

THE DRIVERS AND MECHANISMS OF C₄ AND C₃ GRASS DISTRIBUTIONS IN
HAWAII UNDER CURRENT AND FUTURE CLIMATES

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF THE
UNIVERSITY OF HAWAII AT MANOA IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

IN

BOTANY
(ECOLOGY, EVOLUTION, AND CONSERVATION BIOLOGY)

AUGUST 2012

By

Courtney L. Angelo

Dissertation Committee:
Curtis Daehler, Chairperson
Don Drake
Creighton Litton
Tamara Ticktin
Susan Cordell

DEDICATION

For my family, friends, and teachers that have influenced me to follow my dreams
and shoot for the stars.

For my gentle friend, Neeva Shrestha, who untimely passed away in 2009. May
her passion for botany live on in my work.

ACKNOWLEDGEMENTS

I want to thank my advisor, Curt Daehler, who taught me so much over my five years in Hawai'i. His strong support and guidance throughout my PhD made this work possible. Words cannot express my gratitude for his immense contribution to my work and to the development of my abilities as a scientist. He dedicated uncountable hours working with me in the field, teaching me grass species identification, reading drafts of grant proposals, dissertation chapters, and manuscripts, and helping me prepare PowerPoint presentations for conferences. His door was always open when I needed to discuss my research.

I want to also thank my committee members: Susan Cordell, Don Drake, Creighton Litton and Tamara Ticktin, each of whom have supported me along the way and made very thoughtful contributions to my dissertation work. I would like to also thank my committee members for reading drafts of manuscripts. I want to give a special thanks to Susan Cordell for showing me how to perform carbon uptake (A) versus internal CO_2 (C_i) curves. Learning how to do these curves gave me a greater understanding of the internal workings of C_4 and C_3 photosynthesis in plants.

I want to thank the Daehler Lab: Jennifer Bufford, Ayres Christ, Melody Euaparadorn, Matt Lurie, Alexandre Sampaio, and Seana Walsh. Your support and guidance helped me push through challenges and complete my PhD.

I want to thank Stephanie Saephan in the Botany GIS Lab. With her endless effort and teaching abilities, I was able to master the ArcGIS software system. I want to also thank Stephanie for making me instruction guides while I was in California, and for her work developing my future climate layers for the Hawaiian Islands. Her support through the years will not be forgotten.

I want to also thank Cliff Morden for his continued support and encouragement of my research working with grasses. His love for grasses was contagious.

Additionally, I would like to thank Tim Gallaher, who spent hours helping me construct additional light apparatuses for my CO₂ chambers. I would also like to thank Amanda Uowolo for helping me take A/C_i curve measurements. I would like to thank Alexandre Sampaio for our many conversations on C₄ plant biology, help in the greenhouse and with my CO₂ experiment, guidance, and friendship.

I would like to thank my three wonderful and dedicated undergraduate research assistants, Maria Perez, Patra Foulk, and Seana Walsh. Their lab help was invaluable to my dissertation progress. Their dedication to my research and meticulous work ethics gave me room to breathe when there were too many simultaneous tasks that needed completion. A big Mahalo!

I would like to thank all of the faculty and students in the Botany Department for being so supportive and helpful over the years. The positive energy in the Botany Department made this work possible. I cannot imagine completing my PhD in a

more supportive department. I want to also thank Patty Bedoya and Kori Phillips in the Botany office.

I would like to thank my fellow female Botany graduate friends: Lisa Mandle, Isabel Schmidt, Vandana Krishnamurthy, Georgia Hart, Jennifer Bufford, Marian Chau, Maggie Sporck, and Rachael Wade for their continued friendship, guidance, and support over the years. Without their friendship and support, obtaining my PhD would have been more painful. I would like to especially thank Lisa Mandle and Isabel Schmidt for sticking by me all of these years and bringing so much light, laughter, and good times to this journey. I also would like to thank two other amazing female scientists in other UH departments, Cadie Buckley and Martha Gauthier for their support and friendship from the beginning to the end of this journey.

I would like to thank my friends back in California. You have supported me through this entire process from applying to grad school till graduating with my PhD. Throughout this journey, you have helped me stay connected to other things I love besides, botany.

I would like to thank Ingrid Parker and Becky Hufft Kao for seeing potential in me as an undergraduate at UC Santa Cruz and taking me under your wing. You were the initial catalysts of this journey.

I would like to thank my family for always supporting me in all of my endeavors and telling me to shoot for the stars. Without their support the dream of obtaining

a PhD would not have become a reality! I would like to also thank my Dad, Amadeo Angelo, for flying out to Hawai'i to build my CO₂ chambers and my Mom, Kim Angelo, for supporting me every week through this journey. Thank you to my sisters, Amanda and Jenna Angelo for being my sisters and my life's cheerleaders.

I would also like to thank the Abresch/Price family and extended family for allowing me to stay at their houses during my California visits and for always giving me support and loving care.

Finally, I would like to thank Jamey Abresch, for sticking by me through this long process and always loving me. Jamey, you have given me so much strength and support to pursue my goals even though we were apart. I'm grateful that we made it through this journey together.

This work was funded by the USDA National Institute of Food and Agriculture Biology of Weedy and Invasive Species Program, University of Hawai'i Ecology, Evolution and Conservation Biology Program, Maybelle Roth Scholarship in Conservation Biology, University of Hawai'i Graduate Student Organization, University of Hawai'i Research Corporation, University of Hawai'i Botany and Biology Departments. Thank you to all of my funding sources for making my PhD research possible.

ABSTRACT

The two most common photosynthetic pathways in flowering plants are C₄ and C₃ photosynthesis. Forty percent of species in the Poaceae (the grass family) have C₄ photosynthesis while the other 60% use the C₃ photosynthetic pathway. C₄ plants generally have a high optimum temperature range; while C₃ plants have a lower optimum temperature range. Over the last 200 years, over 400 grass species having both C₄ and C₃ photosynthetic pathways have been introduced to Hawai'i, with 100 of these species becoming naturalized. In Hawai'i, most nonnative grasses that have altered the grass fire cycle and threaten native plant communities are C₄ grasses. Therefore, it is important to understand the drivers and limitations of C₄ and C₃ grass distributions in Hawai'i. In addition, to understanding current distributions of C₄ and C₃ grasses, it is also important to determine how these distributions will be impacted by aspects of global change such as climate warming, altered precipitation patterns, and elevated CO₂. This work used field surveys across broad elevation transects, historical data, manipulative experiments, and climate-niche modeling to determine what climatic factors drive C₄ and C₃ grass distributions, along with determining how these distributions might change in response to global change. Relative C₄/C₃ grass abundance and richness patterns were found to be broadly driven by temperature. This suggests that the C₄-C₃ transition point (the point of dominance between C₄ and C₃ grasses) will shift upward in elevation with climate warming. Distributional patterns for individual C₄ species were found to be complex and require species-specific evaluation. C₃ species consistently

responded as predicted with climate warming and elevated CO₂ revealing that these species will likely have smaller distributions in the future at higher elevations in Hawai‘i and may become more competitive in drought conditions with increased CO₂. C₄ plants were found to have positive growth and physiological responses to elevated CO₂, however, some species may have physiological limitations under drought stress that cannot be overcome with increased CO₂. Similar patterns are expected for ecosystems elsewhere in the tropics, where both C₄ and C₃ grass persist.

TABLE OF CONTENTS

DEDICATION	ii
ACKNOWLEDGEMENTS.....	iii
ABSTRACT	vii
TABLE OF CONTENTS	ix
LIST OF TABLES	xii
LIST OF FIGURES	xiii
Chapter 1. C ₄ and C ₃ grass distributions in Hawai'i: Where we are now and where we need to go	1
LITERATURE CITED	11
Chapter 2. Distribution patterns of C ₄ and C ₃ grasses along tropical elevation gradients in Hawai'i	14
ABSTRACT	15
INTRODUCTION	17
METHODS.....	21
RESULTS.....	24
DISCUSSION	28
LITERATURE CITED	32
TABLES.....	35
FIGURES	43
APPENDIX	46
Chapter 3. Upward expansion of fire-adapted C ₄ and C ₃ grasses along a warming tropical elevation gradient	51
ABSTRACT	52
INTRODUCTION	54
METHODS.....	57
RESULTS.....	60

DISCUSSION	63
LITERATURE CITED	68
TABLES.....	72
FIGURES	74
APPENDIX	80
Chapter 4. Impacts of future climates on fire-promoting invasive grass distributions in the Hawaiian Islands: C ₄ vs C ₃	83
ABSTRACT	84
INTRODUCTION	86
METHODS.....	91
RESULTS.....	97
DISCUSSION	104
LITERATURE CITED	115
TABLES.....	120
FIGURES	130
APPENDIX	145
Chapter 5. Growth, physiological and biochemical responses of C ₄ and C ₃ grasses to aspects of global change: Is there a true winner?	170
ABSRACT.....	171
INTRODUCTION	173
METHODS.....	180
RESULTS.....	186
DISCUSSION	194
LITERATURE CITED	207
TABLES.....	213
FIGURES	217

Chapter 6. Past, current, and future distributions of C ₄ and C ₃ grasses in the Hawaiian Islands: What we know now, limitations, and future directions.....	235
LITERATURE CITED.....	249

LIST OF TABLES

Table 2.1. Spearman's correlation: r_s values for relative percent cover and relative species richness data and climatic variables.....	36
Table 2.2. Spearman's correlation: r_s values for absolute percent cover and climatic variables.....	37
Table 2.3. Transition temperatures for C_4 and C_3 grass distributions on the islands of Hawai'i and Maui.....	38
Table 2.4. Transition elevations for C_4 and C_3 grass distributions on the islands of Hawai'i and Maui.....	39
Table 2.5. Global summary of C_4 and C_3 grass transition points, temperature, and/or main climatic driving factor.....	40
Table 3.1. Elevational changes documented over a 40 year time period for fire-adapted vs. non-fire adapted C_3 and C_4 grass species in Hawai'i.....	73
Table 4.1. PRISM AUC values and species model climatic constraints.....	121
Table 4.2. Giambelluca AUC values and species model climatic constraints...	122
Table 4.3. <i>P</i> -values for site species distribution differences between PRISM and Giambelluca climate data.....	123
Table 4.4. Range change estimates for across the Hawaiian Islands.....	124
Table 4.5. Range change values across Hawai'i Volcanoes National Park.....	125
Table 4.6. Range change values across Haleakalā National Park.....	126
Table 4.7. Range change values across Koke'e State Park.....	127
Table 4.8. Range change values across Mauna Kea Forest Reserve.....	128
Table 4.9. Range change values across Pohakuloa Training Area.....	129
Table 5.1. C_4 and C_3 species used in the experiment.....	214
Table 5.2. Mixed model of analysis of variance	215
Table 5.3. Mixed model of analysis of variance.....	216

LIST OF FIGURES

Figure 2.1. Distribution of grass surveys on the islands of Kaua'i, Maui, and Hawai'i.....	44
Figure 2.2. July mean maximum transition temperatures for elevation gradients in the Hawaiian Islands.....	45
Figure 3.1. Survey sites and fires sites on the island of Hawai'i all within Hawai'i Volcanoes National Park.....	75
Figure 3.2. Monthly temperature averages for Hawai'i Volcanoes National Park in July and January 1965-2009.....	76
Figure 3.3. Transition elevations for % relative cover and relative species richness of C ₃ and C ₄ grasses.....	77
Figure 3.4. C ₄ grass distributions in 2008 versus 1966/1967	78
Figure 3.5. C ₃ grass distributions in 2008 versus 1966/1967	79
Figure 4.1. Distribution projections for <i>Anthoxanthum odoratum</i>	131-132
Figure 4.2. Distribution projections for <i>Cenchrus ciliaris</i>	133-134
Figure 4.3. Distribution projections for <i>Holcus lanatus</i>	135-136
Figure 4.4. Distribution projections for <i>Hyparrhenia rufa</i>	137-138
Figure 4.5. Distribution projections for <i>Melinis minutiflora</i>	139-140
Figure 4.6. Distribution projections for <i>Paspalum dilatatum</i>	141-142
Figure 4.7. Distribution projections for <i>Pennisetum setaceum</i>	143
Figure 4.8. Distribution projections for <i>Schizachyrium condensatum</i>	144
Figure 5.1. Mean daily relative humidity and chamber temperatures for ambient and elevated CO ₂ chambers.....	218
Figure 5.2. Mean values for the effects of CO ₂ and Photosynthetic Pathway (PP) for the variables total plant biomass, aboveground biomass, and underground biomass.....	219
Figure 5.3. Mean values for the effects of water treatment on C ₃ and C ₄ grass species for the variables total plant biomass, aboveground biomass, and underground biomass.....	220
Figure 5.4. Mean values for the effects of CO ₂ and Photosynthetic Pathway (PP) for the variables A _{max} , g _s , and WUE.....	221

Figure 5.5. Mean values among species variation in A_{\max} in response to CO ₂ levels.....	222
Figure 5.6. Mean values for the effects of water treatment on C ₃ and C ₄ grass species for the variables A_{\max} , WUE, and F _v /F _m	223
Figure 5.7. Mean values for the effects of CO ₂ and water treatment on stomatal conductance (g _s) and relative water content (RWC).....	224
Figure 5.8. Mean Values for leaf Nitrogen (%) for CO ₂ and water treatments, by photosynthetic pathway.....	225
Figure 5.9. Mean values for light-adapted quantum yield of photosystem II (Φ_{PSII}) in response to CO ₂ and water treatments.....	226
Figure 5.10. Mean values for dark-adapted photochemical efficiency (F _v /F _m) in response to CO ₂ by water treatments.....	227
Figure 5.11. Mean values for C ₃ A/c _i curves for <i>Bromus diandrus</i> and <i>Ehrharta calycina</i> for ambient and elevated CO ₂ , well-watered conditions.....	228
Figure 5.12. Mean values for C ₃ A/c _i curves for <i>Bromus diandrus</i> and <i>Ehrharta calycina</i> for ambient and elevated CO ₂ , drought conditions.....	229
Figure 5.13. Mean values for C ₄ A/c _i curves for <i>Cenchrus ciliaris</i> and <i>Paspalum dilatatum</i> for ambient and elevated CO ₂ , well-watered conditions.....	230
Figure 5.14. Mean values for C ₄ A/c _i curves for <i>Cenchrus ciliaris</i> and <i>Paspalum dilatatum</i> for ambient and elevated CO ₂ , drought conditions.....	231
Figure 5.15. Mean values for V _{cmax} for C ₃ species in response to CO ₂ and water treatments.....	232
Figure 5.16. Mean values for J _{max} for C ₃ species in response to CO ₂ and water treatments.....	233
Figure 5.17. Mean values for V _{pmax} values C ₄ species in response to CO ₂ and water treatments.....	234

CHAPTER 1

C₄ and C₃ grass distributions in Hawai‘i: Where we are now and where we need to go

Differences in photosynthesis among vascular plant species can have important ecological consequences. The two most common photosynthetic pathways are C₃ and C₄ photosynthesis. Among angiosperms, the C₄ photosynthetic pathway has the highest occurrence in the Poaceae (the grass family) where it comprises 40% of the species, with the other 60% using the C₃ photosynthetic pathway (Brown 1977). Anatomical and biochemical differences between C₃ and C₄ plants contribute to how these plants respond to their environments (Sage 1999). C₄ plants generally have a high optimum temperature range, a high light saturation point, and minimal photorespiration. In turn, C₃ plants have a lower optimum temperature range (10-25°C), a much lower light saturation point, and commonly experience photorespiration. C₄ plants also have a CO₂ concentrating mechanism that allows these plants to accumulate CO₂ at the site of carbon uptake. This in turn, gives C₄ plants the capability to acquire high concentrations of CO₂, while keeping their stomatal conductance relatively low compared to C₃ plants (Sage 1999). These physiological characteristics give C₄ plants a competitive advantage in warm and arid environments (Long 1999). Many tropical grasses have C₄ photosynthesis, while C₃ photosynthesis is more common in temperate grasses (Ehleringer 1978).

The Poaceae (Grass Family) is one of the largest families of angiosperms, comprising 600 genera and 10,000 species. In Hawai'i, the grass family is represented by 39 endemic species and 8 indigenous species in 19 genera (Wagner et al. 1999). Over the last 200 years, over 400 grass species having both C₃ and C₄ photosynthetic pathways have been introduced into the Hawaiian

Islands (Rotar 1968), with around 100 of these species becoming naturalized (Wagner et al. 1999). In the Hawaiian Islands, extreme elevation gradients spanning more than 3000 m occur on the islands of Hawai'i and Maui. Over relatively short distances, tropical conditions can be found at warm, low elevations and alpine conditions can be found at cold, mountain summits. Elevation gradients like those found in Hawai'i are ideal places to study the assortment and distributions of C₄ and C₃ grass species due to differences in temperature and precipitation along these gradients.

In Hawai'i, most nonnative grasses that have altered the grass fire-cycle and threatened native plant communities are C₄ grasses. Therefore, it is important to understand the potential ranges of C₄ grasses in Hawai'i, and how they may interact with C₃ grasses. Over the last 30 plus years, many studies have looked at C₄ and C₃ grass distributions in relation to climate (Cabido et al. 1997; Hattersley 1983; Rundel 1980; Teeri and Stowe 1976). Considering precipitation and temperature, it has been speculated that precipitation may be the most critical factor influencing C₄ and C₃ grass distributions in tropical areas (Chazdon 1978). In contrast, in temperate regions temperature may be a more critical factor in determining C₄ and C₃ grass distributions (Teeri and Stowe 1976). By understanding the factors that promote competitive ability of C₄ versus C₃ grasses in the tropics, predictions about future invasions and impacts can be made.

Typically, broad patterns of C₄ to C₃ grass distributions have been studied. Along latitudinal gradients, C₄ plants generally decrease in both species richness

and cover with increasing latitude or elevation, while C₃ plants increase with increasing latitude or elevation (Ehleringer 1978; Rundel 1980; Teeri and Stowe 1976). Previous studies on C₄ and C₃ grasses and climate have calculated transitional latitudes, elevations, and temperatures associated with the switch in dominance between C₄ and C₃ grasses, where the transition point is defined as the location or conditions at which C₄ and C₃ dominance both equal 50% relative abundance. At this transition point, the quantum yield (the ratio of photosynthetic carbon gain to photons absorbed) of C₄ and C₃ grasses is presumed to be similar. This has become known as the “crossover temperature hypothesis” (Ehleringer 1978; Ehleringer et al. 1997). Among studies conducted across different elevation and latitudinal gradients in both tropical and temperate locations, average crossover temperatures range between 21 – 28 °C monthly mean maximum temperature for the warmest month of the year (Cabido et al. 1997; Hattersley 1983; Rundel 1980; Tieszen et al. 1979). Ehleringer (1978) proposed that variations in the quantum yields might be the reason for the observed geographical distribution differences of C₄ and C₃ grass species. In addition, Ehleringer and Pearcy (1983) found that C₄ grass subtypes have varying quantum yields and that C₄ grasses have higher quantum yields than C₄ eudicots. The C₄/C₃ crossover temperature for C₄ grasses at CO₂ concentrations of 350 ppm occurs at a daytime temperature of 21°C for C₄/C₃ grasses having quantum yields between 0.060 and 0.065 µmol/ mol (Ehleringer and Pearcy 1983).

Conversely, some researchers have suggested that the “crossover temperature hypothesis” of C₄/C₃ plants may be too simplistic (Edwards and Still 2008; Hattersley 1983), as C₄ photosynthesis has independently evolved in different grass lineages and it may be important to consider the evolutionary history of grass species in order to understand their ecological distributions. Research clarifying phylogenetic relationships among major lineages of grass species found that most species belong to either the BEP or PACCMA clades (Barker et al. 2001). Edwards and Still (2008) analyzed temperature divergence within the major grass lineages, “BEP, C₃” and “PACCMA, C₄ and C₃” clades and found that there was not a significant divergence of the temperature at which plants were found growing in the field within the C₄ and C₃PACCMA clade (both pathways in this clade were found at higher temperatures than C₃ plants in the BEP clade). Thus, the major factor driving ecological differentiation between C₄ and C₃ grasses may not be photosynthetic pathway, but rather phylogeny. However, the study by Edwards and Still (2008) was based on geo-referenced herbarium specimens, and it was not a systematic survey. Edwards and Still (2008) also did not investigate the climatic drivers of relative abundance patterns of C₄ and C₃ grasses along elevational gradients.

Along with understanding the climatic factors that influence C₄ and C₃ grass distributions it is also important to determine if these distributions are likely to be altered by a changing climate. Climate change has been reported for the tropics over the last century (IPCC 2007). However, little research has been done in Hawai‘i investigating how climate change has impacted tropical plant

distributions (Feeley 2012; Feeley et al. 2011; Juvik et al. 2011) or how it will impact future plant distributional patterns (Colwell et al. 2008; Feeley and Silman 2010a; Feeley and Silman 2010b; Kriticos et al. 2003a, b; Thomas et al. 2004). In the Hawaiian Islands, Giambelluca et al. (2008) found that a long term increase of temperature of 0.04°C/decade has occurred in the Hawaiian Islands from 1919 - 2006 while a more rapid increase of 0.164°C/decade occurred from 1975 - 2006. In addition, when these temperature trends are broken up between high and low elevations, high elevation sites have warmed by a factor of three (0.27°C/decade) compared to lower elevations (0.09°C/decade). In addition, warming trends are lower for summer and higher for winter (Giambelluca et al. 2008). Precipitation has been predicted to also change across the Hawaiian Islands in response to climate change. A 5 - 10% decrease in precipitation in the wet season and a 5% increase in the dry season has been predicted (Timm and Diaz 2009). These documented and predicted changes in climate in the Hawaiian Islands may alter the ecological distribution of C₄ and C₃ grasses, along with potentially disrupting the intact native ecosystems at high elevations (Giambelluca et al. 2008).

In addition to changes in temperature and precipitation, the global atmospheric carbon dioxide concentration (CO₂) is expected to reach concentrations of 600 ppm by the year 2050 ± 20 years (Prentice et al. 2001) and since CO₂ is a primary component in photosynthesis it will also impact C₄ and C₃ grass distributions. Positive C₃ plant responses to elevated CO₂ are more consistent than responses of C₄ plants (Ainsworth and Long 2005; Wand et al.

1999). Contrary to the photosynthetic theory which states that C₄ plants will generally not benefit from increased CO₂, a meta-analysis by Wand et al. (1999) found that non-crop C₄ grasses responded to elevated CO₂ with carbon uptake increases of 25%. Increases in total plant biomass and water use efficiency, along with decreases in stomatal conductance were also found in C₄ grasses at elevated CO₂ concentrations. In addition, Kellogg et al. (1999) found that not all C₄ grasses respond in the same way to elevated CO₂. Their study showed that variation among species within a genus in response to elevated CO₂ was as great as the variation between genera within a subfamily and between subfamilies within the Poaceae. Furthermore, Ziska and Bunce (1997) found that C₄ grasses with different biochemical subtypes varied in their response to elevated CO₂ and that weedy species (fast growing, non-crop species) responded more favorably than non-weedy species. In contrast, Leakey et al. (2009) found that C₄ plants responded to elevated CO₂ when the plant was experiencing drought stress, but there was no CO₂ effect on carbon uptake at any other time. Additionally, a review reported that C₄ plants exhibit only a limited number of consistent changes with elevated CO₂ such as reduced stomatal conductance and increased leaf area, while responses in terms of leaf tissue N concentration varied among studies (Ghannoum et al. 2000). Responses of C₄ and C₃ grasses to elevated CO₂ could have dramatic ecological implications when coupled with changes in temperature and rainfall.

Questions and Hypotheses

Chapter 2 - Distribution Patterns of C₄ and C₃ grasses Along Tropical Elevation Gradients in Hawai‘i

How do distributions of C₄ and C₃ grasses vary with elevation? Is precipitation or temperature the most critical factor in determining grass distributions? Are transition temperatures of C₄ and C₃ grasses lower in Hawai‘i compared to temperate areas?

I hypothesized that temperature will be the most influential climate factor determining C₄ and C₃ grass distributions along elevation gradients in Hawai‘i based on previous studies (Livingstone and Clayton 1980; Teeri and Stowe 1976). I also hypothesized that distributional patterns of C₄ and C₃ grasses in the Hawaiian Islands have lower transition temperatures compared to temperate areas because of limited seasonality and lack of extreme low temperatures in the Hawaiian Islands.

Chapter 3 - Upward Expansion of Fire-Adapted C₄ and C₃ Grasses Along a Warming Tropical Elevation Gradient

Have C₄ and C₃ grass distributions shifted upward in elevation in response to climate warming or other global change factors in Hawai‘i Volcanoes National Park? Has species composition or dominance of grasses changed in Hawai‘i Volcanoes National Park?

I hypothesized that C₄ and C₃ grass transition points are now established at higher elevations compared to transition points in 1966/1967 due to climate warming over the past forty years and increased fire frequency. I also

hypothesized that fire-adapted grasses are now a more dominant component of the landscape compared to initial surveys in 1966/1967.

Chapter 4 - Impacts of Future Climates on Fire-Promoting Invasive Grass Distributions in the Hawaiian Islands: C₄ vs C₃

Will dominant fire-promoting grass species ranges increase, decrease or stay stable with climate change by the year 2050 and will there be a shift in upper montane invasions with climate change?

I hypothesized that C₃ fire-promoting grass distributions will be reduced by 2050, while C₄ fire-promoting grass distributions will expand due the physiological preferences of the respective grass species. However, species distributional changes will also vary by species, as has been shown in previous studies (Parker-Allie et al. 2009). I also hypothesized that fire-promoting species within conservation areas (e.s., nature reserves, state/national parks) will vary in their response to climate change depending on the location of the conservation area.

Chapter 5 - Growth, Physiological and Biochemical Responses of C₄ and C₃ Grasses to Aspects of Global Change: Is There a True Winner?

