several factors, such as, growth suppression, exceeding bioclimatic tolerance limits, or age. Mortality due to exceeding a bioclimatic limit for a plant functional type is implemented if the minimum monthly temperature over the past 20 years falls below a plant functional type's specified minimum survival temperature. Mortality due to age and growth suppression is stochastically implemented for each individual in a patch by a random draw from a Normal distribution defined by a mortality probability. The mortality probability is the sum of the non-stressed age and growth efficiency mortality probability, and is given by:

$$(15)\ \textit{Mortality probability} = \min(\textit{mort}_{\text{age}} + \textit{mort}_{\text{greff}}, 1)$$

Where $\textit{mort}_{\text{age}} = \min(1.0 \text{ or } -\log(F) * (Q+1)/\textit{longevity}*(\textit{age}/\textit{longevity})^{Q})$

F = Fraction of population expected to survive to specified longevity

Q = Shape parameter

and $mort_{\text{greff}}$ =

$$\begin{cases} 0 & \text{if the 5 year average growth efficiency (kg C/m}^2\text{ leaf/year) is greater than a plant functional type specified threshold;} \\ 0.3 & \text{if the 5 year average growth efficiency (kg C/m}^2\text{ leaf/year) is less than a plant functional type specified minimum threshold;} \end{cases}$$

$\frac{\text{crown area-1}}{\text{crown area}}$ if the summed crown area exceeds 100 in a patch, and is ≥ 0.3

Establishment

Establishment for each plant functional type is randomly implemented annually after mortality, and is constrained by a bioclimatic limit, light availability at the forest floor, a plant functional type maximum establishment rate, and a specified net C allocation to reproduction. The expected density of new individuals (saplings / m^2 /year) is given in Equation (16).

(16) Establishment = $est_{\text{max}} * (k_{\text{reprod}} * C_{\text{repr}} + k_{\text{bgestab}}) * \exp[\alpha(1 - 1/F)]$

where $est_{\max}$ is the maximum establishment rate (saplings / m^2 /year); k_{reprod} is a constant for establishment; C_{repr} is the net carbon allocated to reproduction (10%); and k_{bgestab} is a constant that accounts for a spatial mass effect of the propagule pool within a patch; α is a plant functional type specific constant where higher values represent a steeper decline in the establishment rate due to environmentally limiting factors (i.e. limited light availability, limited soil water, low temperatures); F represents potential productivity as a fraction of the maximum possible for the current plant functional type at the forest floor. The number of individuals added to a patch is determined stochastically by making a random draw from a Poisson distribution if the expected number of individuals establishing is less than or equal to 100, or using a normal distribution otherwise. The distributions are constrained by the expected number of individuals establishing. Saplings are allocated biomass that is proportional to the potential NPP at the forest floor and do not exceed 1.2 m in height. Grass is modeled as one individual and initial biomass establishment is limited by potential forest floor net assimilation (kg C/m^2/year).

APPENDIX D

LPJ-GUESS Parameterization Definition

LPJ-GUESS uses a variety of parameters to define and determine vegetation dynamics. These parameters can be set by the user to represent specific conditions that may exist in the area being modeled. Table D1 lists the parameters used for all model simulations and Table D2 provides descriptions of the parameters. This study re-defined the following parameters.

Shade tolerance parameters: alphar, est_max, greff_min, parff_min, and turnover_sap were defined to distinguish between shade tolerant and intolerant plant functional types' establishment, minimum growth efficiency, minimum light requirements, and sap wood turnover rate according to Hickler et al. (2008). Hickler's vegetation dynamics parameters were calibrated using data on pristine forest vegetation dynamics, composition, and structure in different biomes (P. Miller & T. Hickler, unpublished data). Tree species planted at the Hickler et al. (2008) young plantation study sites (FACE) were not explicitly used to define these parameter definitions. Hickler et al's. (2008) parameter settings were used since these settings resulted in more realistic representations of the percent open patches than the original settings of Smith et al. (2001). Extended simulations with Hickler's parameters resulted in similar percentages of open forest cover as observed by Takaoka & Swanson (2008) and Dailey (2007) (~5%). Also, Hickler's est_max definition most closely matched empirical measurements from Bunchgrass Meadow Special Habitat Area plot used in Chapter 3.

The five Hickler et al. (2008) parameter settings were found to result in minimal differences of output annual net primary productivity, carbon biomass, and tree cover output for the baseline and the climate, CO_2, and fire scenarios (Chapter 4, Table 4.2, Scenario 1 and 12) as compared to outputs run with original parameters from Smith et al. 2001.

The distinterval parameter was defined to better represented the average occurrence of generic disturbances in Pacific Northwest forests (Halpern, 2009, unpublished dendrochronology data), and to allow a better representation of older tree age classes. The fire resistance parameter, fireresist, was defined to distinguish between less fire resistant plant functional types (e.g. Pacific silver fir) and more fire resistant plant functional types (e.g. Douglas-fir) based on parameter settings from Thonicke et al. (2001) for all plant functions types except BE, for which Smith et al. (2001) was used. The ITNE fireresist parameter was based on empirical data for Douglas-fir and Ponderosa pine from the western U.S. (Hood et al. 2007). Longevity values were set to define maximum non-stressed lifespans in years for each plant functional type based on Franklin & Dyrness (1988). The pstemp_high and pstemp_low parameters were defined to represent optimal high and low photosynthesis temperatures of temperate conifer plant functional types (ITNE and TTNE) according to Hickler (2009). The shade tolerance of BE was defined to represent shade tolerant species of the Pacific Northwest (e.g. *Quercus chrysolepis* (Canyon Live Oak), *Arbutus menziesii* (Pacific Madrone), *Castanopsis chrysophilia* (Giant Chinkpin). Higher minimum light requirements of parff_min values for grass are used to represent higher light requirements for meadow species found by

Haugo and Halpern (2007). The tcmax_est parameter was defined to represent the maximum temperature for establishment for Pacific Northwest boreal needleleaved evergreen (e.g. Pacific silver fir, Lodgepole pine) and broadleaved evergreen plant functional types according to Silvics (1990) and Thompson (1999). Temperate needleleaved evergreen plant functional types, ITNE and TTNE (e.g. Douglas-fir, Western hemlock) were defined to distinguish between boreal and temperate plant functional types. Parameters of: tcmax_est, tcmin_est, and tcmin_surv were defined to represent maximum and minimum temperatures for establishment and the minimum temperature for survival according to Silvics (1990) and Thompson (1999). Parameters in table D1 not marked with a special character are original parameter values used by Smith et al. (2001).

Table D1. Plant Functional Types Parameter Values Settings Used For All Model Runs

Parameter Name	TBNE	IBNE	TTNE	ITNE	TBS	IBS	BE	GRASS
alphar[*]	0.8[*]	2[*]	0.8[*]	2[*]	0.8[*]	2[*]	2[*]	10
crownarea_max	27.3	27.3	27.3	27.3	27.3	27.3	27.3	
cton_leaf	29	29	29	29	29	29	29	29
cton_root	29	29	29	29	29	29	29	29
cton_sap	330	330	330	330	330	330	330	
distinterval[+]	200[+]	200[+]	200[+]	200[+]	200[+]	200[+]	200[+]	200[+]
emax	5	5	5	5	5	5	5	5
est_max[*]	0.05[*]	0.15[*]	0.05[*]	0.15[*]	0.05[*]	0.15[*]	0.15[*]	
estinterval	1	1	1	1	1	1	1	
fireresist†,[§]	0.12[§]	0.12[§]	0.12[§]	0.6†	0.12[§]	0.12[§]	0.12	0.5
gdd5min_est[¶]	600	600	600[¶]	600[¶]	1000	500	1200	0
gmin	0.3	0.3	0.3	0.3	0.5	0.5	0.5	0.5
greff_min[*]	0.09[*]	0.11[*]	0.09[*]	0.11[*]	0.09[*]	0.11[*]	0.09[*]	
include	1	1	1	1	1	1	1	1
intc	0.06	0.06	0.06	0.06	0.02	0.02	0.02	0.01
k_allom1	150	150	150	150	200	200	200	
k_allom2	40	40	40	40	40	40	40	
k_allom3	0.67	0.67	0.67	0.67	0.67	0.67	0.67	
k_chilla	0	0	0	0	0	0	0	
k_chillb	100	100	100	100	100	100	100	
k_chillk	0.05	0.05	0.05	0.05	0.05	0.05	0.05	

Table D1. Plant Functional Types Parameter Values Settings Used for All Model Runs (Continued)

Parameter Name	TBNE	IBNE	TTNE	ITNE	TBS	IBS	BE	GRASS
k_latosa	3000	3000	3000	3000	4000	4000	4000	
k_rp	1.6	1.6	1.6	1.6	1.6	1.6	1.6	
kest_bg	1	1	1	1	1	1	1	
kest_pres	0	0	0	0	0	0	0	
kest_repr	200	200	200	200	200	200	200	
lambda_max	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8
leaflong	2	2	2	2	0.5	0.5	2	1
leaftype	Needle-leaf	Needle-leaf	Needle-leaf	Needle-leaf	Broad-leaf	Broad-leaf	Broad-leaf	
lifeform	TREE	TREE	TREE	TREE	TREE	TREE	TREE	GRASS
litterme	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.2
longevityǂ	500	500	500ǂ	800ǂ	430	300	400	
ltor_max	1	1	1	1	1	1	1	0.5
parff_min[*]	1000000[*]	200000[*]	1000000[*]	2000000[*]	1000000[*]	2000000[*]	2000000[*]	2500000[×]
pathway	C3	C3	C3	C3	C3	C3	C3	C3
phengdd5ramp	0	0	0	0	200	150		50
phenology	EVER GREEN	EVER GREEN	EVER GREEN	EVER GREEN	SUMMER GREEN	SUMMER GREEN	EVER GREEN	
pstemp_high[*]	25	25	25[*]	25[*]	25	25	30	30
pstemp_low[*]	10	10	15[*]	15[*]	15	10	20	10
pstemp_max	38	38	38	38	38	38	42	45
pstemp_min	-4	-4	-4	-4	-2	-4	-4	-5
reprfrac	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
respcoeff	1	1	1	1	1	1	1	1
rootdist	0.67/ 0.33	0.67/ 0.33	0.67/ 0.33	0.67/ 0.33	0.67/ 0.33	0.67/ 0.33	0.67/ 0.33	0.9/ 0.1
shadetolerance‡	Shade-tol	Shade-intol	Shade-tol	Shade-intol	Shade-tol	Shade-intol	Shade-tol ‡	
sla	21.73	21.73	21.73	21.73	41.11	41.11	21.73	29.89
tcmax_est‡[,¶]	2‡[¶]	2‡[¶]	10‡[¶]	10‡[¶]	6	1000	9‡[¶]	1000
tcmin_est‡[¶]	-32	-32	-10‡[¶]	-10‡[¶]	-18	-1000	3	-1000
tcmin_surv‡[¶]	-32	-32	-10‡[¶]	-10‡[¶]	-18	-1000	3	-1000
turnover_leaf	0.5	0.5	0.5	0.5	1	1	0.5	1
turnover_root	0.5	0.5	0.5	0.5	1	1	0.5	0.5
turnover_sap[*]	0.03[*]	0.08[*]	0.03[*]	0.08[*]	0.03[*]	0.08[*]	0.03[*]	
twmin_est	-1000	-1000	-1000	-1000	-1000	1000	-1000	-1000
twminusc	0	0	0	0	0	0	0	0
wooddens	200	200	200	200	200	200	200	
wscal_min	0.35	0.35	0.35	0.35	0.35	0.35	0.35	0.35

Parameters defined by Smith et al. 2001 unless otherwise noted below

* Hickler et al. (2008) Validated establishment values most closely matched Bunchgrass Meadow Special Habitat Area Plots used in Chapter 3
† Hood et al. (2007) Fire resistance values for Douglas-fir.
‡ Silvics of North America USDA Forest Service Agricultural Handbook 654.
¶ U.S. Geological Survey Atlas (1999).
ǂ Franklin & Dyrness (1988).
§ Thonicke et al. (2001) Fire resistance values.
+ Halpern, C., et al. Unpublished dendrochronology data for Bunchgrass Meadow Special Habitat Area 2009.
x Smith et al. (2001); Haugo & Halpern (2007), higher minimum PAR values for grass are used to represent higher light requirements for meadow species found by Haugo & Halpern, 2007.

Table D2. Plant Functional Type Parameter Values Description

Parameter	**Description**
alphar	Shape parameter for recruitment-juvenile growth rate relationship
crownarea_max	Maximum tree crown area (m^2)
cton_leaf	Leaf C:N mass ratio
cton_root	Fine root C:N mass ratio
cton_sap	Sapwood C:N mass ratio
distinterval	Average return time for a generic patch destroying disturbance
emax	Maximum evapotranspiration rate (mm/day)
est_max	Maximum sapling establishment rate (individual/m^2/year)
estinterval	Years between establishment events
fireresist	Fire resistance (0-1)
gdd5min_est	Minimum GDD on 5 ºC base for establishment
gmin	Canopy conductance not assoc with photosynthesis (mm/s)
greff_min	Threshold for growth suppression mortality (kg C/m_2 leaf/yr)
include	Include Plant Functional Type in analysis
intc	Interception coefficient
k_allom1	Constant in allometry equations scaling crown area
k_allom2	Constant in allometry equations scaling tree height
k_allom3	Constant in allometry equations scaling tree height
k_chilla	Constant in equation for budburst chilling time requirement
k_chillb	Coefficient in equation for budburst chilling time requirement
k_chillk	Exponent in equation for budburst chilling time requirement
k_latosa	Tree leaf to sapwood cross section area ratio
k_rp	Constant in allometry equations scaling crown area
kest_bg	Constant in equation for tree establishment rate
kest_pres	Constant in equation for tree establishment rate
kest_repr	Constant in equation for tree establishment rate

Parameter	**Description**
lambda_max	Non-water-stressed ratio of intercellular to ambient CO_2 ppm
leaflong	Leaf longevity (years)
leaftype	Single word parameter for leaf type ('needleleaf', 'broadleaf')
lifeform	Life form ("TREE" or "GRASS")
litterme	Litter moisture flammability threshold (fraction of AWC)
longevity	Expected longevity under lifetime non-stressed conditions (yr)
ltor_max	Non-water-stressed leaf:fine root mass ratio
parff_min	Minimum forest floor PAR for grass growth/tree establishment ($J/m^2/day$)
pathway	Biochemical pathway ("C3" or "C4")
phengdd5ramp	GDD on 5 ºC base to attain full leaf cover
phenology	Phenology ("EVERGREEN", "SUMMERGREEN", "RAINGREEN" or "ANY")
pstemp_high	Approximate higher range of temperature optimum for photosynthesis (ºC)
pstemp_low	Approximate lower range of temperature optimum for photosynthesis (ºC)
pstemp_max	Maximum temperature limit for photosynthesis (ºC)
pstemp_min	Approximate low temp limit for photosynthesis (ºC)
reprfrac	Fraction of NPP allocated to reproduction
respcoeff	Respiration coefficient (0-1)
rootdist	Fraction of roots in each soil layer (first value=upper layer)
shadetolerance	Single word parameter for shade tolerance ('shadetol', 'shadeintol')
sla	Specific leaf area (m^2/kg C)
tcmax_est	Max 20-year coldest month mean temp for establishment (ºC)
tcmin_est	Min 20-year coldest month mean temp for establishment (ºC)
tcmin_surv	Min 20-year coldest month mean temp for survival (ºC)
turnover_leaf	Leaf turnover (fraction/year)
turnover_root	Fine root turnover (fraction/year)
turnover_sap	Sapwood turnover (fraction/year)
twmin_est	Min warmest month mean temp for establishment (ºC)
twminusc	larch parameter
wooddens	Sapwood and heartwood density (kg C/m^3)
wscal_min	Water stress threshold for leaf abscission (raingreen Plant Functional Types)

APPENDIX E

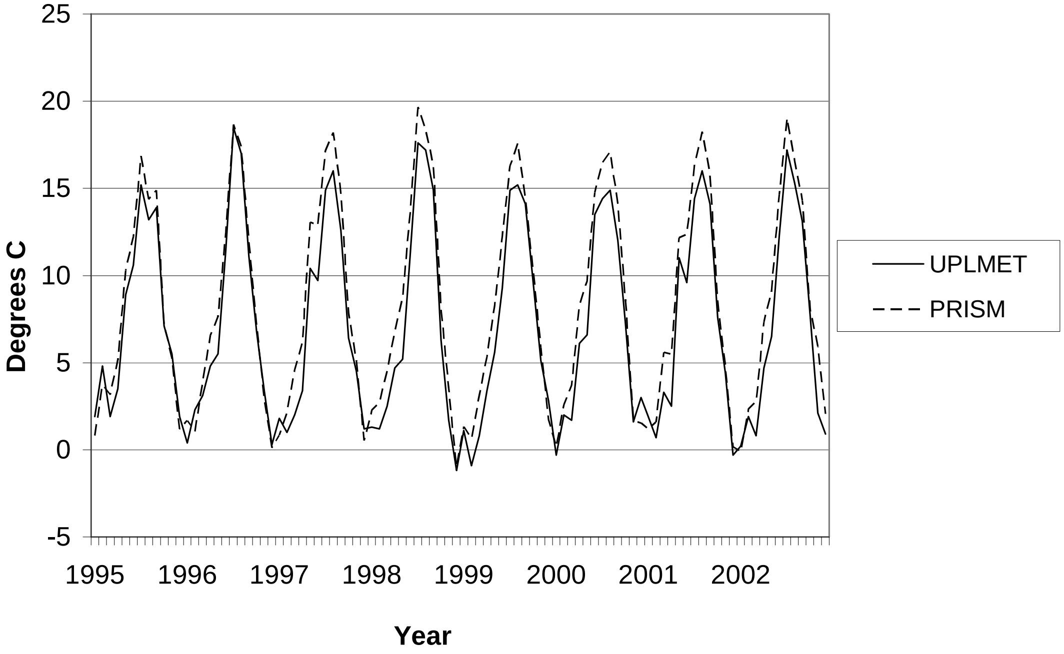
LPJ-GUESS Validation and Model Uncertainty

Model Input Climate Data Validation

Observed temperature and precipitation data for Lookout Mountain were obtained from the H. J. Andrews Upper Lookout meteorological station (UPLMET) for January, 1995 through December 2002 (Daly & McKee 2009; http://www.fsl.orst.edu/climhy/). These data were compared with estimated temperature and precipitation from the PRISM data set (Daly et al. 1994; http://www.prism.oregonstate.edu/) for the 2.5 arc-minute (~16 km^2) PRISM grid cell including UPLMET (Figures E1-E4). Observed snow water equivalent (SWE) for the H. J. Andrews reference stand 4 that is of similar elevation to UPLMET and the modeled grid cell (Daly & Levno 2009; http://andrewsforest.oregonstate.edu/data/abstract.cfm?dbcode=MS007) was compared to LPJ-GUESS output for snow water equivalents.

Interpolated temperatures for the UPMET weather station by the PRISM model tended to overestimate temperatures especially during spring, summer and fall (Figure E1 & E3). The r^2 value for 7 years of PRISM temperatures as compared to actual meteorological station data was 0.97. The range of differences between actual and PRISM data was + 3.8 °C to – 1.5 °C, and the average difference was 1.3 °C.

Figure E1. Mean monthly temperature (°C) for Lookout from the PRISM (dotted line; Daly 1994; http://www.prism.oregonstate.edu/) and UPLMET (solid line; H. J. Andrews Upper Lookout Meteorological station, (Daly & McKee 2009; http://www.fsl.orst.edu/climhy/) data sets for January 1995 – December 2002.



PRISM precipitation values for the UPLMET weather station site tended to underestimate observed precipitation, especially during the fall and winter (Figure E2 & E4). The r^2 value for 7 years of PRISM precipitation as compared to measured data at the H. J. Andrews Upper Lookout Met station was 0.95. The range of differences between actual measurements and PRISM data was + 79mm to - 190 mm, and the average difference was -20 mm.

Figure E2. Mean monthly precipitation (mm) for Lookout from the PRISM (dotted line; Daly et al. 1994; http://www.prism.oregonstate.edu/) and UPLMET (solid line; H. J. Andrews Upper Lookout Meteorological station (Daly & Levno 2009; http://www.fsl.orst.edu/climhy/) data sets for January 1995 – December 2002.