Do C₄ and C₃ grasses have growth and physiological responses to elevated CO₂? Does CO₂ ameliorate the effects of drought? Do these responses vary between C₄ and C₃ plants?

I hypothesized that NADP-ME (Panicoideae subfamily) C₄ and C₃ grass species will have biomass and physiological responses to elevated CO₂ under well-watered and drought conditions due to increased carbon uptake (*A*) at the site of photosynthesis. I also hypothesized that the effects of drought will be ameliorated for both C₄ and C₃ grass species under elevated CO₂ due to a reduction in

photosynthesis inhibition caused by stomatal limitations and increased water-use efficiency.

LITERATURE CITED

- Ainsworth EA, Long SP (2005) What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO₂. *New phytologist* 165:351-372
- Barker NP, Clark LG, Davis JI, et al. (2001) Phylogeny and subfamilial classification of the grasses (Poaceae). *Annals of the Missouri Botanical Garden*:373-457
- Brown WV (1977) The Kranz syndrome and its subtypes in grass systematics. *Mem. Torrey Bot. Club* 23:1-97
- Cabido M, Ateca N, Astegiano M, et al. (1997) Distribution of C₃ and C₄ grasses along an altitudinal gradient in Central Argentina. *J. biogeogr.* 24:197-204
- Chazdon RL (1978) Ecological aspects of the distribution of C₄ grasses in selected habitats of Costa Rica. *Biotropica*:265-269
- Colwell RK, Brehm G, Cardelus CL, et al. (2008) Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322:258-261
- Edwards EJ, Still CJ (2008) Climate, phylogeny and the ecological distribution of C₄ grasses. *Ecology letters* 11:266-276
- Ehleringer J, Pearcy RW (1983) Variation in quantum yield for CO₂ uptake among C₃ and C₄ plants. *Plant physiology* 73:555
- Ehleringer JR (1978) Implications of quantum yield differences on the distributions of C₃ and C₄ grasses. *Oecologia* 31:255-267
- Ehleringer JR, Cerling TE, Helliker BR (1997) C₄ photosynthesis, atmospheric CO₂, and climate. *Oecologia* 112:285-299
- Feeley KJ (2012) Distributional migrations, expansions, and contractions of tropical plant species as revealed in dated herbarium records. *Glob. change biol.* 18: 1335-1341
- Feeley KJ, Silman MR (2010a) Land-use and climate change effects on population size and extinction risk of Andean plants. *Glob. change biol.* 16:3215-3222

Feeley KJ, Silman MR (2010b) Modelling the responses of Andean and Amazonian plant species to climate change: the effects of georeferencing errors and the importance of data filtering. *J. biogeogr.* 37:733-740

Feeley KJ, Silman MR, Bush MB, et al. (2011) Upslope migration of Andean trees. *J. biogeogr.* 38:783-791

Ghannoum O, Caemmerer SV, Ziska L, et al. (2000) The growth response of C₄ plants to rising atmospheric CO₂ partial pressure: a reassessment. *Plant, cell & environment* 23:931-942

Giambelluca TW, Diaz HF, Luke MSA (2008) Secular temperature changes in Hawaii. *Geophys. res. lett.* 35

Hattersley PW (1983) The distribution of C₃ grass and C₄ grasses in Australia in relation to climate. *Oecologia* 57:113-128

IPCC (2007) Climate Change 2007: The Physical Science Basis: Working Group I Contribution to the Fourth Assessment Report of the IPCC. Cambridge University Press, UK

Juvik JO, Rodomsky BT, Price JP, et al. (2011) "The upper limits of vegetation on Mauna Loa, Hawaii": a 50th-anniversary reassessment. *Ecology* 92:518-525

Kellogg EA, Farnsworth EJ, Russo ET, et al. (1999) Growth Responses of C₄ Grasses of Contrasting Origin to Elevated CO₂. *Annals of botany* 84:279

Kriticos D, Sutherst R, Brown J, et al. (2003a) Climate change and biotic invasions: a case history of a tropical woody vine. *Biol. invasions* 5:147-165

Kriticos D, Sutherst R, Brown J, et al. (2003b) Climate change and the potential distribution of an invasive alien plant: *Acacia nilotica* ssp. *indica* in Australia. *J. appl. ecol.* 40:111-124

Leakey ADB, Ainsworth EA, Bernacchi CJ, et al. (2009) Elevated CO₂ effects on plant carbon, nitrogen, and water relations: six important lessons from FACE. *Journal of experimental botany* 60:2859

Livingstone D, Clayton W (1980) An altitudinal cline in tropical African grass floras and its paleoecological significance. *Quaternary research* 13:392-402

Long SP (1999) Environmental responses. In: Sage RM, Monson RK (eds) C₄ Plant Biology. Academic Press, San Diego, CA, pp. 215-249

Parker-Allie F, Musil C, Thuiller W (2009) Effects of climate warming on the distributions of invasive Eurasian annual grasses: a South African perspective. *Climatic change* 94:87-103

Prentice IC, Farquhar G, Fasham M, et al. (2001) The carbon cycle and atmospheric carbon dioxide. In: Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Dai X, Maskell K, Johnson CA (eds) *Climate change 2001: the scientific basis*. Cambridge University Press, Cambridge, UK, pp. 183–237

Rotar P (1968) *Grasses of Hawaii*. University of Hawaii Press, Honolulu, HI

Rundel PW (1980) The ecological distribution of C₄ and C₃ grasses in the Hawaiian Islands. *Oecologia* 45:354-359

Sage RF (1999) Why C₄ photosynthesis. In: Sage RF, Monson RK (eds) *C₄ plant biology*. Academic Press, San Diego, CA, pp. 3-16

Teeri J, Stowe L (1976) Climatic patterns and the distribution of C₄ grasses in North America. *Oecologia* 23:1-12

Thomas CD, Cameron A, Green RE, et al. (2004) Extinction risk from climate change. *Nature* 427:145-148

Tieszen LL, Senyimba MM, Imbamba SK, et al. (1979) The distribution of C₃ and C₄ grasses and carbon isotope discrimination along an altitudinal and moisture gradient in Kenya. *Oecologia* 37:337-350

Timm O, Diaz HF (2009) Synoptic-statistical approach to regional downscaling of IPCC Twenty-first-century climate projections: Seasonal rainfall over the Hawaiian Islands. *Journal of climate* 22:4261-4280

Wagner WL, Herbst DR, Sohmer SH (1999) *Manual of the Flowering Plants of Hawai'i*, Vols. 1 and 2. University of Hawai'i and Bishop Museum Press, Honolulu, HI

Wand SJE, Midgley GYF, Jones MH, et al. (1999) Responses of wild C₄ and C₃ grass (Poaceae) species to elevated atmospheric CO₂ concentration: a meta-analytic test of current theories and perceptions. *Glob. change biol.* 5:723-741

Ziska LH, Bunce JA (1997) Influence of increasing carbon dioxide concentration on the photosynthetic and growth stimulation of selected C₄ crops and weeds. *Photosynthesis research* 54:199-208

CHAPTER 2

Distribution patterns of C₄ and C₃ grasses along tropical elevation gradients in Hawai'i

ABSTRACT

The distributional patterns of C₄ and C₃ grasses in relation to latitude and climate have attracted much attention but few studies have examined grass distributions along tropical elevation gradients. Previous studies on C₄ and C₃ grass distributional patterns identified either temperature, precipitation, or both as the key climatic factor(s) influencing grass distributions. I hypothesized that temperature would be the key climatic factor determining C₄ versus C₃ grass distributions in Hawai'i based on findings from temperate localities. C₄ grasses were also hypothesized to dominate at lower mean temperatures in Hawai'i, relative to at higher latitudes, because of relatively constant year round temperatures. I surveyed grass species and cover from field plots at 100 - 150 m elevation intervals and correlated relative dominance by C₃ grasses to temperature and precipitation. The transition temperature between C₄-C₃ grasses was determined from the inflection point of a best fit logistic regression model. I found that July mean maximum temperature was correlated with relative cover and species richness of C₄ and C₃ grasses along all elevation transects, while precipitation was only correlated with C₄ and C₃ grasses when it was also correlated with temperature. Absolute cover data for C₄ and C₃ grasses also supported this trend. Temperature appears to be the key climatic factor shaping distributional patterns of C₄ and C₃ grasses, and C₄-C₃ grass transition temperatures ranged from 20 – 22 °C and 21 – 22 °C July mean maximum for relative cover and species data, respectively. These Hawaiian transition

temperatures are lower than transition temperatures in temperate localities. Increasing temperatures associated with climate change are likely to shift C₄ grass dominance upward in elevation, which may promote an expanded grass-fire cycle that threatens native communities.

INTRODUCTION

The grass family (Poaceae) is one of the largest angiosperm families, comprising 600 genera and 10,000 species (Mabberley 2008). The family is widely distributed with species inhabiting a range of ecological niches. Around 40% of grass species make use of the C₄ photosynthetic pathway, while the remainder uses the C₃ photosynthetic pathway (Brown 1977). In comparison to C₃ plants, C₄ plants generally have a higher optimum temperature range and a high light saturation point for photosynthesis, and minimal photorespiration (Sage 1999). The physiological characteristics of C₄ plants give them an advantage in warm and dry environments (Long 1999). Many tropical grasses have C₄ photosynthesis, while C₃ photosynthesis is more common in temperate grasses (Cabido et al. 1997).

A number of previous studies have looked for relationships between C₄ and C₃ grass distributional patterns and climate (Cabido et al. 1997; Hattersley 1983; Mo et al. 2004; Rundel 1980; Teeri and Stowe 1976). In comparing the importance of precipitation and temperature, temperature may be a more critical factor in determining C₄ and C₃ grass distributions in temperate regions (Cavagnaro 1988). It has been speculated, however, that precipitation may be the most critical factor influencing C₄ and C₃ grass distributions in tropical areas (Chazdon 1978).

Typically, broad patterns of C₄ and C₃ grass distributions are studied either along latitudinal or elevation gradients. The transition latitude, elevation, or temperature is defined as the point at which C₄ and C₃ grasses are equally

abundant, on average. The transition latitude of C₄ and C₃ grasses usually ranges from 30° to 45° (Sage et al. 1999). Along latitudinal gradients, C₄ plants generally become less common with increasing latitude, where they are replaced by C₃ plants (Hattersley 1983; Sage et al. 1999; Still et al. 2003; Teeri and Stowe 1976). Along elevation gradients C₄ species tend to dominate lowlands, being replaced by C₃ species at higher elevations. Typically the transition elevation for C₄ and C₃ grasses occurs between 1500 - 3000 m (sites ranging from 0° to 42° latitude), with lower transition elevations in higher latitudes (Sage et al. 1999).

Ehleringer (1978) proposed that variability in quantum yields (the ratio of photosynthetic carbon gain to photons absorbed) might be the reason for the observed distribution differences of C₄ and C₃ species. At the transition temperature, the quantum yields of C₄ and C₃ grasses are expected to be similar, and this has become known as the “crossover temperature hypothesis”. Among studies conducted across different elevation and latitudinal gradients, average crossover temperatures range between 21 – 28 °C monthly mean maximum temperature for the warmest month of the year (Cabido et al. 1997; Cavagnaro 1988; Hattersley 1983; Rundel 1980; Tieszen et al. 1979).

However, recent evidence suggests that the “crossover temperature hypothesis” of C₄/C₃ plants may be too simplistic (Edwards and Still 2008). Research clarifying phylogenetic relationships among major lineages of grass species found that most species belong to either the BEP or PACCMA clades (Barker et al. 2001). Edwards and Still (2008) analyzed the temperature divergence of species distributions within the “PACCMA” grass clade, which

includes species that evolved in warm climates, both C₄ and C₃ species. They found no significant divergence of species temperature ranges among C₄ and C₃ grasses within the PACCMA clade, while C₃ grasses in a separate clade (BEP) that evolved in temperate areas were associated with colder environments. That is, the major factor driving climate differentiation between grass distributions may be phylogeny rather than photosynthetic pathway. Edwards and Still (2008) also found that Hawaiian grasses did not appear to sort along a precipitation gradient by either photosynthetic pathway or major lineage when analyzed across species. However, the study by Edwards and Still (2008) was based on geo-referenced herbarium specimens, and it not a systematic survey. Edwards and Still (2008) also did not investigate the climatic drivers of relative abundance patterns of C₄ and C₃ grasses along elevational gradients.

In Hawai‘i, the grass family is represented by 39 endemic species and 8 indigenous species (Wagner et al. 1999). Nonnative grasses have also become dominant over large areas and have displaced many native grass species in Hawai‘i (Daehler and Carino 1998). Over the last 200 years, more than 400 grass species, both C₄ and C₃, have been introduced to the Hawaiian Islands (Rotar 1968). Around 100 of these species have become naturalized (Wagner et al. 1999), and a number of them, primarily C₄ grasses, have become dominate invasive species. The wide elevational range provided by high volcanoes in the Hawaiian Islands provides steep gradients in temperature and precipitation, allowing testing of hypotheses about the climatic distribution of C₄ and C₃ grasses. Many C₄ grasses in the tropics are associated with a grass-fire cycle

that can transform landscapes (D'Antonio and Vitousek 1992). Therefore, understanding the factors that promote dominance of C₄ or C₃ grasses in the tropics will aid in predicting future invasions and impacts.

The goal of this study was to compare the relative distributions of C₄ and C₃ grasses along multiple elevation gradients on the islands of Hawai'i, Maui, and Kaua'i and to statistically test their associations with temperature and precipitation. I also aimed to review previous studies on C₄ and C₃ grass distributional patterns worldwide to determine if these patterns are different in the tropics versus temperate localities. Based on previous studies, I hypothesized that temperature would be the most influential climate factor determining C₄ and C₃ grass distributions. I also hypothesized that transition temperatures for C₄ and C₃ grasses in the Hawaiian Islands would be lower compared to temperate regions, because of limited seasonality, specifically lack of extreme minimum temperatures in the Hawaiian Islands.

METHODS

Field Surveys

Field plots ($n = 177$) were surveyed along five elevation gradients on the islands of Kaua‘i (Koke‘e State Park, 0- 1300 m), Maui (Haleakalā National Park, 500 – 3000 m), and Hawai‘i (Hilo-Mauna Kea, 350 – 2900 m; Kona-Mauna Kea, 500 – 2900 m; Hawai‘i Volcanoes National Park ; 0 – 2100 m) during June 2008 and April 2009 (Figure 2.1). Field plots were 50 m x 2 m, and were surveyed for grass species and cover at 100 – 150 m elevation intervals, both immediately along the roadside and ~30 m away from the road (natural or pasture habitat). Roadside and away from the road plots were both done to determine if there were differences in distributional patterns between habitat types. At each elevation, the side of the road (right versus left) chosen for each plot was randomly selected and then away from the road transects were surveyed on the same side of the road. All grass species found in the plots were recorded and cover estimates for each species were made within five 10 m x 2 m subplots. Cover estimates were visually made based on one of six cover categories: 0-1, 2-5, 6- 25, 26-50, 51-75, 76-100. Initially, surveys for roadside and off road plots were analyzed separately, however, differences in transition temperatures were less than 1° C; therefore, roadside and off road data were combined by averaging relative percent cover and relative species richness between roadside and off-road plots at each survey site.

Data Analysis

The photosynthetic pathway of all grasses was determined using Brown (1977) and relative percent cover, relative species richness, and absolute cover of C₄ and C₃ grasses were calculated for each plot (Appendix A). The transition temperature and elevation between C₄ and C₃ grass dominance, defined as the point where C₄ and C₃ grasses both equal 50% in relative percent cover or species richness, were determined from the inflection point of a best fit logistic regression model($y= 1/(1+(x/x_0)^b)$), where x= elevation (m), x₀= crossover elevation or temperature, y= relative percent cover or species richness of C₃ grasses, and b = a fitted shape parameter (SigmaPlot version 10, SSPS Inc., Chicago, IL)). Transition temperatures using annual mean maximum (maximum temperature averaged across the year), July mean maximum (monthly maximum temperature for the warmest month of the year), July mean minimum (monthly minimum temperature for the warmest month of the year), January mean maximum (monthly maximum temperature for the coldest month of the year), and January mean minimum (monthly minimum temperature for the coldest month of the year), were each determined because I found that previous studies used one of the five listed types of transition temperature data. Relative percent cover, relative species richness, and absolute cover data were arcsine transformed and correlated with climate data (PRISM Climate Group, Oregon State University) using the ArcGIS 9.3.1 (ESRI, Redlands, CA) and Systat 10.2 software (Systat Software, Inc, Chicago, IL).

A literature review of key climatic variables and transition temperatures for C₄ and C₃ grass distributions around the world was conducted by searching the databases Biological Abstracts, Web of Science, and Google Scholar using the key words C₄ and C₃ grass distributions. For each published study, I determined if the study was done in tropical or temperate latitudes, the key climatic factor reported to drive C₄ and C₃ grass distributional patterns, transition elevation or latitude, and temperatures. In addition, I differentiated studies that identified key climatic factors using statistical analyses versus those that used only subjective methods. Hattersley (1983), was evaluated as both a tropical and temperate study because it spanned both latitudes. Data from the literature review were then compared to results from the current study.

RESULTS

Comparison of PACCMAD C₄ and PACCMAD C₃

In my surveys, I found only 2 PACCMAD C₃ species, *Rytidosperma pilosum* (R. Br.) Connor & Edgar and *Sacciolepis indica* (L.) Chase. These two species were found at opposing ends of the elevation gradients and their distributions did not overlap. *Sacciolepis indica* was found between 348 -1700 m and *Rytidosperma pilosum* was found between 2040 - 2744 m. The July mean maximum temperatures for *Sacciolepis indica* ranged from 21 – 26 °C, comparable to July mean maximum temperatures for PACCMAD C₄ species with at least 30 % cover (21 – 29 °C); however, the temperature range for *Rytidosperma pilosum* (14 - 18 °C) reflected closely that of the C₃ BEP species. Since there was no clear trend differentiating the two PACCMAD C₃ and BEP C₃ species, they were grouped together as C₃ species for subsequent comparisons of C₄ and C₃ grasses.

Percent C₄ and C₃ Grass Composition and Climatic Correlations

July mean maximum temperature was significantly correlated with relative cover and relative species richness of C₃ grasses along all five elevation transects, while annual precipitation was significantly correlated with C₃ grasses for only three of the transects (Table 2.1). Along the Hilo transect, low elevations have high temperatures and high precipitation, and the positive correlation between temperature and precipitation leads to a negative correlation between precipitation and C₃ grass dominance (Table 2.1). In contrast, along the Kona and Koke'e transects, low elevations have high temperature and low

precipitation, and a negative correlation between temperature and precipitation (Table 2.1) leads to a positive correlation between C₃ dominance and precipitation (Table 2.1). When precipitation is not correlated with temperature (Volcano and Haleakalā transects, Table 2.1), relative cover and relative species richness of C₃ grasses are correlated only with temperature and not precipitation. This is strong evidence that temperature is the key climatic factor influencing relative cover and species richness of C₄ to C₃ grasses in Hawai‘i. However, precipitation may be causing the observed difference in C₄ to C₃ transition elevations between the Kona and Hilo sides of Mauna Kea; under dry conditions (Kona side) the transition occurs at higher elevation and cooler temperatures. July mean maximum temperature was also significantly correlated with absolute cover of C₄ and C₃ grasses along all five elevation transects (excluding Hilo C₃ data), while annual precipitation was significantly correlated with C₄ and C₃ grasses for only three of the transects (excluding Hilo C₃ data) (Table 2.2).

Comparison of Transition Temperatures and Elevations Across Elevation Gradients

Transition temperatures for all elevation gradients on Hawai‘i and Maui were similar (Table 2.3, Figures 2.2). July mean maximum and minimum temperatures ranged between 20.4 - 22.3 °C and 9.2 – 12.1 °C, respectively, depending on the location of the gradient (Table 2.3). Transition temperatures differed by about 3 °C between July and January minimums and maximums (Table 2.3). Transition elevations varied by as much as 662 m and 484 m for the relative percent cover and relative species richness data (Table 2.4). The

transition temperature and elevation for the Koke‘e transect (Kaua‘i) were not statistically determined because the road did not reach a high enough elevation to observe clear dominance by C₃ grasses and footpaths accessing higher elevations were forested, with very little grass. Nevertheless, the pattern for Koke‘e is qualitatively similar to other transect (Figures 2.2).

Comparison of Worldwide Data

From the literature review, I found that 7 out of 15 locations reported that C₄ and C₃ grass distributions had a statistically significant relationship with temperature, while an additional 6 out of 15 studies reported a possible relationship with temperature without any statistical test (Table 2.5). Five out of 15 studies reported a statistically significant trend with precipitation or soil moisture, while an additional 3 out of 15 locations reported a relationship between C₄ and C₃ grass distributions and precipitation or soil moisture without any statistical test (Table 2.5). Out of the five locations that had a statistically significant trend with precipitation or soil moisture, three also reported a significant correlation with temperature. However, these studies did not test whether temperature and precipitation were correlated. Tropical studies varied in their conclusions regarding the climatic factor or factor(s) driving distributional patterns of C₄ and C₃ grasses. In the tropics, I found three studies that reported an interplay between temperature and precipitation, while temperature and precipitation/soil moisture were reported two times each as the most critical climatic factor determining grass distributional patterns. Temperate studies concluded that distributional patterns of C₄ and C₃ grasses were more influenced

by temperature (67%) than precipitation or an interplay of climatic factors (Table 2.5).

Transition temperatures were around 21 - 31 °C mean maximum for the warmest month of the year for both tropical and temperate latitudes (Table 2.5). Transition temperatures appeared to be lower in the Hawaiian Islands for the warmest month of the year (20 - 22 °C) (Table 2.3) compared to localities at higher latitudes (26 - 31 °C) and similar to transition temperatures for localities at tropical latitudes (21 - 22 °C) (Table 2.5). However, I did find outliers in transition temperatures for two temperate studies (Batanouny et al. 1988; Cabido et al. 1997). Transition elevations reported in previous studies varied by location from 1000 – 3000 m, emphasizing the greater value of reporting transition temperature in place of transition elevation (Table 2.5).

DISCUSSION

Determining the climatic factors that influence BEP (C_3) and PACCMAD (C_4 or C_3) grass distributions in the Hawaiian Islands can be essential in understanding the ecology and behavior of these grasses (Edwards and Still 2008), and this information can be applied for conservation and management purposes. However, the PACCMAD C_4 species have been more successful than the PACCMAD C_3 species, both in terms of lineage diversification and ecological importance (Edwards and Still 2008). The low ecological importance and rarity of PACCMAD C_3 grass species was reflected in my surveys and thus they did not affect overall patterns. Instead, the C_3 patterns discussed in this paper were determined primarily by BEP C_3 species. Due to the limited number and abundance of PACCMAD C_3 species in this study, my data cannot confirm previous findings by Edwards and Still (2008) that PACCMAD C_3 species have temperature niches similar to those of PACCMAD C_4 species. One of the two PACCMAD C_3 species had a distribution pattern consistent with BEP C_3 species, rather than PACCMAD C_4 species.

Previous studies on C_4 and C_3 grass distributions, which did not distinguish PACCMAD and BEP clades, have identified either temperature, precipitation, or both, as the key climatic factor influencing distributions depending on the location of the study (Cavagnaro 1988; Chazdon 1978; Rundel 1980). Previous work in the tropics has suggested that precipitation is the key climatic factor influencing grass distributions (Chazdon 1978). In addition, other studies have shown that soil moisture is an important factor determining

distributional patterns of C₄ and C₃ grasses in the tropics (Tieszen et al. 1979; Young and Young 1983). However, this study shows that temperature is the principal climatic factor determining these distributions in Hawai‘i, as hypothesized. I found precipitation to be correlated with C₄ and C₃ grass distributions only when it also was correlated with temperature. Based on decoupling of precipitation across multiple elevation gradients, Livingstone and Clayton (1980) also suggested that temperature was the principal climatic factor influencing C₄ and C₃ grass distributions in tropical Africa. Whereas other studies in the tropics suggested an interplay between temperature and precipitation (Rundel 1980; Tieszen et al. 1979), but these studies did not attempt to statistically distinguish which of the two factors was responsible for grass distributional patterns.

Hawaiian C₄ to C₃ grass transition temperatures were lower than transition temperatures in temperate areas, as hypothesized. In the tropics, lower transition temperatures were also reported in earlier work from Costa Rica (Chazdon 1980), tropical Africa (Tieszen et al. 1979), and Hawai‘i (Rundel 1980). These lower transition temperatures may be due to relatively consistent temperatures year round in the tropics. In temperate localities, C₄ grasses face larger temperature extremes. The temperature optimum of light-saturated CO₂ uptake (A_{sat}) in C₄ species is typically 10 °C higher than in C₃ species (Long 1999) making it difficult for C₄ species to survive or compete at lower temperature extremes. C₄ and C₃ grass populations along an elevation gradient have also been shown to vary in their chill tolerance, with high elevation C₃ grasses being

more chill resistant than low to mid elevation C₄ grasses (Earnshaw et al. 1990). Thus, C₄ grass species in temperate localities would be excluded at higher elevation sites for most of the year and might not be able to compete with the dominant C₃ species once warmer temperatures occur in the spring and summer. This would restrict C₄ grasses in temperate regions to lower elevations, compared to C₄ grasses growing in the tropics. Furthermore, Teeri and Stowe (1976) found that high minimum temperatures during the growing season have the strongest correlation with the relative abundance of C₄ grass species across a latitudinal gradient in North America. Thus, C₄ grass species seem to require warm summer nights for distribution into higher latitudes (Mo et al. 2004). In Hawai‘i, I found that there was only a 3 °C difference between July minimum and maximum and January minimum and maximum transition temperatures allowing mean transition temperatures to more closely reflect likely physiological limits of C₄ grasses (Long 1983; Osborne et al. 2008).

My study, which was dominated by grasses belonging to the BEP C₃ clade and PACCMAD C₄ clade, supports a majority of studies worldwide that have concluded that temperature is the key climatic factor determining C₄ and C₃ grass distributions (Batanouny et al. 1988; Cavagnaro 1988; Ellis et al. 1980; Hofstra et al. 1972; Livingstone and Clayton 1980; Mo et al. 2004; Teeri and Stowe 1976; Wan and Sage 2001). However, this is the first study to statistically indicate temperature as the most critical climatic factor determining C₄ and C₃ distributional patterns in the tropics using multiple elevation gradients.

Furthermore, determining that temperature is the key climatic factor influencing

dominance patterns of C₄ and C₃ grasses has implications for understanding how grass distributions may shift in the future with climate change. This is particularly important in the Hawaiian Islands where nonnative C₄ grasses have become dominant across wide regions and changed ecosystem processes such as fire cycles (D'Antonio and Vitousek 1992; Smith and Tunison 1992). In addition, my study highlights that transition temperatures of C₄ and C₃ grass distributions maybe lower in the tropics than in temperate localities. Thus, C₄ grasses are established at higher elevations in the tropics than expected based on temperature-elevation relationships in temperate areas, and with small changes in temperature, high elevation mountains will become suitable habitat for invasive C₄ species.

LITERATURE CITED

- Barker NP, Clark LG, Davis JI, et al. (2001) Phylogeny and subfamilial classification of the grasses (Poaceae). Annals of the Missouri Botanical Garden:373-457
- Batanouny KH, Stichler W, Ziegler H (1988) Photosynthetic pathways, distribution, and ecological characteristics of grass species in Egypt. Oecologia 75:539-548
- Brown WV (1977) The Kranz syndrome and its subtypes in grass systematics. Mem. Torrey Bot. Club 23:1-97
- Cabido M, Ateca N, Astegiano M, et al. (1997) Distribution of C₃ and C₄ grasses along an altitudinal gradient in Central Argentina. J. biogeogr. 24:197-204
- Cavagnaro JB (1988) Distribution of C₃ and C₄ grasses at different altitudes in a temperate arid region of Argentina. Oecologia 76:273-277
- Chazdon RL (1978) Ecological aspects of the distribution of C₄ grasses in selected habitats of Costa Rica. Biotropica:265-269
- D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annu. rev. ecol. syst. 23:63-87
- Daehler CC, Carino DA (1998) Recent replacement of native pili grass (*Heteropogon contortus*) by invasive African grasses in the Hawaiian Islands. Pacific science 52:220-227
- Earnshaw M, Carver K, Gunn T, et al. (1990) Photosynthetic pathway, chilling tolerance and cell sap osmotic potential values of grasses along an altitudinal gradient in Papua New Guinea. Oecologia 84:280-288
- Edwards EJ, Still CJ (2008) Climate, phylogeny and the ecological distribution of C₄ grasses. Ecology letters 11:266-276
- Ehleringer JR (1978) Implications of quantum yield differences on the distributions of C₃ and C₄ grasses. Oecologia 31:255-267
- Ellis RP, Vogel J, Fuls A (1980) Photosynthetic pathways and the geographical distribution of grasses in South West Africa/Namibia. S. Afr. j. sci 76:307-14
- Hattersley PW (1983) The distribution of C₃ grass and C₄ grasses in Australia in relation to climate. Oecologia 57:113-128

Hofstra JJ, Aksornkoae S, Atmowidjojo S, et al. (1972) A study on the occurrence of plants with a low CO₂ compensation point in different habitats in the tropics. Ann. bogor 5:143-157

Livingstone D, Clayton W (1980) An altitudinal cline in tropical African grass floras and its paleoecological significance. Quaternary research 13:392-402

Long S (1983) C₄ photosynthesis at low temperatures. Plant, cell & environment 6:345-363

Long SP (1999) Environmental responses. In: Sage RM, Monson RK (eds) C₄ Plant Biology. Academic Press, San Diego, CA, pp. 215-249

Mabberley DJ (2008) Mabberley's plant-book: a portable dictionary of plants, their classification and uses. Cambridge Univ Press, UK

Mo W, Nishimura N, Soga Y, et al. (2004) Distribution of C₃ and C₄ plants and changes in plant and soil carbon isotope ratios with altitude in the Kirigamine Grassland, Japan. Grassland science 50:243-254

Osborne CP, Wythe EJ, Ibrahim DG, et al. (2008) Low temperature effects on leaf physiology and survivorship in the C₃ and C₄ subspecies of *Alloteropsis semialata*. Journal of experimental botany 59:1743-1754

Rotar P (1968) Grasses of Hawaii. University of Hawaii Press, Honolulu, HI

Rundel PW (1980) The ecological distribution of C₄ and C₃ grasses in the Hawaiian Islands. Oecologia 45:354-359

Sage RF (1999) Why C₄ photosynthesis. In: Sage RF, Monson RK (eds) C₄ plant biology. Academic Press, San Diego, CA, pp. 3-16

Sage RF, Wedin DA, Li M (1999) The biogeography of C₄ photosynthesis: patterns and controlling factors. In: Sage RF, Monson RK (eds) C₄ plant biology. Academic Press, San Diego, CA, pp. 313-373

Smith CW, Tunison JT (1992) Fire and alien plants in Hawaii: research and management implications for native ecosystems. University of Hawaii Press, Honolulu, HI

Still CJ, Berry JA, Collatz GJ, et al. (2003) Global distribution of C₃ and C₄ vegetation: Carbon cycle implications. Glob. biogeochem. cycle 17

Teeri J, Stowe L (1976) Climatic patterns and the distribution of C₄ grasses in North America. Oecologia 23:1-12

Tieszen LL, Senyimba MM, Imbamba SK, et al. (1979) The distribution of C₃ and C₄ grasses and carbon isotope discrimination along an altitudinal and moisture gradient in Kenya. *Oecologia* 37:337-350

Vogel J, Fuls A, Danin A (1986) Geographical and environmental distribution of C₃ and C₄ grasses in the Sinai, Negev, and Judean deserts. *Oecologia* 70:258-265

Wagner WL, Herbst DR, Sohmer SH (1999) Manual of the Flowering Plants of Hawai'i, Vols. 1 and 2. University of Hawai'i and Bishop Museum Press, Honolulu, HI

Wan CSM, Sage RF (2001) Climate and the distribution of C₄ grasses along the Atlantic and Pacific coasts of North America. *Canadian journal of botany* 79:474-486

Young HJ, Young TP (1983) Local distribution of C₃ and C₄ grasses in sites of overlap on Mount Kenya. *Oecologia* 58:373-377

TABLES

Table 2.1. Spearman's correlation: r_s values for relative percent cover and relative species richness data and climatic variables

Elevation Gradient	July mean Temperature	Annual mean Precipitation	Temperature correlated with Precipitation
Volcanoes National Park			-0.109
% C ₃ Relative Cover	-0.846*	-0.063	
% C ₃ Species Richness	-0.879*	-0.049	
Kona			-0.550*
% C ₃ Relative Cover	-0.969*	0.565*	
% C ₃ Species Richness	-0.952*	0.581*	
Hilo			0.937*
% C ₃ Relative Cover	-0.865*	-0.790*	
% C ₃ Species Richness	-0.852*	-0.799*	
Haleakalā National Park			0.082
% C ₃ Relative Cover	-0.925*	-0.073	
% C ₃ Species Richness	-0.965*	-0.038	
Koke'e State Park			-0.906*
% C ₃ Relative Cover	-0.719*	0.651*	
% C ₃ Species Richness	-0.725*	0.656*	

*=P-value =.01 significance

Table 2.2. Spearman's correlation: r_s values for absolute percent cover and climatic variables

	July mean Temperature		Annual mean Precipitation	
	C ₄ Grasses	C ₃ Grasses	C ₄ Grasses	C ₃ Grasses
Volcanoes National Park	0.442**	-0.747*	0.126	0.072
Kona	0.721*	-0.859*	-0.608*	0.647*
Hilo	0.874*	-0.313	0.850*	-0.123
Haleakalā National Park	0.897*	-0.358**	0.081*	-0.264
Koke'e State Park	0.720*	-0.756*	-0.550*	0.684*

* and ** = P -value = .01 and .05 significance, respectively

Table 2.3. Transition temperatures for C₄ and C₃ grass distributions on the islands of Hawai'i and Maui

Elevation Gradient	July mean min (°C)	January mean min (°C)	July mean max (°C)	January mean max (°C)	Annual mean max (°C)
Relative Cover Data					
Volcanoes National Park	11.41	8.67	21.38	18.77	20.05
Kona	9.18	6.22	20.73	17.64	19.16
Hilo	11.71	8.78	22.33	19.85	21.06
Haleakalā National Park	11.03	8.22	20.40	17.10	18.83
Species Richness Data					
Volcanoes National Park	11.68	8.91	21.56	18.96	20.23
Kona	9.8	6.69	21.15	18.24	19.72
Hilo	11.60	8.64	22.22	19.72	20.95
Haleakalā National Park	12.10	9.44	21.48	18.11	19.90

* maximum = max; minimum = min

Table 2.4. Transition elevations for C₄ and C₃ grass distributions on the islands of Hawai'i and Maui

Elevation Gradient	Transition point (m) using Relative Cover data	Transition point (m) using Species Richness data
Volcanoes National Park	1442	1394
Kona	1914	1726
Hilo	1252	1242
Haleakalā National Park	1656	1427

Table 2.5. Global summary of C₄ and C₃ grass transition points, temperature, and/or main climatic driving factor

Study Location	Tropical or Temperate	Important Climatic Variable	Transition Elevation(m)/ Latitude (°)	Transition Temperature (°C)	Statistically Derived	Author
North America	Temperate	Temperature	No data	July min = 21°C	Statistically Derived	Teeri and Stowe 1976
Atlantic and Pacific Coasts of North America	Temperate	Temperature	Pacific 25°/ Atlantic 40°	July min = 20°C (Pacific) July min = 17.5°C(Atlantic)	Statistically Derived	Wan and Sage 2001
Japan	Temperate	Temperature	1670 – 1770m	August min = 12 – 13°C	Statistically Derived	Mo et al. 2004
South West Africa/Namibia	Temperate	Temperature	Decrease of % C ₄ with increase in latitude	July max = 17.5°C July min = 10.1°C C ₄ never below 80%	Not Statistically Derived	Ellis et al. 1980
Egypt	Temperate	Temperature	Decrease of % C ₄ with increase in latitude	Hottest month mean max = 33.3 – 39.8°C Coldest month mean min = 2.1 – 10.4°C	Not Statistically Derived	Batanouny et al. 1988
Sinai, Negev, and Judean deserts	Temperate	Temperature and Precipitation	No data	No data	Statistically Derived	Vogel et al. 1986
Argentina	Temperate	Temperature	Mixed distribution 1100 – 1600m	Jan mean max 28°C Jan mean min 14°C	Statistically Derived	Cavagnaro 1988

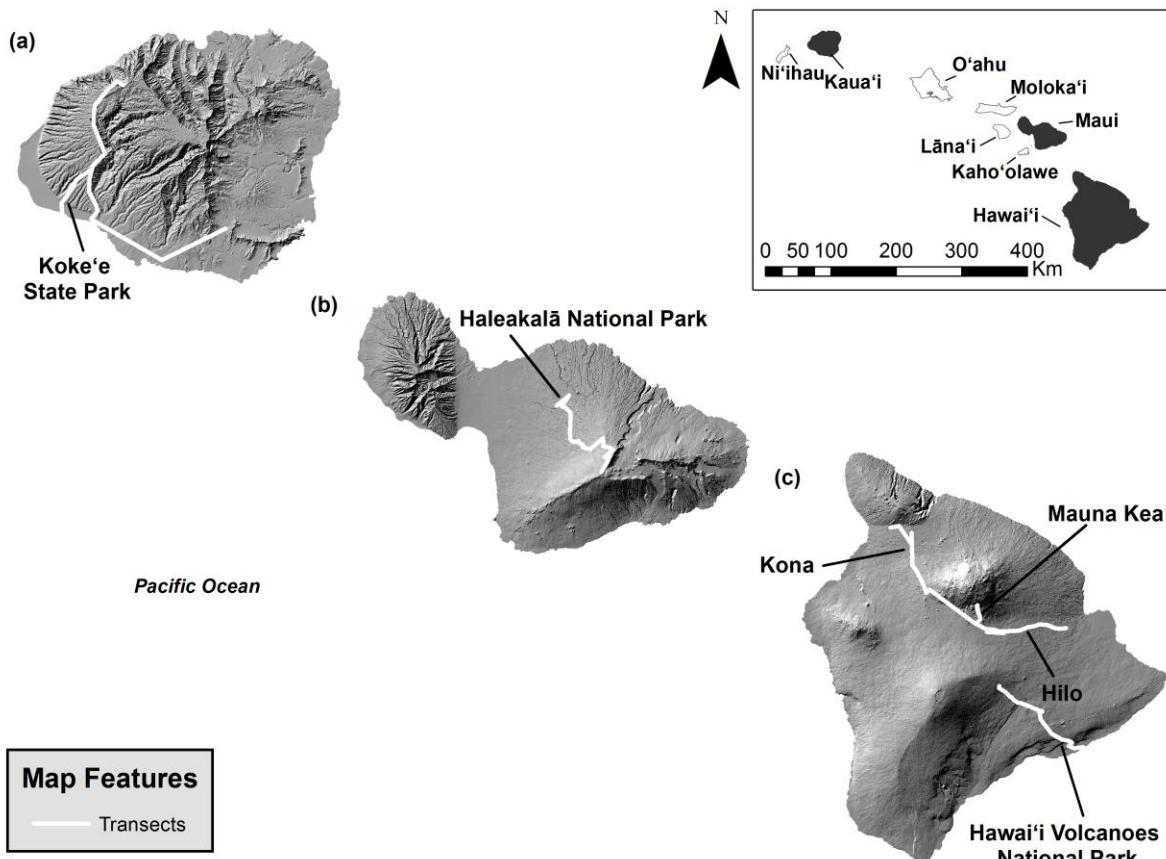
Table 2.5. (Continued) Global summary of C₄ and C₃ grass transition points, temperature, and/or main climatic driving factor

Central Argentina	Temperate	Temperature and Precipitation	Species Richness = 1500m Percent Cover = 1000m	Species Richness Jan mean min = 12°C Jan mean max = 21 to 22°C; Percent Cover Jan mean max = 26 to 27°C Jan mean min = 14.7°C	Statistically Derived	Cabido et al. 1997
Australia	Both	Temperature and Precipitation	Decrease of % C ₄ with increase in latitude, above 32° latitude	Jan mean max = 28 to 31°C Jan mean min = 14 to 15°C	Statistically Derived	Hattersley 1983
Hawaiian Islands	Tropical	Temperature and Precipitation	1400m	July mean max = 21°C Jan mean min = 9°C	Not Statistically Derived	Rundel 1980
Java	Tropical	Temperature	~1600m	No data	Not Statistically Derived	Hofstra et al. 1972
Tropical East Africa	Tropical	Temperature	2682m +/- 85m	No data	Not Statistically Derived	Livingstone and Clayton 1980

Table 2.5. (Continued) Global summary of C₄ and C₃ grass transition points, temperature, and/or main environmental driving factor

Mount Kenya	Tropical	Soil Moisture	2800 – 3000m	No data	Statistically Derived	Young and Young 1983
Kenya	Tropical	Temperature and Soil Moisture	Mixed distribution 2300m	July mean max = 22°C	Not Statistically Derived	Tieszen et al. 1979
Costa Rica	Tropical	Precipitation	Decrease of % C ₄ with increase in elevation Mixed distribution ~ 1750m	Annual Mean max 19 – 23°C Mean min 9 – 11°C	Not Statistically Derived	Chazdon 1978

FIGURES



* Both the Hilo and Kona transects terminate at Mauna Kea

Figure 2.1. Distribution of Grass Surveys on the islands of a) Kaua'i, b) Maui, and c) Hawai'i. The elevation gradients chosen for the surveys included: Hawai'i Volcanoes National Park, Hilo-Mauna Kea, Kona-Mauna Kea, Hawai'i; Haleakalā National Park, Maui, and Koke'e State Park, Kaua'i

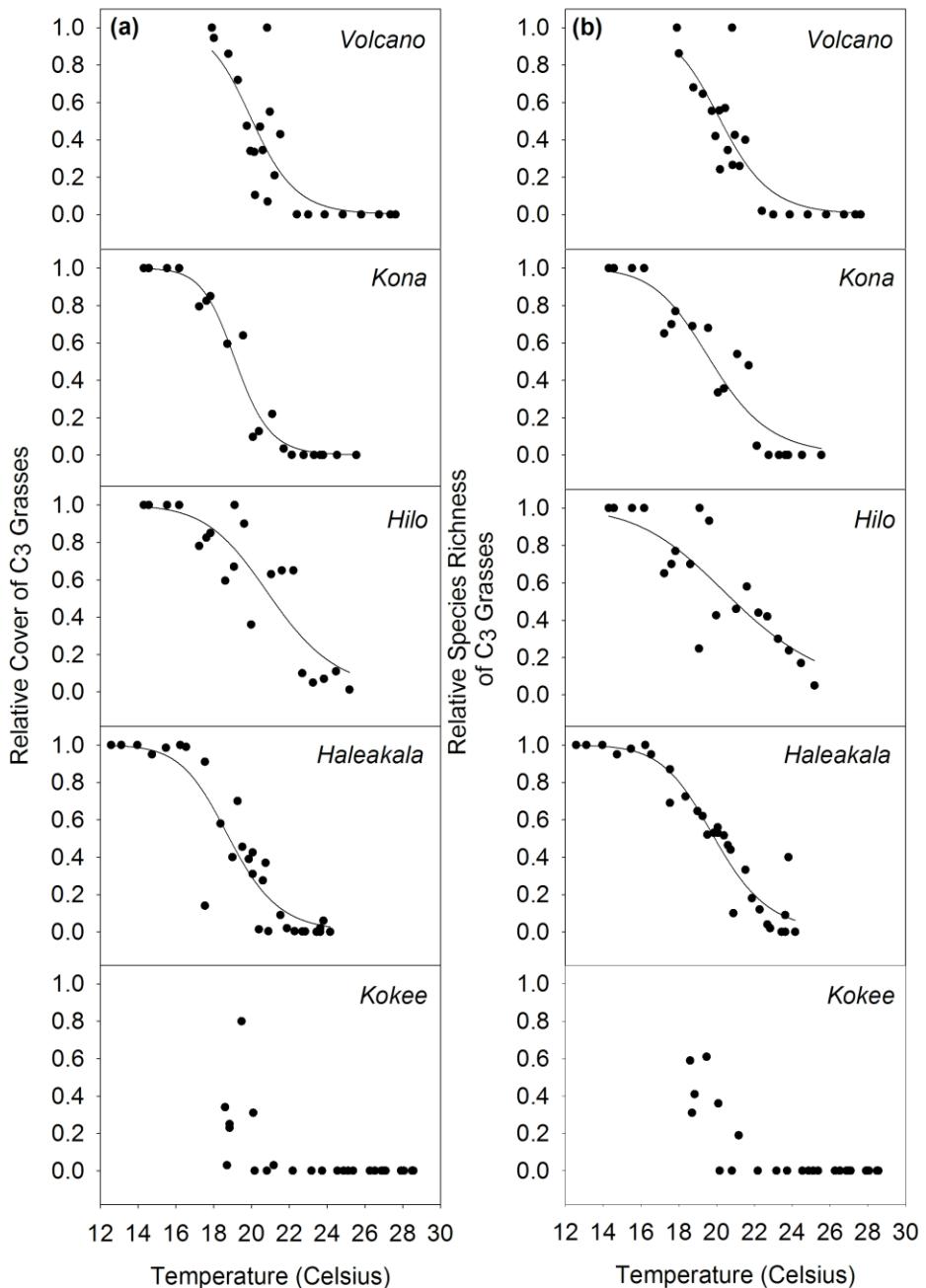


Figure 2.2 (a) and (b). July mean maximum transition temperatures for elevation gradients in the Hawaiian Islands using (a) relative percent cover data and (b) relative species richness data determined by a best fit regression model ($y = 1/(1+(x/x_0)^b)$).

APPENDIX

Appendix A. GPS points, Elevation (m), Annual maximum temperature (°C), July mean maximum temperature (°C), July mean minimum temperature (°C), January mean maximum temperature (°C), January mean minimum temperature (°C), Relative percent cover of C₃ grasses (PC), Relative percent species richness of C₃ grasses (SR), Absolute cover of C₃ grasses (AC C₃), and Absolute cover of C₄ grasses (AC C₄)

Location	X_UTM	Y_UTM	Elev	Annual	July max	July min	Jan max	Jan min	PC	SR	AC C ₃	AC C ₄
Volcanoes National Park	279131	2134604	36	27.62	28.5	19.88	26.41	17.52	0	0	0	0.26
	276138	2134187	67	27.35	28.22	19.66	26.18	17.23	0	0	0	0.82
	273967	2135131	174	26.74	27.7	18.79	25.63	16.33	0	0	0	0.2
	275150	2136373	303	25.8	26.92	17.75	24.72	15.02	0	0	0	0.51
	273975	2137034	553	24.82	26.13	17.03	23.64	14.2	0	0	0	0.37
	273905	2136993	679	23.87	25.31	16.7	22.66	13.86	0	0	0	0.15
	271495	2137606	866	23	24.51	15.86	21.73	12.97	0	0	0	0.04
	268045	2139773	979	22.4	23.86	15.03	21.14	12.14	0	0	0	0.33
	264221	2145037	1102	21.52	22.9	13.9	20.28	10.98	0.43	0.4	0.20	0.34
	263859	2147559	1157	21.22	22.49	13.42	20.02	10.5	0.21	0.26	0.15	0.55
	264931	2147935	1207	20.97	22.24	13.05	19.76	10.1	0.55	0.43	0.14	0.14
	258108	2150824	1200	20.85	22.11	12.81	19.64	9.82	0.07	0.27	0.05	0.65
	257630	2151092	1252	20.82	22.09	12.77	19.61	9.78	1	1	0.29	0.04
	256967	2151330	1307	20.59	21.87	12.42	19.35	9.41	0.35	0.35	0.33	0.35
	256054	2151418	1354	20.45	21.74	12.17	19.21	9.17	0.47	0.57	0.17	0.5
	255132	2152234	1400	20.18	21.49	11.74	18.91	8.77	0.11	0.24	0.13	0.93
	254806	2152283	1438	20.14	21.46	11.66	18.88	8.72	0.34	0.56	0.44	0.67
	253991	2153447	1537	19.94	21.27	11.34	18.67	8.47	0.34	0.42	0.09	0.19
	253422	2153721	1550	19.75	21.09	11	18.46	8.27	0.48	0.56	0.21	0.43
	251954	2155265	1700	19.27	20.65	10.18	17.97	7.71	0.72	0.65	0.19	0.16
	250824	2156062	1850	18.77	20.15	9.29	17.44	7.21	0.86	0.68	0.41	0.04
	249616	2156967	2040	18.01	19.44	8.38	16.65	6.35	0.95	0.86	0.24	0.02
	249713	2157675	2100	17.9	19.37	8.16	16.54	6.2	1	1	0.09	0
Kona	212384	2216294	500	25.54	26.14	17.26	24.32	13.49	0	0	0	0.94
	215474	2216745	650	24.52	25	15.9	23.47	12.17	0	0	0	0.61
	219603	2210212	800	23.78	24.19	14.75	22.72	10.88	0	0	0	0.45

Appendix A. (Continued)

	219901	2214084	817	23.64	24	14.46	22.63	10.64	0	0	0	0.66
	219811	2204307	950	23.3	23.91	13.79	22.16	9.88	0	0	0	0.78
	219796	2202293	1100	22.75	23.57	13.04	21.55	9.28	0	0	0	0.88
	221087	2200483	1250	22.13	23.18	12.4	20.83	8.8	0	0	0	0.75
	222069	2198705	1369	21.7	22.88	11.9	20.35	8.42	0.04	0.48	0.03	0.75
	222829	2196964	1550	21.09	22.45	11.34	19.67	7.98	0.22	0.54	0.09	1
	223626	2194754	1700	20.39	21.87	10.61	18.9	7.28	0.13	0.36	0.15	1
	224377	2192228	1763	20.07	21.61	10.07	18.56	6.97	0.1	0.34	0.08	1
	225632	2193345	1850	19.55	21.11	9.72	18.02	6.51	0.64	0.68	0.23	0.14
	242043	2180378	2050	18.72	20.38	8.61	17.17	5.66	0.6	0.69	0.44	0.28
	243643	2181903	2150	17.82	19.4	7.89	16.33	5.29	0.85	0.77	0.56	0.14
	243642	2182272	2238	17.61	19.18	7.74	16.12	5.34	0.83	0.7	0.58	0.11
	243498	2183054	2300	17.23	18.8	7.46	15.74	5.08	0.8	0.65	0.67	0.09
	242949	2184446	2450	16.17	17.75	6.71	14.62	4.29	1	1	0.48	0
	242814	2185436	2600	15.53	17.13	6.22	13.97	3.79	1	1	0.32	0
	242578	2186509	2750	14.57	16.21	5.68	12.97	3.12	1	1	0.19	0
	242886	2187111	2900	14.3	15.95	5.51	12.68	2.77	1	1	0.21	0
Hilo	274531	2177776	348	25.18	26.05	17.32	24.35	14.55	0.01	0.05	0.01	0.85
	272829	2177512	500	24.47	25.36	16.6	23.64	13.81	0.11	0.17	0.02	0.54
	270745	2177712	650	23.83	24.73	15.88	22.97	13.11	0.07	0.24	0.04	0.66
	267459	2179205	800	23.25	24.19	14.96	22.33	12.15	0.05	0.3	0.05	1
	264933	2179397	950	22.68	23.7	14.11	21.67	11.28	0.1	0.42	0.11	1
	263125	2178897	1100	22.21	23.27	13.5	21.13	10.66	0.65	0.44	0.76	0.39
	260510	2178415	1250	21.6	22.77	12.66	20.46	9.84	0.65	0.58	0.76	0.42
	257612	2177408	1400	21.03	22.28	11.74	19.82	8.94	0.63	0.46	0.7	0.41
	245855	2177369	1550	19.07	20.58	8.96	17.66	6.14	0.67	0.25	0.55	0.27
	251919	2176717	1700	19.98	21.38	10.3	18.66	7.27	0.36	0.43	0.42	0.73
	249094	2177968	1815	19.61	21.06	9.74	18.25	6.82	0.9	0.93	0.51	0.10
	245296	2178493	1942	19.1	20.64	9.02	17.67	6.11	1	1	0.22	0
	242022	2180395	2050	18.61	20.27	8.52	17.07	5.52	0.6	0.7	0.44	0.28
	243643	2181903	2150	17.82	19.4	7.89	16.33	5.29	0.85	0.77	0.56	0.14
	243642	2182272	2238	17.61	19.18	7.74	16.12	5.34	0.83	0.7	0.58	0.11
	243498	2183054	2300	17.23	18.8	7.46	15.74	5.08	0.78	0.65	0.67	0.09