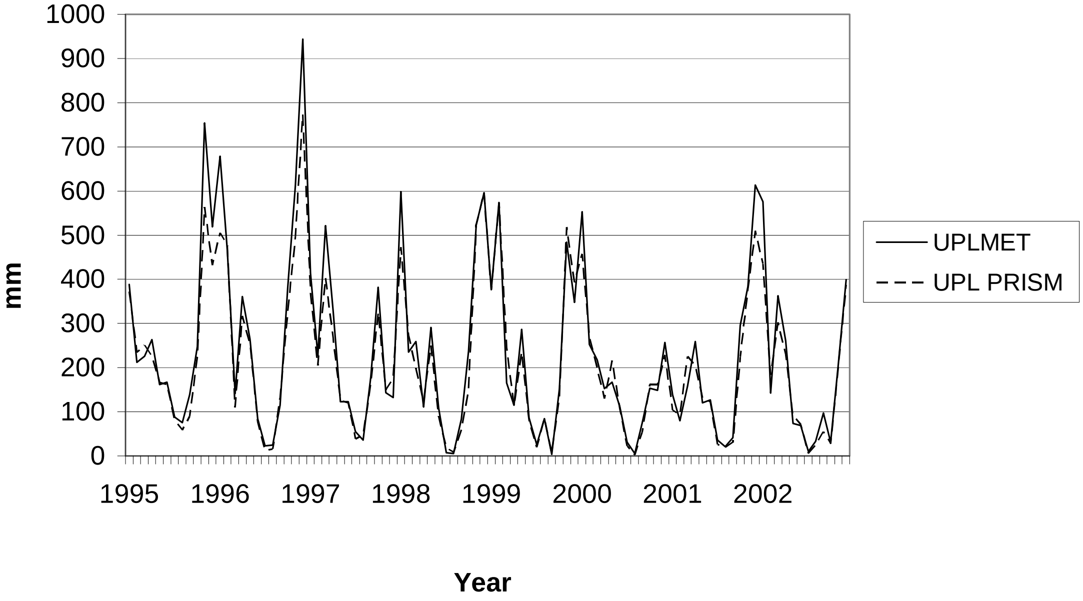


Figure E3. PRISM monthly precipitation minus UPLMET precipitation (January 1995 – December 2002)

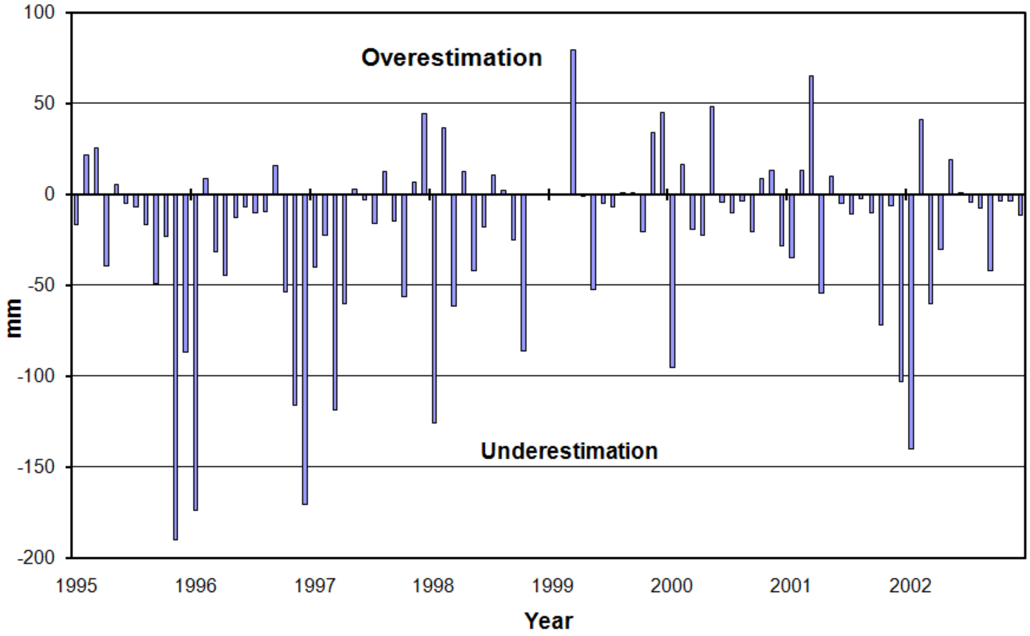
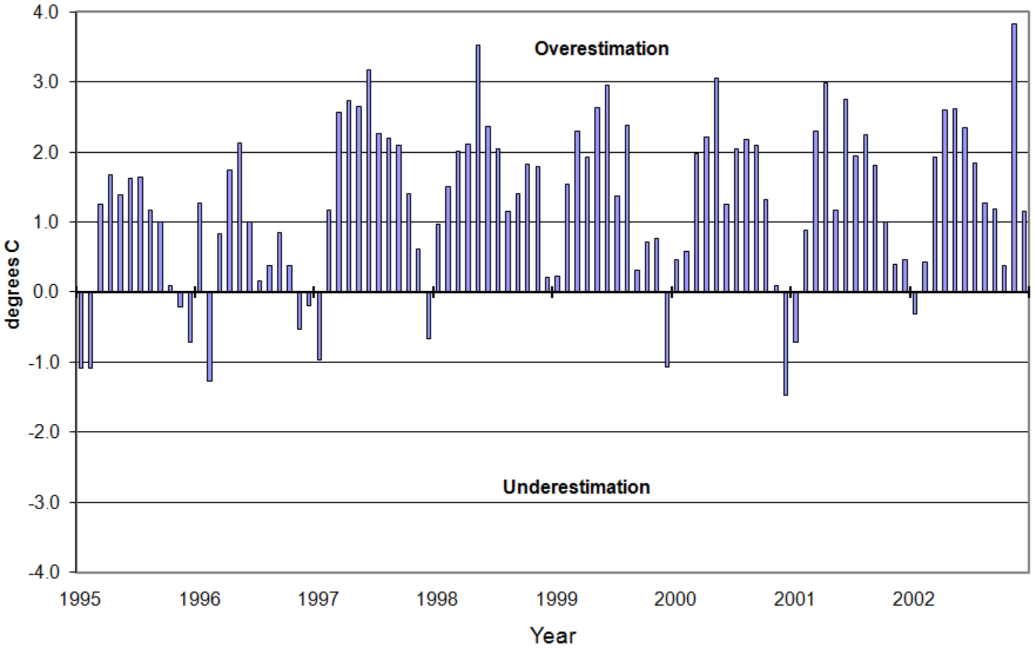


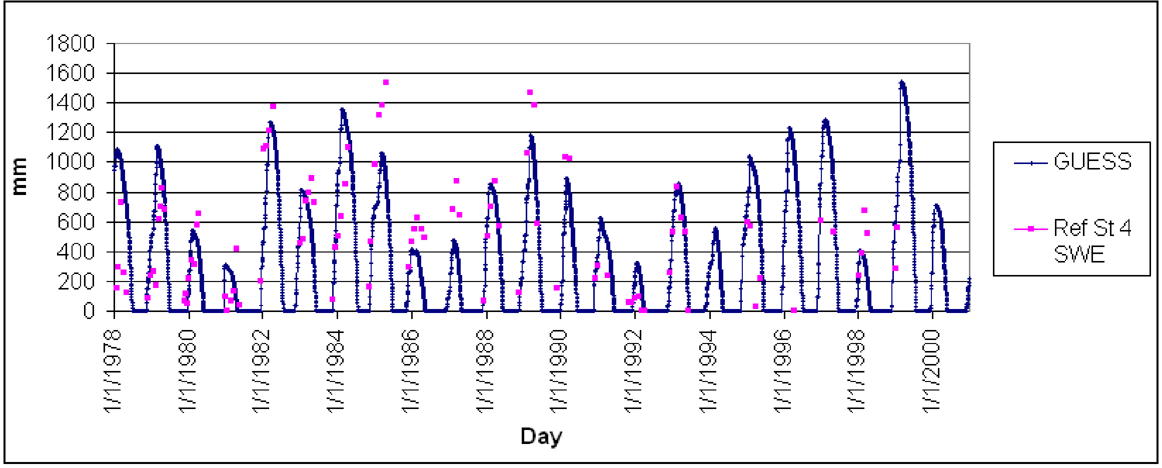
Figure E4. PRISM mean monthly temperatures minus UPLMET mean monthly temperatures for Lookout Mountain (January 1995– December 2002)



LPJ-GUESS snow water equivalent (SWE) simulated for temperature and precipitation from 1978 – 2000 (precipitation ranged from 300 mm to >1500 mm (Figure E5)). LPJ-GUESS snowpack estimates were similar or slightly lower than measured SWE at H.J. Andrews Reference Stand 4 (elevation 1300 m, <1 km east from modeled site, 1978-2000) but showed a similar seasonal pattern of SWE accumulation.

LPJ-GUESS Output Compared to Observed Data

Figure E5. Daily snow water equivalent (mm) simulated by LPJ-GUESS using 1978-1998 climate and CO_2 data inputs (blue line), and measured at H.J. Andrews Reference Stand 4 (purple squares; Daly & Levno 2009) for the years 1978-2000.



LPJ-GUESS daily precipitation was estimated by redistributing monthly precipitation among a user-specified number of rain days (Figure E6), and was not correlated to observed daily precipitation (Correlation Coefficient= 0.12). However, the frequency of rain amounts (mm) closely matched observed precipitation frequencies (Figure E7 and E8).

Figure E6. LPJ-GUESS daily precipitation and modeled rain days for the year 1996

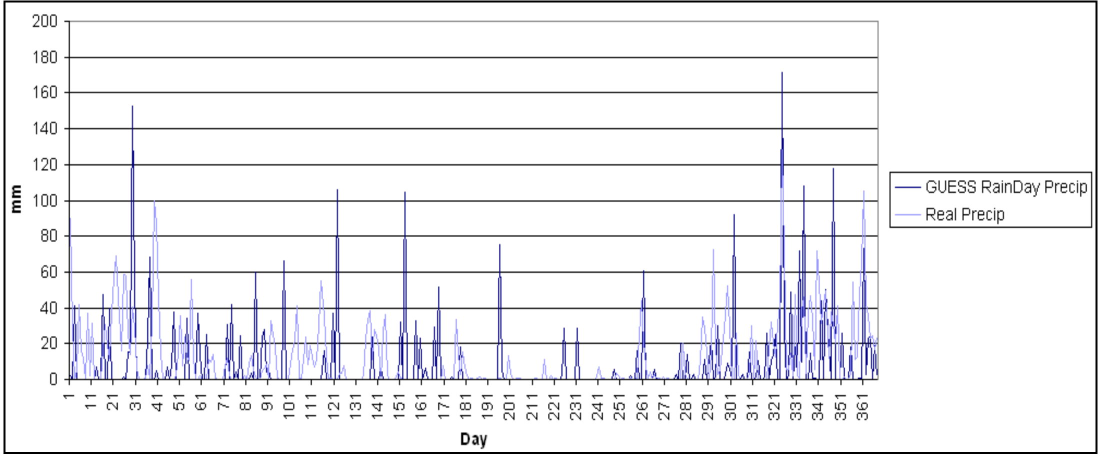


Figure E7. Frequency of precipitation amounts (mm) for UPLMET observed data (1995 – 2002)

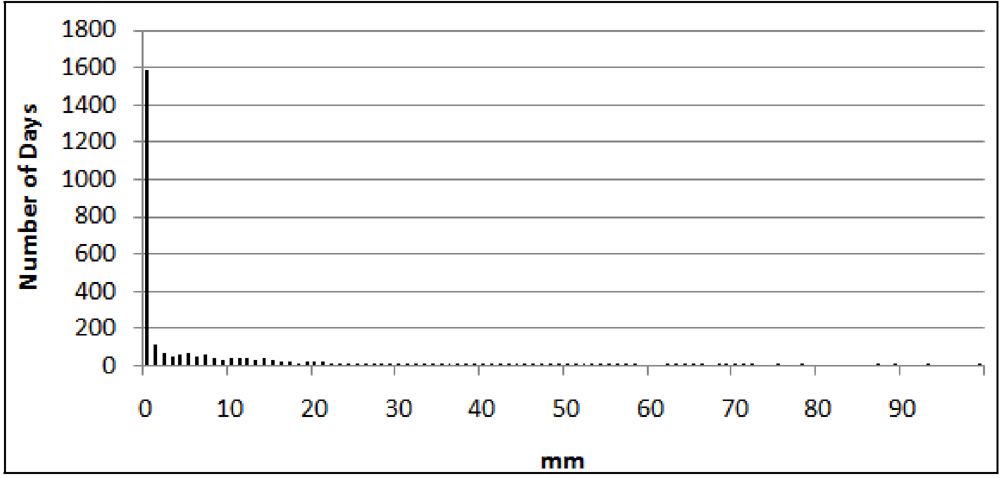


Figure E8. Frequency of precipitation amounts (mm) for LPJ-GUESS simulated rain days (1995 – 2002) of the Climate-CO_2-Fire Suppression scenario (Chapter 4, Table 4.3)

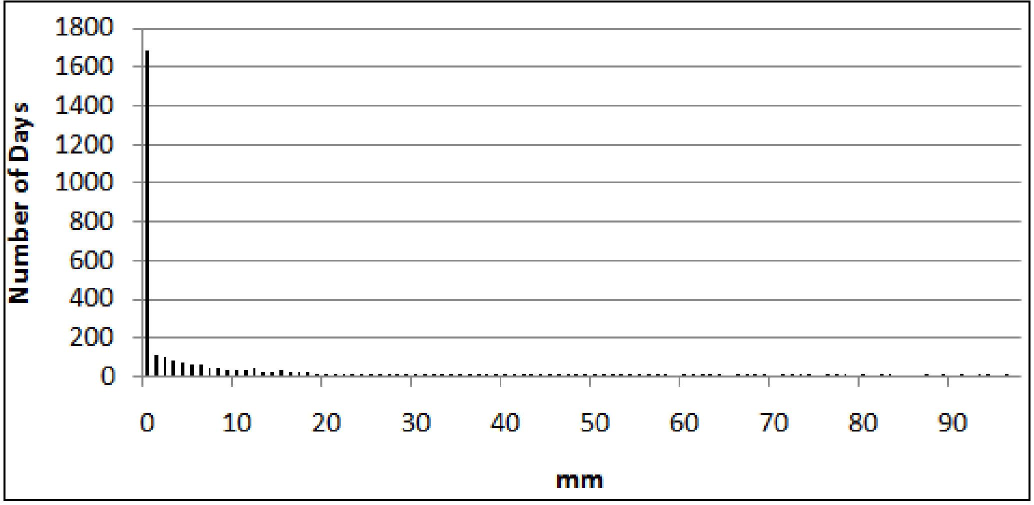


Figure E9 a) LPJ-GUESS soil moisture in the upper (0-0.5m) and lower (0.5-1 m) soil layers simulated for the year 2006 of the Climate-CO2 Scenario 6 (Chapter 4, Table4.4) and b) UPLMET soil moisture for the year 2006 measured at 0.1 m, 0.2 m, 0.5 m and 1.0 m depth.

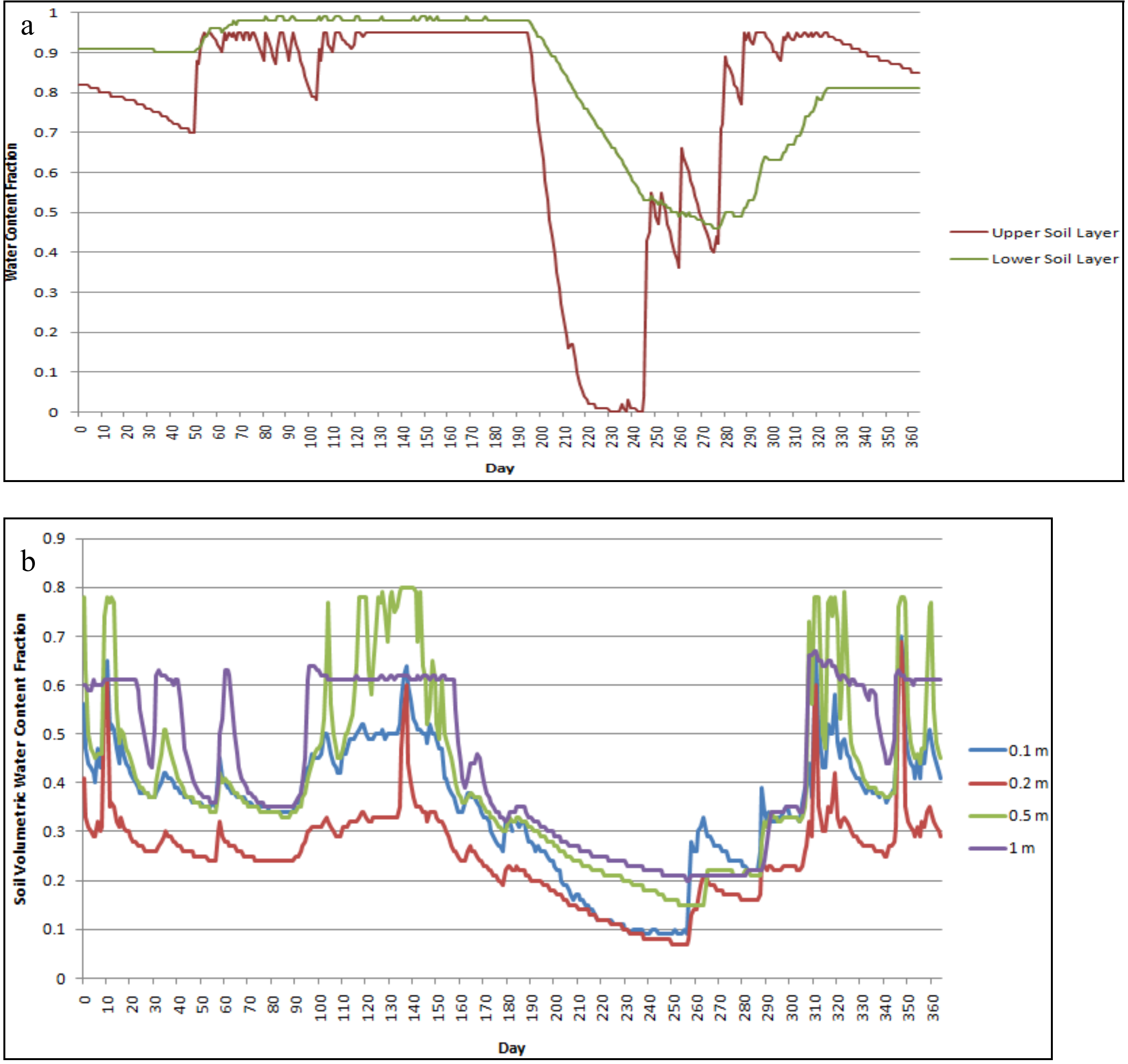
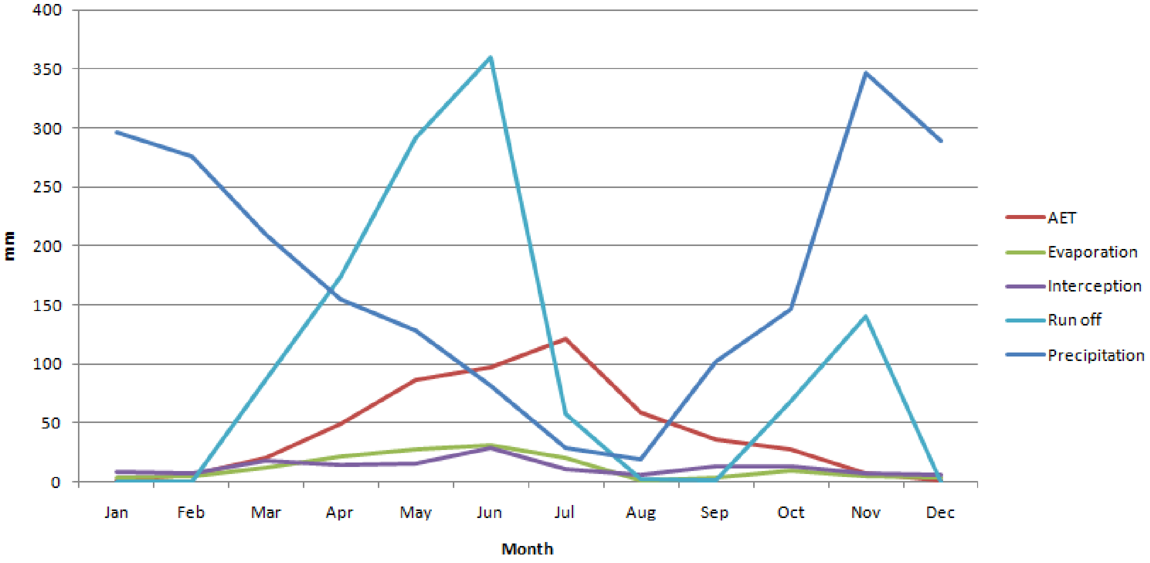


Figure E10. LPJ-GUESS simulated monthly water budget for simulation year 2006. of the Climate-CO_2 Scenario 6 (Chapter 4, Table 4.4). Annual total actual evapotranspiration (AET) is 480 mm, annual total runoff is 1190 mm, annual total evaporation is 140 mm, annual total interception is 150 mm, and annual total precipitation is 2080 mm.



An LPJ-GUESS simulation of 2000 years (Figures E11-E14), repeats the input climate and atmospheric CO_2 data for the years 1971-2000 with fire suppression (Extended Scenario, Chapter 4, Figure 4.7) is compared with observed measurements for Leaf Area Index, Annual Net Primary Productivity, Carbon Biomass, and Mortality (Tables E3-E6) by the eight Plant Functional Types.

Figure E11. LPJ-GUESS Simulated Leaf Area Index (LAI) (m^2/m^2) for Eight Plant Functional Types. Figure generated by LPJ-GUESS (Smith et al. 2001).

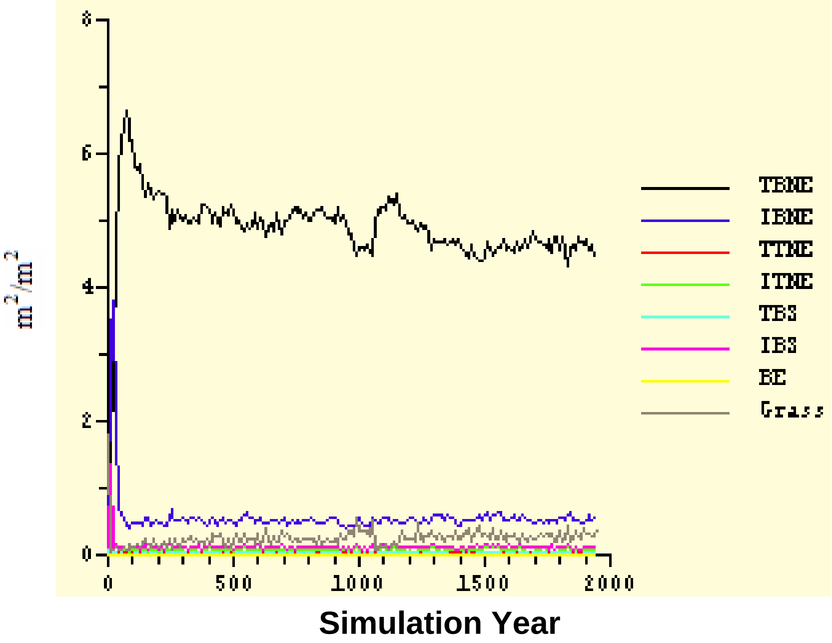


Table E1. Empirical Leaf Area Index (LAI)

Source	LAI
Waring et al. (1999); OTTER Project Santiam, Oregon (Pacific silver fir)	3
Waring et al. (1999); OTTER Project Scio, Oregon (Douglas-fir)	8.5
Hessl et al. (2004); PNW Tree Database (Pacific silver fir)	2 - 15

Figure E12. LPJ-GUESS Simulated Annual Net Primary Productivity (ANPP, kg C/m^2) for Eight Plant Functional Types. Figure Generated by LPJ-GUESS (Smith et al. 2001).