Appendix A. (Continued)

	242949	2184446	2450	16.17	17.75	6.71	14.62	4.29	1	1	0.48	0
	242866	2185447	2600	15.53	17.13	6.22	13.97	3.79	1	1	0.32	0
	242602	2186503	2750	14.57	16.21	5.68	12.97	3.12	1	1	0.19	0
	242877	2187104	2900	14.3	15.95	5.51	12.68	2.77	1	1	0.21	0
Haleakalā National Park	777705	2305706	537	24.16	25.61	17.61	22.3	14.3	0	0	0	1
	780085	2307702	579	23.8	25.23	17.55	22.06	14.19	0.06	0.40	0.07	1
	778670	2305568	617	23.63	25.08	17.21	21.8	13.95	0.02	0.09	0.02	1
	778627	2305571	618	23.63	25.08	17.21	21.8	13.95	0	0	0	1
	779366	2305359	659	23.44	24.89	17.02	21.64	13.82	0	0	0	1
	780357	2304395	776	22.83	24.33	15.96	21.05	13	0	0	0	1
	780360	2303275	825	22.69	24.2	15.52	20.85	12.62	0	0	0	1
	780239	2300993	927	22.28	23.85	14.58	20.35	11.82	0	0	0	1
	780331	2299285	1045	21.87	23.43	13.85	19.95	11.28	0.02	0.18	0.04	0.40
	780720	2298830	1082	21.53	23.09	13.53	19.62	10.96	0.09	0.33	0.02	1
	781525	2298700	1250	20.89	22.46	12.82	19.02	10.39	0	0	0	1
	781887	2298971	1275	20.74	22.32	12.78	18.88	10.28	0.37	0.44	0.33	0.65
	782067	2298542	1328	20.6	22.18	12.69	18.75	10.13	0.28	0.46	0.54	0.60
	781863	2298434	1334	20.39	21.97	12.53	18.56	9.91	0.01	0.52	0.05	1
	782323	2298403	1424	20.06	21.64	12.22	18.26	9.6	0.31	0.53	0.36	0.77
	782504	2298344	1451	20.06	21.64	12.22	18.26	9.6	0.43	0.56	0.46	0.59
	782808	2298076	1496	19.85	21.44	12.03	18.05	9.4	0.39	0.53	0.45	0.69
	782728	2297710	1553	19.51	21.09	11.77	17.75	9.16	0.46	0.52	0.49	0.65
	783123	2297625	1611	19.26	20.84	11.69	17.51	9.1	0.70	0.62	0.75	0.32
	783370	2297500	1695	18.99	20.57	11.43	17.25	8.74	0.40	0.65	0.43	0.54
	784191	2297378	1842	18.36	19.92	10.86	16.67	7.89	0.58	0.73	0.57	0.43
	786628	2299513	2012	17.53	19.1	9.61	15.91	6.74	0.14	0.69	0.65	0.07
	786643	2299515	2014	17.53	19.1	9.61	15.91	6.74	0.91	0.87	0.15	0.95
	786659	2297898	2161	16.54	18.08	8.84	14.95	5.96	0.99	0.95	0.36	0.03
	787750	2297717	2322	16.23	17.76	8.56	14.64	5.65	1	1	0.37	0
	788511	2297264	2443	15.47	17	7.83	13.91	4.92	0.99	0.98	0.21	0.14
	786917	2295790	2585	14.73	16.22	7.43	13.19	4.56	0.95	0.95	0.07	0
	787828	2295840	2744	13.96	15.43	6.84	12.45	3.92	1	1	0.16	0
	787221	2294535	2883	13.11	14.55	6.2	11.62	3.33	1	1	0.01	0

Appendix A. (Continued)

	787228	2294535	2885	13.11	14.55	6.2	11.62	3.33	1	1	0.01	0
	786256	2293040	2990	12.57	13.99	5.86	11.1	3.01	1	1	0.02	0
Koke'e State Park	430670	2428373	1	28.53	30.03	21.12	26.36	17.46	0	0	0	0.95
	425904	2429475	27	28.56	30.13	21.07	26.38	17.45	0	0	0	0.87
	431575	2427730	31	28.53	30.02	21.26	26.37	17.48	0	0	0	1
	425902	2430876	36	28.49	30.05	20.83	26.31	17.32	0	0	0	0.84
	441260	2422352	61	28.04	29.46	21.31	26.05	17.3	0	0	0	1
	431440	2429402	148	28.06	29.55	20.54	25.9	16.83	0	0	0	0.48
	426642	2432225	151	27.91	29.42	19.9	25.73	16.42	0	0	0	0.81
	431478	2429442	158	28.06	29.55	20.54	25.9	16.83	0	0	0	1
	450892	2426985	215	26.52	27.66	20.13	24.87	16.25	0	0	0	1
	431317	2430600	290	27.09	28.56	19.18	24.94	15.55	0	0	0	0.75
	427115	2433296	340	26.98	28.47	18.44	24.79	15.13	0	0	0	1
	430229	2432380	395	26.87	28.34	18.56	24.73	15.1	0	0	0	0.83
	427763	2434287	440	26.26	27.79	17.7	24.03	14.4	0	0	0	1
	430248	2434146	509	25.37	26.93	16.95	23.12	13.52	0	0	0	1
	429020	2435327	557	25.11	26.59	16.59	22.9	13.21	0	0	0	0.73
	430553	2435879	616	24.87	26.48	16.64	22.56	13.11	0	0	0	0.73
	430040	2435894	641	24.54	26.08	16.17	22.27	12.68	0	0	0	0.57
	431295	2437267	777	23.17	24.76	15.1	20.84	11.39	0	0	0	0.27
	430731	2436659	842	23.73	25.33	15.49	21.33	11.94	0	0	0	0.43
	432113	2438382	883	22.18	23.78	14.38	19.86	10.43	0	0	0	0.27
	431597	2440655	984	21.17	22.8	13.61	18.82	9.46	0.03	0.19	0.01	0.53
	430736	2442791	1068	20.81	22.44	13.4	18.49	9.11	0	0	0	0.46
	432100	2447295	1118	19.47	21.25	12.52	17.03	8.04	0.8	0.61	0.74	0.28
	430919	2445749	1123	20.09	21.8	12.96	17.69	8.63	0.31	0.36	0.20	0.44
	430915	2445126	1125	20.16	21.87	12.97	17.73	8.66	0	0	0	0.47
	432480	2447686	1196	18.84	20.58	11.85	16.42	7.5	0.25	0.41	0.14	0.48
	433216	2448636	1242	18.6	20.39	11.66	16.15	7.38	0.34	0.59	0.19	0.39
	434406	2449402	1248	18.84	20.63	11.88	16.46	7.69	0.23	0.41	0.10	0.32
	434907	2449274	1275	18.7	20.48	11.76	16.29	7.52	0.03	0.31	0.02	0.69

CHAPTER 3

Upward expansion of fire-adapted C₄ and C₃ grasses along a warming tropical elevation gradient

ABSTRACT

High mountain regions in the tropics have thus far been impacted relatively little by anthropogenic activity or species invasion. However, they are unlikely to be immune to impacts of global change, including climate change and other anthropogenic disturbances. Changes in fire regimes, for example, are known to accelerate the spread of invasive C₄ grasses and interactions between changes in fire and climate can alter species distributions. The aim of this study was to compare grass distributions along an elevational gradient in Hawai‘i between the 1960’s and 2008 to determine whether C₄ and C₃ grass distributions are shifting upward in response to alterations in fire and climate patterns. Field plots at Hawai‘i Volcanoes National Park were surveyed for grass species and cover at ~150 m elevation intervals and compared to previous surveys done in the 1960’s. I found that the transition elevation, marking a shift in dominance between C₄ and C₃ grasses based on relative cover, shifted upward over 40 years (1476 m ± 130 m in 2008 versus 1200 m ± 106m in 1966/1967). On the other hand, maximum elevation across all C₄ or C₃ grasses was not significantly different in 2008 compared to 1960’s. However, a subset of C₄ (and fewer C₃) grasses moved to substantially higher elevations, and these were species adapted to fire. 100% of fire-adapted grasses moved up in elevation compared to 29% of non-fire adapted species, and the change in elevation of fire-adapted species (mean = + 454 m) was significantly greater than the change in elevation of non-fire adapted species ($P = 0.003$). My study documents an upward

expansion of fire-adapted grasses at high elevations in the tropics as an important threat that seems to be compounded by warming trends.

INTRODUCTION

Climate change has been predicted to increase invasions in tropical montane environments more so than in temperate montane environments (Bortenschlager 1991), however, current research has primarily addressed the influence of climate change on plant distributions in temperate ecosystems. Previous studies have investigated plant species distribution shifts upward in elevation in response to climate change (Kelly and Goulden 2008; Kullman 2002; Lenoir et al. 2008; Parolo and Rossi 2008; Penuelas and Boada 2003), but these studies were at high latitudes outside the tropics. Only a few studies on contemporary range shifts in the tropics have been published (Chen et al. 2009; Juvik et al. 2011; Peh 2007; Raxworthy et al. 2008; Seimon et al. 2007); most of these studies have not investigated changes in plant distributions. Even though the IPCC (2007) documented that temperature changes have been smaller at tropical latitudes in comparison to higher latitudes, bioclimatic modeling has shown that distributions of tropical vegetation will ultimately be altered with changes in climate (Colwell et al. 2008; Feeley and Silman 2010). Studies of contemporary plant range shifts in the tropics are needed to test predicted influences of climate change.

Studies comparing distributional shifts between C₄ and C₃ species in response to climate change are lacking. The physiological characteristics of C₄ plants such as a high optimum temperature range and minimal photorespiration give them an advantage in warm environments compared to C₃ plants, which dominate under cooler conditions (Long 1999). As a result, C₄ and C₃ plant

distributional patterns are significantly correlated with temperature (Cabido et al. 1997; Mo et al. 2004; Wan and Sage 2001). Tropical mountain systems, with C₄ grass dominance at lower elevations and C₃ dominance at higher elevations, are ideal environments for studying plant responses to climate change in relation to photosynthetic pathways. The Poaceae (grass family) is one of the largest families of angiosperms found in the tropics with species comprised of both C₃ and C₄ photosynthetic pathways, making them an ideal group for investigating potential shifts in plant distributions in response to climate change; furthermore, because of known associations between many grasses and disturbance we may expect substantial shifts in grass distributions in response to global change.

Disturbance has been shown to disrupt dominant vegetation patterns and promote changes in species distributions (Sousa 1984). In particular, fire can cause important changes in species distributions and composition (Ainsworth and Kauffman 2010; D'Antonio et al. 2001; Fonda and Binney 2011). In many cases, fire can shift vegetation to favor non-native, invasive species (reviewed in D'Antonio 2000). In areas that become invaded by grasses, a feedback cycle enhancing fire and grass expansion can occur (the grass-fire cycle) (D'Antonio and Vitousek 1992). In Hawai'i Volcanoes National Park for example, 36 fires burned an average of 4.5 hectares per fire over a 40 year period before the invasion of fire-adapted grasses. After the invasion of fire-adapted grasses, 93 fires have burned an average of 149 ha/fire in less than 30 years (Smith and Tunison 1992). Furthermore, the impacts of global climate change and altered

disturbance regimes are predicted to interact in altering distributional patterns of many invasive species (Kriticos et al. 2003a, b).

Tropical elevation gradients are excellent sites for investigating ongoing impacts of climate change in the tropics (Malhi et al. 2010). The broad elevation ranges of Hawaiian volcanoes (0 - 4000 m) combined with a wide assortment of C₄ and C₃ grasses makes Hawai'i a valuable tropical location for analyzing species distribution patterns and exploring underlying factors responsible for those patterns. The aim of this study was to compare grass distributions across an elevation gradient in Hawai'i over a forty year period between 1966/1967 (Newell 1968) and 2008 to determine if C₄ and/or C₃ grass distributions have shifted upward in elevation and if the species composition or dominance of grasses has changed. I hypothesized that C₄ and C₃ grasses are now established at higher elevations in response to climate warming over the past forty years and increased fire frequency (Giambelluca et al. 2008; Smith and Tunison 1992). I also hypothesized that fire-adapted grasses would be a more dominant component of the landscape compared to initial surveys in 1966/1967.

METHODS

During June 2008, field plots were surveyed along an elevation gradient on Mauna Loa, Hawai‘i (Figure 3.1). My field surveys were done within Hawai‘i Volcanoes National Park (HAVO) along the Chain of Craters Road and Mauna Loa Road. Original surveys in 1966 and 1967 (Newell 1968) were also done along these two roads documenting the earlier vegetation along this transect. All grass species found in the plots were recorded and cover estimates for each species were made based on one of six cover categories: 0-1, 2- 5, 6- 25, 26- 50, 51-75, 76-100. Forty-three total plots were surveyed at 100 – 150 m elevation intervals from sea level to 2000 m along the road and in natural habitats ~30 m away from the road. At each plot elevation, the side of the road (right versus left) chosen for each plot was randomly selected and then away from the road transects were done on the corresponding side of the road. For comparisons over time, only off road sites ($n = 21$) were used because original survey sites were similarly located off road; however, I also compared the roadside plots with off-road results. The locations of survey plots were matched as closely as possible to those used by Newell in 1966 and 1967. Newell (1968) used variable plot sizes while I used a fixed plot size of 50 m x 2 m divided into five 10 m x 2 m subplots. However, in all cases, my 2008 plot size was equal or smaller in size to that used by Newell (1968) so that any detected upward shift in plant range in 2008 represents a conservative estimate of the shift.

The photosynthetic pathway of all grasses was determined using species lists in Brown (1977), and relative percent cover and relative species richness of

C_4 and C_3 grasses for each plot were quantified. The transition point between C_4 and C_3 grasses, defined as the elevation where C_4 and C_3 grasses both equal 50% in relative cover or richness, was calculated from the inflection point of a best fit three parameter logistic regression model (Sigma Plot version 10, SSPS Inc, Chicago, IL 2007) and compared to the 1966 - 67 transition point calculated in the same manner. The logistic regression model used was $y = a/(1+(x/x_0)^b)$, where x is elevation (m), x_0 is the crossover elevation, y is the proportion of C_3 grasses, $a = 1$, and b is a fitted shape parameter. Significant differences in transition elevations between 1966/1967 and 2008 were determined using 95% confidence intervals calculated by the supporting plane method (PSI-Plot Version 8, Polysoft Software, Pearl River, NY 2007).

In addition to examining the overall transition elevation for C_4 and C_3 grass cover and species richness, distributions of individual grass species recorded in both the 1966/1967 and 2008 surveys were compared. Paired t -tests were used to compare maximum elevations between 1966/1967 and 2008 among all C_4 species or all C_3 species, and to compare the size of the elevation ranges in 1966/1967 and 2008. One-sample t -tests were used to determine if changes in C_4 or C_3 species distributions were different from zero. Species were also classified as either increasing or decreasing in elevation maxima, and the null expectation that half of the species would increase and half would decrease in elevation was tested using a binomial probability test.

Average daily temperatures were obtained for HAVO Park Headquarters for January and July 1965 – 2009 (IRMA 2011) to compare climate conditions

between survey dates and averaged to determine average monthly temperatures. Using GIS data for fires in HAVO, the number and size of fires along my transect over time were determined. Fire-adaption of a species was determined using Smith and Tunison (1992). An exact *chi-square* test (StatExact 4.0, Cytel Software) was used to determine if the proportion of fire-adapted species that moved up in elevation was different than the proportion of non fire-adapted species that moved up in elevation. A Kruskal-Wallis test was used to determine if the average change in elevation for fire and non-fire adapted species was different, while a *t*-test comparing dates of introduction was used to test the hypothesis that fire-adapted grasses were introduced more recently than non-fire adapted grasses.

RESULTS

Temperature Trends Over Time

Warming trends in the immediate vicinity of my transect (Figure 3.2) provide local support for broader warming patterns across the Hawaiian Islands documented by Giambelluca et al. (2008). The average monthly maximum temperatures at HAVO Park Headquarters (1200 m) for July (1966 - 1968) and July (2006 - 2008) were 17.2 °C and 17.9 °C, respectively. The average monthly maximum temperature for January (1966 - 1968) and January (2006 - 2008) were 14 °C and 14.67 °C, respectively (IRMA 2011). Thus, an average warming of about 0.7 °C occurred between survey dates.

Number and Size of Fires

There were six large fires along the transect from 1969 - 2000 that ranged in size from 225 - 1620 ha (Figure 3.1). Additionally, there were six smaller fires (1977 - 2000) within 150 meters of my transect, ranging in size from 0.04 - 156 ha (Figure 3.1). All of the fires that were directly along the transect were larger in size than fires that occurred prior to the earlier survey date (1924-1966, 8 fires, averaging <10 ha).

Comparison of Grass Distributions between 1966/1967 and 2008

In the 1966/1967 surveys, Newell (1968) documented 33 grasses species, 19 C₄ and 14 C₃, 9 of which were native species. As expected due to smaller plots sizes of my survey, in 2008 I found fewer species (22 grass species, 13 C₄ and 9 C₃, 5 of which were native species). The vast majority of species that I failed to detect in my 2008 survey (14 of 16 species) were rare in the 1966/1967

survey (averaging 1% cover in 1966/1967). I also found six new species in the 2008 transect. Four species that were found in the 1966/1967 surveys were only found along the road in 2008 (Appendix B).

Using a best fit three-parameter logistic regression based on Newell's (1968) original data, I found that the C₄ to C₃ transition point in 1966/1967 was at 1200 m (relative cover data, n = 24) and 1137 m (species richness data, n = 24) versus 1476 m (n = 21) and 1407 m (n = 21) in 2008, respectively. Although both trends were in the predicted direction of an upward shift in C₄ dominance, the difference was statistically different only for relative cover, based on 95% confidence intervals ($P = 0.04$) (Figure 3.3). Most grass species had higher elevation maxima in 2008 (Figures 3.4, 3.5), but a few species, both C₃ and C₄, declined in elevation between 1966/1967 and 2008, making the overall pattern statistically non-significant (paired *t*-test, $t = 0.811$, df = 9, $P = 0.43$ for C₄ grasses and $t = -0.038$, df = 4, $P = 0.97$, for C₃ grasses). Although the number of species that moved up in elevation (10) versus downward in elevation (4) was in line with predictions based on warming, this difference was not statistically different from the random expectation of 50% ($P = 0.09$). Considering all grass species, total elevational ranges were also not significantly broader between 1966/1967 and 2008 for either C₄ or C₃ grasses (paired *t*-test, $t = 1.43$, df = 9, $P = 0.18$ and $t = 0.073$, df = 4, $P = 0.94$, respectively).

Despite the lack of statistical support for overall increases in elevation among all C₄ or C₃ grass species, a clear trend was apparent among the grass species adapted to fire (Table 3.1). Significantly more fire-adapted species

moved up in elevation compared to non-fire adapted species (exact chi-square test, $P = 0.007$). In addition, when comparing change in elevation for fire and non-fire adapted species, the fire-adapted species moved up in elevation by a significantly greater amount (mean= 454 m) than non-fire adapted species (mean = -273 m, Kruskal-Wallis, $P = 0.003$) (Table 3.1). This difference was not due to more recent introductions of the fire adapted species, as species introduction dates were not significantly different between fire (mean = 1910) and non-fire adapted grasses (mean = 1904) (t -test, $t = -0.87$, df = 9, $P = 0.40$, native species excluded).

DISCUSSION

My study was limited by the number of plots originally used by Newell (1968) and thus, my small sample size leads to limited power of inference. However, despite this I did find statistically significant patterns that document changes over time. My study revealed an increase in elevation of the C₄-C₃ transition point, consistent with a plant response to warming over the past forty years. In the Hawaiian Islands, lapse rates have varied depending on the source: 0.3 °C per 100 m elevation up to ~ 1500 m (Doty and Mueller-Dombois 1966), 0.55°C per 100 m (Blumenstock 1961) and 0.7°C per 100 m (USDA 2004). Considering that temperatures at HAVO differed by 0.7 °C in the summer and 0.67 °C for the winter between the survey periods (1965 – 2009; IRMA 2011), and using the range of lapse rates reported for Hawai‘i (Doty and Mueller-Dombois 1966), the observed warming in my study is equivalent to the higher range of elevation change based on lapse rates (100 - 233 m). I observed higher transition elevations between 1966/1967 and 2008 with a mean increase of 276 m using relative cover data and 270 m using species richness data. Rundel (1980) used data from Newell (1968) to visually estimate the transition point as 1400 m in 1966/1967, however my estimation method based on fitting a logistic equation provides a consistent and less subjective means of comparing transition points over time.

Changes in tropical vegetation may be lagging behind vegetation trends at higher latitudes (Kelly and Goulden 2008; Kullman 2002; Lenoir et al. 2008; Parolo and Rossi 2008; Penuelas and Boada 2003). The IPCC (2007) reported

that high latitudes in the Northern hemisphere are warming faster than tropical latitudes, with temperature changes in the tropics roughly half of what higher latitudes are experiencing. Furthermore, previous studies that have documented plant distribution shifts have reported on average a change in temperature of 0.3 °C/decade (Penuelas and Boada 2003; Parolo and Rossi 2008), while, I only observed a change in temperature of 0.17 °C/decade (1968-2008) (from local weather station data) or 0.16 °C/decade since 1975 (based on island-wide trends reported by Giambelluca et al. (2008). Thus, in addition to a relatively small sample size of survey plots ($n = 21$), smaller temperature changes at my tropical site may have made some statistical patterns difficult to detect. Nevertheless, significant and non-significant trends in plant distributions were all in the predicted upward direction. As climate warming continues to increase in the future (IPCC 2007), tropical vegetation may more clearly mimic trends seen at higher latitudes (Kelly and Goulden 2008; Kullman 2002; Lenoir et al. 2008; Parolo and Rossi 2008; Penuelas and Boada 2003).

Since 1966/1967, fires have tripled in frequency and have increased in size in HAVO (Smith and Tunison 1992) and most of these fires have been anthropogenic. My data suggest that increased fire frequency is linked to upward range expansion of fire-adapted grasses (grasses that promote and/or tolerate fire). These upward grass expansions are associated with reduced ranges of other grasses, usually lower stature grasses that have minimal cover compared to fire-adapted grasses. Thus, fire may selectively diminish or reduce the ranges of some grasses, perhaps indirectly via competition with fire-adapted grasses,

resulting in high overall variance in distribution changes over time when all C₃ or C₄ grasses were considered together as a group. Road habitats are frequently prone to disturbances and thus contain open niches for species establishment (Alexander et al. 2009; Arteaga et al. 2009; Renth et al. 2005). Roadsides in HAVO were disturbed by automobile usage, human trampling, and vegetation cutting. I found that some species that were found off road in 1966/1967 were restricted to the roadside in 2008 and that species richness along the road in 2008 was also more similar to species richness values away from the road in 1966/1967, suggesting that the competitive nature of fire-adapted grasses now found more abundantly in the natural habitat may have reduced the abundance of some grass species, although successional trends away from the road might also account for this pattern.

In addition to upward expansion, one of nine C₄ grass species (*Schizachyrium condensatum*), had substantial downward expansion (decreased elevation minimum). Two other studies, Kelly and Goulden (2008) and Lenoir et al. (2008) also found downward shifts of 10% and 31% of the studied species, respectively, with climate warming. However, Lenoir et al. (2010) suggested that downslope range shifts of species may be biotic responses to habitat modifications, and in the case of *S. condensatum*, it is likely related to its dominance after fire. Thus, fire may have a more immediate influence on grass distribution patterns than climate warming, but it is difficult to separate these two drivers as increased fire frequency often accompanies climate change (Hemp 2005; Pechony and Shindell 2010; Schumacher and Bugmann 2006). Juvik et al.

(2011) also proposed that anthropogenic impacts along with climate warming may be impacting floristic composition and range changes along another roadside on Mauna Loa. In HAVO, cattle were removed from this study area by 1948 (Cuddihy 1984), while other feral animal populations were controlled before 1968. It is possible that release from grazing prior to 1968 may have also facilitated an expansion of fire-adapted grasses. Juvik et al. (2011) suggested that the dry conditions on Mauna Loa could possibly shift species distributions downslope as a result of increased water stress at higher elevations. This may explain why I did not see more C₃ species expand upward in elevation along my transect, as the higher elevation sites are often above the trade-wind inversion layer and they can experience extreme droughts.

This is the first study to show that transition elevations between C₄ and C₃ grasses are moving upward in the tropics and also contributes to the few studies looking at distributional shifts in response to climate change in the tropics. It shows a significant increase in the C₄-C₃ transition elevation in terms of plant cover, along with showing that grasses adapted to fire have shifted upwards in elevation in the last 40 years. Many of these grasses pose threats to native ecosystems due to their promotion of fire (D'Antonio and Vitousek 1992; D'Antonio et al. 2000). Tropical mountain systems are known to be very diverse in plant taxa (Laurance et al. 2011) and to support endemic montane species found nowhere else in the world (Chen et al. 2009) and Hawaiian montane ecosystems are no different. My study documents an upward dominance of C₄ grasses and expansion of fire-adapted grasses as important threats to Hawaiian

montane ecosystems that is likely to be compounded by further warming trends. Similar patterns are expected for montane ecosystems elsewhere in the tropics, where invasion by fire adapted grasses at lower elevations is already well documented (D'Antonio and Vitousek 1992).

LITERATURE CITED

- Ainsworth A, Kauffman JB (2010) Interactions of fire and nonnative species across an elevation/plant community gradient in Hawaii Volcanoes National Park. *Biotropica* 42:647-655
- Alexander JM, Naylor B, Poll M, et al. (2009) Plant invasions along mountain roads: the altitudinal amplitude of alien Asteraceae forbs in their native and introduced ranges. *Ecography* 32:334-344
- Arteaga MA, Delgado JD, Otto R, et al. (2009) How do alien plants distribute along roads on oceanic islands? A case study in Tenerife, Canary Islands. *Biol. invasions* 11:1071-1086
- Bortenschlager S (1991) The invasion of plants in the Alps: its mechanism. In: Ramakrishnan PS (ed) *Ecology of biological invasion in the tropics*. International Scientific Publications for National Institute of Ecology, New Delhi, pp. 177
- Brown WV (1977) The Kranz syndrome and its subtypes in grass systematics. *Mem. Torrey Bot. Club* 23:1-97
- Blumenstock DI (1961) Climates of the States, Hawaii. *Climatology of the United States*, No. 60-51. U.S. Department of Commerce, Weather Bureau, Washington, D.C.
- Cabido M, Ateca N, Astegiano M, et al. (1997) Distribution of C₃ and C₄ grasses along an altitudinal gradient in Central Argentina. *J. biogeogr.* 24:197-204
- Chen IC, Shiu HJ, Benedick S, et al. (2009) Elevation increases in moth assemblages over 42 years on a tropical mountain. *Proc. natl. acad. sci. U. S. A.* 106:1479-1483
- Colwell RK, Brehm G, Cardelus CL, et al. (2008) Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322:258-261
- Cuddihy L (1984) Effects of cattle grazing on the mountain parkland ecosystem, Mauna Loa, Hawaii. Cooperative National Park Resources Studies Unit, University of Hawaii at Manoa: Technical Report
- D'Antonio CM, Hughes RF, Vitousek PM (2001) Factors influencing dynamics of two invasive C₄ grasses in seasonally dry Hawaiian woodlands. *Ecology* 82:89-104

D' Antonio CM (2000) Fire, plant invasions, and global changes. In: Mooney HA, Hobbs RJ (eds) *Invasive species in a changing world*. Island Press, Covelo, pp. 65-93

D' Antonio CM, Tunison JT, Loh RK (2000) Variation in the impact of exotic grasses on native plant composition in relation to fire across an elevation gradient in Hawaii. *Austral ecology* 25:507-522

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. rev. ecol. syst.* 23:63-87

Doty L, Mueller-Dombois D (1966) *Atlas of bioecology studies in Hawaii Volcanoes National Park*. University of Hawaii, Botanical Science paper no. 2. Manoa, Hawaii, USA

Feeley KJ, Silman MR (2010) Modelling the responses of Andean and Amazonian plant species to climate change: the effects of georeferencing errors and the importance of data filtering. *J. biogeogr.* 37:733-740

Fonda RW, Binney EP (2011) Vegetation response to prescribed fire in Douglas-fir forests, Olympic National Park. *Northwest sci.* 85:30-40

Giambelluca TW, Diaz HF, Luke MSA (2008) Secular temperature changes in Hawaii. *Geophys. res. lett.* 35

Hemp A (2005) Climate change-driven forest fires marginalize the impact of ice cap wasting on Kilimanjaro. *Glob. change biol.* 11:1013-1023

IRMA (2011) Integrated Resource Management Applications Portal, National Park Service. Available at:
<http://nrinfo.nps.gov/Reference.mvc/Profile?Code=2166409> (Accessed on July 15, 2011).

IPCC (2007) *Climate Change 2007: The Physical Science Basis: Working Group I Contribution to the Fourth Assessment Report of the IPCC*. Cambridge University Press, UK

Juvik JO, Rodomsky BT, Price JP, et al. (2011) "The upper limits of vegetation on Mauna Loa, Hawaii": a 50th-anniversary reassessment. *Ecology* 92:518-525

Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent climate change. *Proc. natl. acad. sci. U. S. A.* 105:11823-11826

Kriticos D, Sutherst R, Brown J, et al. (2003a) Climate change and biotic invasions: a case history of a tropical woody vine. *Biol. invasions* 5:147-165

Kriticos D, Sutherst R, Brown J, et al. (2003b) Climate change and the potential distribution of an invasive alien plant: *Acacia nilotica* ssp. *indica* in Australia. *J. appl. ecol.* 40:111-124

Kullman L (2002) Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *J. ecol.* 90:68-77

Laurance WF, Useche DC, Shoo LP, et al. (2011) Global warming, elevational ranges and the vulnerability of tropical biota. *Biol. conserv.* 144:548-557

Lenoir J, Gegout JC, Guisan A, et al. (2010) Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography* 33:295-303

Lenoir J, Gegout JC, Marquet PA, et al. (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science* 320:1768-1771

Long SP (1999) Environmental responses. In: Sage RM, Monson RK (eds) *C₄ Plant Biology*. Academic Press, San Diego, CA, pp. 215-249

Malhi Y, Silman M, Salinas N, et al. (2010) Introduction: Elevation gradients in the tropics: laboratories for ecosystem ecology and global change research. *Glob. change biol.* 16:3171-3175

Mo W, Nishimura N, Soga Y, et al. (2004) Distribution of C₃ and C₄ plants and changes in plant and soil carbon isotope ratios with altitude in the Kirigamine Grassland, Japan. *Grassland science* 50:243-254

Newell C (1968) A phytosociological study of the major vegetation types in Hawaii Volcanoes National Park, Hawaii. MS Thesis, Honolulu: Univ. of Hawaii,

Parolo G, Rossi G (2008) Upward migration of vascular plants following a climate warming trend in the Alps. *Basic appl. ecol.* 9:100-107

Pechony O, Shindell DT (2010) Driving forces of global wildfires over the past millennium and the forthcoming century. *Proc. natl. acad. sci. U. S. A.* 107:19167-19170

Peh KSH (2007) Potential effects of climate change on elevational distributions of tropical birds in Southeast Asia. *Condor* 109:437-441

Penuelas J, Boada M (2003) A global change-induced biome shift in the Montseny mountains (NE Spain). *Glob. change biol.* 9:131-140

Raxworthy CJ, Pearson RG, Rabibisoa N, et al. (2008) Extinction vulnerability of tropical montane endemism from warming and upslope displacement: a preliminary appraisal for the highest massif in Madagascar. *Glob. change biol.* 14:1703-1720

Rentch JS, Fortney RH, Stephenson SL, et al. (2005) Vegetation-site relationships of roadside plant communities in West Virginia, USA. *J. appl. ecol.* 42:129-138

Rundel PW (1980) The ecological distribution of C₄ and C₃ grasses in the Hawaiian Islands. *Oecologia* 45:354-359

Schumacher S, Bugmann H (2006) The relative importance of climatic effects, wildfires and management for future forest landscape dynamics in the Swiss Alps. *Glob. change biol.* 12:1435-1450

Seimon TA, Seimon A, Daszak P, et al. (2007) Upward range extension of Andean anurans and chytridiomycosis to extreme elevations in response to tropical deglaciation. *Glob. change biol.* 13:288-299

Smith CW, Tunison JT (1992) Fire and alien plants in Hawaii: research and management implications for native ecosystems. University of Hawaii Press, Honolulu

Sousa WP (1984) The role of disturbance in natural communities. *Annu. rev. ecol. syst.* 15:353-391

USDA (2004) Experimental Forests and ranges of the USDA Forest Service. Gen. tech. Rep. NE-321. Available at: <http://www.fs.fed.us/psw/ef/hawaii/> (Accessed on June 15, 2012).

Wan CSM, Sage RF (2001) Climate and the distribution of C₄ grasses along the Atlantic and Pacific coasts of North America. *Canadian journal of botany* 79:474-486

TABLES

Table 3.1. Elevational changes documented over a 40 year time period for fire-adapted vs. non-fire adapted C₃ and C₄ grass species in Hawaii, ordered alphabetically and by photosynthetic pathway (Smith and Tunison 1992).

Grass Species	PP	Elevation Change (m)	Fire-Adapted Species
<i>Anthoxanthum odoratum</i>	C ₃	+495	X
<i>Holcus lanatus</i>	C ₃	+185	X
* <i>Agrostis avenacea</i>	C ₃	-138	
<i>Dactylis glomerata</i>	C ₃	+20	
<i>Vulpia myuros</i>	C ₃	-587	
* <i>Heteropogon contortus</i>	C ₄	+5	X
<i>Melinis minutiflora</i>	C ₄	+1150	X
<i>Melinis repens</i>	C ₄	+1195	X
* <i>Panicum tenuifolium</i>	C ₄	+125	X
<i>Paspalum dilatatum</i>	C ₄	+115	X
<i>Schizachyrium condensatum</i>	C ₄	+360	X
* <i>Chrysopogon aciculatus</i>	C ₄	-40	
<i>Cynodon dactylon</i>	C ₄	+40	
<i>Digitaria violascens</i>	C ₄	-1205	
<i>Setaria parviflora</i>	C ₄	+0	

*Native Hawaiian grass

FIGURES

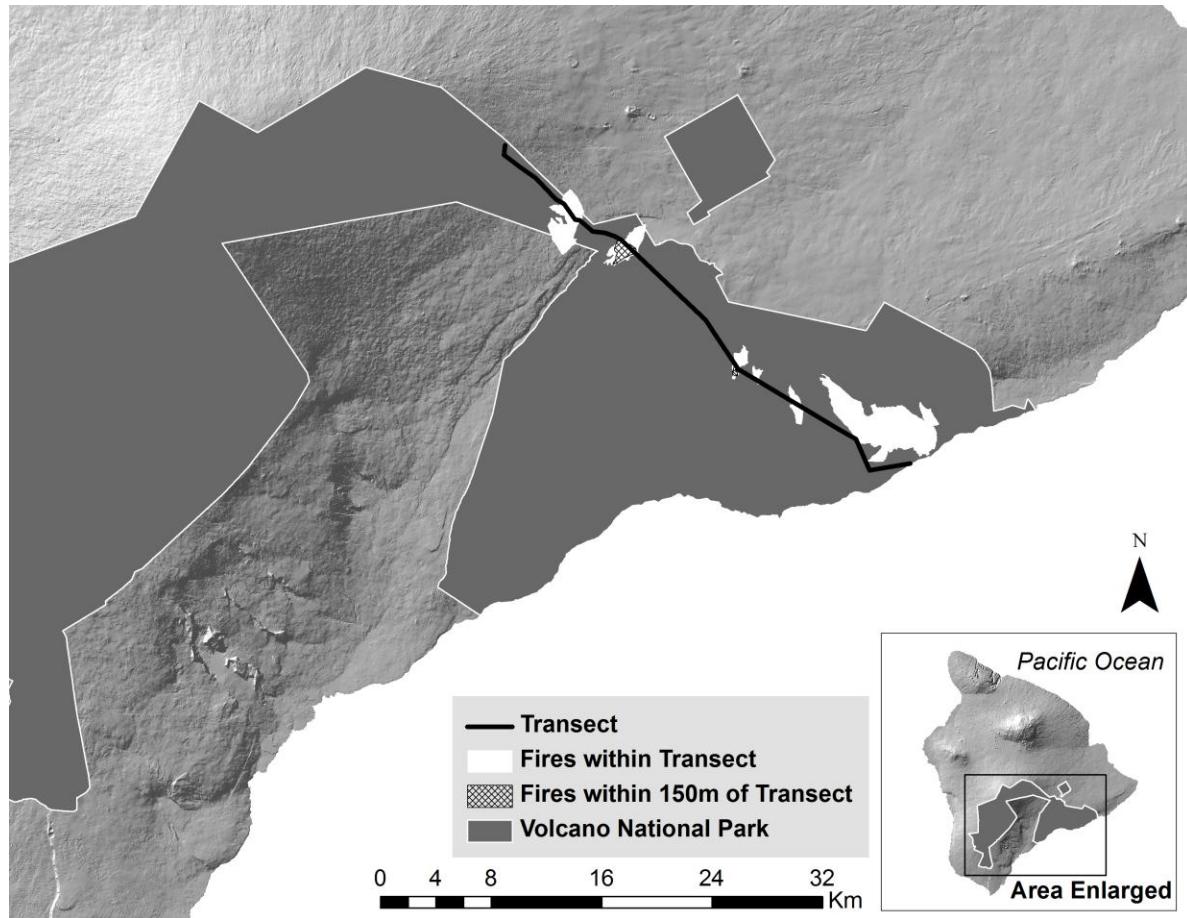


Figure 3.1 Survey sites (black circles, 2008) and fires sites (checkered and white, 1968 - present) on the island of Hawai'i, all within Hawai'i Volcanoes National Park

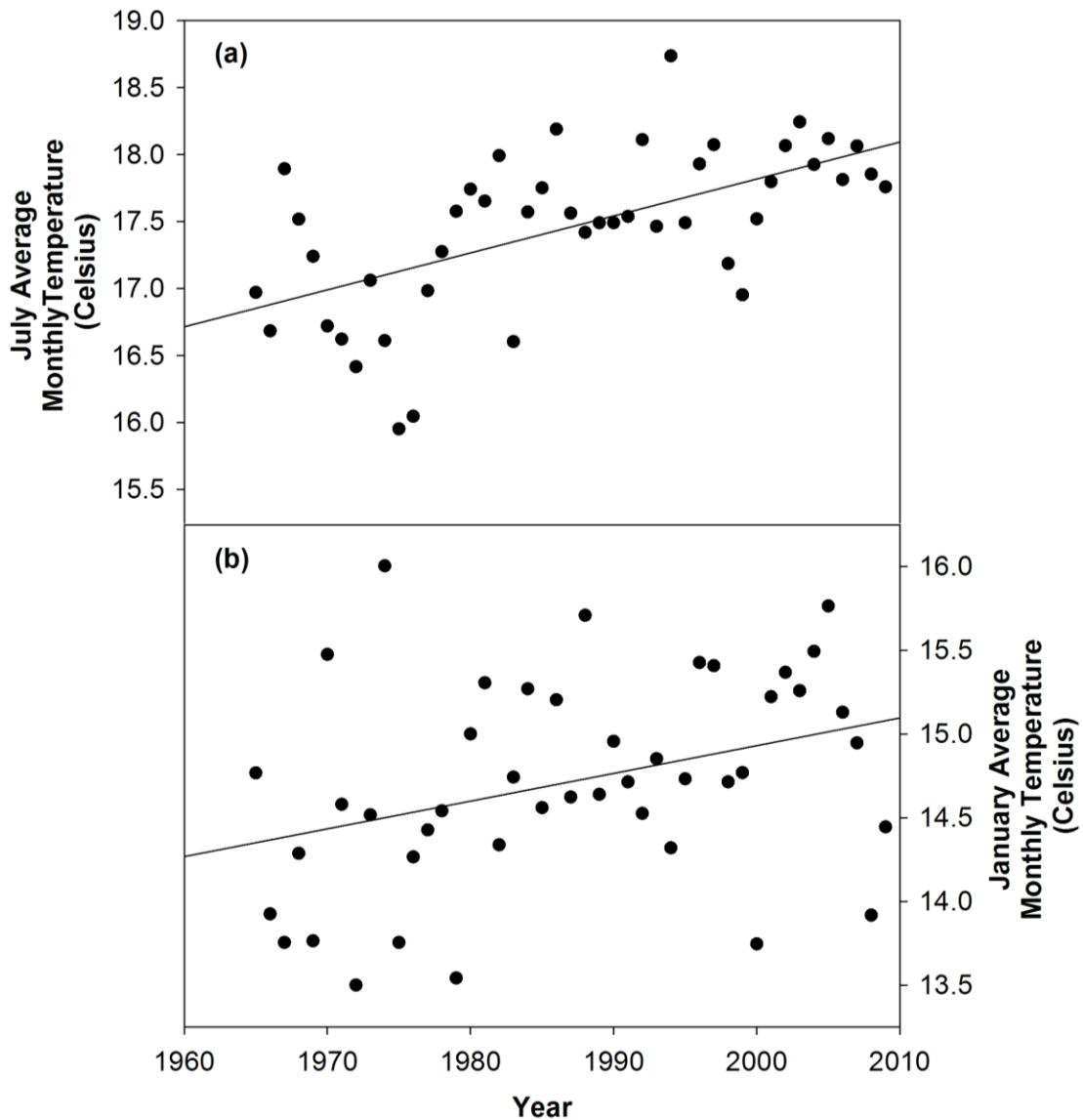


Figure 3.2 Monthly temperature averages for Hawai'i Volcanoes National Park in (a) July and (b) January 1965-2009.

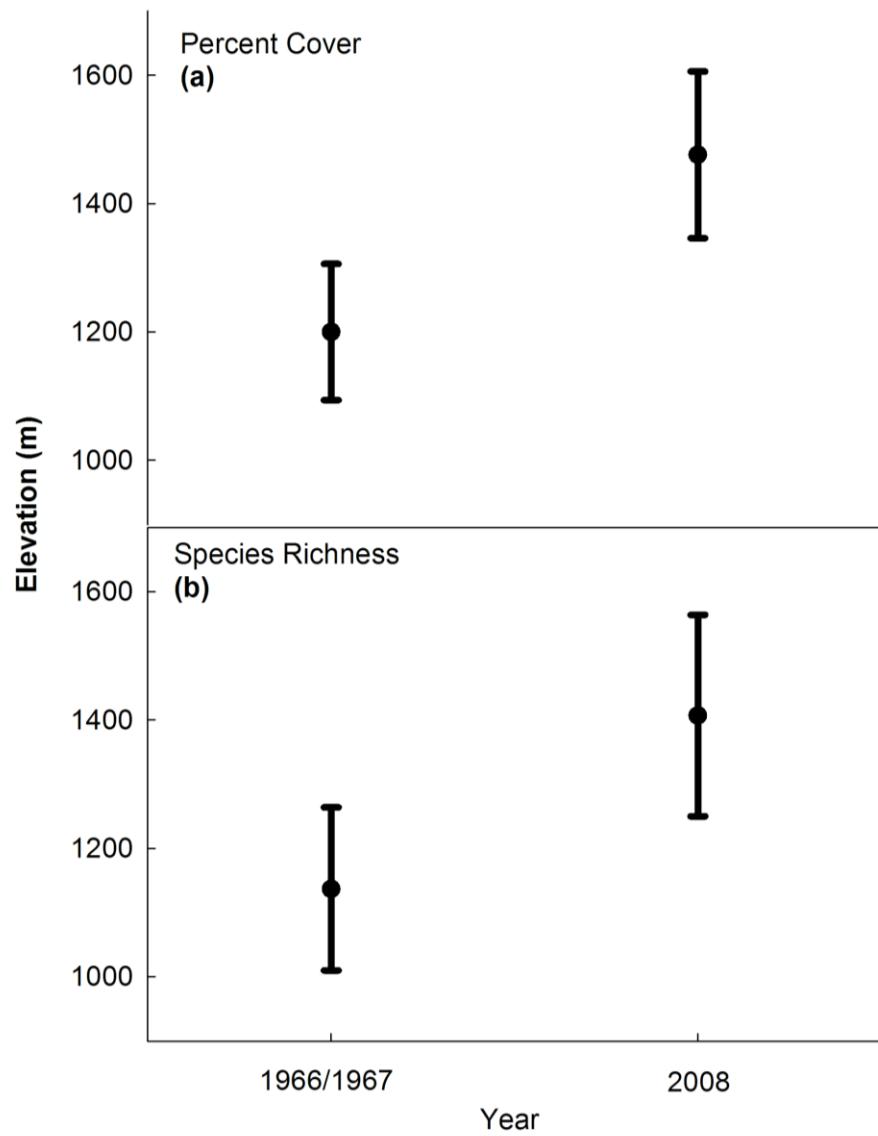


Figure 3.3 (a) Transition elevations for % relative cover of C₃ and C₄ grasses with 95% confidence intervals, and (b) Transition elevations for relative species richness of C₃ and C₄ grass species with 95% confidence intervals (1968 and 2008 surveys).

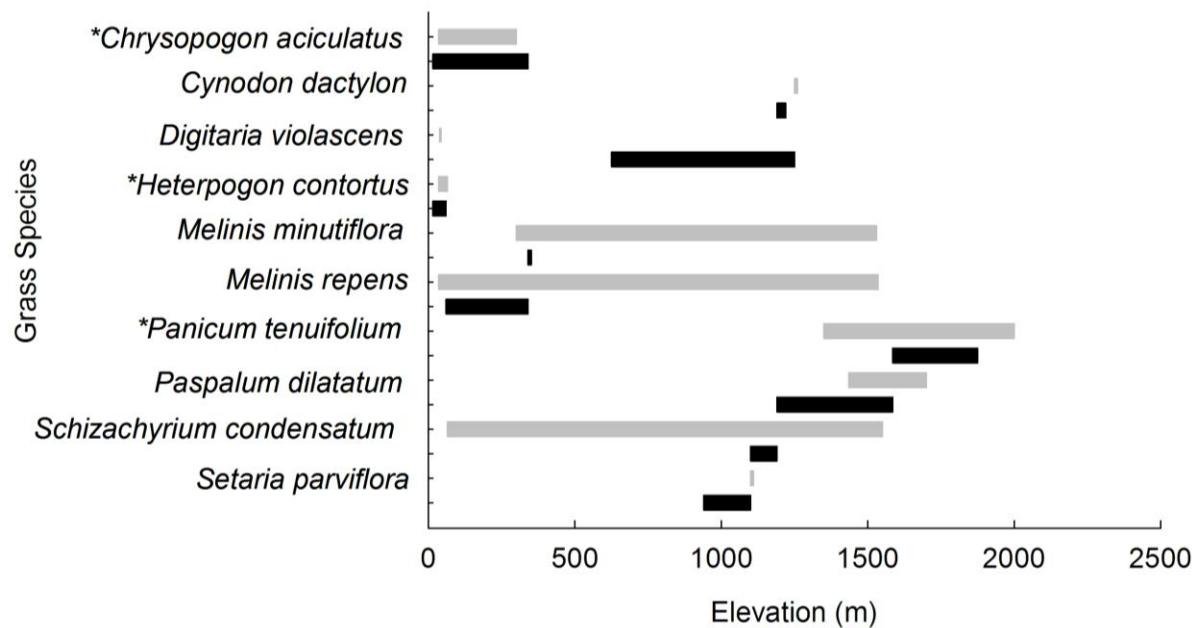


Figure 3.4 C₄ grass distributions in 2008 (gray bars) versus 1966/1967 (black bars), ordered alphabetically from top to bottom. Asterisk indicates native Hawaiian grass.

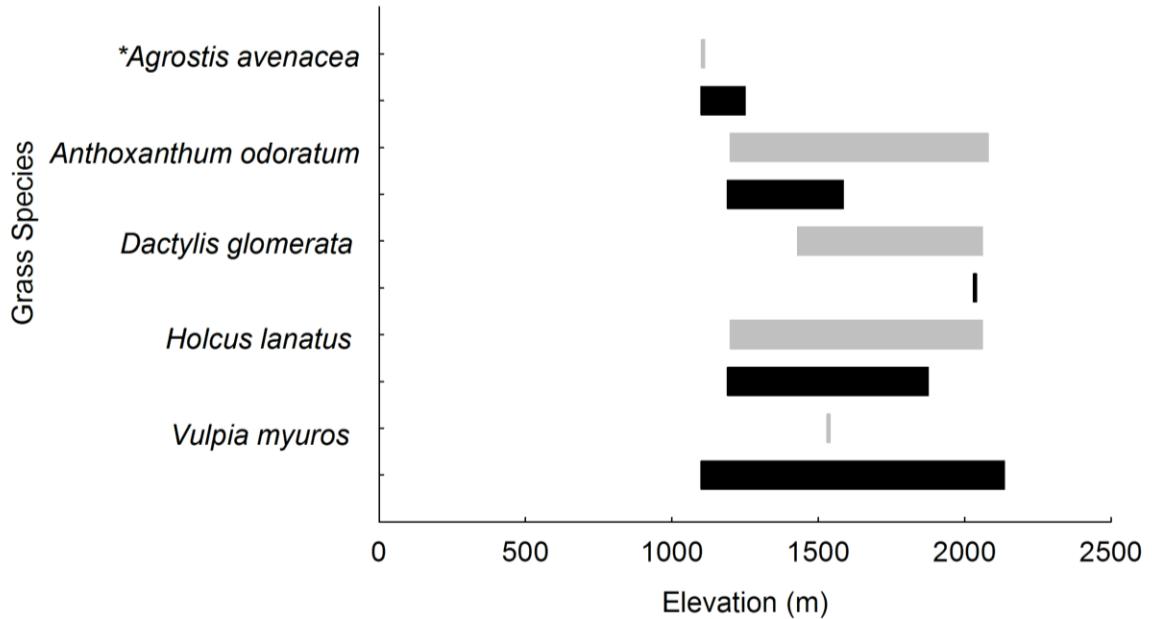


Figure 3.5 C₃ grass distributions in 2008 (gray bars) versus 1966/1967 (black bars), ordered alphabetically from top to bottom. Asterisk indicates native Hawaiian grass.