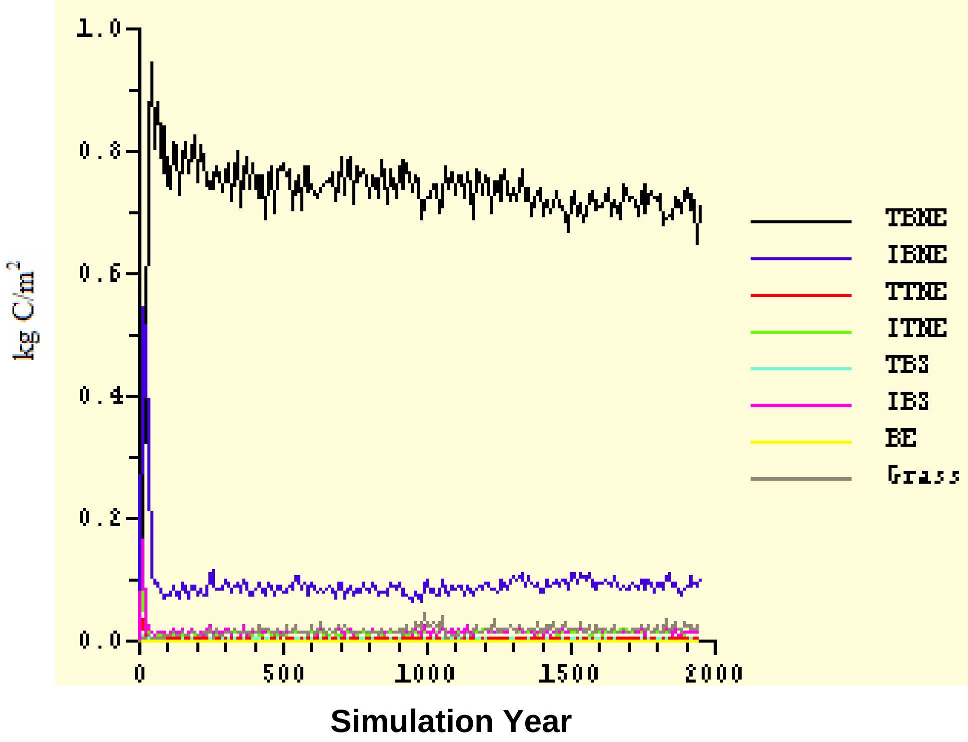


Table E2. Empirical Annual Net Primary Productivity (ANPP)

	ANPP kg/m^2/year
Waring et al. (1999); OTTER Project Santiam, Oregon (Pacific silver fir)	0.5
Waring et al. (1999);OTTER Project Scio, Oregon (Douglas-fir)	1.7
Harmon et al. (2004); Wind River, WA, Old Growth Douglas-fir	0.597
Hessl et al. (2004); PNW Tree Database (Pacific silver fir)	0.5 – 1.5

Figure E13. LPJ-GUESS Modeled Carbon Mass for Eight Plant Functional Types. Figure Generated by LPJ-GUESS (Smith et al. 2001).

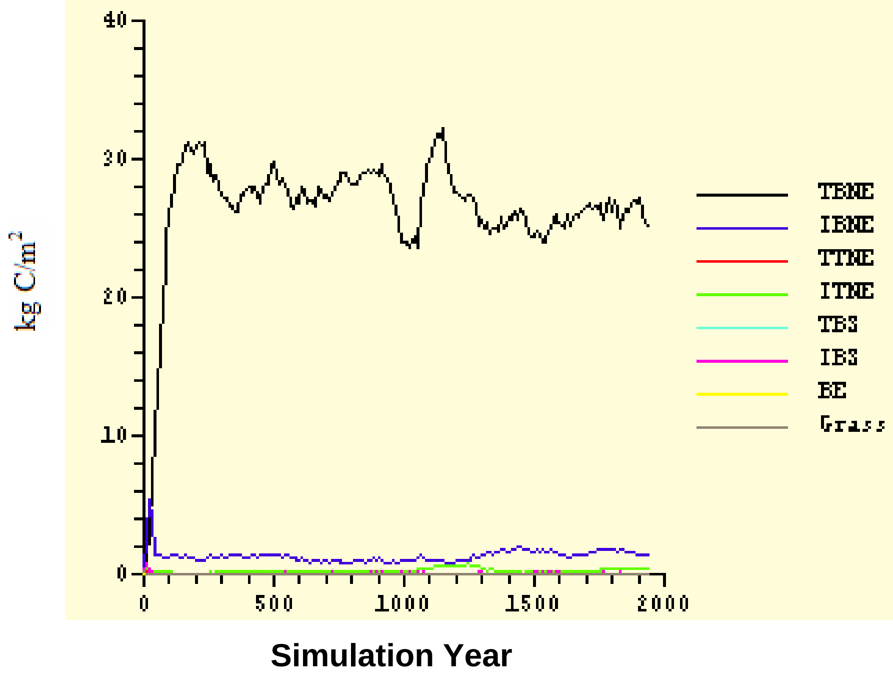


Table E3. Empirical Carbon Mass

	C Mass kg/m^2/year
Hessl et al. (2004) PNW Tree Database Pacific silver fir corresponding to TBNE	7 - 58

Figure E14. LPJ-GUESS Simulated Mortality Fraction Due to Age and Growth Suppression for Eight Plant Functional Types. Figure Generated by LPJ-GUESS (Smith et al. 2001).

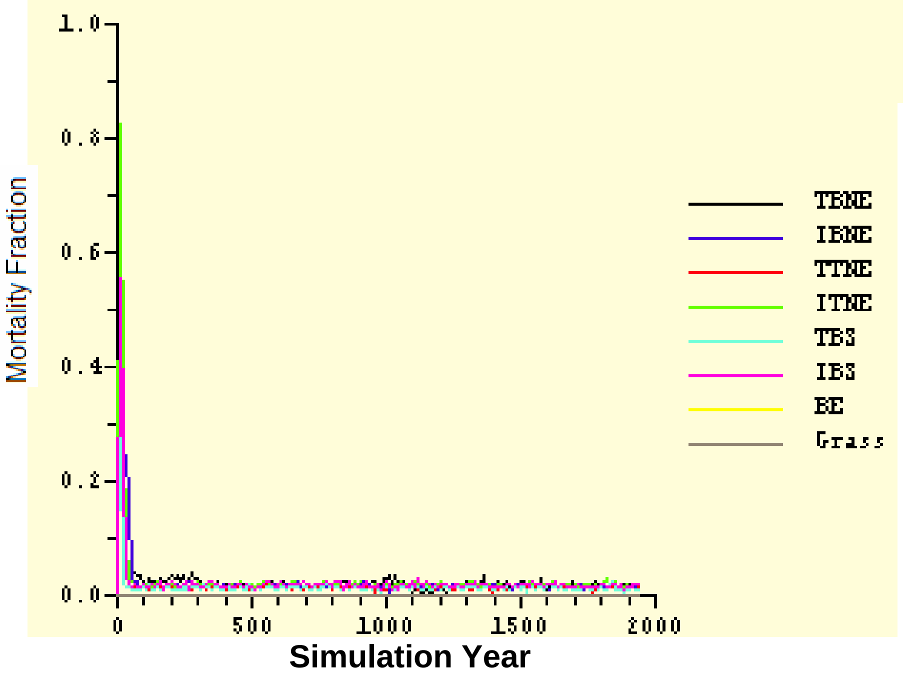


Table E4. Empirical Mortality Percentage

	Percent Mortality
Timber Resource Statistics for Western Oregon, (1997), Resource Bulletin PNW-RB-237	0.02 - 0.25

LPJ-GUESS Model Structure Uncertainty

A number of montane meadow and forest ecosystem characteristics are either not explicitly represented in LPJ-GUESS or are simplified. Model structure uncertainty affecting meadow persistence may result from: 1) the ability of LPJ-GUESS to simulate the spatial scale and temporal persistence of open cover with very few trees, 2) a simple soil module that may overestimate soil moisture conditions and may be more conducive to forest persistence, and 3) an accelerated forest succession process resulting from the establishment of individuals with the characteristics of saplings instead of seedlings.

Montane meadows in the western Cascades of Oregon can exist as disconnected open patches or as connected mosaics of trees and meadow vegetation. Meadow patch sizes can range from several hundred square meters to a dozen or more hectares (Rice, Chapter 2). For this study, LPJ-GUESS simulated 500 independent 1000 m^2 patches that varied from completely treeless to fully forested. Montane meadows have been found to occupy less than 5% of the Willamette National Forest (Dailey, 2007) and, under pre-industrial conditions, 5±1.3% of the simulated patches were classified as meadow. However, some patches classified as forest also contained simulated grass cover. These sub-patch grass areas could represent additional meadow habitat but, since LPJ-GUESS does not simulate the spatial distribution of plant functional types within a patch, grass cover within forest patches could also represent grass existing in forest canopy gaps and thus grass cover from forest patches was not included in estimated meadow cover.

A second, related issue concerns meadow persistence. Montane meadows in the western Cascades of Oregon can be ephemeral landscape features dominated by non-forest vegetation that persists for a short time after a disturbance occurs. In other instances, meadows can persist for several to thousands of years when site conditions inhibit or eliminate tree establishment (Rice Chapter 2, Takaoka and Swanson 2007). The non-forest patches simulated by LPJ-GUESS were created by fire or a generic disturbance randomly implemented throughout the simulation. These individual patches were observed to persist for 1 to over 150 years in the baseline simulation, but average persistence was 6 years. The 6 year average persistence length reflected the numerous occurrences of many non-forest patches that occurred for just 1 year and then were quickly reforested

Montane meadows may be maintained by drought stress where site conditions, such as shallow soils, limit available soil moisture and inhibit tree establishment and survival (Takaoka & Swanson, 2007). For example, Dailey (2007) found that meadows in the Willamette National Forest of Oregon tended to occur on ridge tops and steep south or east facing slopes indicating that shallow soils or higher drought stress conditions tend to maintain meadow areas. In this study, LPJ-GUESS was run using a depth of 0.5 m for an upper and lower soil layer and topographic variability (e.g., aspect, slope, and hill slope position) was not considered. As a result, LPJ-GUESS may overestimate soil moisture (Figure E9). Empirical measurements at lower elevations of the H.J. Andrews Forest record annual actual evapotranspiration (AET) rates of 1000 mm/year (J. Jones, personal communication), while LPJ-GUESS simulates an average of 490 mm/year of AET (Figure E10). This simulated underestimation of AET combined with an overestimation of soil water content could underestimate drought stress. Specifying shallower soils and increasing AET amounts could improve the model's simulation of drought stress. Projected meadow extent and persistence would be expected to increase if these factors were incorporated in simulations.

Inter-specific biotic interactions, such as facilitation, also play an important role in forest encroachment of meadows. In Bunchgrass Meadow, a pioneer shade-intolerant species, Lodgepole pine, appears to modify local site conditions and facilitate the subsequent establishment and dominance of Grand fir, a secondary shade-tolerant species that eventually outcompetes Lodgepole pine over a period of several decades (Rice, Chapter 3). A similar situation occurs in Lookout Meadow, where Noble fir is the facilitative pioneer species and Pacific silver fir appears to play the role of a secondary succession species (J. Rice, personal observation). Forest succession from shade-intolerant to shade-tolerant trees can occur relatively quickly in LPJ-GUESS simulations because initial establishment occurs with individuals that are around breast height (~10 years old), and the subsequent growth and mortality is quickly influenced by a large number of newly established trees competing for light. If the model were modified to incorporate the slower timing of facilitative biotic interactions, modeled meadow persistence might be lengthened.

Model Parameter Uncertainty

There are a number of uncertainties associated with the input data and model parameter values used in this study that may affect the model's simulation of meadow vegetation. Of particular importance are: 1) a possible underestimation of precipitation and overestimation of temperature in the modern input data, 2) mortality and generic disturbance parameterizations, and 3) parameterization of plant functional type establishment rates and bioclimatic limits.

The monthly precipitation and temperature input data used in this study were from the PRISM data set for 1900 – 2000 (Daly et al. 1994) and downscaled ECHAM5 data for 2001-2100 (Climate Impacts Group 2007). Although our study area was located near the center of both the PRISM and ECHAM5 grid cells from which we obtained input data, the grid cells estimated climate for large areas, ~16 km^2 for the PRISM data and ~140 km^2 for the downscaled ECHAM5 data. Comparison of the PRISM data with UPLMET data (Appendix E1) indicates that PRISM data overestimated observed summer temperatures by 2 - 3 °C (Figures E1 and E4) and underestimated observed precipitation by a monthly average of 20 mm over the 1995-2002 record (Figures E2 and E3). Overestimating summer temperatures while underestimating precipitation could increase drought stress simulated by the model, thereby reducing forest productivity and biomass, and potentially overestimating simulated meadow cover.

Simulated meadow cover may also be affected by parameters controlling tree mortality. Plant mortality from non-fire disturbance events, such as wind throw, ice damage, and insect outbreaks, was simulated using a generic disturbance parameter, which stochastically implemented 100% mortality of all simulated individuals every 200 years for a given patch. Other LPJ-GUESS modeling studies have used a 100 year generic disturbance parameter setting (Smith 2001; Hickler 2004 & 2008; Wolf 2008). We used 200 years because this value better represented the average occurrence of these types of disturbances in Pacific Northwest forests (C. Halpern, unpublished dendrochronology data) and to allow a better representation of older tree age classes in the simulations.

Fire resistance parameters for each plant functional type affect the amount of mortality from simulated fire events. We used fire resistance parameters from Thonicke et al. (2001) for all plant functions types except BE, for which we used Smith et al's. (2001) definition, and ITNE, for which we based the parameter value on empirical data for Douglas-fir and Ponderosa pine from the western U.S. (Hood et al. 2007). Although increased fire occurrence had a greater effect on forest attributes than temperature or atmospheric CO_2 in the scenarios and sensitivity analysis, nevertheless it was not a very large effect for the scenarios. The scenarios were dominated by a lower fire resistant plant functional type, TBNE, whose carbon mass, net primary productivity, and leaf area varied by only 3% to 6%, and whose cover varied by only 10% over fire frequencies ranging from 100 yrs to 200 yrs in the scenarios (Chapter 4, Table 4.6). Forest attributes of other plant functional types, especially shade intolerant plant functional types, varied < 2%, and forest cover varied < 4% over fire frequencies ranging from 100 years to 200 years in the scenarios (Table 4.6). Even though the model was more sensitive to fire frequency than to other environmental driver values varied in the model experiment, nevertheless model outputs indicated that forests persist under the projected future changes.

The fire return interval simulated for scenarios involving fire (Table E5) was slightly more frequent for the century 1800-1900 (90 years) than was defined in the model (100 years). The number of fires that occurred were relatively close to the 1700 - 2000 definitions of fire probability that were set in the model, and the model determined fire return from 2000 – 2100 varied between 105 to 140 years.

Table E5. Simulated mean fire return interval for scenarios involving fire over the 4 centuries between 1700 – 2100. (Fire probability setting used in LPJ-GUESS are listed in second row of table)

Scenario Mean Fire Return (years)				
Scenario	**1700-1800 (Fire return set to 200 years)**	**1800-1900 (Fire return set to 100 years)**	**1900-2000 (Fire return set to 1000 years)**	**2000-2100 (Fire return model determined)**
4 Future Fire Suppression	200	90	1000	
5 Future Fire	200	90	1000	140
7 Climate - Future Fire Suppression	200	90	1000	
8 Climate-Future Fire	200	90	1000	105
9 CO_2-Future Fire Suppression	200	90	1000	
10 CO_2-Future Fire	200	90	1000	125
11 Climate-CO_2-Future Fire Suppression	200	90	1000	
12 Climate-CO_2-Future Fire	200	90	1000	105

We set the parameter for maximum seedling establishment rate (est_max, Table D1) at 500 individuals/ha/yr for shade tolerant species, and 1500 individuals/ha/yr for shade intolerant species according to Hickler (2008). These values are used to limit the initial establishment of trees after a disturbance has occurred. In contrast, the Bunchgrass Meadow plot (Chapter 3) had about 50% tree cover, and maximum seedling establishment rates varied depending on the size of area considered. Maximum observed establishment rates of saplings >30 cm in height varied from 220 individuals/ha/yr and 250 individuals/ha/yr for shade intolerant and shade tolerant species respectively in a 1000 m^2 area to 1000 individuals/ha/yr and 6700 individuals/ha/yr for shade intolerant and shade tolerant species respectively in a 30 m^2 area that was fully occupied by trees (Rice, Chapter 3). It is possible that the maximum allowable establishment rates overly constrained tree plant functional type establishment in some cases. Wramneby, et al. (2008) tested the effect of uncertainty in the maximum establishment parameter for LPJ-GUESS and found that at sites dominated by shade tolerant needleleaved evergreen, as our model site is, modeled net primary productivity and carbon biomass had low sensitivity to variations in this parameter. If maximum allowable tree establishment rates were underestimated in this study, non-forest extent may have been slightly overestimated.

Establishment was parameterized to occur every year if light conditions permitted, consistent with the literature (e.g., Silvics, 1998). Because annual establishment may overestimate actual tree establishment, a lower establishment rate of every 5 years was tested, and it had very little impact on model output. The results are representative for areas without significant topographic or soil depth limitations where tree establishment may consistently occur.

Meadow cover can also be influenced by the parameterization of plant functional type bioclimatic limits. Bioclimatic limits are used in LPJ-GUESS simulations to represent plant functional type climate limits, such as minimum and maximum temperature tolerance for survival and photosynthesis, and associated plant mortality. For this study, values of bioclimatic limits from other LPJ-GUESS studies (Smith 2001, Hickler 2004 and 2008, Wolf 2006) were used except where values were adjusted for Pacific Northwest species based on empirical data (Silvics, 1990, Appendix D).

Adjustments to plant functional type parameters made for this study were validated against empirical measurements of biomass, ANPP and LAI from the Pacific Northwest (Figures E11 – E14). The plant functional type parameterization values for shade tolerance photosynthetic temperature limits have been used in other LPJ-GUESS modeling studies for Europe and the eastern United States (Smith et al. 2001, Hickler, 2008, Wolf, 2008). Parameters for the shade-intolerant temperate needleleaved plant functional type (ITNE) were adjusted to more closely match the longevity, bioclimatic limits, and higher fire resistance of Douglas-fir or Ponderosa pine (Hood et al. 2007). These adjustments may give the ITNE plant functional type a competitive advantage over other plant functional types.

APPENDIX F

LPJ-GUESS Sensitivity Analysis

Sensitivity Analysis Methods

The sensitivity of model response to changes in climate, CO_2, and fire that are beyond the historic and projected future variability of the model experiment was tested. This sensitivity analysis incrementally varies values for five sensitivity categories of temperature (Table 4.4a), atmospheric CO_2 (Table 4.4b), fire return intervals (Table4.4c), precipitation (Table 4.4d), and temperature and precipitation (Table 4.4e), while holding other category values to the 1901 – 1931 average baseline. The temperature sensitivity analysis holds CO_2 at 280 ppm and omits fire for each of the separate model runs that increased the temperature of each month by 2, 4, 6, 8 and 12 °C from the baseline average of 6.7 °C. The CO_2 sensitivity analysis test holds temperature and precipitation at the baseline average with fire omitted, and has separate model runs that vary CO_2 from 180 ppm to 980 ppm by increments of 100 ppm. The fire sensitivity analysis test holds temperature, precipitation and CO_2 to the baseline values, and separately simulates the variation in the fire return interval by 10, 25, 50, 100, 250, 500, 1000 years, and also no fire. The precipitation sensitivity analysis holds temperature and CO_2 at the baseline value with fire omitted, for each of the separate model runs that increases precipitation of each month by 15%, 30%, 50%, 100%, and decreases precipitation by 15%, 30%, 50%, 80%, and 90%. The precipitation sensitivity also tested the effect of decreased dry season (for the months June to September) precipitation by 50% and 100%, and both increased wet season (October to May) and decreased dry season (June to September) by 50% and 100%. The temperature and precipitation sensitivity held CO_2 at 280 ppm and omitted fire, while using the precipitation sensitivity values and holding the temperature to a 6 ^{o}C increase from the baseline value.

For each model run, 20 replicate patches were averaged over 1000 years for output values of ANPP, CMass, LAI, FPC, and percent of meadow. Model output random variability was minimized, and computational efficiency was maximized with this method. The monthly input values for each sensitivity increment were kept constant throughout a 1000 year spin-up, and another 1000 years of output. The thousand years after the spin-up was used to calculate the average results for total tree and dominant plant functional types.

Table F1a – e. Sensitivity values used for each model run for temperature, atmospheric CO_2 concentrations, fire return interval, precipitation, and precipitation and temperature.

a.

Temperature ºC (Average Annual)
6.7 (Baseline)
7.7 (+1 ºC)
8.7 (+2 ºC)
10.7 (+4 ºC)
12.7 (+6 ºC)
14.7 (+8 ºC)
18.7 (+12 ºC)

b.

Atmospheric CO_2 Concentration (ppm)
180
280 (Baseline)
380
480
580
680
780
880
980

c.

Fire Return Interval (Years)
10
25
50
100
250
500
1000
No Fire

d.

Precipitation (mm)	
Wet Season (Oct-May)	Dry Season (Jun-Sep)
1847 (Baseline)	115 (-50%)
1847 (Baseline)	0 (-100%)
185 (-90%)	24 (-90%)
369 (-80%)	46 (-80%)
924 (-50%)	115 (-50%)
1293 (-30%)	152 (-30%)
1570 (-15%)	196 (-15%)
1847 (Baseline)	231 (Baseline)
2108 (+15%)	267 (+15%)
2402 (+30%)	300 (+30%)
2771 (+50%)	346 (+50%)
3695 (+100%)	462 (+100%)
2771 (+50%)	115 (-50%)
3695 (+100%)	0 (-100%)

e.

Precipitation (mm) and Temperature (ºC)		
Wet Season (Oct-May)	Dry Season (Jun-Sep)	Temp (ºC)
1847 (Baseline)	115 (-50%)	12.7
1847 (Baseline)	0 (-100%)	12.7
185 (-90%)	24 (-90%)	12.7
369 (-80%)	46 (-80%)	12.7
924 (-50%)	115 (-50%)	12.7
1293 (-30%)	152 (-30%)	12.7
1570 (-15%)	196 (-15%)	12.7
1847 (Baseline)	231 (Baseline)	12.7
2108 (+15%)	267 (+15%)	12.7
2402 (+30%)	300 (+30%)	12.7
2771 (+50%)	346 (+50%)	12.7
3695 (+100%)	462 (+100%)	12.7
2771 (+50%)	115 (-50%)	12.7
3695 (+100%)	0 (-100%)	12.7

LPJ-GUESS Sensitivity Analysis Results

Mean annual temperature modifications over the range from 6.7 °C (1901-1930 average) to 18.7 °C (roughly a tripling of 1901-1930 average) altered the productivity, biomass, leaf area, and cover of plant functional type's (Figure F1a-e). Upper elevation conifer forest (TBNE) was replaced by low elevation conifer forest (TTNE) when the mean annual temperature was 10 °C; TTNE in turn was replaced by broadleaf evergreen forest (BE) when the mean annual temperature was 14 °C; and BE in turn was replaced by shade-intolerant broadleaf summergreen forest (IBS) when the mean annual temperature was 18 °C. However, less forest biomass and percent cover was evident as needleleaved species gave way to broadleaved species. Tree cover dropped from around 0.75 to 0.55, and the percent of open cover was most reduced at +12 ºC (18 °C annual mean) (to 3%), but was otherwise around 7 %.

Precipitation changes of a 100% increase (4156 mm/year) or 50% decrease (1037 mm/year) of pre-industrial precipitation (2078 mm/year) had little impact on altering productivity, biomass, leaf area, cover of plant functional type's, and percent open cover (Figure F2a-e). Productivity, biomass, and leaf area values were reduced when precipitation was reduced by 80% (to 415 mm/year) or 90% (to 207 mm/year), but there was no large change in the amount of forest cover or percent of open cover. The 80% and 90% reduction in precipitation also resulted in an unexpected decrease in the percent of open cover as less area with very low tree cover (<10%) occurred.

Precipitation changes of a 100% increase (4156 mm/year) or 50% decrease (1037 mm/year) combined with a mean annual temperature of 12.7 °C did not result in a large change of productivity, biomass, leaf area or cover of plant functional type's (Figure F3a-e). However, the plant functional type attributes were significantly lowered when a reduction in annual precipitation of 80% (415 mm/year) or 90% (207 mm/year) occurred, with the lowest impact on forest cover and percent of meadow cover. The dominant plant functional type was lower elevation conifer (TTNE) except for the +100% (4156 mm/year) precipitation test where BE dominated measured attributes. The tests for reduced dry season and both reduced dry season with wet season increase did not show a large difference from Baseline levels.

Fire return intervals ranging from no fire to 1000 years to 10 years (Figure F4a-e) showed the largest impact of on productivity, biomass, leaf area, cover, and percent of meadow cover. A consistent decrease in tree attributes, and a consistent increase in percent of meadow cover (up to ~50%) and Grass plant functional type occurred with increasing fire return interval. The most fire tolerant plant functional type, ITNE, took the role of co-dominant plant functional type with higher fire returns, as it replaced IBNE.

The atmospheric CO_2 concentration that span a 500% increase in CO_2, from 180 ppm to 980 ppm, resulted in a 50% increase of forest productivity, a 115% increase in forest carbon mass, a 57% increase in forest leaf area, and no large changes to forest projective cover or percent of meadow cover occurred (Figure F5a-e).

Figure F1a. Temperature sensitivity of Annual Net Primary Productivity for 8 Plant Functional Types

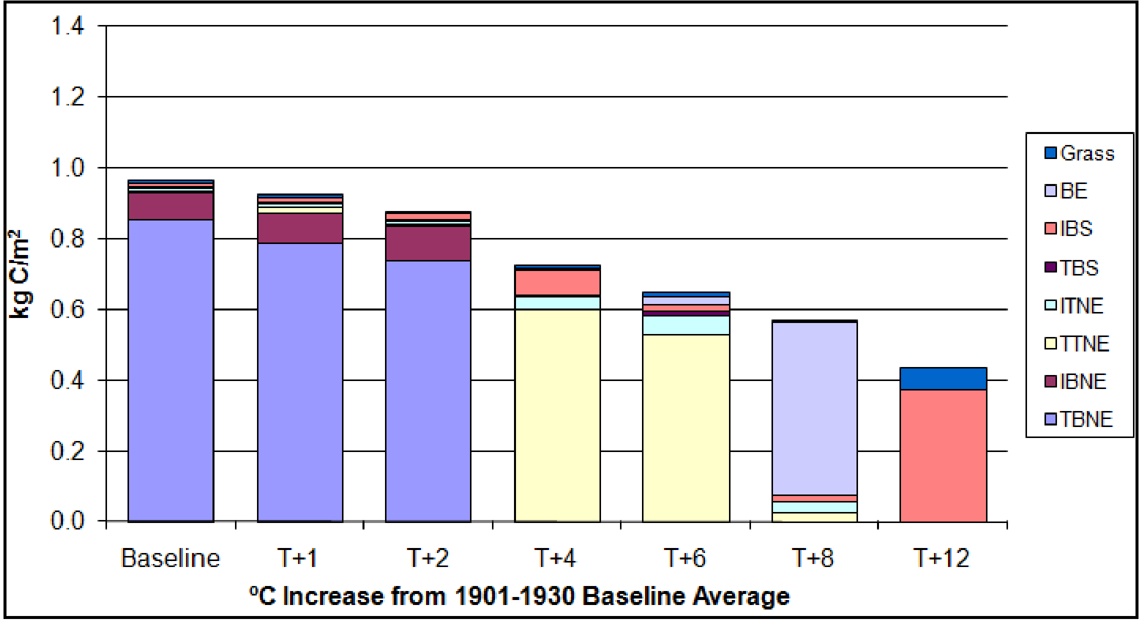


Figure F1b. Temperature sensitivity Carbon Mass for 8 Plant Functional Types

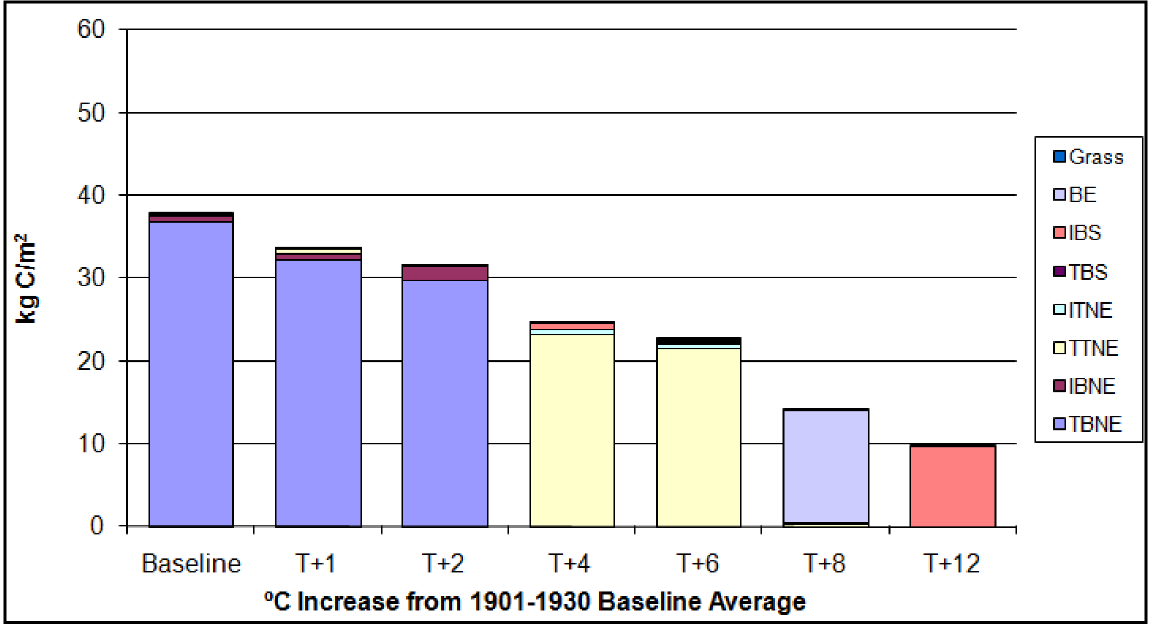


Figure F1c. Temperature sensitivity Leaf Area Index for 8 Plant Functional Types

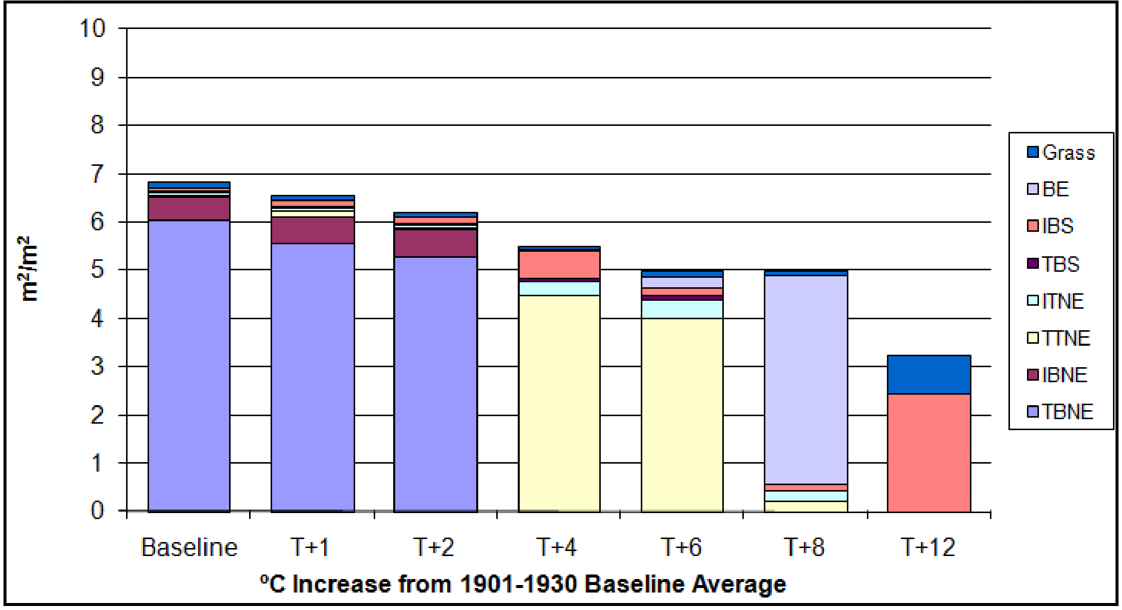


Figure F1d. Temperature sensitivity of Foliar Projective Cover (FPC) for 8 Plant Functional Types

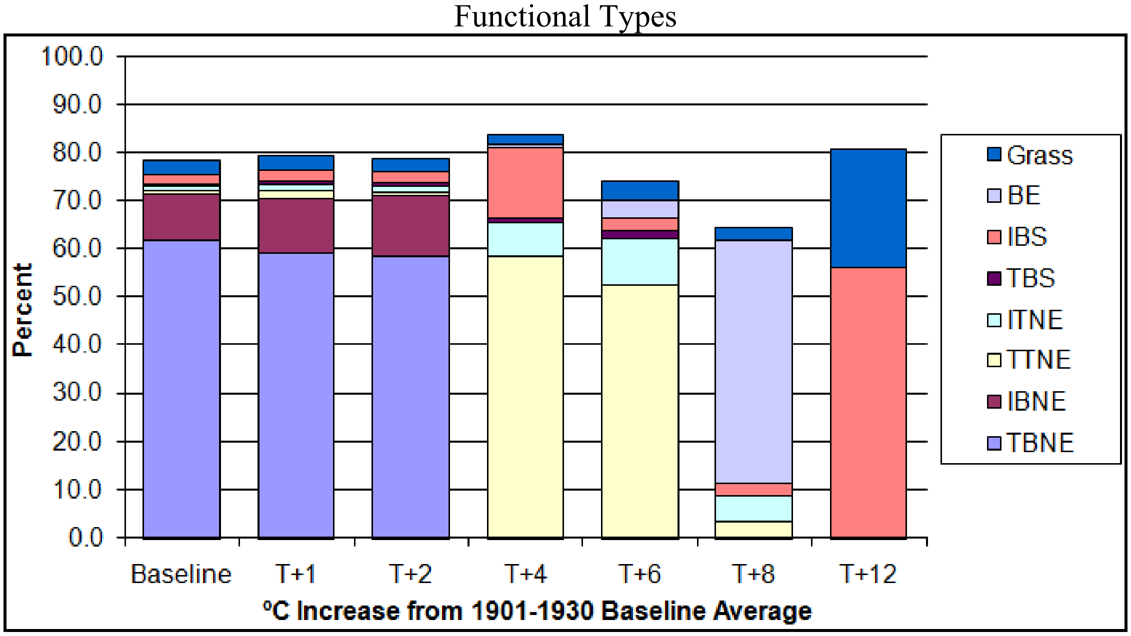


Figure F1e. Temperature sensitivity Percent Open Cover

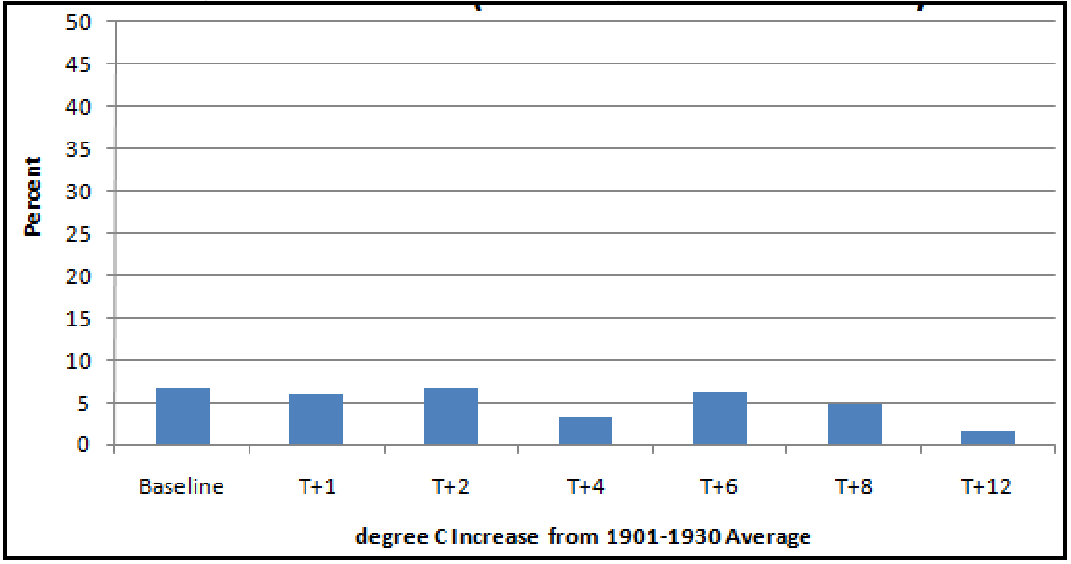


Figure F2a. Precipitation sensitivity of Annual Net Primary Productivity (ANPP) for 7 Plant Functional Types

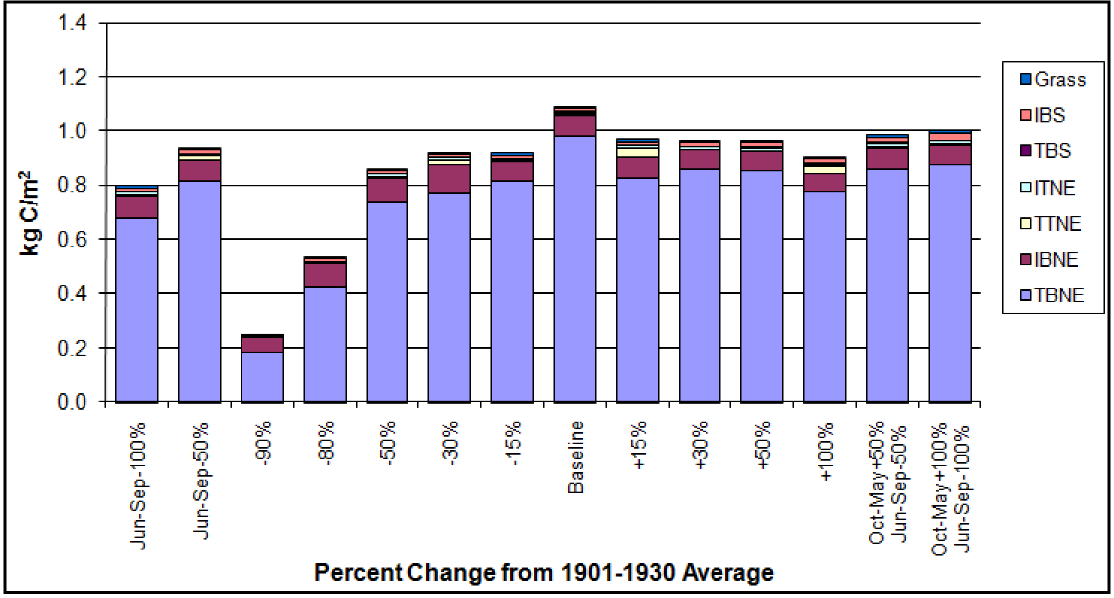


Figure F2b. Precipitation sensitivity of Carbon Mass (C Mass) for 7 Plant Functional Types

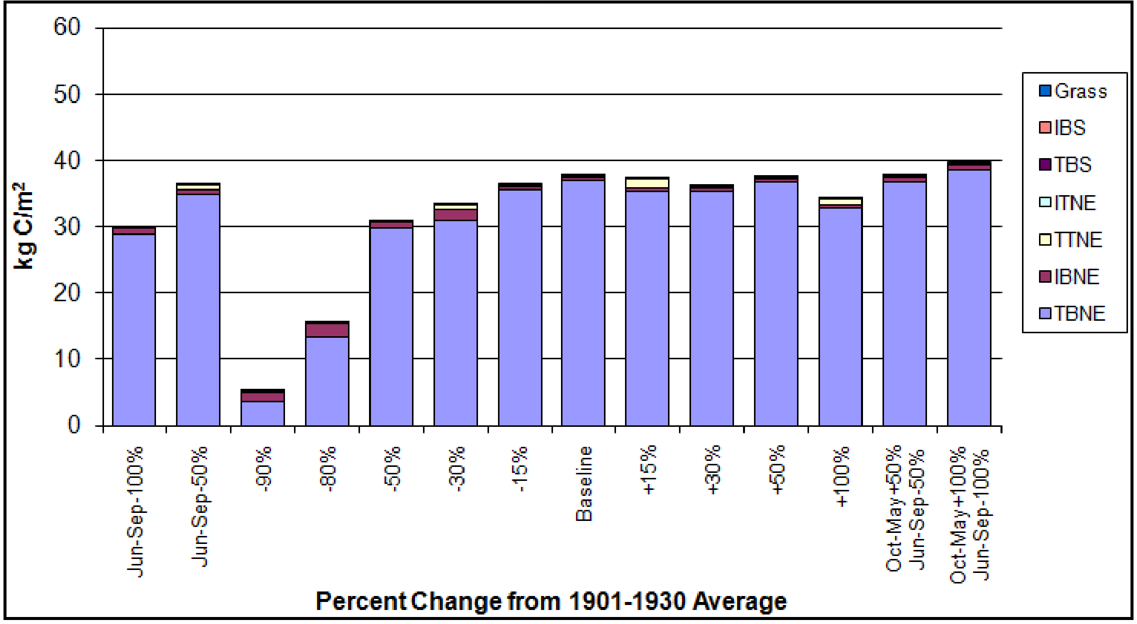


Figure F2c. Precipitation sensitivity of Leaf Area Index (LAI) for 7 Plant Functional Types

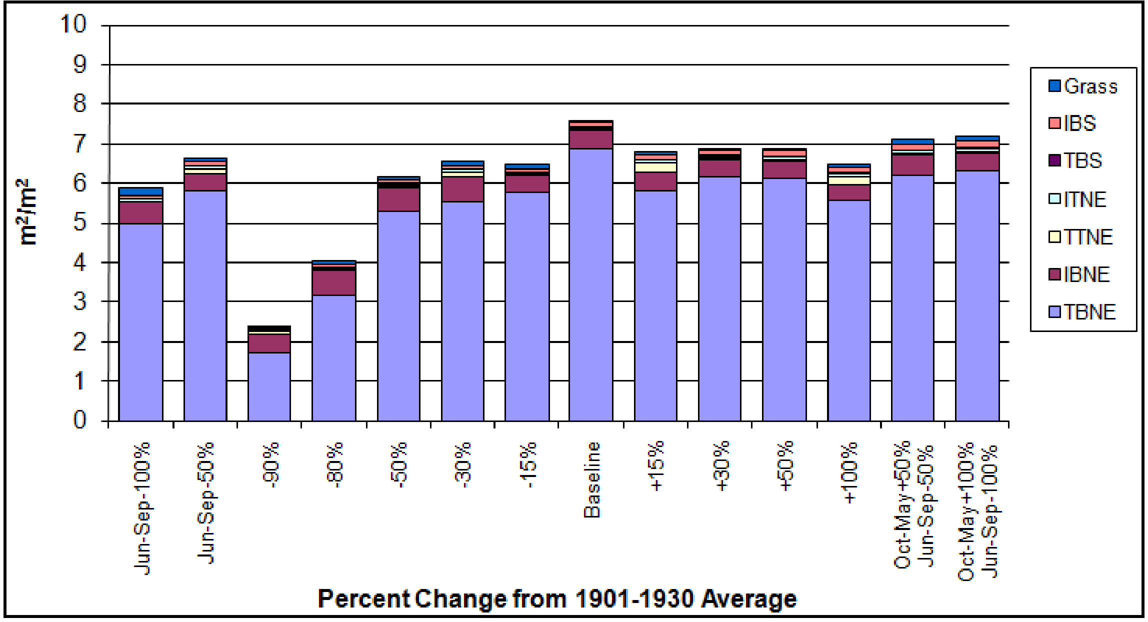


Figure F2d. Precipitation sensitivity Foliar Projective Cover (FPC) for 7 Plant Functional Types