APPENDIX

Appendix B. Species percent cover for 1966/1967 surveys and species roadside percent cover for 2008 surveys

Species Name	PP	Native/ Non-native	1966 - 1967	Average Percent Cover/Transect 1966 - 1967	2008	Average Percent Cover/Transect 2008
<i>Agrostis avenacea</i>	C ₃	native	X	2	X	1
<i>Agrostis sandwicensis</i>	C ₃	native	X	1	-	
<i>Andropogon virginicus</i>	C ₄	non-native	X	20	-	
<i>Anthoxanthum odoratum</i>	C ₃	non-native	X	7.5	X	10.5
<i>Bothriochloa pertusa</i>	C ₄	non-native	X	1	-	
<i>Briza minor</i>	C ₃	non-native	X	1	-	
<i>Bromus willdenowii</i> ‡	C ₃	non-native	X	1	-	
<i>Chrysopogon aciculatus</i>	C ₄	native	X	3.5	X	1
<i>Cynodon dactylon</i>	C ₄	non-native	X	21	X	1
<i>Dactylis glomerata</i>	C ₃	non-native	X	1	X	1
<i>Deschampsia nubigena</i>	C ₃	native	X	17	X	23
<i>Digitaria ciliaris</i>	C ₄	non-native	X	5.5	-	
<i>Digitaria fuscescens</i>	C ₄	non-native	X	1	-	
<i>Digitaria violascens</i>	C ₄	non-native	X	1	X	1
<i>Eragrostis tenella</i>	C ₄	non-native	X	1	-	
<i>Heteropogon contortus</i>	C ₄	native	X	25	X	38
<i>Holcus lanatus</i>	C ₃	non-native	X	21	X	6
<i>Isachne distichophylla</i>	C ₃	native	X	2.5	-	
<i>Melinis minutiflora</i>	C ₄	non-native	X	1	X	19
<i>Melinis repens</i>	C ₄	non-native	X	6	X	7.5
<i>Opismenus hirtellus</i>	C ₃	non-native	X	1	-	
<i>Panicum tenuifolium</i>	C ₄	native	X	6.5	X	8

Appendix B (continued). Species percent cover for 1966/1967 surveys and species roadside percent cover for 2008 surveys

<i>Paspalum conjugatum</i>	C ₄	non-native	X	1	-	
<i>Paspalum dilatatum</i>	C ₄	non-native	X	30	X	50
<i>Paspalum orbiculare</i>	C ₄	native	X	1	-	
<i>Paspalum urvillei</i> ‡	C ₄	non-native	X	1	-	
<i>Sacciolepis indica</i> ‡	C ₃	non-native	X	1	-	
<i>Schizachyrium condensatum</i>	C ₄	non-native	X	1	X	16
<i>Setaria parviflora</i>	C ₄	non-native	X	1	X	5
<i>Sporobolus africanus</i> ‡	C ₄	non-native	X	1	-	
<i>Trisetum glomeratum</i>	C ₃	native	X	1	-	
<i>Vulpia myuros</i>	C ₃	non-native	X	1	X	25
<i>Vulpia octoflora</i>	C ₃	non-native	X	1	-	
New Species Found in 2008						
<i>Bromus diandrus</i>	C ₃	non-native	-		X	1
<i>Ehrharta stipoides</i>	C ₃	non-native	-		X	10
<i>Hyparrhenia rufa</i>	C ₄	non-native	-		X	27
<i>Pennisetum clandestinum</i>	C ₄	non-native	-		X	50
<i>Poa pratensis</i>	C ₃	non-native	-		X	1
<i>Sporobolus diander</i>	C ₄	non-native	-		X	1

‡ Indicates species only found along the roadside in 2008

CHAPTER 4

Impacts of future climates on fire-promoting invasive grass
distributions in the Hawaiian Islands: C₄ vs C₃

ABSTRACT

Climate warming in the tropics has been documented during the past century. Warming has been predicted to increase invasions in tropical montane environments more so than in temperate montane environments, however, current research has primarily addressed the influence of climate change on plant distributions in temperate ecosystems. Invasive C₄ and few C₃ grasses are known to change fire-frequencies, alter ecosystem processes and displace native species in the tropics. To predict changes in fire-promoting invasive C₄ and C₃ grass distributions in response to climate change in the Hawaiian Islands, bioclimatic models were developed for nine grasses using the maximum-entropy approach for species distribution modeling (MAXENT). Average minimum temperature during January, average maximum temperature during July, wettest quarter and driest quarter were the environmental constraints used to build the models. For future projections, I altered climate layers based on expected warming and precipitation trends for the Hawaiian Islands for the year 2050. Changes in species distributions were analyzed across the Hawaiian Islands, along with five conservation areas. I found that C₃ species had habitat loss and decreases in range size at most locations. C₄ species varied in their response to climate alterations, with these species contracting or increasing in range size depending on species and location. C₃ species were primarily limited by temperature constraints, whereas the C₄ species were limited by a combination of temperature and precipitation constraints. Projections of future ranges of fire-

promoting grasses can be used to help guide conservation of rare, high elevation plant communities in the tropics.

INTRODUCTION

Changes in climate will ultimately alter the distributions of many plants in the 21st century (Bradley et al. 2010; Colwell et al. 2008; Hijmans and Graham 2006; Pearson and Dawson 2003; Peterson et al. 2008; Thomas et al. 2004; Thuiller 2004). The principal mechanism that affects biota under climate change is a shift in the distribution of areas with climatically suitable conditions, which forces species to migrate to new areas where their bioclimatic niches persist (Colwell et al. 2008; Feeley and Silman 2011; Grabherr et al. 1994; Kelly and Goulden 2008; Kullman 2002; Lenoir et al. 2008; Parolo and Rossi 2008; Penuelas and Boada 2003). These shifts in distributions can cause species ranges to be reduced or expanded in size, ultimately impacting plant community structure (Beaumont et al. 2009; Bradley 2009; Colwell et al. 2008; Thomas et al. 2004). In areas with elevational gradients, species distributions are predicted to move towards higher elevations as the climate warms (Feeley 2012). The degree to which climate will change across a particular area, however, is expected to depend on latitude (IPCC 2007). High latitude areas have seen higher increases in temperature than low latitude, tropical areas (IPCC 2007). Furthermore, changes in climate have been empirically shown (Giambelluca et al. 2008) and projected (Bradley et al. 2006; Timm and Diaz 2009) for different tropical areas. Studies documenting tropical species range shifts in response to climate change have been minimal (Feeley et al. 2011; Juvik et al. 2011; Feeley 2012). In addition, studies that have determined how current plant distributions may change in the future with climate change in the tropics have focused on plants in

Central America, South America or Australia (Colwell et al. 2008; Feeley and Silman 2010a, Feeley and Silman 2010b, Kriticos et al. 2003a, Kriticos et al. 2003b; Thomas et al. 2004). Thus, more research is needed in other tropical localities such as the Hawaiian Islands.

Invasive species are known to transform ecosystems and have been identified as a major component of global change (Vitousek et al. 1996). Grasses (Poaceae) are now well-known invaders of many habitats on most continents, and they possess growth and reproductive traits that give them the ability to alter ecosystems (D'Antonio and Vitousek 1992). In areas that become invaded by grasses, a feedback cycle enhancing fire and grass expansion can occur (the grass-fire cycle). In many cases, this grass-fire cycle can shift vegetation to favor non-native, invasive species. In the tropics, invasive C₄ grasses have become dominant components of ecosystems, altering ecosystem processes such as the frequency and/or intensity of fire (D'Antonio and Vitousek 1992). The physiological characteristics of C₄ plants, such as a high optimum temperature range and minimal photorespiration give them an advantage in warm environments compared to C₃ plants, which dominate under cooler and moister conditions (Long 1999). Furthermore, in New Zealand an extreme heat event favored the expansion of C₄ grasses relative to C₃ species, shifting the distribution of these species (White et al. 2000). Thus, the prevalence of invasive C₄ species may be exacerbated by climate change, as has been predicted more generally for other invasive species (IPCC 2007).

Determining an invasive species' climatic habitat under current and future climates using bioclimatic envelope modeling can assess the area of land that may be at risk or areas that may open up for restoration with climate change (Bradley et al. 2009). A climatic habitat can be described as the biogeographic area that possesses the climatic attributes essential to a species' survival and growth (Bradley et al. 2010; Kearney 2006). Areas that become less climatically suitable for invasive species under climate change might provide opportunities for ecological restoration (Bradley et al. 2009). In addition, predicting how invasive species will impact protected areas under climate change is a major obstacle for land managers and conservation planners (Bradley 2009), and there is limited understanding of the potential interactions between invasive species and climate change in conservation areas (Beaumont et al. 2009; Hannah et al. 2007; MacDonald 1994). To sustain conservation and restoration efforts, the potential effects of climate change on invasive species' distributions needs to be incorporated into management strategies (Beaumont et al. 2009; Bradley 2009).

Bioclimatic envelope models (BEMs) can be used to statistically describe a species' climatic habitat (Pearson and Dawson 2003; Phillips et al. 2006). These models have proven to be useful tools to predict invasive species distributions under current climates (Thuiller et al. 2005) and both native and invasive species distributions under climate change (Colwell et al. 2008; Hijmans and Graham 2006; Pearson and Dawson 2003; Thomas et al. 2004; Thuiller 2004). In addition, these models have shown that invasive species distributions have the potential for both expansion (Bradley 2009; Bradley et al. 2010; Kriticos

et al. 2003) and contraction (Beaumont et al. 2009; Bradley 2009; Bradley et al. 2009; Parker-Allie et al. 2009; Peterson et al. 2008) under climate change. These models have limitations, however, since other factors besides climate can limit a species distribution, including competition and other biotic interactions (Guisan and Zimmermann 2000; Pearson and Dawson 2003), and other abiotic factors such as increases in atmospheric CO₂ can affect invasive plant distributions (Ainsworth and Long 2005). Despite these limitations, bioclimatic models are still useful for identifying the climatic constraints that define a species distribution (Hirzel et al. 2002), along with the potential distribution of a species under climate change (Bradley 2009; Hijmans and Graham 2006; Pearson and Dawson 2003).

Feeley and Silman (2011) emphasized that there has so far been relatively little modeling on current and future distributions of species in the tropics. Furthermore, Malhi et al. (2010) argue that tropical elevation gradients are excellent sites for examining ongoing climate change impacts in the tropics. The Hawaiian Island chain is an ideal place to investigate invasive C₄ and C₃ grass distributions due to the accessibility of these plants near roadsides, extensive GIS data, climate data specific for the Hawaiian Islands, extensive elevation/climate gradients, and numerous conservation areas. A recent study in Hawai‘i (Juvik et al. 2011) found that anthropogenic impacts, along with climate warming, may be impacting the floristic composition and species distributions along the Mauna Loa Volcano, highlighting that shifts in plant distributions in response to climate change are likely already underway and need to be further

investigated. In addition, high elevation sites in Hawai‘i may be particularly vulnerable to climate change because they include some of the last relatively intact ecosystems in the Hawaiian Islands (Loope and Giambelluca 1998) and also because climate warming is occurring faster at these higher elevations compared to lower elevation sites (Giambelluca et al. 2008). In Hawai‘i, vegetation clearly changes across climatic gradients, and therefore climate change has been predicted to influence plant distributions over time (Crausbay and Hotchkiss 2010).

The aim of this study was to project the potential distributions of invasive, fire-promoting C₄ and C₃ grasses for the year 2050 using MAXENT, a BEM that has been shown to produce models with good predictive power (Hijmans and Graham 2006). I hypothesized that overall, C₃ grass distributions would be reduced because of expected physiological disadvantages at higher temperatures, while C₄ grass distributions would expand due to their competitive advantage at high temperatures. However, I also expected that distributional changes would vary based on individual species' climatic preferences, as was found in previous studies (Kelly and Goulden 2008; Lenoir et al. 2008). I hypothesized that distribution changes within valuable conservation areas (nature reserves, state/national parks) would vary, depending on the location of these conservation areas, with greater changes in conservation areas at high elevations, where projected temperature changes are greater.

METHODS

Field surveys and Supplemental Species Occurrence Data

Field surveys were done on the islands of O'ahu, Maui, Kaua'i, and Hawai'i during 2008, 2009, and 2010 to obtain GPS points for bioclimatic envelope modeling (BEM). Surveys were conducted along major roads, immediately on the roadside and 30 m away from the road. My GPS points for species observations were supplemented with collection points derived from herbarium records (Edwards and Still 2008). Data filtering has been shown to be necessary when using herbarium data (Feeley and Silman 2010a). GPS points from Edwards and Still (2008) were screened for anomalies by plotting them using ArcMap, and 40 out of 222 points were removed from analysis because they were well outside of the species known distributional range, suggesting either that the locality data had been erroneous/imprecise or that those environments only rarely can sustain growth. All points (field survey and herbarium) were then compiled and evaluated in ArcMap to determine the distance between GPS points. If recorded GPS points were closer than 500 m, one point was randomly removed from analysis to avoid overweighing of particular localities in the models (Appendix C).

Species Selection

Grass species selection for modeling was based on previous papers (D'Antonio and Vitousek 1992; Smith and Tunison 1992) that documented important fire-promoting non-native grasses in the Hawaiian Islands. The species selected for the modeling were *Anthoxanthum odoratum*, *Cenchrus ciliaris*,

Holcus lanatus, *Hyparrhenia rufa*, *Megathyrsus maximus*, *Melinis minutiflora*,

Paspalum dilatatum, *Pennisetum setaceum*, *Schizachyrium condensatum*.

Holcus lanatus and *Anthoxanthum odoratum* are C₃ grasses, while all of the other species are C₄ grasses. All of the grass species used in the study are non-native grasses.

Climate Layers

Climate data from PRISM (Prism Climate Group, Oregon State University 2004) and from Tom Giambelluca (Giambelluca et al. 2011; Tom Giambelluca, Personal Communication) were used to build species models. PRISM climate data has a resolution of 500m, while the Giambelluca data has a resolution of 250m. Variation in time periods and statistical approaches used to construct original temperature data have been reported (Tom Giambelluca, Personal Communication). PRISM climate data was based on the years, 1971-2000, whereas, Giambelluca temperature data was based on period of record data for each climate station (Tom Giambelluca, Personal Communication). There have also been reported differences between Giambelluca et al. (2011) and PRISM's precipitation layers. Some reasons for this are that the methodologies used are different. Giambelluca et al. (2011) incorporated variables such as vegetation and radar data in the creation of their precipitation layers. PRISM precipitation layers were also used in the creation of Giambelluca et al. (2011)'s precipitation layers as one of the contributing variables. Giambelluca et al. (2011) also used more than double the number of climate stations used by PRISM (with higher quality control on climate station data). Whereas the PRISM climate data have

been widely used, the Giambelluca climate data have become available only recently, so models were developed separately from these two data sources to check for consistency. The island of Ni‘ihau was not included in my analyses because the Giambelluca data did not include the island of Ni‘ihau. The climate factors used in my study were July mean maximum temperature (T_{\max}), January mean minimum temperature (T_{\min}), wettest quarter, and driest quarter. Monthly temperature layers were chosen based on previous literature that has shown January and July temperatures to influence grass distributions (Batanouny et al. 1988; Cabido et al. 1997; Rundel 1980). The wettest and driest quarters for each pixel were determined from monthly means by obtaining precipitation values for the driest and wettest consecutive three months using ArcGIS 10. Precipitation layers were expressed as wettest and driest quarters because extremes in water seasonal availability (as opposed to simply total annual precipitation) often have a stronger influence on species distributions, and because future precipitation projections were available for changes in the wettest and driest seasons (Timm and Diaz 2009).

Future climate layers were created based on empirical trends and modeled projections for the Hawaiian Islands for the year 2050 (Giambelluca et al. 2008; Timm and Diaz 2009). GIS layers were manipulated using ArcGIS 10. Precipitation was increased by 3% in the driest quarter and decreased by 5% in the wettest quarter. Future temperature layers were created with the assumption of greater temperature increases at higher elevations, as has been observed empirically. At elevations ranging from 0 m to 4200 m, temperatures were

increased from 0.12°C to 0.35°C (July mean maximum) and 0.73°C to 1.84°C (January mean minimum). Temperature increases were applied at 100 m elevation intervals using the following equation in ArcGIS 10:

```
if [RASTERVALU] <=100 Then [tmin_new]=[GRID_CODE] + .732 ELSEIF  
[RASTERVALU] > 100 and [RASTERVALU] <=200 Then [tmin_new]=  
[GRID_CODE] + .759.... ELSEIF [RASTERVALU] >4100 and [RASTERVALU]  
<= 4200 Then [tmin_new]=[GRID_CODE] + 1.839. This equation is for increases  
in January mean minimum, but was analogously applied to July mean maximum.
```

Bioclimatic Envelope Model Construction

Bioclimatic envelope models were developed using the Maximum Entropy approach (MAXENT) (Phillips et al. 2006; Phillips and Dudík 2008). MAXENT was chosen due to its good performance when projecting species distributions under current (Elith et al. 2006) and future climates (Hijmans and Graham 2006). Models were constructed using GPS points from the island of Hawai'i (training data) and tested using GPS points from the other islands in the Hawaiian Island chain (testing data) except for *Schizachyrium condensatum*, which only had GPS points from the island of Hawai'i. The model for *S. condensatum* was built using my field-collected GPS points from the island of Hawai'i (training data) and tested using herbarium data. Models were determined to be acceptable based on training and testing AUC (Area under the Curve) values of 0.7 or higher and if they had biologically realistic response curves (probability of species presence in relation to environmental variables). The value of AUC ranges from 0 to 1, with a value of 0.5 indicating that model predictions are no better than random. The

higher the testing AUC (above 0.5), the better the model is at predicting the presences broadly across the Hawaiian Islands. AUC values were ranked as excellent (AUC = 0.9 - 1), good (AUC = 0.80 - 0.89), fair (AUC = 0.70 – 0.79) or poor (AUC = 0.6 – 0.69) based on Parker-Allie et al. (2009). All possible combinations of climatic variables were assessed. More than one model was retained if testing AUC values for the models were within ten percent of each other and if the response curves for each of those models were biologically feasible.

Species Suitability

For the purpose of predicting area lost or gained with climate change, probability layers produced by the MAXENT program were converted to binary layers (areas that were suitable and not suitable for specific species) based on the maximum test sensitivity plus specificity logistic threshold. Using the logistic threshold and ArcMap, a map layer was made with both suitable and unsuitable areas for each species. Area of species suitability vs. total area of the Hawaiian Islands was determined using ArcMap. To determine percent suitable habitat area for particular conservation areas, the species suitability layer was cut to produce shapefiles for each individual conservation area. To determine percent area suitable for fire-promoting species as an aggregate group, shapefiles for all species were united and then dissolved using ArcGIS 10 to form an aggregate shapefile. This process was then repeated separately for the functional groups, C₄ and C₃. If two or more models were made for a species then distributional

area and percent changes for that species are given as a range. A paired *t*-test was used to compare range sizes for current and future ranges among all species at each location for the two climate data sets (PRISM versus Giambelluca data).

RESULTS

Model Predictive Power

Of the nine species modeled, seven species had over 40 records. Most species had two best-fit models with comparable AUC values for both the PRISM and Giambelluca data sets, except for *Pennisetum setaceum* and *Schizachyrium condensatum*, which only had one best-fit model per climate data set each (Tables 4.1, 4.2). *Schizachyrium condensatum* had excellent predictive power using both data sets, while *Cenchrus ciliaris* had excellent predictive power only for the Giambelluca data set. Seven out of 16 models had good predictive power using the PRISM climate data based on AUC criteria proposed by Parker-Allie et al. (2009). For the Giambelluca data set, only three out of the 16 models had good predictive power. For both data sets there were similar numbers of models in the fair category, six for the PRISM and seven for the Giambelluca data sets (Tables 4.1, 4.2). Poor model predictive power was found for *Megathyrsus maximus* with both sources of climate data probably due to its wide distributional and environmental range. For the Giambelluca data set, the models for *Paspalum dilatatum* also had poor predictive power (Tables 4.1, 4.2). *Megathyrsus maximus* was excluded from further analysis due to poor AUC values for both Giambelluca and PRISM data sets.

Environmental Constraints determining Species Distributions

Three out of the eight species had temperature contributing more than 50% to the model; while five out of the eight species had a precipitation constraint contributing more than 50% of the model. Mean temperature of the

warmest (T_{\max}) and coldest (T_{\min}) months were the main climatic constraints for species with the C₃ photosynthetic pathway, followed by wettest quarter. In contrast, the main climatic constraint varied among C₄ species. One C₄ species, *Paspalum dilatatum* had (T_{\max}) as their main climatic constraints. The remaining five C₄ species had either wettest quarter (40%) or driest quarter (60%) constraints contributing more than 50 % to the model (Tables 4.1, 4.2). The C₄ species that were determined mainly by wettest quarter were classified with the NADP-ME subtype, Panicoideae subfamily, and in the Andropogoneae tribe. The C₄ species having distributions determined either by driest quarter or by a temperature constraint were either the NADP-ME or PCK subtype, Panicoideae subfamily, and in the Paniceae tribe. The percent contribution of each environmental constraint was similar for 6 out of the 8 species for both PRISM and Giambelluca data sets. For the Giambelluca climate data temperature contributions were 10% - 20% more for three C₄ species compared with PRISM climate data contributions (Tables 4.1, 4.2).

Comparison of Predicted Ranges using Two Different Climate Data Sets

Two climate data sets were used for bioclimatic envelope models (BEMs) and using paired *t*-tests, I did not find a significant overall difference in range sizes for either predicted current or future ranges for all species at each conservation area or across the Hawaiian Islands. As a whole, there was no tendency for one climate data set (PRISM versus Giambelluca) to predict greater ranges relative to the other. The climate data set predicting the largest mean range size for either current or future ranges varied by conservation area location.

That is, one climate data set did not always predict larger areas over the other (Table 4.3). The average percent difference between predicted area based on the two climate data sets across sites was 1.5% to 22% for current distributions and 1.5% to 14% for future distributions. The largest variation in species range changes between the two climate data sets were in Koke‘e State Park, Mauna Kea Forest Reserve, and Pohakuloa Training Area.

Impact of Climate Change on Fire-Promoting Species Distributions across the Hawaiian Islands

Overall I found that fire-promoting species grouped together had minimal distributional changes with climate changes predicted for the Hawaiian Islands in 2050. Throughout the Hawaiian Islands, fire-promoting species grouped as a whole decreased in range size less than 3% for both climate data sets (Table 4.4). For C₃ species, overall decreases occurred across the Hawaiian Islands of up to 7%. For C₄ species, overall decreases occurred across the Hawaiian Islands of up to 3% (Table 4.4). Larger range changes were predicted for the grouped fire-promoting species and the grouped C₄ species with the PRISM climate data, while, differences did not occur for the C₃ species. For individual species, most species had more habitat lost than habitat gained, reducing the net range sizes for most species across the Hawaiian Islands (-1% to -2%) except for *Melinis minutiflora* which increased in range size by about 2% (Figures 4.1 – 4.8).

Predicted Species Distribution Changes in Key Conservation Areas

Hawai‘i Volcanoes National Park (HAVO)

Fire-promoting species grouped as a composite did not change range size in HAVO, while C₃ species grouped decreased almost twice as much as C₄ species grouped. All individual C₃ species decreased in range size in HAVO under climate change at lower elevations. Four out of the six C₄ species decreased in range size, while two increased in range size in HAVO. The C₄ species that decreased had distributional models with over 50% contribution from a precipitation constraint. *Melinis minutiflora* also had over 50% contribution from a precipitation constraint, but it increased in range size. HAVO, which includes a substantial lowland area, was the park that had the smallest range changes with only one species having a change in range size of over 5% (Table 4.5).

Haleakalā National Park

Fire-promoting species and C₃ species grouped were only reduced at most by 2% in range size in Haleakalā National Park, while C₄ species as a group increased in the park, 2 to 3%. Individual C₃ species mainly decreased at low elevations, while 60% (3/5) of C₄ species increased in range size in the park. The two C₄ species that were modeled solely from precipitation constraints had reductions in range size. Three species had range changes of 5% or more (*Holcus lanatus*, *Hyparrhenia rufa*, and *Melinis minutiflora*). The C₄ species, *Cenchrus ciliaris* is not present in the park and was not projected to be there with climate change, thus only seven out the eight invasive fire-promoting species have potential ranges within Haleakalā NP (Table 4.6).

Koke‘e State Park

Fire-promoting species and C₄ species grouped did not change range size in Koke‘e State Park, while C₃ species grouped did not decrease using the PRISM data set, but decreased substantially (26%) using the Giambelluca data set. Four species had range changes of 5% or more in the park (Table 4.7). A reduction in individual C₃ species ranges was not seen using the PRISM data set, but large habitat loss was seen for these species using the Giambelluca data at low elevations. These discrepancies were also seen between climate data sets for the individual C₄ grass, *Melinis minutiflora*, which increased 3 - 4% respectively using the Giambelluca data set, but was not predicted as present, respectively, using the PRISM data set. The C₄ species that had 100% contribution from precipitation constraints, *Schizachyrium condensatum*, was reduced by 16 to 19 % for the Giambelluca and PRISM data sets under climate change, respectively.

Mauna Kea State Reserve (MKR)

Using either climate data set, fire-promoting species as a composite and C₄ species as a composite did not change range size in MKR. However, again there was a large discrepancy between the PRISM and Giambelluca data sets for the C₃ species grouped. The Giambelluca climate data predicted C₃ species as a group to increase 22% in area at higher elevations, while there was no increase in area using the PRISM data. Using the PRISM data, C₃ species as a group occupied the full area of Mauna Kea State Reserve in both current and future data sets. Three C₄ species did not have predicted distributions at all in

Mauna Kea State Reserve, while two others had small predicted distributions using the PRISM data set and no distributions with the Giambelluca data set. The individual C₃ species had the largest range changes with *Anthoxanthum odoratum* (~ 22%) and *Holcus lanatus* (~32%), however, using the PRISM data set *A. odoratum* did not change in range size. *Pennisetum setaceum* was the only C₄ species with a predicted distribution in MKR using both climate data sets (Table 4.8). This could be due to the dry and cool conditions found at MKR.