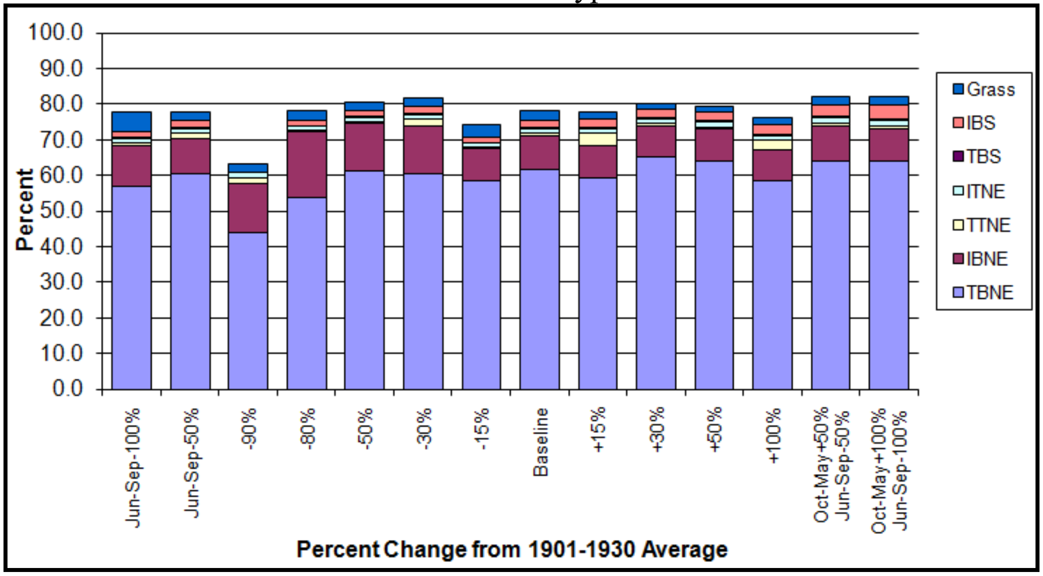


Figure F2e. Precipitation sensitivity of Percent of Open Cover

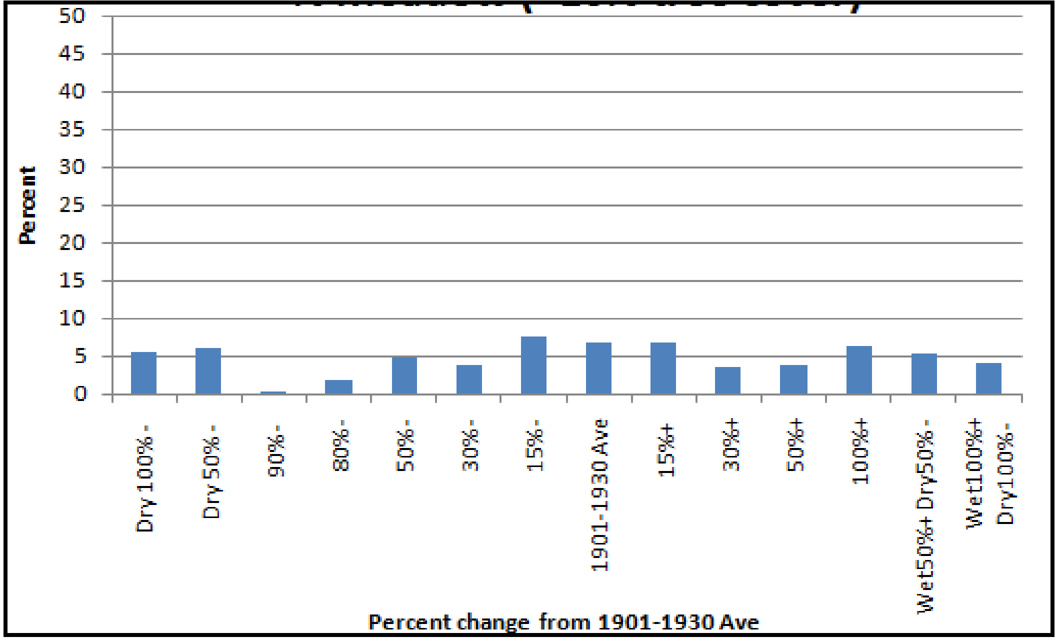


Figure F3a. Precipitation and temperature sensitivity of Annual Net Primary Productivity (ANPP) for 6 Plant Functional Types

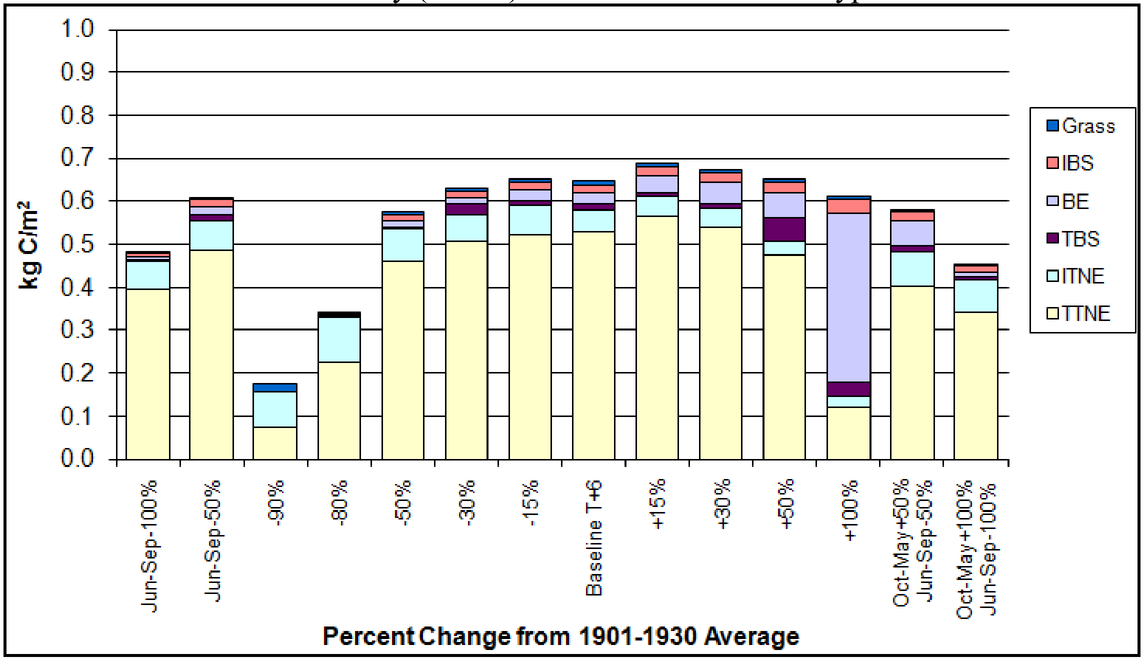


Figure F3b. Precipitation and temperature sensitivity of Carbon Mass (C Mass) for 8 Plant Functional Types

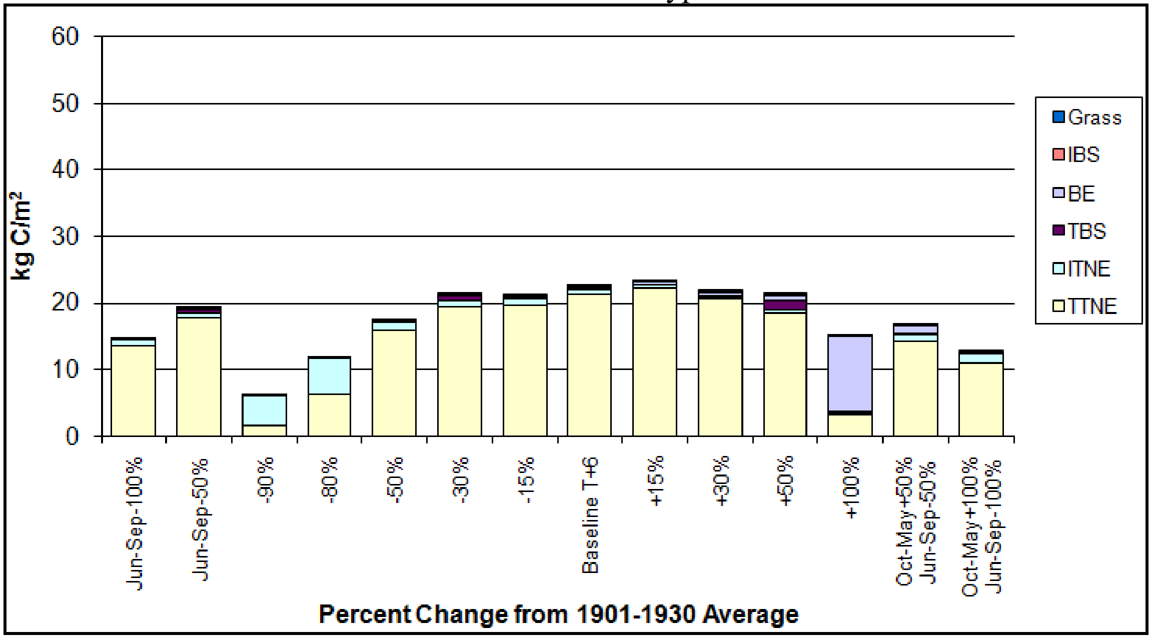


Figure F3c. Precipitation and temperature sensitivity Leaf Area Index (LAI) for 6 Plant Functional Types

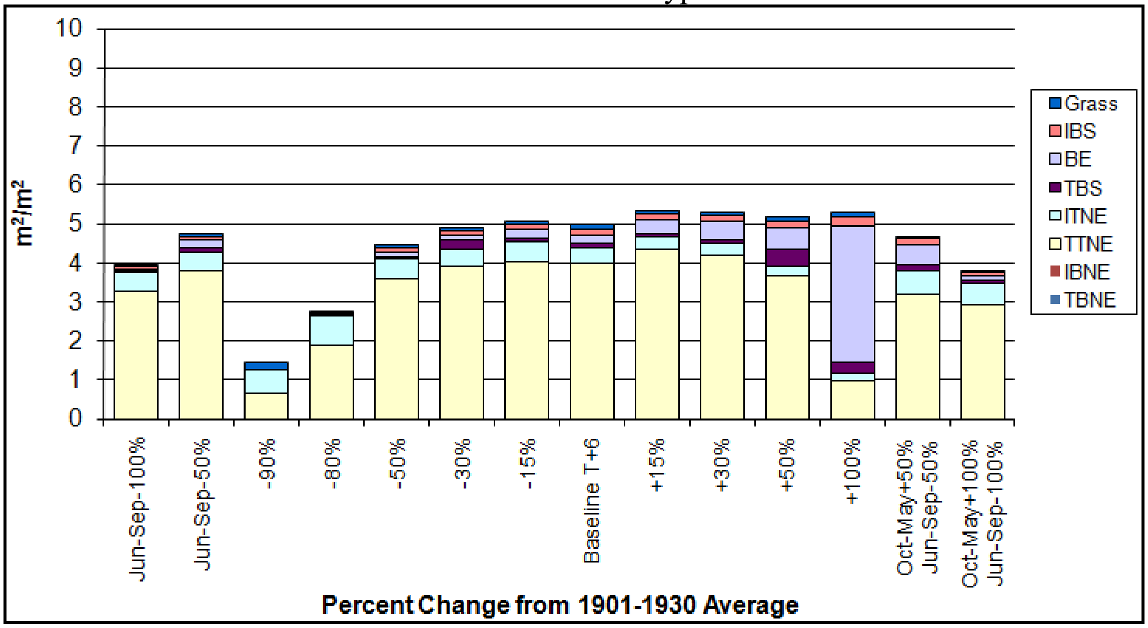


Figure F3d. Precipitation and temperature sensitivity of Foliar Projective Cover (FPC) for 6 Plant Functional Types

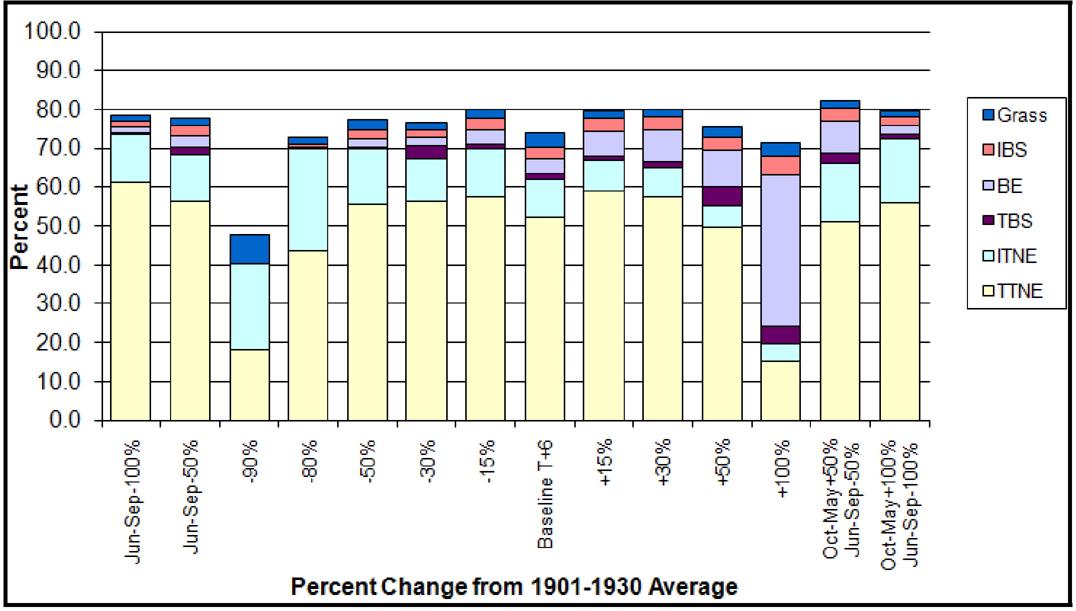


Figure F3e. Precipitation and temperature sensitivity Percent of Open Cover

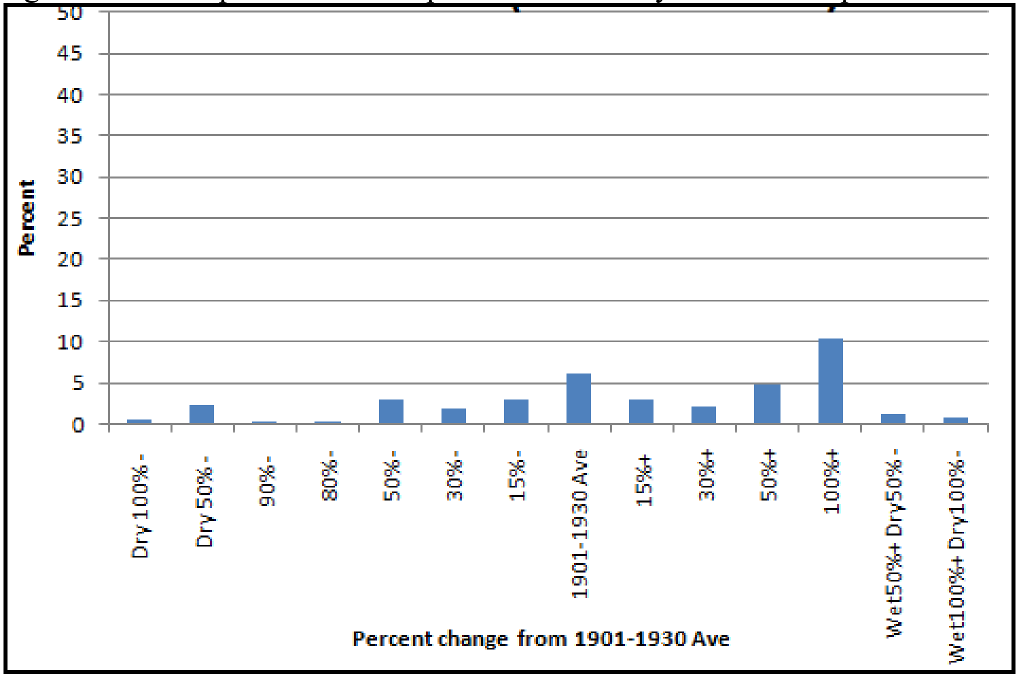


Figure F4a. Fire sensitivity of Annual Net Primary Productivity (ANPP) for 7 Plant Functional Types

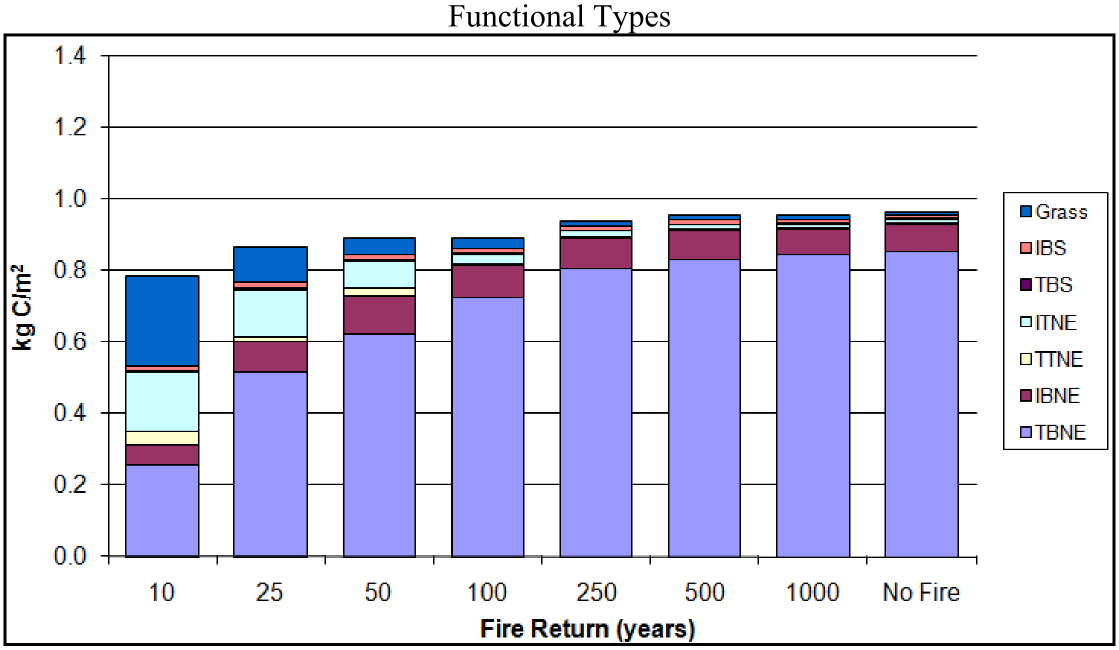


Figure F4b. Fire sensitivity of Carbon Mass (C Mass) for 7 Plant Functional Types

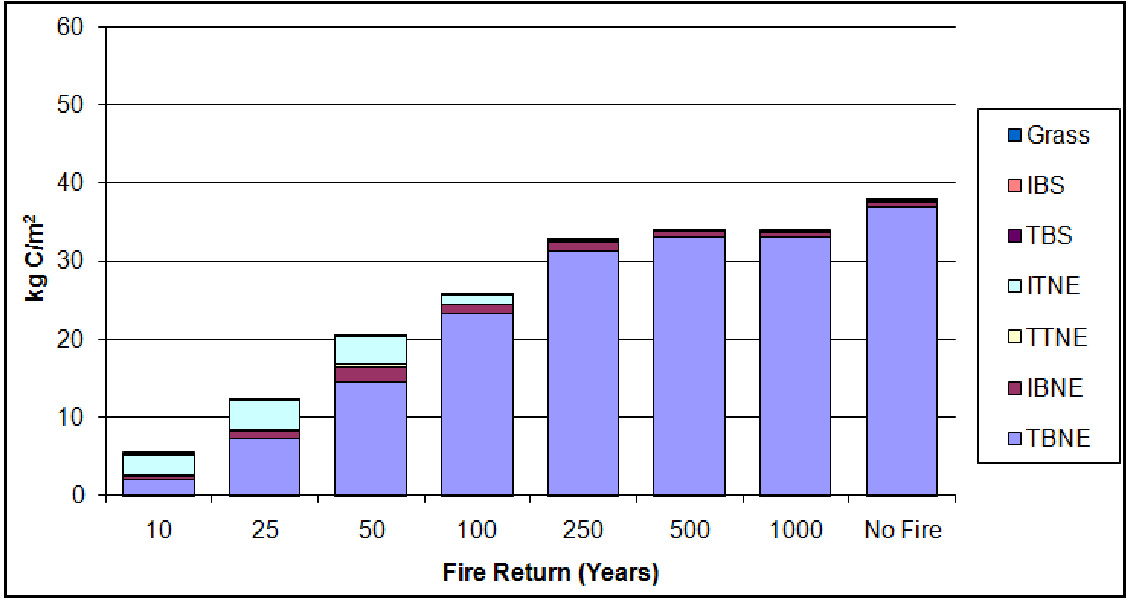


Figure F4c. Fire sensitivity of Leaf Area Index (LAI) for 7 Plant Functional Types

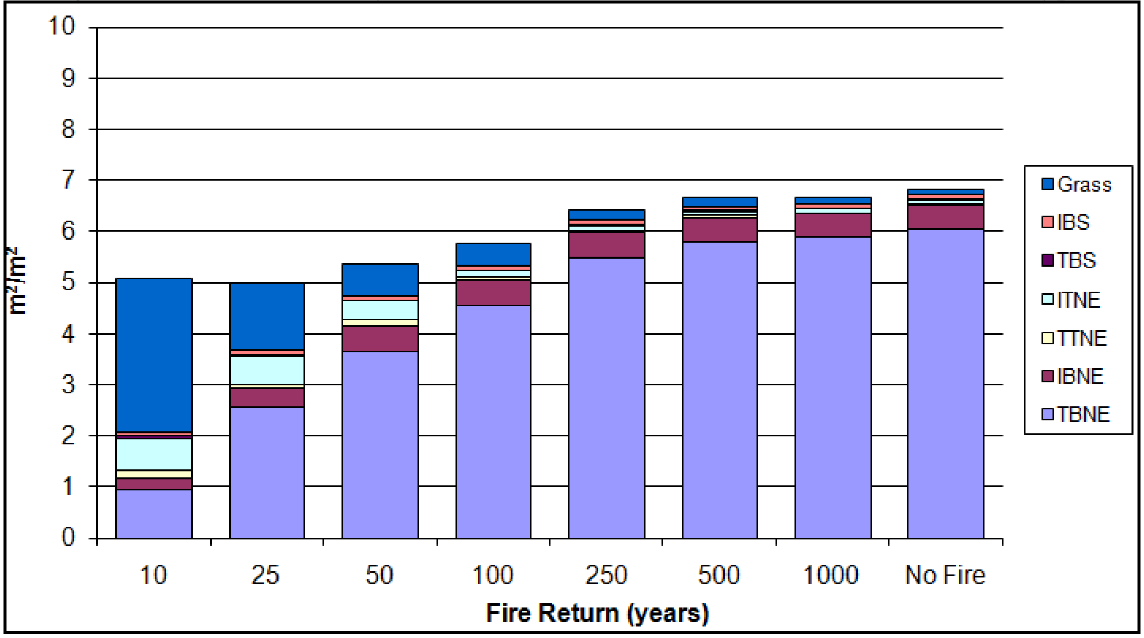


Figure F4d. Fire sensitivity of Foliar Projective Cover (FPC) for 7 Plant Functional Types