Pohakuloa Training Area (PTA)

The composite distributions of fire-promoting species and C₄ species did not change in size at PTA, while C₃ species grouped decreased from 6 to 38%. PTA was projected as suitable for only five out of the eight fire-promoting species. In PTA, there were three species that had range changes of 5% or more. There was variation in individual C₃ range changes between the two climate data sets. In addition, for both C₃ species, the models built using mean temperature of the warmest month and wettest quarter did not have ranges in PTA using the PRISM data set, however, for the C₃ species having models built using mean temperature of the coldest month and wettest quarter, PRISM range changes were 2 to 3 times larger than C₃ range changes using the Giambelluca data set. The C₄ species, *Cenchrus ciliaris*, both increased in predicted range size, while *Paspalum dilatatum* and *Pennisetum setaceum* did not substantially change in range size. The *P. dilatatum* tmax and wettest quarter model did not occur in PTA using the PRISM data set. The C₄ species *C. ciliaris*, *P. setaceum*, are known to tolerate low precipitation and have on average large predicted

range sizes in PTA. While the few C₄ species present in PTA mainly increased in suitable habitat, C₃ species decreased in suitable habitat (Table 4.9).

DISCUSSION

I used two climate data sets (Prism Climate Group, Oregon State University 2004, Giambelluca et al. 2011; Personal Communication) and adjusted them for future projections under climate change for the Hawaiian Islands. The AUC values for each species varied by data set. There were more excellent species' models using the Giambelluca data set, however, there were more good species models using the PRISM data set. Thus, the predictive power of the species' models varied by which climate data set was used. In addition, three C₄ species' models had temperature contributions 10% higher using the Giambelluca data compared with models for the same species using the PRISM data set. As a whole, however, there was no tendency for one climate data set to project larger species ranges relative to the other for either current or future ranges for each conservation area. Yet there was potentially important variation for the projected range changes for C₃ grasses in Koke'e State Park, Mauna Kea Forest Reserve, and Pohakuloa Training Area. In Koke'e State Park, the PRISM data set projected the distribution of C₃ grasses as the entire area of the park in both current and future climates, while for the Giambelluca data set, the distribution of C₃ grasses was reduced in the future projections at mid-elevations (lower section of the park). In Mauna Kea Forest Reserve, the projected distributions of the C₃ grass *Anthoxanthum odoratum* were different between the two climate data sets. The PRISM data set projected that the distribution of *A. odoratum* covered MKR in both the current and future climates, whereas the Giambelluca data set projected the distributions of this grass as more restricted

today but increasing under future climate conditions. In Pohakuloa Training Area, C₃ species varied in their magnitude of range change between climate data sets, and the PRISM climate data set did not predict the grasses in the area using the mean temperature of the warmest month and the wettest quarter model. There were also discrepancies for range changes for the C₄ species, *Melinis minutiflora* in Koke‘e State Park. Furthermore, *Melinis minutiflora* was not predicted in Koke‘e State Park using the PRISM data, while it was predicted to increase using the Giambelluca data set. Other modeling differences also occurred for C₄ species in Mauna Kea Forest Reserve and PTA. Thus my findings suggest that both climate data sets should be used to give a range of possible species distribution scenarios.

Overall, fire-promoting grasses grouped together appear to contract in range size by less than 5% due to climate change in the Hawaiian Islands. Previous studies using BEMs have also shown the contraction of invasive plant species ranges with climate change (Beaumont et al. 2009; Bradley 2009; Bradley et al. 2009; Parker-Allie et al. 2009; Peterson et al. 2008). The percent range change for species in my study is smaller compared with temperate studies (Bradley 2009; Bradley et al. 2009; Parker-Allie et al. 2009) and even other tropical studies (Feeley and Silman 2010a; Feeley and Silman 2010b; Thomas et al. 2004). The magnitude of change for species is expected to be smaller in the tropics than in temperate localities because low latitude areas are warming slower than high latitude areas (IPCC 2007). However, differences between my study and other modeling studies performed for the tropics could be

due to the differences in projected increases in temperature and the projected year under study. Some studies used large temperature increases expected for periods at the end of the century (Colwell et al. 2008; Feeley and Silman 2010a; Feeley and Silman 2010b), and/or they used a static increase in temperature (Colwell et al. 2008; Feeley and Silman 2010a; Feeley and Silman 2010b; Kriticos et al. 2003a, Kriticos et al. 2003b; Thomas et al. 2004). It has been shown in Hawai'i that temperature is not increasing at the same rate along elevation gradients, but is increasing faster at higher elevations (Giambelluca et al. 2008); thus smaller range changes were expected (and modeled in my study) for low elevations compared to higher elevations. In addition, novel climates under climate change may not be present in current climates in Hawai'i, thus resulting in modeled species ranges that are truncated and not representing species' true climatic tolerances (Feeley and Silman 2010b). If modeled species ranges are truncated at higher temperatures (lower elevations), bioclimatic modeling may show a loss of area at these temperatures under future climates. This has been shown for tropical plants in previous studies for tropical systems (Feeley and Silman 2010b; van Klinken et al. 2009). In addition, relatively small and static increases and decreases in precipitation layers modeled for Hawaii under future climates may also have reduced the range changes seen in my study compared to other tropical studies (Timm and Diaz 2009).

The mean temperature of both the warmest (T_{\max}) and coldest (T_{\min}) months were the principal climatic constraints for the C₃ grass species with precipitation being secondary. Temperature was also the climatic variable of

most importance in models described in Parker-Allie et al. (2009) with precipitation being a secondary determinant of the relative success of C₃ grasses. Large-scale grass distributional patterns have been shown to be correlated with temperature and not correlated with precipitation (Cavagnaro 1988; Mo et al. 2004). Wan and Sage (2001) also suggested that precipitation may be a more secondary climatic constraint for C₄ and C₃ grass distributional patterns using species richness data for North America. In contrast, Bradley (2009) states that the use of precipitation data in BEMs may also be important for accurate climate projections for the C₃ grass, *Bromus tectorum*. Bradley (2009) found that decreased and increased precipitation changed the area suitable for *B. tectorum* by 45% and 70%, respectively, and that using temperature data alone may be inadequate for future species distribution projections. Models for 4 out of the 5 conservation areas studied suggest that C₃ grasses will likely disappear at mid elevation sites and increase at high elevation sites. My results concur with Parker-Allie et al. (2009) who found that C₃ grasses experienced habitat loss at warmer central interior or at lower altitudes. Bradley (2009) and Bradley et al. (2009) also found that the C₃ grass, *B. tectorum*, moved towards cooler temperatures (higher latitudes) with climate change projections. A reduction in range size for C₃ grass species is expected due to a loss of habitat area as these species move up in elevation to cooler climatic conditions that match their physiologies. C₃ grass species grouped together decreased in range size up to 38% in my study and these contractions in C₃ grass species have also been seen in previous studies of C₃ grass distributions in temperate localities

(Bradley 2009; Bradley et al. 2009; Parker-Allie et al. 2009). Thus, an increase in temperature may potentially negatively impact the range sizes of these temperate C₃ grasses in Hawai‘i as they move up in elevation because less habitat area remains available at higher elevations.

In contrast, temperature and precipitation were found to be key climatic constraints for C₄ species depending on the species. Five out of the six C₄ species had a precipitation constraint contributing over 50% to the model, while the other one species had temperature as the principal climatic constraint. Both precipitation constraints (wettest and driest quarters) were seen to be principle constraints for C₄ species. Previous studies have found that the proportional representation of both aspartate (NAD-ME) and malate (NADP-ME) forming C₄ species have correlations with precipitation gradients (Ellis et al. 1980; Hattersley 1992). Proportional representation of NAD-ME grasses was higher than any other C₄ subtype in arid extremes, while NADP-ME was found at the high-precipitation extremes of the precipitation gradients; the response by the PCK subtype varied by study. More recently, Taub (2000) and Cabido et al. (2008) suggested that subfamily association may be responsible for the geographic patterns seen among C₄ grasses. However, the species in my study were found to have the enzyme subtypes NADP-ME or PCK, and they were also in the same subfamily, Panicoideae; even though, half of them were found in very dry areas and the other half were found in very wet areas. Nonetheless, within the Panicoideae subfamily, the two species that had the wettest quarter as their principle climatic constraint were found to be in the tribe Andropogoneae, while

the other species with temperature or driest quarter constraints were found to be in the tribe Paniceae. My study suggests that characteristics other than decarboxylation type may be responsible for the variance in climatic constraints for the C₄ species. Parker-Allie et al. (2009) found variance in principle climatic constraints for C₄ species. In addition, Parker-Allie et al. (2009) also found that *Digitaria sanguinalis*, a C₄ NADP-ME species, had temperature as its principal climatic component for its BEM with precipitation being the least important climatic component, even though NADP-ME species should be expected to be influenced by precipitation (Taub 2000). *D. sanguinalis* also is found in the tribe Paniceae and fits in with the pattern of C₄ tribes and climatic constraints I found in the Hawaiian Islands.

The C₄ species were the most divergent in their response to aspects of climate change in the Hawaiian Islands due to the variation in climatic factors driving these distributions. C₄ species individually had potential increases, decreases, and stability in range size with climate change. While a large expansion in range size should be expected for C₄ grasses as more area becomes climatically suitable due to increases in temperature; this was not seen in my study. Range changes were smaller than expected for C₄ grasses in my study. These smaller range changes for C₄ species are likely due to a combination of several factors: smaller modeled increases in temperature at low elevations where these species persist, projection of truncated temperature niches in future climates, and the heavy reliance of precipitation constraints in C₄ models (with only small modeled changes in precipitation). One species,

Paspalum dilatatum had temperature as an environmental constraint that contributed more than 50% to the model, however, truncated temperature niches were probably not seen for *P. dilatatum* since it was found mainly at intermediate elevations. Since five of my models for C₄ species had a precipitation constraint contributing more than 50% to the model, small changes in ranges would be expected based on only small static increases and decreases predicted for precipitation in 2050. Contrasting responses of C₄ grasses were also seen in Parker-Allie et al. (2009) who found C₄ species responses were species-specific in South Africa. This suggests that C₄ species range changes under climate change maybe harder to predict than for C₃ species. Due to the complexity of the C₄ photosynthetic pathway lumping C₄ species together and predicting range changes as a functional group may give misleading results.

While other factors besides climate also affect invasion risk, climate is one of the most important limiting factors at regional scales (Guisan and Thuiller 2005; Pearson and Dawson 2003). Species distributional predictions presented in this study are based on climate suitability and do not take into consideration vegetation types, and or other environmental factors such as increased atmospheric CO₂ concentrations under global change that may impede or promote the spread of certain fire-promoting grasses. Thus, some areas that are currently predicted to have a suitable climate for fire-promoting grasses may be occupied by other vegetation which might reduce the spread of these fire-promoting grasses, and the future impact of these grasses might be less than reported in this study. Thus, the size of range changes in the future may be

smaller than presented due to preexisting vegetation in some areas.

Nonetheless, with increasing anthropogenic alterations of landscapes in Hawai‘i these currently occupied areas could be opened up in the future for invasion; especially if they co-occur with preexisting areas dominated by fire-promoting grasses. Furthermore, previous work investigating the responses of C₄ and C₃ grasses to increases in atmospheric CO₂ have shown consistent growth and physiological responses for C₃ plants (Ainsworth and Long 2005; Wand et al. 1999), while, variation in growth and physiological responses have been reported for C₄ plants (Ainsworth and Long 2005; Wand et al. 1999). With increases in atmospheric CO₂, C₃ grasses may be able to sustain distributions at lower elevations than projected in this study due to increased tolerance of warmer temperatures and increases in water-use efficiency (Ainsworth and Long 2005; Wand et al 1999). C₃ grasses may have enhanced competitiveness with C₄ plants at lower elevations under elevated CO₂. These complex interactions are not reflected in this study. Thus, species' model projections presented in this study provide a spatial estimation of invasion risk a regional scale, which can later be refined for conservation areas or transitional areas between C₄/C₃ grasses using smaller scalel assessments that consider risk factors appropriate to those scales (e.g., land use, competitive ability) (Guisan and Thuiller 2005; Pearson and Dawson 2003). Thus, it is best to use these species projections as an estimate of where species distributions may be found currently and in the future in Hawai‘i.

While the impact of invasive plants on protected areas in the Hawaiian Islands has been documented (Ainsworth and Kauffman 2010; D'Antonio et al. 2000; Smith and Tunison 1992), our understanding of potential changes in invasive species within conservation areas in response to climate change is limited. In the Hawaiian Islands there are 334 conservation areas, and I chose five large and important areas to evaluate (Hawai'i State GIS Program). Within the conservation areas, I found that not all of them contained suitable habitat for all of the fire-promoting grass species and that species responses to potential future climate change within these areas varied. Thus, each conservation area should be evaluated individually for potential risks of expansion and contractions of invasive fire-promoting grasses. The differences in species responses within each conservation area are likely due to the broad differences in temperature and precipitation gradients, along with the elevation span of each area. Furthermore, HAVO had the smallest predicted species range changes compared to the other conservation areas in the study. This could be due to the large lowland area that HAVO encompasses, which was projected to be less impacted by changes in temperature in the future (Giambelluca et al. 2008). I found that grasses in Koke'e, Haleakalā and PTA had comparatively larger predicted range changes for half of the species in the study compared with species in HAVO. Greater predicted range changes for C₃ grasses were also seen for MKR compared with HAVO. This supports the hypothesis that greater changes would be seen in conservation areas that have most of their area at higher elevations. However, other factors such as the size and location of the

park along an elevation gradient may have also contributed to larger range changes seen for Koke‘e and PTA. These parks have elevation cutoffs due to the location of the parks occurring at both low (664m, 750m; respectively) and medium elevations (1290m, 1746m; respectively) providing a narrower elevational range in which shifts could be projected. Furthermore, Mauna Kea State Reserve and HAVO had C₃ species that gained suitable habitat into higher elevations, while Haleakalā did not have suitable habitat for C₃ species to move into higher elevations.

Thus, since not all fire-promoting grass species responded to climate change in the same manner at all sites, species-specific and site-specific risk assessments appear critical for land management and conservation planning in Hawai‘i. In Hawai‘i, where fire-promoting grasses have already changed ecosystems (D'Antonio and Vitousek 1992) and climate warming has already been documented (Giambelluca et al. 2008), species-specific projections like those made here are increasingly important to help develop mitigating conservation strategies for areas at risk.

In conclusion, this work adds to the limited amount of work addressing species' distributional shifts in the Hawaiian Islands under climate change and highlights the need for further research. It is the first study to examine distributional changes using BEMs of C₃ and C₄ grasses in the tropics under climate change. It also highlights the complex responses of C₄ plants to aspects of climate change and draws attention to the fact these species should not be

lumped together as a functional group when evaluating plant responses to climate change due to differential species responses.

LITERATURE CITED

- Ainsworth A, Kauffman JB (2010) Interactions of fire and nonnative species across an elevation/plant community gradient in Hawaii Volcanoes National Park. *Biotropica* 42:647-655
- Ainsworth EA, Long SP (2005) What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO₂. *New phytologist* 165:351-372
- Araújo MB, New M (2007) Ensemble forecasting of species distributions. *Trends in ecology & evolution* 22:42-47
- Batanouny KH, Stichler W, Ziegler H (1988) Photosynthetic pathways, distribution, and ecological characteristics of grass species in Egypt. *Oecologia* 75:539-548
- Beaumont LJ, Gallagher RV, Downey PO, et al. (2009) Modelling the impact of *Hieracium* spp. on protected areas in Australia under future climates. *Ecography* 32:757-764
- Bradley BA (2009) Regional analysis of the impacts of climate change on cheatgrass invasion shows potential risk and opportunity. *Glob. change biol.* 15:196-208
- Bradley BA, Oppenheimer M, Wilcove DS (2009) Climate change and plant invasions: restoration opportunities ahead? *Glob. change biol.* 15:1511-1521
- Bradley BA, Wilcove DS, Oppenheimer M (2010) Climate change increases risk of plant invasion in the Eastern United States. *Biol. invasions* 12:1855-1872
- Bradley RS, Vuille M, Diaz HF, et al. (2006) Threats to water supplies in the tropical Andes. *Science* 312:1755
- Cabido M, Pons E, Cantero JJ, et al. (2008) Photosynthetic pathway variation among C₄ grasses along a precipitation gradient in Argentina. *J. Biogeogr.* 35:131-140
- Colwell RK, Brehm G, Cardelus CL, et al. (2008) Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322:258-261
- Crausbay SD, Hotchkiss SC (2010) Strong relationships between vegetation and two perpendicular climate gradients high on a tropical mountain in Hawai'i. *J. biogeogr.* 37:1160-1174

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. rev. ecol. syst.* 23:63-87

D'Antonio CM, Tunison JT, Loh RK (2000) Variation in the impact of exotic grasses on native plant composition in relation to fire across an elevation gradient in Hawaii. *Austral ecology* 25:507-522

Edwards EJ, Still CJ (2008) Climate, phylogeny and the ecological distribution of C₄ grasses. *Ecology letters* 11:266-276

Elith J, Graham CH, Anderson RP, et al. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129-151

Ellis RP, Vogel J, Fuls A (1980) Photosynthetic pathways and the geographical distribution of grasses in South West Africa/Namibia. *S. Afr. J. Sci* 76:307-14

Feeley KJ (2012) Distributional migrations, expansions, and contractions of tropical plant species as revealed in dated herbarium records. *Glob. change biol.* 18: 1335-1341

Feeley KJ, Silman MR, Bush MB, et al. (2011) Upslope migration of Andean trees. *J. biogeogr.* 38:783-791

Feeley KJ, Silman MR (2011) The data void in modeling current and future distributions of tropical species. *Glob. change biol.* 17:626-630

Feeley KJ, Silman MR (2010a) Modelling the responses of Andean and Amazonian plant species to climate change: the effects of georeferencing errors and the importance of data filtering. *J. biogeogr.* 37:733-740

Feeley KJ, Silman MR (2010b) Biotic attrition from tropical forests correcting for truncated temperature niches. *Glob. change biol.* 16:1830-1836.

Giambelluca TW Chen Q, Frazier AG, Price JP, Chen Y-L, Chu P-S, Eischeid J, and Delparte D (2011) The Rainfall Atlas of Hawai'i.
<http://rainfall.geography.hawaii.edu>.

Giambelluca TW, Diaz HF, Luke MSA (2008) Secular temperature changes in Hawaii. *Geophys. Res. lett.* 35

Grabherr G, Gottfried M, Pauli H (1994) Climate effects on mountain plants. *Nature* 369:448-44

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecological modelling* 135:147-186

Hannah L, Midgley G, Andelman S, et al. (2007) Protected area needs in a changing climate. *Frontiers in ecology and the environment* 5:131-138

Hattersley P (1992) C₄ photosynthetic pathway variation in grasses (Poaceae): its significance for arid and semi-arid lands. In: Chapman, GP ed. *Desertified grasslands: their biology and management*. Linn. Soc. Symp. No. 13. Academic Press: London, UK, pp. 181-212

Hijmans RJ, Graham CH (2006) The ability of climate envelope models to predict the effect of climate change on species distributions. *Glob. change biol.* 12:2272-2281

Hirzel A, Hausser J, Chessel D, et al. (2002) Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? *Ecology* 83:2027-2036

IPCC (2007) *Climate Change 2007: The Physical Science Basis: Working Group I Contribution to the Fourth Assessment Report of the IPCC*. Cambridge University Press, UK

Juvik JO, Rodomsky BT, Price JP, et al. (2011) "The upper limits of vegetation on Mauna Loa, Hawaii": a 50th-anniversary reassessment. *Ecology* 92:518-525

Kearney M (2006) Habitat, environment and niche: what are we modelling? *Oikos* 115:186-191

Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent climate change. *Proc. natl. acad. sci. U. S. A.* 105:11823-11826

Kriticos D, Sutherst R, Brown J, et al. (2003a) Climate change and biotic invasions: a case history of a tropical woody vine. *Biol. invasions* 5:147-165

Kriticos D, Sutherst R, Brown J, et al. (2003b) Climate change and the potential distribution of an invasive alien plant: *Acacia nilotica* ssp. *indica* in Australia. *J. appl. ecol.* 40:111-124

Kullman L (2002) Rapid recent range margin rise of tree and shrub species in the Swedish Scandes. *J. ecol.* 90:68-77

Lenoir J, Gegout JC, Marquet PA, et al. (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science* 320:1768-1771

Long SP (1999) Environmental responses. In: Sage R, Monson RK (eds) *C₄ Plant Biology*. Academic Press, San Diego, CA, pp. 215-249

Loope LL, Giambelluca TW (1998) Vulnerability of island tropical montane cloud forests to climate change, with special reference to East Maui, Hawaii. *Climatic change* 39:503-517

MacDonald I (1994) Global change and alien invasions: implications for biodiversity and protected area management. In: Solbrig Oea (ed) *Biodiversity and Global Change*. CABI Publisher, pp. 199-209

Mack MC, D'Antonio CM (1998) Impacts of biological invasions on disturbance regimes. *Trends in Ecology & Evolution* 13:195-198

Malhi Y, Silman M, Salinas N, et al. (2010) Introduction: Elevation gradients in the tropics: laboratories for ecosystem ecology and global change research. *Glob. change biol.* 16:3171-3175

Mo W, Nishimura N, Soga Y, et al. (2004) Distribution of C₃ and C₄ plants and changes in plant and soil carbon isotope ratios with altitude in the Kirigamine grassland, Japan. *Grassland science* 50:243-254

Parker-Allie F, Musil C, Thuiller W (2009) Effects of climate warming on the distributions of invasive Eurasian annual grasses: a South African perspective. *Climatic change* 94:87-103

Parolo G, Rossi G (2008) Upward migration of vascular plants following a climate warming trend in the Alps. *Basic appl. ecol.* 9:100-107

Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global ecology and biogeography* 12:361-371

Penuelas J, Boada M (2003) A global change-induced biome shift in the Montseny mountains (NE Spain). *Glob. change biol.* 9:131-140

Peterson AT, Stewart A, Mohamed KI, et al. (2008) Shifting global invasive potential of European plants with climate change. *PLoS one* 3:e2441

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. *Ecological modelling* 190:231-259

Phillips SJ, Dudík M (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31:161-175

Rundel PW (1980) The ecological distribution of C₄ and C₃ grasses in the Hawaiian Islands. *Oecologia* 45:354-359

Smith CW, Tunison JT (1992) Fire and alien plants in Hawaii: research and management implications for native ecosystems. University of Hawaii Press, Honolulu, HI

Taub DR (2000) Climate and the US distribution of C₄ grass subfamilies and decarboxylation variants of C₄ photosynthesis. American journal of Botany 87:1211-1215

Thomas CD, Cameron A, Green RE, et al. (2004) Extinction risk from climate change. Nature 427:145-148

Thuiller W (2004) Patterns and uncertainties of species' range shifts under climate change. Glob. change biol. 10:2020-2027

Thuiller W, Richardson DM, Pysek P, et al. (2005) Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. Glob. change biol. 11:2234-2250

Timm O, Diaz HF (2009) Synoptic-statistical approach to regional downscaling of IPCC Twenty-first-century climate projections: Seasonal rainfall over the Hawaiian Islands. Journal of climate 22:4261-4280

van Klinken RD, Lawson BE, Zalucki MP (2009) Predicting invasions in Australia by a Neotropical shrub under climate change: the challenge of novel climates and parameter estimation. Global ecology and biogeography 18: 688-700

Vitousek PM, D'Antonio CM, Loope LL, et al. (1996) Biological invasions as global environmental change. American scientist 84:468-478

Wan CSM, Sage RF (2001) Climate and the distribution of C₄ grasses along the Atlantic and Pacific coasts of North America. Canadian journal of botany 79:474-486

Wand SJE, Midgley GYF, Jones MH, et al. (1999) Responses of wild C₄ and C₃ grass (Poaceae) species to elevated atmospheric CO₂ concentration: a meta-analytic test of current theories and perceptions. Glob. change biol. 5:723-741

White TA, Campbell BD, Kemp PD, et al. (2000) Sensitivity of three grassland communities to simulated extreme temperature and rainfall events. Glob. change biol. 6:671-684

TABLES

Table 4.1. PRISM AUC Values and Species Model Climatic Constraints

Species	PP	n	Training	Testing	Logistic	Climatic Variables	July mean max	July mean min	Wettest Quarter	Driest Quarter
			AUC	AUC	Threshold					
<i>Anthoxanthum odoratum</i>	C ₃	64	0.875	0.846	0.321	67.3	x	32.7	x	
<i>Anthoxanthum odoratum</i>	C ₃	64	0.884	0.77	0.163	x	68.3	31.7	x	
<i>Cenchrus ciliaris</i>	C ₄	37	0.893	0.821	0.158	14	x	x	x	86
<i>Cenchrus ciliaris</i>	C ₄	37	0.904	0.847	0.292	x	15.5	x	x	84.5
<i>Holcus lanatus</i>	C ₃	81	0.902	0.879	0.33	70.3	x	29.7	x	
<i>Holcus lanatus</i>	C ₃	81	0.906	0.845	0.175	x	70.8	29.2	x	
<i>Hyparrhenia rufa</i>	C ₄	34	0.876	0.718	0.24	11.7	x	88.3	x	
<i>Hyparrhenia rufa</i>	C ₄	34	0.882	0.734	0.196	x	14.6	85.4	x	
<i>Melinis minutiflora</i>	C ₄	76	0.826	0.821	0.429	1.6	x	x	x	98.6
<i>Melinis minutiflora</i>	C ₄	76	0.834	0.801	0.41	x	5.4	x	x	94.6
<i>Megathyrsus maximus</i>	C ₄	115	0.764	0.633	0.243	100	x	x	x	x
<i>Megathyrsus maximus</i>	C ₄	115	0.71	0.672	0.438	x	100	x	x	x
<i>Paspalum dilatatum</i>	C ₄	46	0.883	0.707	0.322	x	55.2	44.8	x	
<i>Paspalum dilatatum</i>	C ₄	46	0.883	0.741	0.35	53	x	47	x	
<i>Pennisetum setaceum</i>	C ₄	53	0.835	0.717	0.336	x	x	x	x	100
<i>Schizachyrium condensatum</i>	C ₄	45	0.862	0.933	0.566	x	x	100	x	