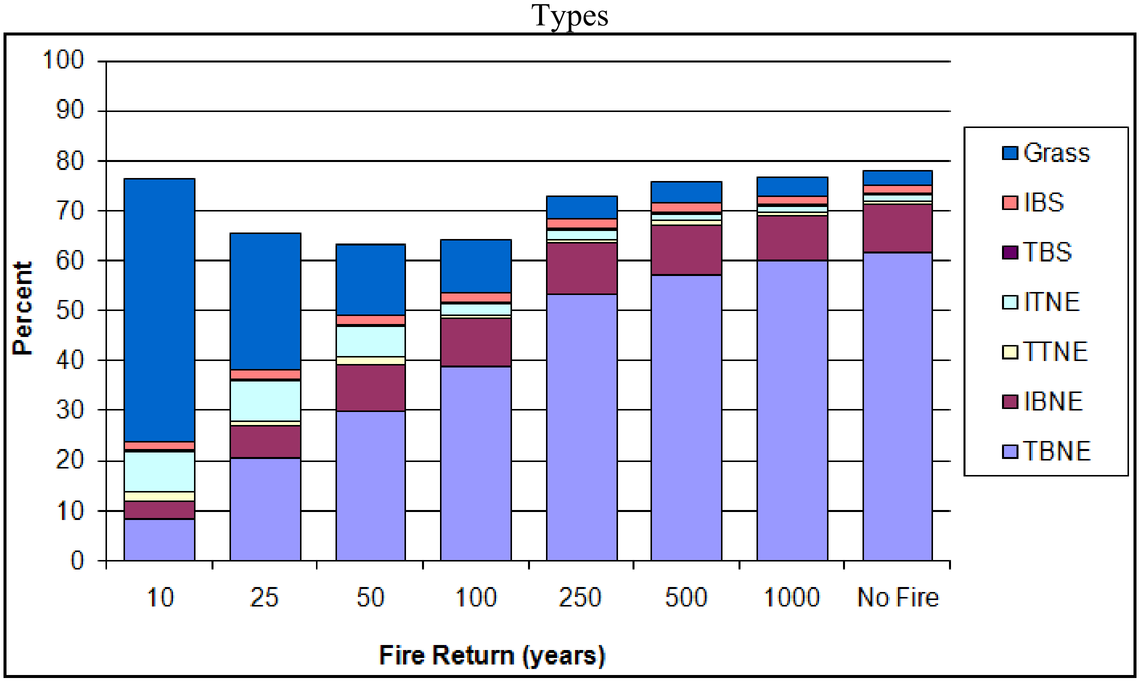


Figure F4e. Fire sensitivity of Percent of Open Cover

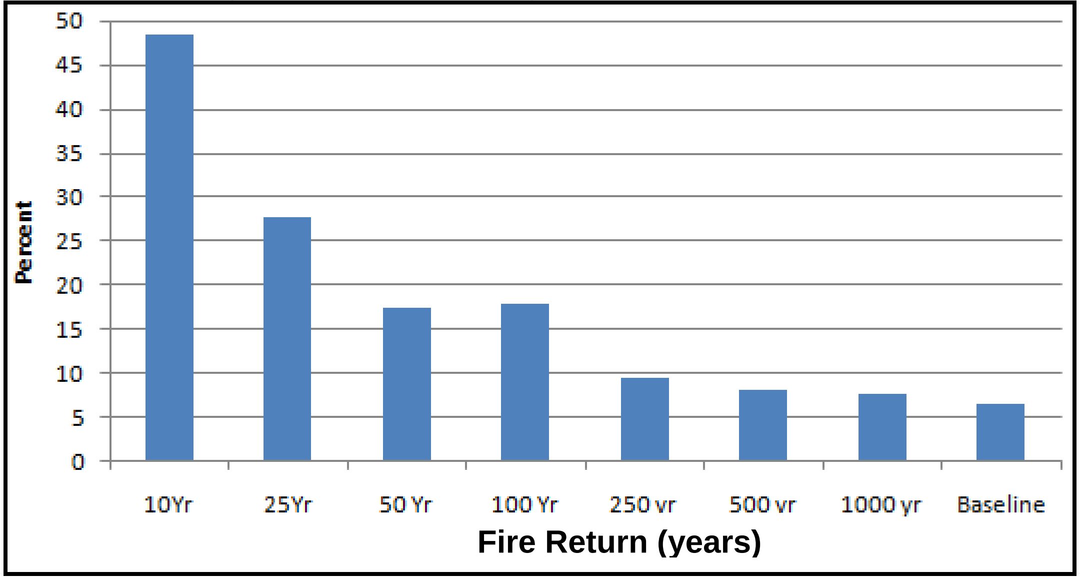


Figure F5a. CO_2 sensitivity of Annual Net Primary Productivity (ANPP) for 7 Plant Functional Types

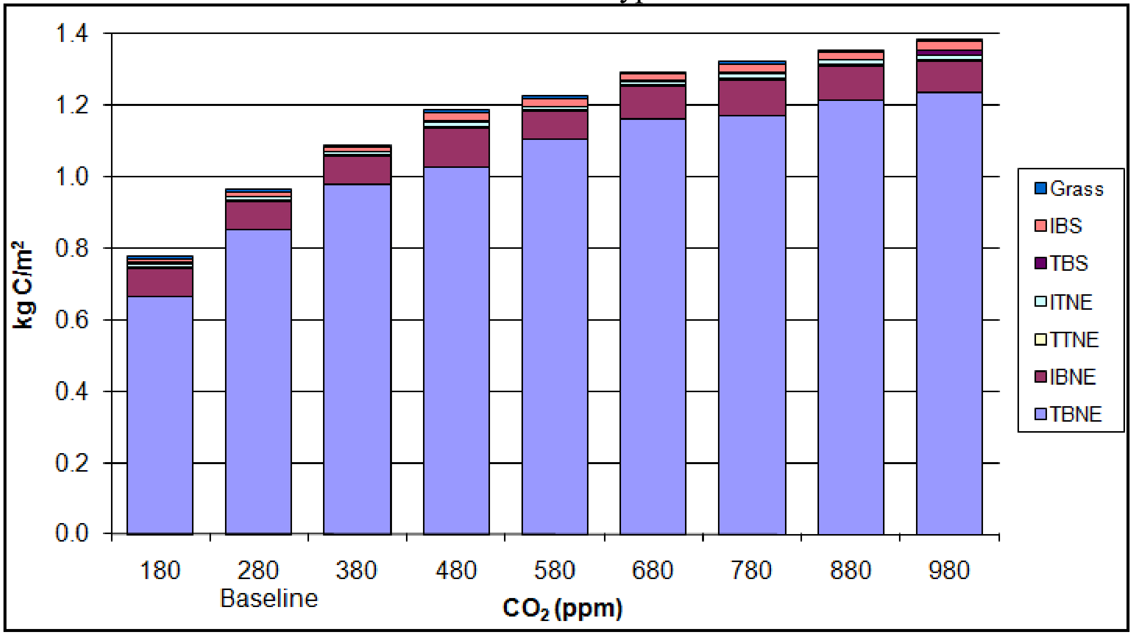


Figure F5b. CO_2 sensitivity of Carbon Mass (C Mass) for 7 Plant Functional Types

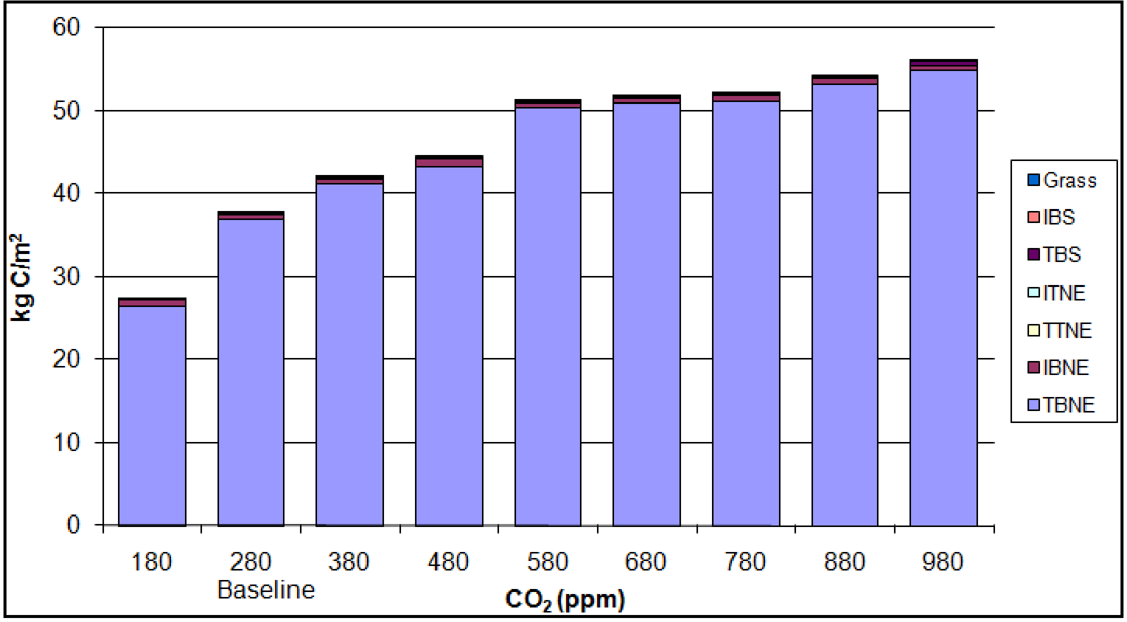


Figure F5c. CO_2 sensitivity of Leaf Area Index (LAI) for 7 Plant Functional Types

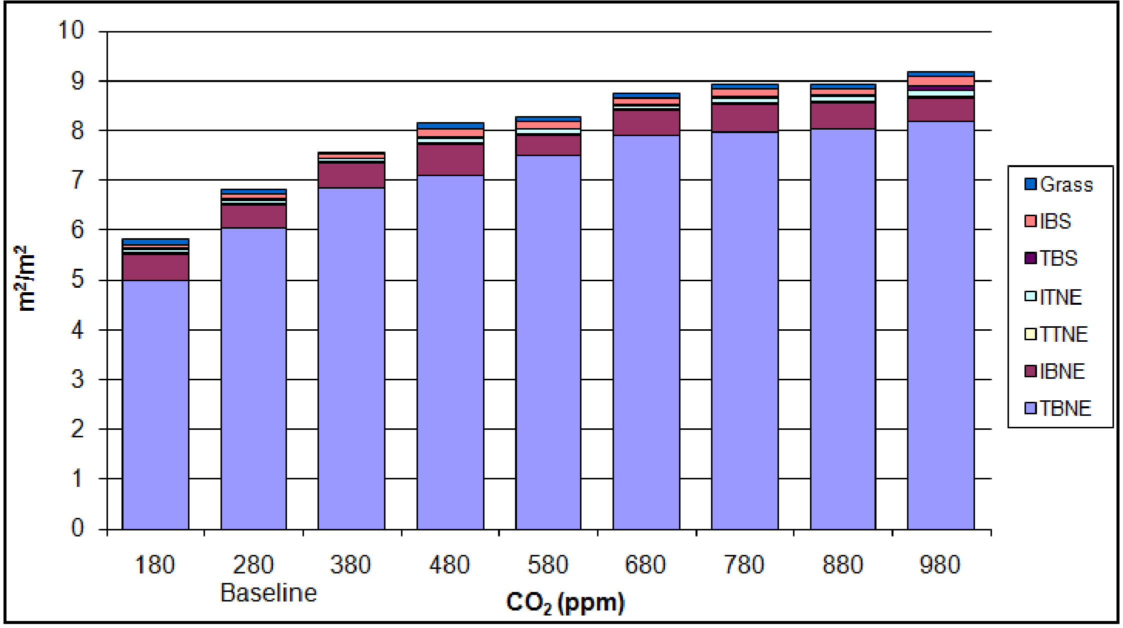


Figure F5d. CO_2 sensitivity of Foliar Projective Cover (FPC) for 7 Plant Functional Types

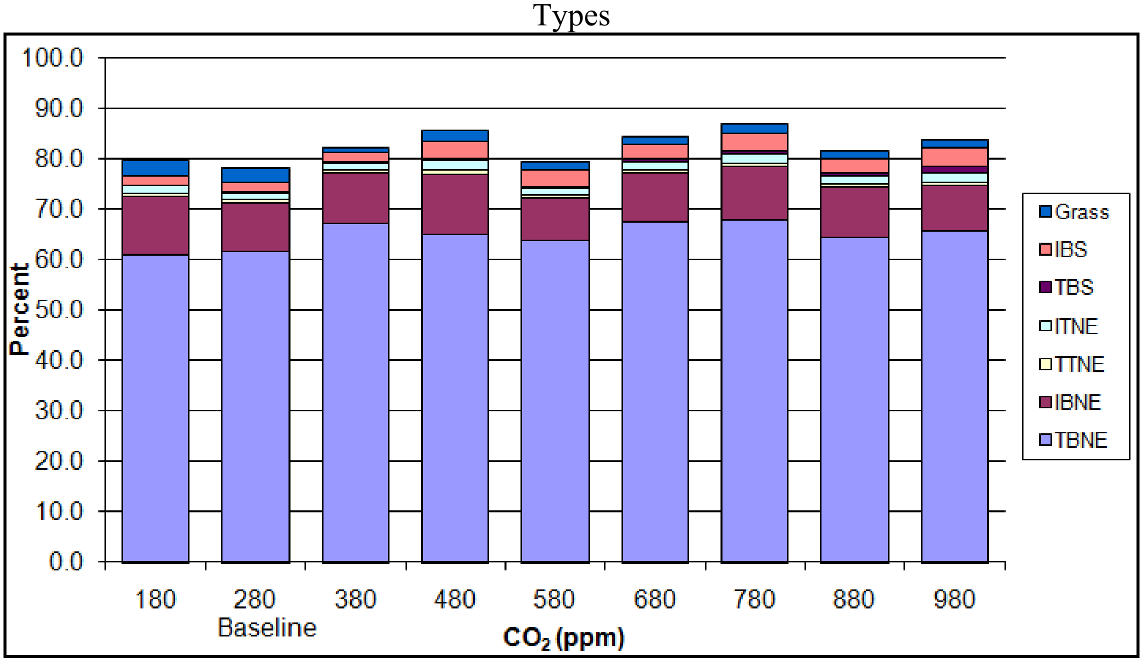
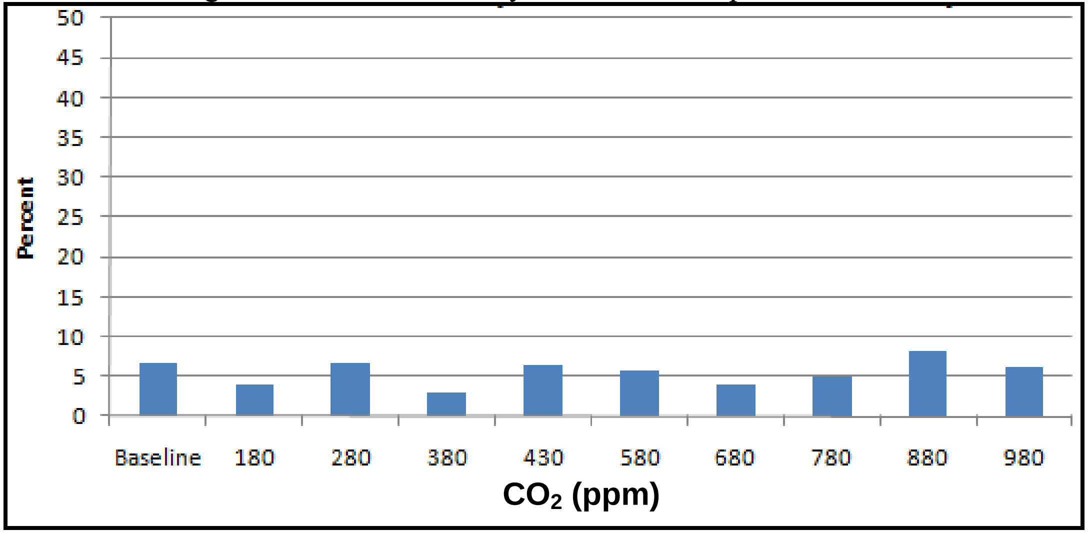


Figure F5e. CO_2 sensitivity of Percent of Open Cover

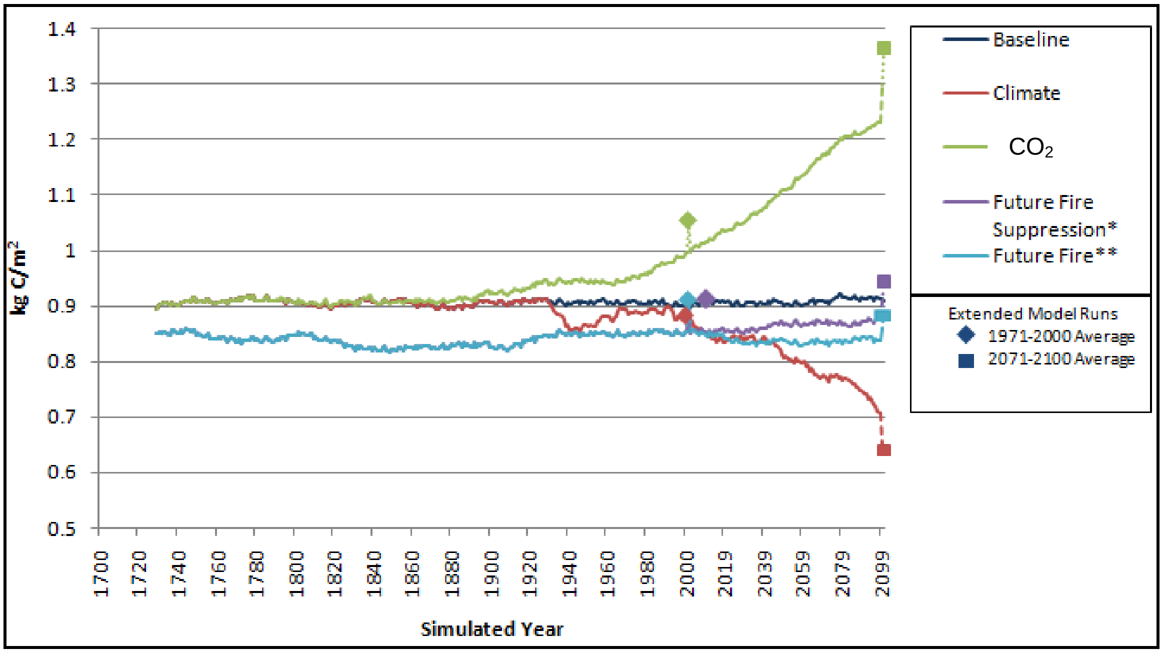


APPENDIX G

The output created by LPJ-GUESS (Smith et al. 2001) for the 12 scenarios (Chapter 4, Table 4.2) are graphed for single, double and triple driver scenarios in Tables G1a-d to G3a-d. The diamond and square symbols on dotted lines outside the scenario output averages signify 1000-year averages of extended model runs.

G.1 LPJ-GUESS Single Driver Scenario Graphs

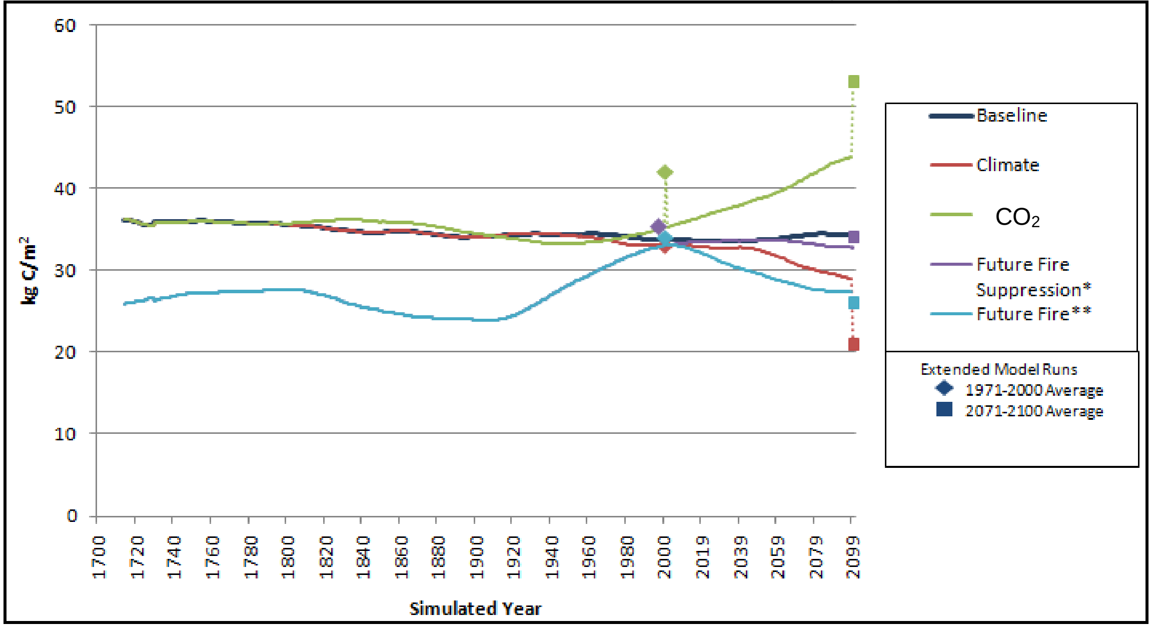
Figure G1a. LPJ-GUESS Tree Annual Net Primary Productivity (ANPP) 30-year Moving average output and extended model run average for single environmental driver Scenarios (Climate, CO2, Future Fire Suppression, and Future Fire) during the years 1700 – 2100.



*Future Fire Suppression Scenario simulated a 1000 year fire return from 1920-2100.

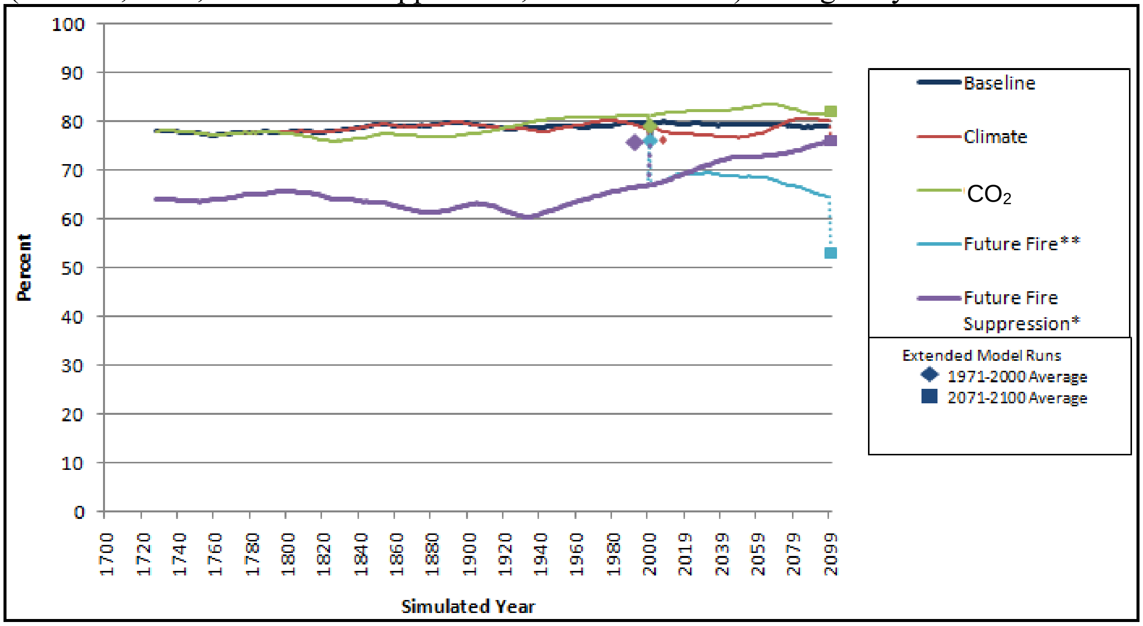
**Future Fire Scenario simulated a 1000 year fire return from 1920-2000 and model determined fire from 2000-2100.

Figure G1b. LPJ-GUESS Tree Carbon Mass (CMASS) 30-year moving average output and extended model run average for single environmental driver scenarios (Climate, CO2, Future Fire Suppression, and Future Fire) during the years 1700 – 2100.



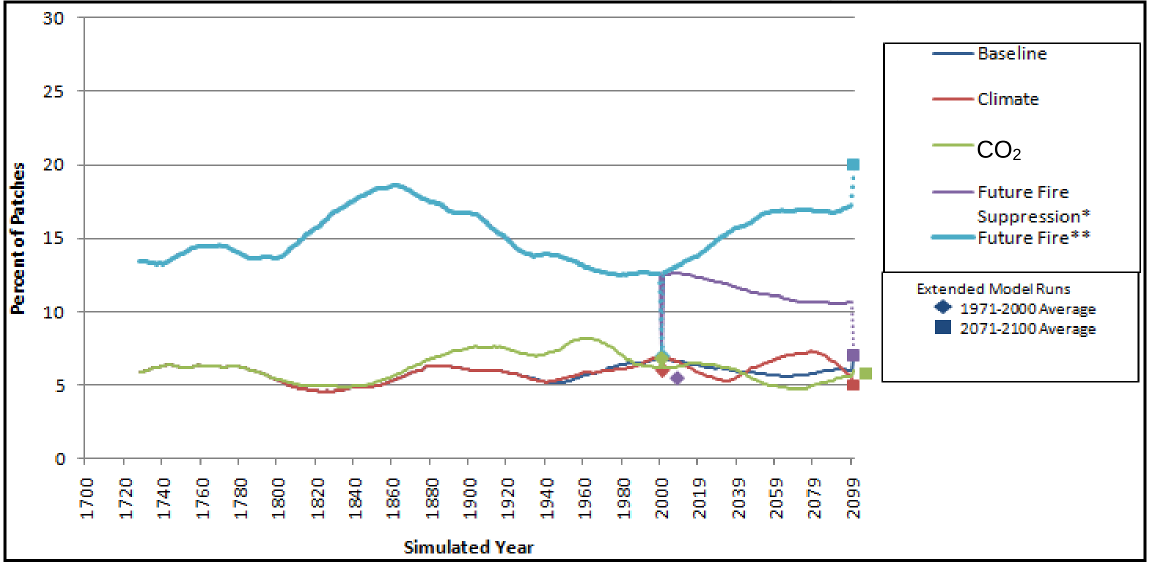
*Future Fire Suppression Scenario simulated a 1000 year fire return from 1920-2100.
**Future Fire Scenario simulated a 1000 year fire return from 1920-2000 and model determined fire from 2000-2100.

Figure G1c. LPJ-GUESS Tree Foliar Projective Cover (FPC) 30-year moving average output and extended model run average for single environmental driver scenarios (Climate, CO2, Future Fire Suppression, and Future Fire) during the years 1700 – 2100.



*Future Fire Suppression Scenario simulated a 1000 year fire return from 1920-2100.
**Future Fire Scenario simulated a 1000 year fire return from 1920-2000 and model determined fire from 2000-2100.

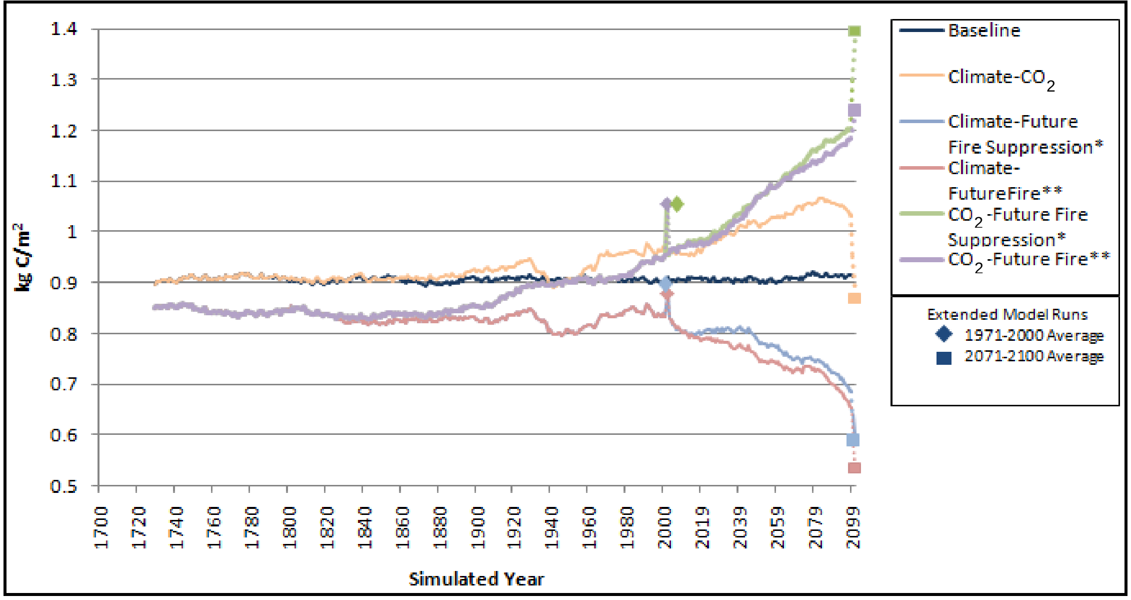
Figure G1d. LPJ-GUESS Percent of Open Cover Patches 30-year moving average output and extended model run average for single environmental driver scenarios (Climate, CO2, Future Fire Suppression, and Future Fire) during the years 1700 – 2100.



*Future Fire Suppression Scenario simulated a 1000 year fire return from 1920-2100.

**Future Fire Scenario simulated a 1000 year fire return from 1920-2000 and model determined fire from 2000-2100.

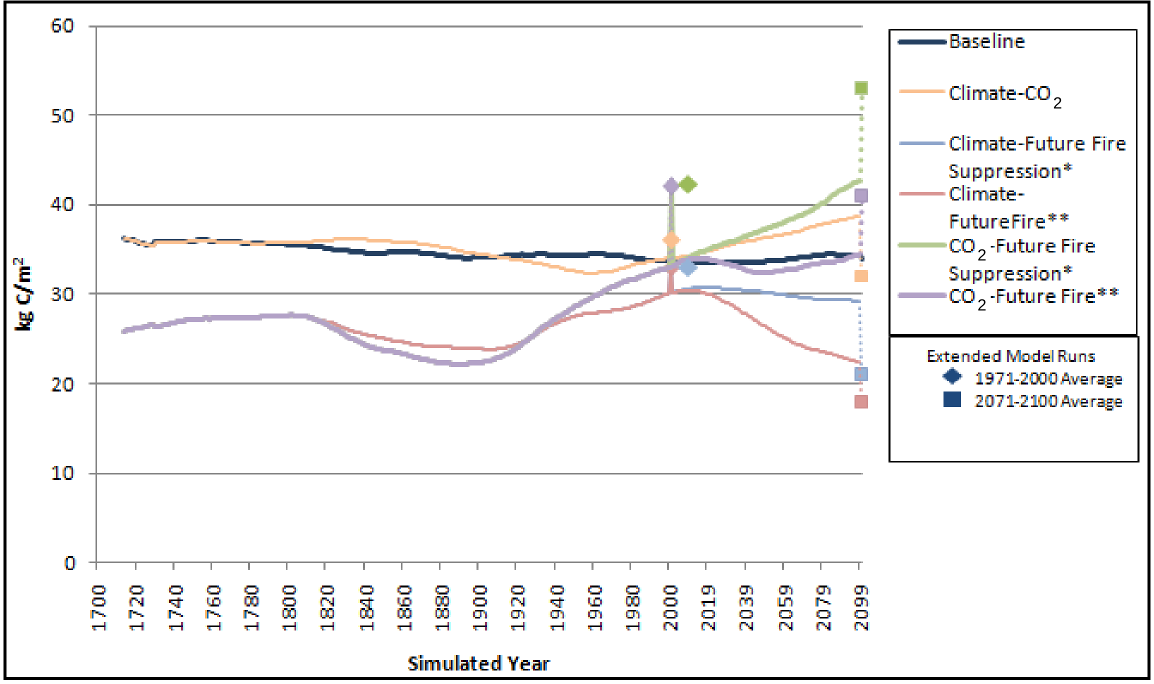
Figure G2a. LPJ-GUESS Tree Annual Net Primary Productivity (ANPP) 30-year moving average output and extended model run average for double environmental driver scenarios (Climate-CO_2, Climate-Future Fire Suppression, Climate-Future Fire, CO_2-Future Fire Suppression, and CO_2-Future Fire) during the years 1700 – 2100.



*Future Fire Suppression Scenario simulated a 1000 year fire return from 1920-2100.

**Future Fire Scenario simulated a 1000 year fire return from 1920-2000 and model determined fire from 2000-2100.

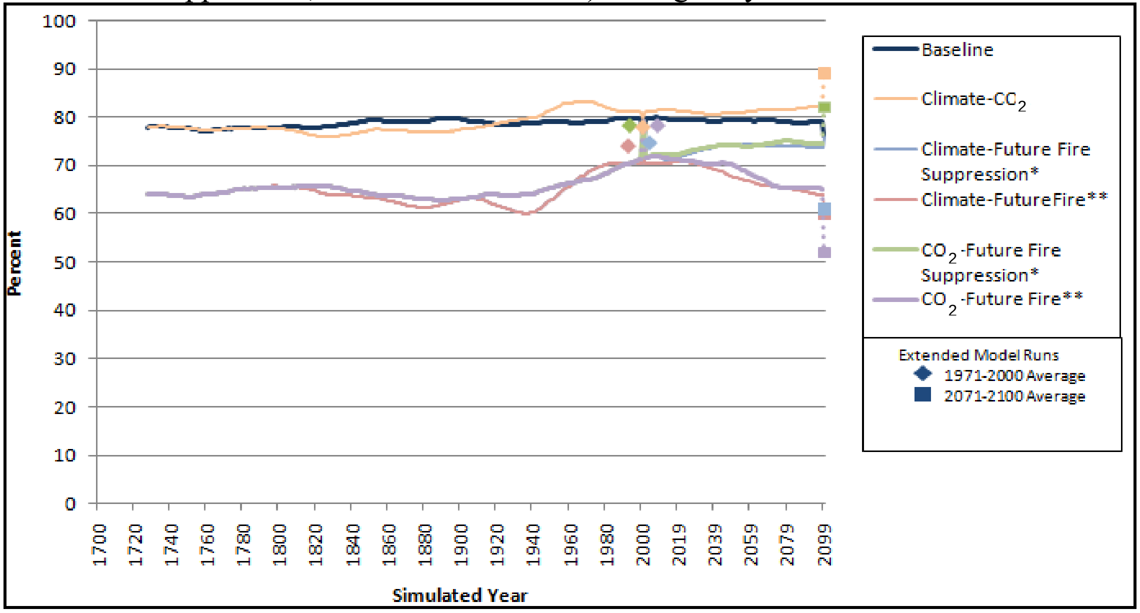
Figure G2b. LPJ-GUESS Tree Carbon Mass (CMASS) 30-year moving average output and extended model run average for double environmental driver scenarios (Climate-CO_2, Climate-Future Fire Suppression, Climate-Future Fire, CO_2-Future Fire Suppression, and CO_2-Future Fire) during the years 1700 – 2100.



*Future Fire Suppression Scenario simulated a 1000 year fire return from 1920-2100.

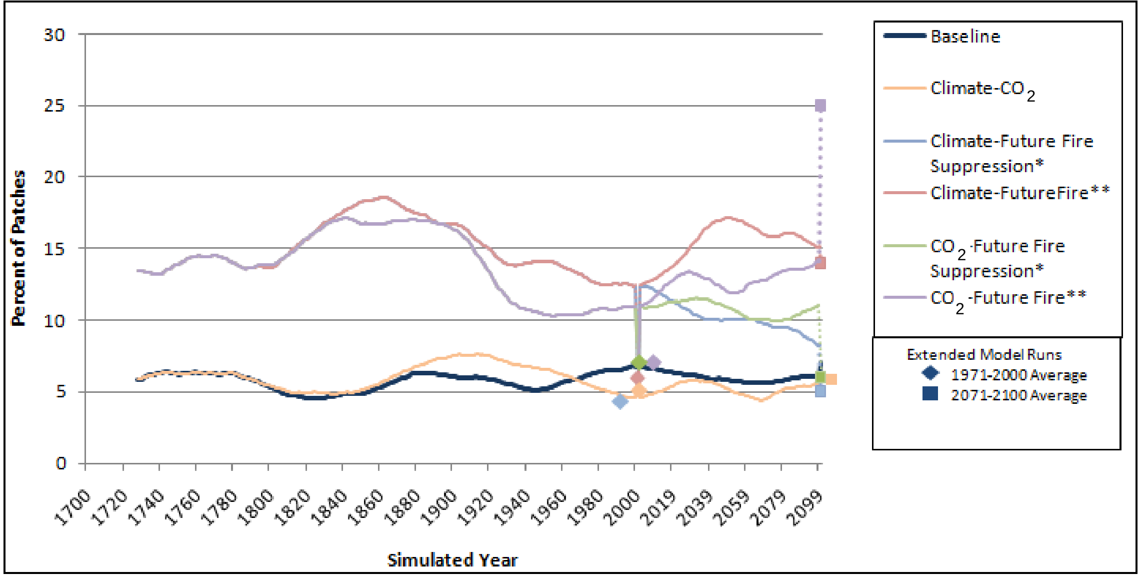
**Future Fire Scenario simulated a 1000 year fire return from 1920-2000 and model determined fire from 2000-2100.

Figure G2c. LPJ-GUESS Tree Foliar Projective Cover (FPC) 30-year moving average output and extended model run average for double environmental driver scenarios (Climate-CO_2, Climate-Future Fire Suppression, Climate-Future Fire, CO_2-Future Fire Suppression, and CO_2-Future Fire) during the years 1700 – 2100.



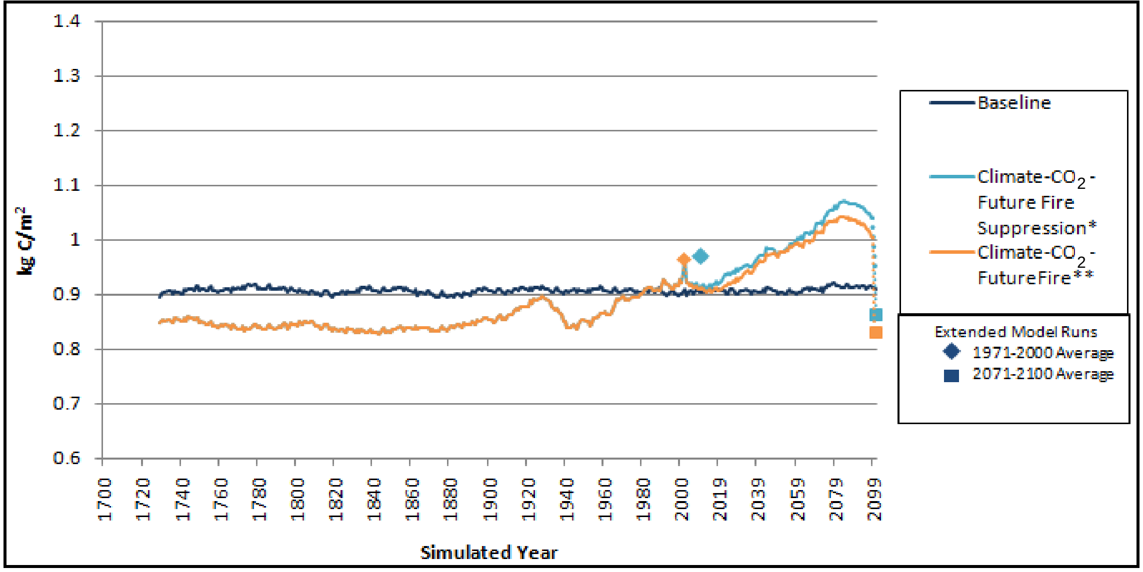
*Future Fire Suppression Scenario simulated a 1000 year fire return from 1920-2100.
**Future Fire Scenario simulated a 1000 year fire return from 1920-2000 and model determined fire from 2000-2100.

Figure G2d. LPJ-GUESS Percent of Open Cover Patches 30-year moving average output and extended model run average for double environmental driver scenarios (Climate-CO_2, Climate-Future Fire Suppression, Climate-Future Fire, CO_2-Future Fire Suppression, and CO_2-Future Fire) during the years 1700 – 2100.



*Future Fire Suppression Scenario simulated a 1000 year fire return from 1920-2100.
**Future Fire Scenario simulated a 1000 year fire return from 1920-2000 and model determined fire from 2000-2100.

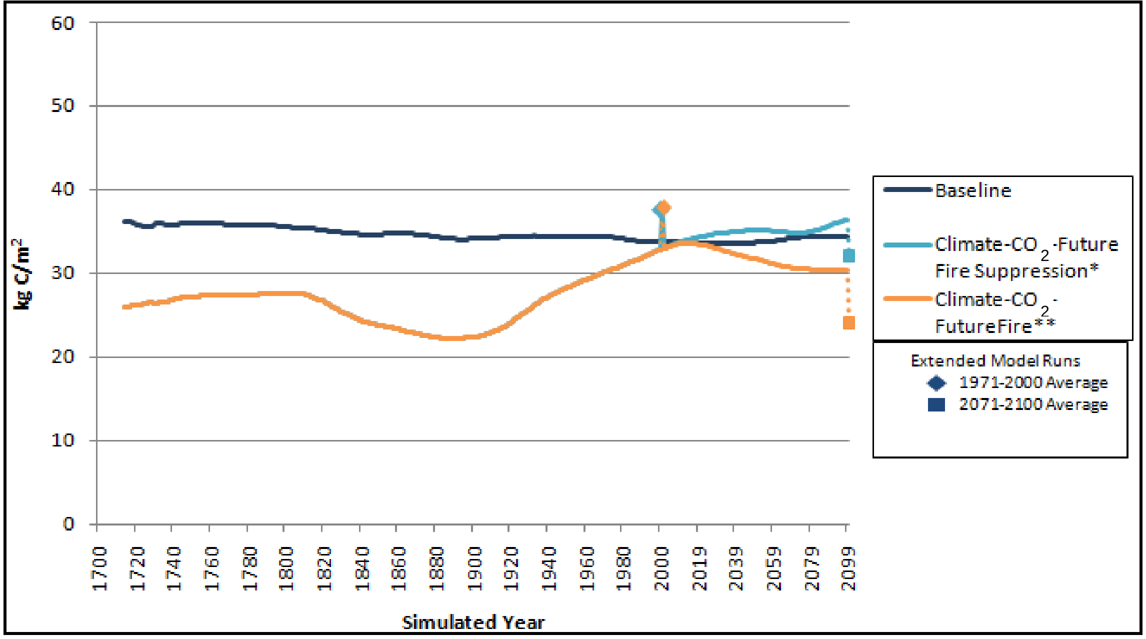
Figure G3a. LPJ-GUESS Tree Annual Net Primary Productivity (ANPP) 30-year moving average output and extended model run average for triple environmental driver scenarios (Climate-CO_2-Future Fire Suppression, Climate-CO_2-Future Fire) during the years 1700 – 2100.



*Future Fire Suppression Scenario simulated a 1000 year fire return from 1920-2100.

**Future Fire Scenario simulated a 1000 year fire return from 1920-2000 and model determined fire from 2000-2100.

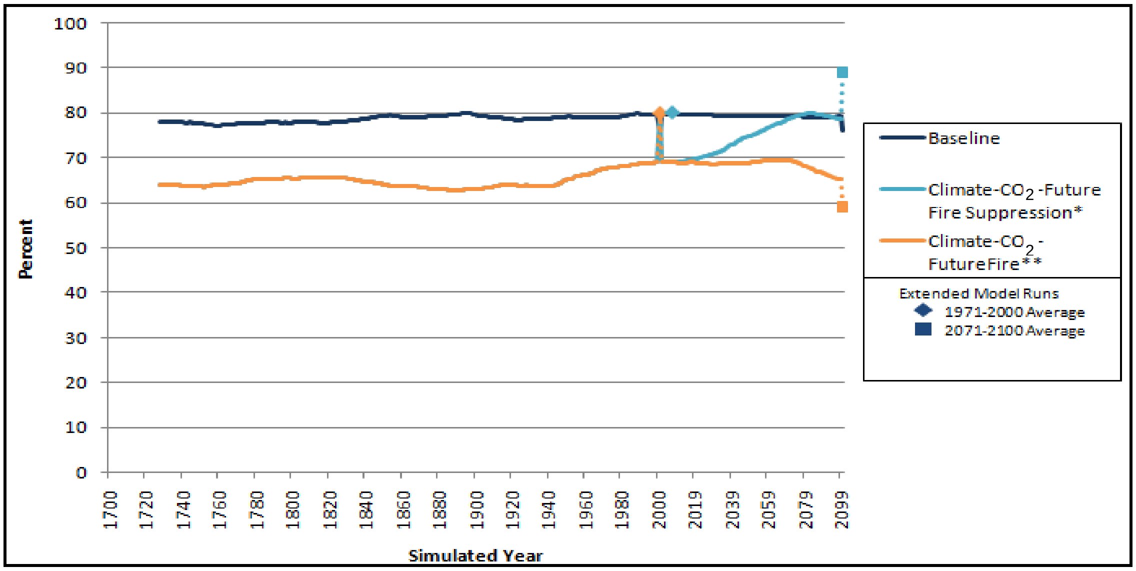
Figure G3b. LPJ-GUESS Tree Carbon Mass (CMASS) 30-year moving average output and extended model run average for triple environmental driver scenarios (Climate-CO_2-Future Fire Suppression, Climate-CO_2-Future Fire) during the years 1700 – 2100.



*Future Fire Suppression Scenario simulated a 1000 year fire return from 1920-2100.

**Future Fire Scenario simulated a 1000 year fire return from 1920-2000 and model determined fire from 2000-2100.

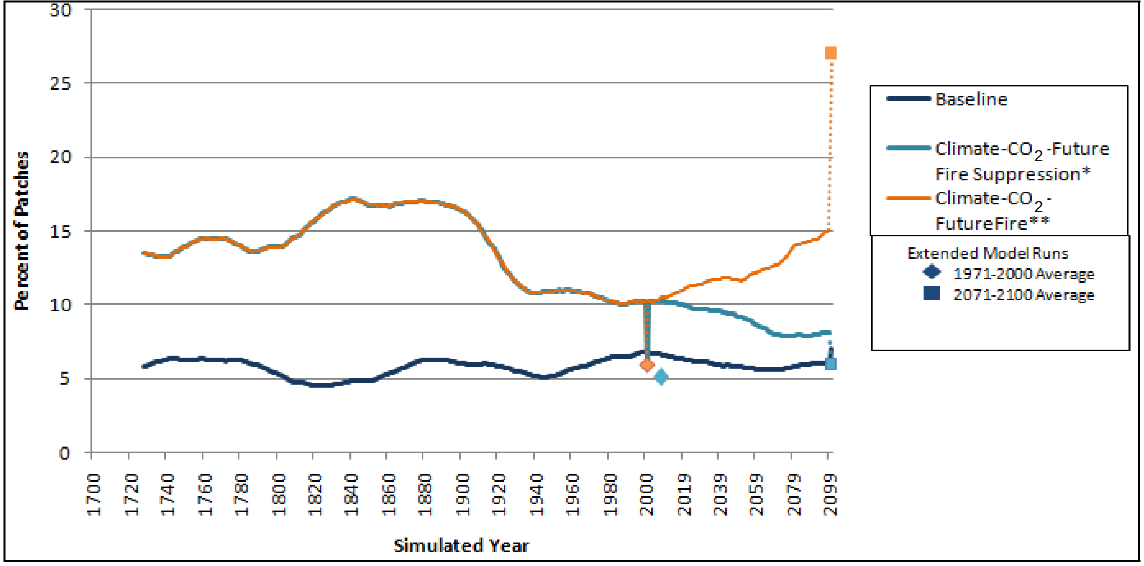
Figure G3c. LPJ-GUESS Tree Foliar Projective Cover (FPC) 30-year moving average output and extended model run average for triple environmental driver scenarios (Climate-CO_2-Future Fire Suppression, Climate-CO_2-Future Fire) during the years 1700–2100.



*Future Fire Suppression Scenario simulated a 1000 year fire return from 1920-2100.

**Future Fire Scenario simulated a 1000 year fire return from 1920-2000 and model determined fire from 2000-2100.

Figure G3d. LPJ-GUESS Percent of Open Cover Patches 30-year moving average output and extended model run average for triple environmental driver scenarios (Climate-CO_2 -Future Fire Suppression, Climate- CO_2-Future Fire) during the years 1700 – 2100.



*Future Fire Suppression Scenario simulated a 1000 year fire return from 1920-2100.

**Future Fire Scenario simulated a 1000 year fire return from 1920-2000 and model determined fire from 2000-2100.

Model Experiment Results by Plant Functional Type

The historic scenario results for plant functional type annual net primary productivity (Table G1), carbon mass (Table G2), and fractional projective cover (Table G3) showed that shade tolerant boreal needleleaved evergreen (TBNE) dominated productivity (0.51-1.11 kg C/m^2), carbon biomass (20.4-40.3 kg C/ m^2), and percent foliar projective cover (37%-65%) for all scenario averages of the last 30 years the centuries 1700, 1800, 1900, and 2000. Shade intolerant boreal needleleaved evergreen (IBNE) had the second highest level of productivity, carbon mass, and percent cover, and shade tolerant and intolerant temperate needleleaved evergreen (TTNE and ITNE) comprised a minor component of productivity , carbon biomass, and percent foliar projective cover for all scenario averages of the last 30 years the centuries 1700, 1800, 1900, and 2000. Shade tolerant and intolerant temperate broadleaved summer-green (TBS and IBS) also comprised a minor component of productivity, carbon biomass, and percent foliar projective cover. Grass comprised another minor component of productivity, carbon biomass, and percent foliar projective cover for all scenario averages of the last 30 years of the four centuries.

The future scenario results by plant functional type (Tables G1 – G3) showed that shade tolerant boreal needleleaved evergreen (TBNE) continued to dominate productivity, carbon biomass, and percent foliar projective cover for all scenarios in 2071-2100. Scenarios involving temperature increase (Scenarios 2, 6, 7, 8, 11, and 12) were the only scenarios with a change in plant functional type composition by the year 2100. These scenarios involving a 5 °C temperature increase resulted in a reduction of the dominant shade tolerant boreal needleleaved evergreen (TBNE) and co dominant shade intolerant boreal needleleaved evergreen (IBNE) productivity, carbon mass, and percent foliar projective cover. Lower elevation (temperate) conifer plant functional types, shade tolerant temperate needleleaved evergreen (TTNE), and especially shade intolerant temperate needleleaved evergreen (ITNE) increased productivity, carbon mass , and percent foliar projective cover. These temperature increase scenarios also allowed broadleaved evergreen (BE) to be present. Shade tolerant broadleaved summer-green (TBS), and especially shade intolerant broadleaved evergreen (IBS) productivity increased, carbon mass, and projective cover. Grass remained a minor component; however increased grass productivity, carbon mass, and projective cover occurred when fire frequency was higher (Scenarios 4, 5, 8, 10, and 12).

Table G1. Annual Net Primary Productivity (kg C/m^2) average for the years 1771-1800, 1871-1900, 1971-2000, and 2071-2100 by scenario for each Plant Functional Type.

Scenario	Year	TBNE	IBNE	TTNE	ITNE	TBS	IBS	BE	Grass
1 Baseline	1771-1800	0.80	0.07	0.01	0.01	0.00	0.01	0.00	0.01
	1871-1900	0.78	0.09	0.01	0.01	0.00	0.01	0.00	0.01
	1971-2000	0.78	0.09	0.01	0.01	0.00	0.01	0.00	0.01
	2071-2100	0.80	0.08	0.01	0.01	0.00	0.01	0.00	0.01
2 Climate	1771-1800	0.80	0.07	0.01	0.01	0.00	0.01	0.00	0.01
	1871-1900	0.78	0.09	0.01	0.01	0.00	0.01	0.00	0.01
	1971-2000	0.77	0.08	0.01	0.01	0.00	0.01	0.00	0.01
	2071-2100	0.58	0.04	0.02	0.03	0.00	0.03	0.01	0.01
3 CO_2	1771-1800	0.81	0.07	0.01	0.01	0.00	0.01	0.00	0.01
	1871-1900	0.81	0.08	0.01	0.01	0.00	0.01	0.00	0.01
	1971-2000	0.89	0.08	0.01	0.01	0.00	0.01	0.00	0.01
	2071-2100	1.11	0.08	0.01	0.01	0.00	0.02	0.00	0.01
4 Future Fire Suppression	1771-1800	0.72	0.09	0.00	0.02	0.00	0.01	0.00	0.02
	1871-1900	0.69	0.09	0.00	0.02	0.00	0.01	0.00	0.03
	1971-2000	0.74	0.08	0.00	0.01	0.00	0.01	0.00	0.01
	2071-2100	0.74	0.10	0.00	0.01	0.00	0.01	0.00	0.01
5 Future Fire	1771-1800	0.72	0.09	0.00	0.02	0.00	0.01	0.00	0.02
	1871-1900	0.69	0.09	0.00	0.02	0.00	0.01	0.00	0.03
	1971-2000	0.74	0.08	0.00	0.01	0.00	0.01	0.00	0.01
	2071-2100	0.71	0.09	0.00	0.02	0.00	0.01	0.00	0.02
6 Climate-CO_2	1771-1800	0.81	0.07	0.01	0.01	0.00	0.01	0.00	0.01
	1871-1900	0.81	0.08	0.01	0.01	0.00	0.01	0.00	0.01
	1971-2000	0.85	0.08	0.01	0.01	0.00	0.02	0.00	0.01
	2071-2100	0.88	0.03	0.03	0.03	0.01	0.05	~0.0	0.01
7 Climate-Future Fire Suppression	1771-1800	0.72	0.09	0.00	0.02	0.00	0.01	0.00	0.02
	1871-1900	0.69	0.09	0.00	0.02	0.00	0.01	0.00	0.03
	1971-2000	0.71	0.09	0.00	0.01	0.00	0.01	0.00	0.01
	2071-2100	0.56	0.05	0.01	0.02	0.00	0.03	0.01	0.01
8 Climate-Future Fire	1771-1800	0.72	0.09	0.00	0.02	0.00	0.01	0.00	0.02
	1871-1900	0.69	0.09	0.00	0.02	0.00	0.01	0.00	0.03
	1971-2000	0.71	0.09	0.00	0.01	0.00	0.01	0.00	0.01
	2071-2100	0.51	0.06	0.01	0.03	0.01	0.02	0.01	0.03
9 CO_2-Future Fire Suppression	1771-1800	0.72	0.09	0.00	0.01	0.00	0.01	0.00	0.02
	1871-1900	0.71	0.10	0.00	0.02	0.00	0.02	0.00	0.03
	1971-2000	0.81	0.10	0.01	0.01	0.00	0.02	0.00	0.01
	2071-2100	1.08	0.08	0.00	0.01	0.00	0.02	0.00	0.01
10 CO_2-Future Fire	1771-1800	0.72	0.09	0.00	0.01	0.00	0.01	0.00	0.02
	1871-1900	0.71	0.10	0.00	0.02	0.00	0.02	0.00	0.03
	1971-2000	0.81	0.10	0.01	0.01	0.00	0.02	0.00	0.01
	2071-2100	1.04	0.10	0.00	0.01	0.00	0.02	0.00	0.02
11 Climate-CO_2-Future Fire Suppression	1771-1800	0.72	0.09	0.00	0.01	0.00	0.01	0.00	0.02
	1871-1900	0.71	0.10	0.00	0.02	0.00	0.02	0.00	0.03
	1971-2000	0.80	0.08	0.00	0.01	0.00	0.01	0.00	0.01
	2071-2100	0.88	0.05	0.01	0.03	0.01	0.05	0.01	0.01
12 Climate-CO_2-Future Fire	1771-1800	0.72	0.09	0.00	0.01	0.00	0.01	0.00	0.02
	1871-1900	0.71	0.10	0.00	0.02	0.00	0.02	0.00	0.03
	1971-2000	0.80	0.08	0.00	0.01	0.00	0.01	0.00	0.01
	2071-2100	0.81	0.06	0.02	0.04	0.02	0.05	0.02	0.02

Table G2. Carbon biomass (kg C/m^2) average for the years 1771-1800, 1871-1900, 1971-2000, and 2071-2100 by scenario for each Plant Functional Type.

Scenario	Year	TBNE	IBNE	TTNE	ITNE	TBS	IBS	BE	Grass
1 Baseline	1771-1800	34.6	0.7	0.2	0.0	0.0	0.0	0.0	0.0
	1871-1900	32.8	0.8	0.4	0.0	0.0	0.1	0.0	0.0
	1971-2000	32.6	0.8	0.3	0.0	0.0	0.1	0.0	0.0
	2071-2100	33.4	0.7	0.2	0.0	0.0	0.1	0.0	0.0
2 Climate	1771-1800	34.6	0.7	0.2	0.0	0.0	0.0	0.0	0.0
	1871-1900	32.8	0.8	0.4	0.0	0.0	0.1	0.0	0.0
	1971-2000	32.1	0.7	0.2	0.0	0.0	0.0	0.0	0.0
	2071-2100	27.8	0.5	0.1	0.2	0.0	0.2	~0.0	0.0
3 CO_2	1771-1800	34.8	0.7	0.2	0.0	0.0	0.0	0.0	0.0
	1871-1900	33.4	0.7	0.3	0.0	0.0	0.1	0.0	0.0
	1971-2000	34.2	0.6	0.2	0.0	0.0	0.1	0.0	0.0
	2071-2100	43.0	0.6	0.3	0.0	0.0	0.1	0.0	0.0
4 Future Fire Suppression	1771-1800	26.1	1.1	0.0	0.3	0.0	0.1	0.0	0.0
	1871-1900	21.9	1.5	0.0	0.5	0.0	0.1	0.0	0.0
	1971-2000	30.8	1.7	0.0	0.4	0.0	0.1	0.0	0.0
	2071-2100	31.1	1.4	0.0	0.2	0.0	0.1	0.0	0.0
5 Future Fire	1771-1800	26.1	1.1	0.0	0.3	0.0	0.1	0.0	0.0
	1871-1900	21.9	1.5	0.0	0.5	0.0	0.1	0.0	0.0
	1971-2000	30.8	1.7	0.0	0.4	0.0	0.1	0.0	0.0
	2071-2100	25.3	1.6	0.0	0.4	0.1	0.1	0.0	0.0
6 Climate-CO_2	1771-1800	34.8	0.7	0.2	0.0	0.0	0.0	0.0	0.0
	1871-1900	33.4	0.7	0.3	0.0	0.0	0.1	0.0	0.0
	1971-2000	32.9	0.7	0.4	0.0	0.0	0.1	0.0	0.0
	2071-2100	37.4	0.4	0.6	0.2	0.0	0.3	~0.0	0.0
7 Climate-Future Fire Suppression	1771-1800	26.1	1.1	0.0	0.3	0.0	0.1	0.0	0.0
	1871-1900	21.9	1.5	0.0	0.5	0.0	0.1	0.0	0.0
	1971-2000	28.2	1.5	0.0	0.3	0.0	0.1	0.0	0.0
	2071-2100	27.5	1.0	0.1	0.4	0.0	0.2	0.0	0.0
8 Climate-Future Fire	1771-1800	26.1	1.1	0.0	0.3	0.0	0.1	0.0	0.0
	1871-1900	21.9	1.5	0.0	0.5	0.0	0.1	0.0	0.0
	1971-2000	28.2	1.5	0.0	0.3	0.0	0.1	0.0	0.0
	2071-2100	20.4	1.2	0.1	0.3	0.1	0.1	0.1	0.0
9 CO_2-Future Fire Suppression	1771-1800	26.0	1.2	0.0	0.3	0.0	0.1	0.0	0.0
	1871-1900	20.4	1.4	0.0	0.4	0.0	0.1	0.0	0.0
	1971-2000	30.9	1.7	0.0	0.4	0.0	0.1	0.0	0.0
	2071-2100	41.6	0.9	0.0	0.3	0.0	0.1	0.0	0.0
10 CO_2-Future Fire	1771-1800	26.0	1.2	0.0	0.3	0.0	0.1	0.0	0.0
	1871-1900	20.4	1.4	0.0	0.4	0.0	0.1	0.0	0.0
	1971-2000	30.9	1.7	0.0	0.4	0.0	0.1	0.0	0.0
	2071-2100	32.8	1.4	0.0	0.1	0.0	0.1	0.0	0.0
11 Climate-CO_2-Future Fire Suppression	1771-1800	26.0	1.2	0.0	0.3	0.0	0.1	0.0	0.0
	1871-1900	20.4	1.4	0.0	0.4	0.0	0.1	0.0	0.0
	1971-2000	30.7	1.4	0.0	0.6	0.0	0.1	0.0	0.0
	2071-2100	34.8	0.9	0.1	0.4	0.1	0.2	0.0	0.0
12 Climate-CO_2-Future Fire	1771-1800	26.0	1.2	0.0	0.3	0.0	0.1	0.0	0.0
	1871-1900	20.4	1.4	0.0	0.4	0.0	0.1	0.0	0.0
	1971-2000	30.7	1.4	0.0	0.6	0.0	0.1	0.0	0.0
	2071-2100	28.0	1.2	0.1	0.5	0.1	0.2	0.1	0.0

Table G3. Foliar projective cover (%) average for the years 1771-1800, 1871-1900, 1971-2000, and 2071-2100 by scenario for each Plant Functional Type.

Scenario	Year	TBNE	IBNE	TTNE	ITNE	TBS	IBS	BE	Grass
1 Baseline	1771-1800	61	10	1	1	0	2	0	3
	1871-1900	60	11	1	1	0	2	0	3
	1971-2000	60	12	1	2	0	2	0	3
	2071-2100	61	10	1	1	0	2	0	3
2 Climate	1771-1800	61	10	1	1	0	2	0	3
	1871-1900	60	11	1	1	0	2	0	3
	1971-2000	61	11	1	1	0	2	0	3
	2071-2100	58	7	2	4	1	5	1	3
3 CO_2	1771-1800	61	10	1	1	0	2	0	2
	1871-1900	59	10	1	1	0	2	0	3
	1971-2000	65	9	1	1	0	2	0	2
	2071-2100	65	9	1	2	1	3	0	2
4 Future Fire Suppression	1771-1800	44	11	1	2	0	2	0	6
	1871-1900	37	11	1	2	0	2	0	10
	1971-2000	47	11	1	2	0	2	0	4
	2071-2100	53	13	1	2	0	2	0	4
5 Future Fire	1771-1800	44	11	1	2	0	2	0	6
	1871-1900	37	11	1	2	0	2	0	10
	1971-2000	47	11	1	2	0	2	0	4
	2071-2100	42	10	1	2	0	2	0	8
6 Climate-CO_2	1771-1800	61	10	1	1	0	2	0	2
	1871-1900	59	10	1	1	0	2	0	3
	1971-2000	64	10	1	1	0	2	0	2
	2071-2100	61	5	2	4	1	7	1	2
7 Climate-Future Fire Suppression	1771-1800	44	11	1	2	0	2	0	6
	1871-1900	37	11	1	2	0	2	0	10
	1971-2000	50	12	1	2	0	2	0	4
	2071-2100	52	8	1	3	1	4	1	4
8 Climate-Future Fire	1771-1800	44	11	1	2	0	2	0	6
	1871-1900	37	11	1	2	0	2	0	10
	1971-2000	50	12	1	2	0	2	0	4
	2071-2100	37	8	1	4	1	4	1	9
9 CO_2-Future Fire Suppression	1771-1800	43	11	1	2	0	2	0	6
	1871-1900	37	12	1	2	0	2	0	9
	1971-2000	50	12	1	2	0	3	0	4
	2071-2100	58	9	1	2	0	3	0	2
10 CO_2-Future Fire	1771-1800	43	11	1	2	0	2	0	6
	1871-1900	37	12	1	2	0	2	0	9
	1971-2000	50	12	1	2	0	3	0	4
	2071-2100	45	10	1	2	1	3	0	4
11 Climate-CO_2-Future Fire Suppression	1771-1800	43	11	1	2	0	2	0	6
	1871-1900	37	12	1	2	0	2	0	9
	1971-2000	51	10	1	2	0	2	0	3
	2071-2100	57	7	2	4	1	6	1	2
12 Climate-CO_2-Future Fire	1771-1800	43	11	1	2	0	2	0	6
	1871-1900	37	12	1	2	0	2	0	9
	1971-2000	51	10	1	2	0	2	0	3
	2071-2100	40	5	2	4	2	6	1	5

The scatter plots for LAI versus other LPJ-GUESS model outputs showed a similar relationship between carbon biomass and annual net primary productivity. The LAI output results were omitted from Chapter 4.

Figure G4a-d. Scatter plots showing linear regression line and LAI's similar relation to CMASS (a), % Foliar Projective Cover (b), ANPP (c), and % Open Cover (d). Black line indicated linear regression fitted to points