X = environmental parameter not used in the present model

Table 4.2. Giambelluca AUC Values and Species Model Climatic Constraints

Species	PP	n	Training AUC	Testing AUC	Logistic Threshold	Climatic Variables	July mean max	July mean min	Wettest Quarter	Driest Quarter
<i>Anthoxanthum odoratum</i>	C ₃	65	0.836	0.779	0.32	72.9	x	27.1	x	
<i>Anthoxanthum odoratum</i>	C ₃	65	0.856	0.82	0.346	x	72.7		27.3	x
<i>Cenchrus ciliaris</i>	C ₄	37	0.92	0.915	0.181	27.5	x	x	x	72.5
<i>Cenchrus ciliaris</i>	C ₄	37	0.927	0.9	0.204	x	24.1	x	x	75.9
<i>Holcus lanatus</i>	C ₃	81	0.864	0.808	0.349	72.2	x	27.8	x	
<i>Holcus lanatus</i>	C ₃	81	0.875	0.838	0.353	x	77	23	x	
<i>Hyparrhenia rufa</i>	C ₄	34	0.866	0.723	0.156	24.7	x	75.3	x	
<i>Hyparrhenia rufa</i>	C ₄	34	0.844	0.732	0.092	x	14.8	85.2	x	
<i>Melinis minutiflora</i>	C ₄	73	0.815	0.759	0.362	21.2	x	x	x	78.8
<i>Melinis minutiflora</i>	C ₄	73	0.809	0.736	0.369	x	16.2	x	x	83.8
<i>Megathyrsus maximus</i>	C ₄	111	0.771	0.71	0.254	100	x	x	x	x
<i>Megathyrsus maximus</i>	C ₄	111	0.734	0.666	0.326	x	100	x	x	x
<i>Paspalum dilatatum</i>	C ₄	46	0.88	0.697	0.348	51.4	x	48.6	x	
<i>Paspalum dilatatum</i>	C ₄	46	0.88	0.671	0.221	51.6	x	x	x	48.4
<i>Pennisetum setaceum</i>	C ₄	55	0.807	0.718	0.389	x	x	x	x	100
<i>Schizachyrium condensatum</i>	C ₄	45	0.837	0.917	0.538	x	x	100	x	

X = environmental parameter not used in the present model

Table 4.3. *P*-values for Site Species Distribution Differences between PRISM and Giambelluca Climate Data

Site	Current Range Mean (PRISM) km ³	Current Range Mean (GIAM) km ³	<i>P</i> -value	Future Range Mean (PRISM) km ³	Future Range Mean (GIAM) km ³	<i>P</i> -value
Hawaiian Islands	6,307,143	6,236,213	0.825	6,071,886	5,927,541	0.631
Hawai'i Volcanoes National Park	588,453	581,830	0.831	579,551	572,893	0.832
Mauna Kea Forest Reserve	147,278	115,543	0.123	118,187	136,572	0.186
Pohakuloa Training Area	43,549	34,589	0.366	38,111	42,468	0.642
Haleakalā National Park	61,328	56,040	0.217	63,261	56,816	0.091
Koke'e State Park	9,416	10,785	0.098	9,062	10,241	0.293

Table 4.4. Range Change Estimates for Across the Hawaiian Islands

Species Name	PP	Current range size %	Future range size %	Δ hectares	Δ range %	Habitat gained %	Habitat lost %
Fire Species(PRISM)	Both	99 - 100	96 - 100	-45,000 to -1900	-3, --	--	3,--
Fire Species (GIAM)	Both	99 - 100	99 - 100	-2,200 to -870	--, --	--, --	--, --
C ₃ Species (PRISM)	C ₃	38 - 49	36 - 42	-106,900 to -38,000	-2, -7	--, --	2, 7
C ₃ Species (GIAM)	C ₃	35 - 43	29 - 41	-90,700 to -40,000	-6, -2	1,1	7, 3
C ₄ Species (PRISM)	C ₄	96 - 99	93 - 99	-37,000 to -580	-3, --	1,--	4,--
C ₄ Species (GIAM)	C ₄	96 - 98	95 - 98	-8,300 to 2,600	-1, --	--,--	1,--
<i>Anthoxanthum odoratum</i> (PRISM)	C ₃	37 - 49	35 - 42	-107,500 to -37,200	-2, -7	--,--	2, 7
<i>Anthoxanthum odoratum</i> (GIAM)	C ₃	34 - 42	28 - 40	-90,500 to -38,300	-6, -2	1,--	7, 2
<i>Holcus lanatus</i> (PRISM)	C ₃	31 - 42	29 - 36	-91,300 to -30,900	-2, -6	--, 1	2, 7
<i>Holcus lanatus</i> (GIAM)	C ₃	29 - 38	25 - 36	-68,600 to -24,900	-4, -2	2,--	6, 2
<i>Cenchrus ciliaris</i> (PRISM)	C ₄	24 - 36	22 - 35	-34,100 to -17,100	-2, -1	2, 1	4, 2
<i>Cenchrus ciliaris</i> (GIAM)	C ₄	26, 25	26 - 27	-4,794 to 35,000	--, 2	--, 3	--,1
<i>Hyparrhenia rufa</i> (PRISM)	C ₄	42 - 44	40 - 42	-32,800 to -27,800	-2,-2	--,1	2, 3
<i>Hyparrhenia rufa</i> (GIAM)	C ₄	46 - 54	44 - 53	-27,300 to -24,000	-2, --	--,--	2, --
<i>Melinis minutiflora</i> (PRISM)	C ₄	38 - 40	41, 41	20,700 to 37,900	3, 1	4, 1	1, --
<i>Melinis minutiflora</i> (GIAM)	C ₄	39 - 42	40 - 45	19,200 to 42,400	1, 3	1, 3	--,--
<i>Paspalum dilatatum</i> (PRISM)	C ₄	18 - 25	18 - 25	-11,500 to -410	--,--	--,--	--,--
<i>Paspalum dilatatum</i> (GIAM)	C ₄	19 - 33	18 - 33	-11,500 to 2,200	-1,--	1,1	2, 1
<i>Pennisetum setaceum</i> (PRISM)	C ₄	39	39	-13,100	-1	--	1
<i>Pennisetum setaceum</i> (GIAM)	C ₄	42	41	-17,700	-1	--	1
<i>Schizachyrium condensatum</i> (PRISM)	C ₄	17	16	-18,900	-1	1	2
<i>Schizachyrium condensatum</i> (GIAM)	C ₄	23	22	-13,500	-1	1	2

Data is given in a range if there was more than 1 model made for a species. Future percent range size for each model is then subtracted from the current percent range size for the corresponding model and data is shown as two values for Δ range %. Areas gained and lost were calculated in ArcGIS 10. If the difference between the future and current models was less than 0.5, a dashed line is shown (--). Values are presented as negative (lost area) and positive (gained area). GIAM = Giambelluca data, PRISM = Prism Data

Table 4.5. Range Change Values Across Hawai‘i Volcanoes National Park

Species Name	PP	Current range size %	Future range size %	Δ hectares	Δ range %	Habitat gained %	Habitat lost %
Fire Species(PRISM)	Both	100, 100	100, 100	0	0, 0	0, 0	0, 0
Fire Species (GIAM)	Both	100, 100	100, 100	0	0, 0	0, 0	0, 0
C ₃ Species (PRISM)	C ₃	75 - 81	72 - 75	-8,800 to -3,800	-3, -6	0	3, 6
C ₃ Species (GIAM)	C ₃	61 - 71	55 - 67	-8,000 to -5,800	-6, -4	5,--	11, 4
C ₄ Species (PRISM)	C ₄	86 - 96	84 - 96	-3,600 to -10	-2,--	1,--	3,--
C ₄ Species (GIAM)	C ₄	78 - 94	77 - 95	-1,400 to 1,490	-1, 1	--, 2	1,1
<i>Anthoxanthum odoratum</i> (PRISM)	C ₃	75 - 81	72 - 75	-8,800 to -3,900	-3, -6	--, --	3, 6
<i>Anthoxanthum odoratum</i> (GIAM)	C ₃	60 - 71	55 - 67	-8,200 to -5,900	-5, -4	5,--	10, 4
<i>Holcus lanatus</i> (PRISM)	C ₃	57 - 64	55 - 61	-4,100 to -3,100	-2, -3	1, 4	3, 7
<i>Holcus lanatus</i> (GIAM)	C ₃	50 - 60	47 - 57	-4,500 to -3,500	-3, -3	--, 7	3,10
<i>Cenchrus ciliaris</i> (PRISM)	C ₄	6, --	5, --	-870 to -120	-1, --	--, --	1,--
<i>Cenchrus ciliaris</i> (GIAM)	C ₄	3 - 4	4, 4	-142 to 1,560	1,--	1,--	--,--
<i>Hyparrhenia rufa</i> (PRISM)	C ₄	40 - 41	39, 39	-3,200 to -2,300	-1, -2	1,--	2, 2
<i>Hyparrhenia rufa</i> (GIAM)	C ₄	43 - 50	42 - 50	-1,800 to -580	-1,--	--,--	1,--
<i>Melinis minutiflora</i> (PRISM)	C ₄	32, 32	34, 34	2,200 to 4,000	2, 3	2, 3	--,--
<i>Melinis minutiflora</i> (GIAM)	C ₄	37 - 38	39 - 41	2,500 to 4,400	2,3	2, 3	--,--
<i>Paspalum dilatatum</i> (PRISM)	C ₄	25 - 47	25 - 49	-460 to 3,300	--, 2	2, 3	2,--
<i>Paspalum dilatatum</i> (GIAM)	C ₄	29 - 56	30 - 58	590 to 2,600	1, 2	1, 2	--,--
<i>Pennisetum setaceum</i> (PRISM)	C ₄	34	32	-3,200	-2	--	2
<i>Pennisetum setaceum</i> (GIAM)	C ₄	24	22	-2,200	-2	--	2
<i>Schizachyrium condensatum</i> (PRISM)	C ₄	24	24	-702	--	2	2
<i>Schizachyrium condensatum</i> (GIAM)	C ₄	29	26	-3,900	-3	--	3

Data is given in a range if there was more than 1 model made for a species. Future percent range size for each model is then subtracted from the current percent range size for the corresponding model and data is shown as two values for Δ range %. Areas gained and lost were calculated in ArcGIS 10. If the difference between the future and current models was less than 0.5, a dashed line is shown (--). Values are presented from negative (lost area) to positive (gained area). GIAM = Giambelluca data, PRISM = Prism Dat

Table 4.6. Range Change Values Across Haleakalā National Park

Species Name	PP	Current range size %	Future range size %	Δ hectares	Δ range %	Habitat gained %	Habitat lost %
Fire Species(PRISM)	Both	100, 100	99 - 100	-90	-1, 0	0, 0	1, 0
Fire Species (GIAM)	Both	98 - 100	99 - 100	7 to 50	1, 0	1, --	--, 0
C ₃ Species (PRISM)	C ₃	93 - 92	91 - 92	-160 to -45	-2,--	--, 1	2,--
C ₃ Species (GIAM)	C ₃	91 - 92	89 - 93	-270 to 120	-2,1	--, 1	2,--
C ₄ Species (PRISM)	C ₄	94 - 97	97 - 98	80 to 400	3,1	4, 1	1,--
C ₄ Species (GIAM)	C ₄	84 - 100	86 - 100	5 to 240	2,--	2,--	--,--
<i>Anthoxanthum odoratum</i> (PRISM)	C ₃	92 - 93	91 - 92	-160 to -50	-1,-1	--,--	1,1
<i>Anthoxanthum odoratum</i> (GIAM)	C ₃	91 - 92	89 - 93	-270 to 120	-2, 1	--,1	2,--
<i>Holcus lanatus</i> (PRISM)	C ₃	82 - 89	82 - 83	-740 to 20	--, -6	1,--	1, 6
<i>Holcus lanatus</i> (GIAM)	C ₃	82, 82	80 - 85	-240 to 320	-2, 3	--, 3	2,--
<i>Cenchrus ciliaris</i> (PRISM)	C ₄	Not in park					
<i>Cenchrus ciliaris</i> (GIAM)	C ₄	Not in park					
<i>Hyparrhenia rufa</i> (PRISM)	C ₄	41 - 50	43 - 60	180 to 1130	2,10	2,11	--, 1
<i>Hyparrhenia rufa</i> (GIAM)	C ₄	31 - 84	33 - 82	-190 to 180	2, -2	2,--	--, 2
<i>Melinis minutiflora</i> (PRISM)	C ₄	36 - 42	44 - 45	260 to 1090	9, 3	10, 3	1, --
<i>Melinis minutiflora</i> (GIAM)	C ₄	20 - 28	21 - 34	80 to 640	1, 6	1, 6	--,--
<i>Paspalum dilatatum</i> (PRISM)	C ₄	38 - 61	40 - 63	240 to 260	2, 2	2, 3	--,1
<i>Paspalum dilatatum</i> (GIAM)	C ₄	27 - 47	29 - 47	75 to 270	2, 1	3, 1	1,--
<i>Pennisetum setaceum</i> (PRISM)	C ₄	34	32	-210	-2	0	2
<i>Pennisetum setaceum</i> (GIAM)	C ₄	36	35	-90	-1	0	1
<i>Schizachyrium condensatum</i> (PRISM)	C ₄	23	23	-20	--	2	2
<i>Schizachyrium condensatum</i> (GIAM)	C ₄	20	19	-140	-1	2	3

Data is given in a range if there was more than 1 model made for a species. Future percent range size for each model is then subtracted from the current percent range size for the corresponding model and data is shown as two values for Δ range %. Areas gained and lost were calculated in ArcGIS 10. If the difference between the future and current models was less than 0.5, a dashed line is shown (--). Values are presented from negative (lost area) to positive (gained area).

GIAM = Giambelluca data, PRISM = Prism Data

Table 4.7. Range Change Values Across Koke'e State Park

Species Name	PP	Current range size %	Future range size %	Δ hectares	Δ range %	Habitat gained %	Habitat lost %
Fire Species(PRISM)	Both	100, 100	100, 100	0	0, 0	0, 0	0, 0
Fire Species (GIAM)	Both	100, 100	100, 100	0	0, 0	0, 0	0, 0
C ₃ Species (PRISM)	C ₃	100, 100	100, 100	0	0, 0	0, 0	0, 0
C ₃ Species (GIAM)	C ₃	94, 94	68 - 91	-50 to -1	-26, -3	--, 1	26, 4
C ₄ Species (PRISM)	C ₄	100, 100	100, 100	0	0, 0	0, 0	0, 0
C ₄ Species (GIAM)	C ₄	100, 100	100, 100	0	0, 0	0, 0	0, 0
<i>Anthoxanthum odoratum</i> (PRISM)	C ₃	100, 100	99 - 100	-1	-1, 0	0, 0	* , 0
<i>Anthoxanthum odoratum</i> (GIAM)	C ₃	93 - 94	67 - 89	-480 to -60	-27, -4	--, --	27, 4
<i>Holcus lanatus</i> (PRISM)	C ₃	100, 100	99 - 100	-4	--, 0	0, 0	--, 0
<i>Holcus lanatus</i> (GIAM)	C ₃	94, 94	64 - 91	-540 to -50	-31, -3	--, 1	31, 4
<i>Cenchrus ciliaris</i> (PRISM)	C ₄	1 - 9	4 - 6	-70 to 60	3, -3	3, --	--, 3
<i>Cenchrus ciliaris</i> (GIAM)	C ₄	3 - 7	9 - 6	-14 to 110	6, -1	7, --	--, 1
<i>Hyparrhenia rufa</i> (PRISM)	C ₄	81 - 100	80 - 100	-15	-1, --	--, --	1, --
<i>Hyparrhenia rufa</i> (GIAM)	C ₄	100	100	0	0	0	0
<i>Melinis minutiflora</i> (PRISM)	C ₄	Not in park					
<i>Melinis minutiflora</i> (GIAM)	C ₄	16, 16	19 - 20	55 to 70	3, 4	3, 4	--, --
<i>Paspalum dilatatum</i> (PRISM)	C ₄	96 - 100	96 - 100	-8	--, 0	--, 0	1, 0
<i>Paspalum dilatatum</i> (GIAM)	C ₄	94 - 100	94 - 100	2 to 6	0	1	1
<i>Pennisetum setaceum</i> (PRISM)	C ₄	Not in park					
<i>Pennisetum setaceum</i> (GIAM)	C ₄	Not in park					
<i>Schizachyrium condensatum</i> (PRISM)	C ₄	19	0	-340	-19	0	19
<i>Schizachyrium condensatum</i> (GIAM)	C ₄	79	63	-290	-16	0	16

Data is given in a range if there was more than 1 model made for a species. Future percent range size for each model is then subtracted from the current percent range size for the corresponding model and data is shown as two values for Δ range %. Areas gained and lost were calculated in ArcGIS 10. If the difference between the future and current models was less than 0.5, an asterisk is shown (--). Values are presented from negative (lost area) to positive (gained area). GIAM = Giambelluca data, PRISM = Prism Data

Table 4.8. Range Change Values Across Mauna Kea Forest Reserve

Species Name	PP	Current range size %	Future range size %	Δ hectares	Δ range %	Habitat gained %	Habitat lost %
Fire Species(PRISM)	Both	100, 100	100, 100	0	0, 0	0, 0	0, 0
Fire Species (GIAM)	Both	100, 100	100, 100	0	0, 0	0, 0	0, 0
C ₃ Species (PRISM)	C ₃	100, 100	100, 100	0	0, 0	0, 0	0, 0
C ₃ Species (GIAM)	C ₃	72 - 100	94 - 100	5,400	22	22	0
C ₄ Species (PRISM)	C ₄	100, 99	99, 99	-130 to 30	-1, --	0, --	1, --
C ₄ Species (GIAM)	C ₄	98, 98	98, 98	-90 to -60	--, --	0, --	--, --
<i>Anthoxanthum odoratum</i> (PRISM)	C ₃	100, 100	99 - 100	-60	--, 0	0	--, 0
<i>Anthoxanthum odoratum</i> (GIAM)	C ₃	72 - 100	94 - 100	5,400	22, --	22, --	0
<i>Holcus lanatus</i> (PRISM)	C ₃	73 - 79	75 - 98	480 to 4,500	2, 19	2,19	0
<i>Holcus lanatus</i> (GIAM)	C ₃	28 - 81	60 - 84	650 to 7,900	32, 3	32, 3	0
<i>Cenchrus ciliaris</i> (PRISM)	C ₄	0 - 31	1- 31	70 to 140	--, --	1, 1	--, 1
<i>Cenchrus ciliaris</i> (GIAM)	C ₄	Not in park					
<i>Hyparrhenia rufa</i> (PRISM)	C ₄	Not in park					
<i>Hyparrhenia rufa</i> (GIAM)	C ₄	Not in park					
<i>Melinis minutiflora</i> (PRISM)	C ₄	Not in park					
<i>Melinis minutiflora</i> (GIAM)	C ₄	Not in park					
<i>Paspalum dilatatum</i> (PRISM)	C ₄	--, --	--, 1	-100 to 190	--, 1	0, 1	--, 0
<i>Paspalum dilatatum</i> (GIAM)	C ₄	Not in park					
<i>Pennisetum setaceum</i> (PRISM)	C ₄	98	98	-93	0	0	0
<i>Pennisetum setaceum</i> (GIAM)	C ₄	98	98	-90	0	0	0
<i>Schizachyrium condensatum</i> (PRISM)	C ₄	Not in park					
<i>Schizachyrium condensatum</i> (GIAM)	C ₄	Not in park					

Data is given in a range if there was more than 1 model made for a species. Future percent range size for each model is then subtracted from the current percent range size for the corresponding model and data is shown as two values for Δ range %. Areas gained and lost were calculated in ArcGIS 10. If the difference between the future and current models was less than 0.5, an asterisk is shown (--). Values are presented from negative (lost area) to positive (gained area). GIAM = Giambelluca data, PRISM = Prism Data

Table 4.9. Range Change Values Across Pohakuloa Training Area

Species Name	PP	Current range size %	Future range size %	Δ hectares	Δ range %	Habitat gained %	Habitat lost %
Fire Species(PRISM)	Both	100, 100	100, 100	0	0, 0	0, 0	0, 0
Fire Species (GIAM)	Both	100, 100	100, 100	0	0, 0	0, 0	0, 0
C ₃ Species (PRISM)	C ₃	73, not in park	35, not in park	-3,600	-38	0	38
C ₃ Species (GIAM)	C ₃	13 - 17	7, 3	-1,330 to -520	-6, -14	0	6, 14
C ₄ Species (PRISM)	C ₄	100, 100	100, 100	0	0, 0	0, 0	0, 0
C ₄ Species (GIAM)	C ₄	100, 100	100, 100	0	0, 0	0, 0	0, 0
<i>Anthoxanthum odoratum</i> (PRISM)	C ₃	68, not in park	33, not in park	-3330	-36	--	36
<i>Anthoxanthum odoratum</i> (GIAM)	C ₃	11 - 13	6, 1	-1120 to -440	-5, -12	--, --	5, 12
<i>Holcus lanatus</i> (PRISM)	C ₃	73, not in park	35, not in park	-3550	-38	--	38
<i>Holcus lanatus</i> (GIAM)	C ₃	17, 14	3 - 8	-1340 to -500	-14, -6	--, --	14, 6
<i>Cenchrus ciliaris</i> (PRISM)	C ₄	95 - 100	99 - 100	450	5, --	5, --	--, --
<i>Cenchrus ciliaris</i> (GIAM)	C ₄	55 - 66	68, 65	-50 to 1230	13, -1	13, --	--, 1
<i>Hyparrhenia rufa</i> (PRISM)	C ₄	Not in park					
<i>Hyparrhenia rufa</i> (GIAM)	C ₄	Not in park					
<i>Melinis minutiflora</i> (PRISM)	C ₄	Not in park					
<i>Melinis minutiflora</i> (GIAM)	C ₄	Not in park					
<i>Paspalum dilatatum</i> (PRISM)	C ₄	--, not in park	0	-1	--	0	--
<i>Paspalum dilatatum</i> (GIAM)	C ₄	1 - 44	0 - 42	-210 to -50	-1, -2	0	1, 2
<i>Pennisetum setaceum</i> (PRISM)	C ₄	100	100	0	0	0	0
<i>Pennisetum setaceum</i> (GIAM)	C ₄	100	100	0	0	0	0
<i>Schizachyrium condensatum</i> (PRISM)	C ₄	Not in park					
<i>Schizachyrium condensatum</i> (GIAM)	C ₄	Not in park					

Data is given in a range if there was more than 1 model made for a species. Future percent range size for each model is then subtracted from the current percent range size for the corresponding model and data is shown as two values for Δ range %. Areas gained and lost were calculated in ArcGIS 10. If the difference between the future and current models was less than 0.5, a dashed line is shown (--). Values are presented from negative (lost area) to positive (gained area). GIAM = Giambelluca data, PRISM = Prism Data

FIGURES

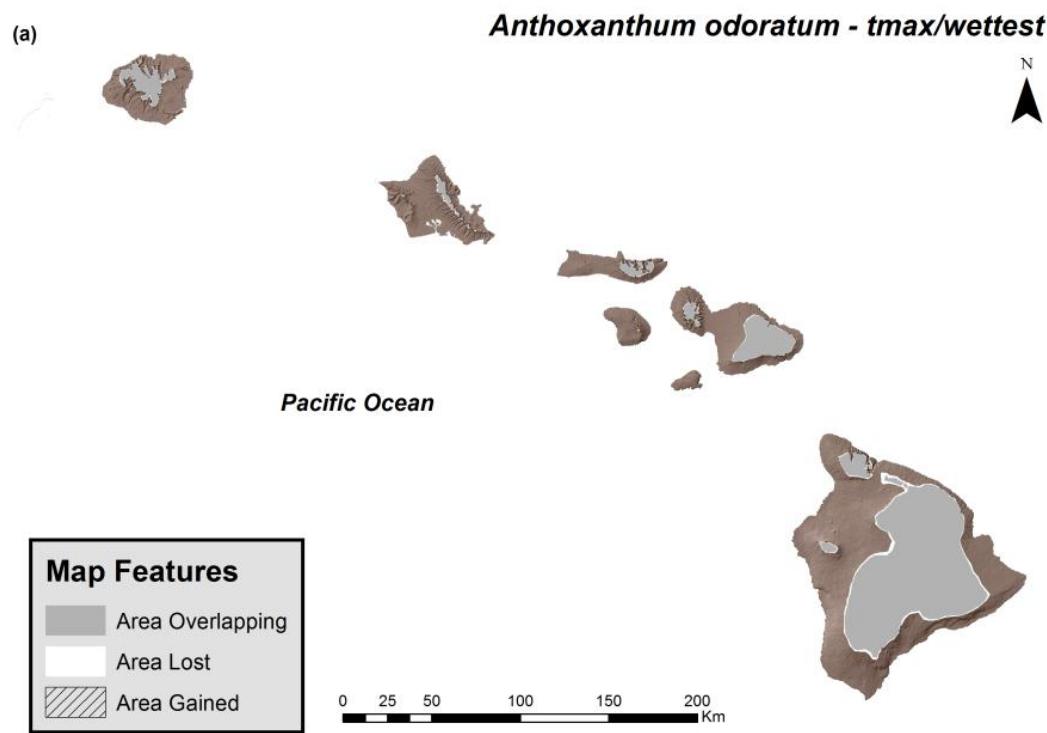


Figure 4.1 (a) Distribution projections for *Anthoxanthum odoratum* using *tmax/wettest* constraints. Distribution projections are made using PRISM model predictions.

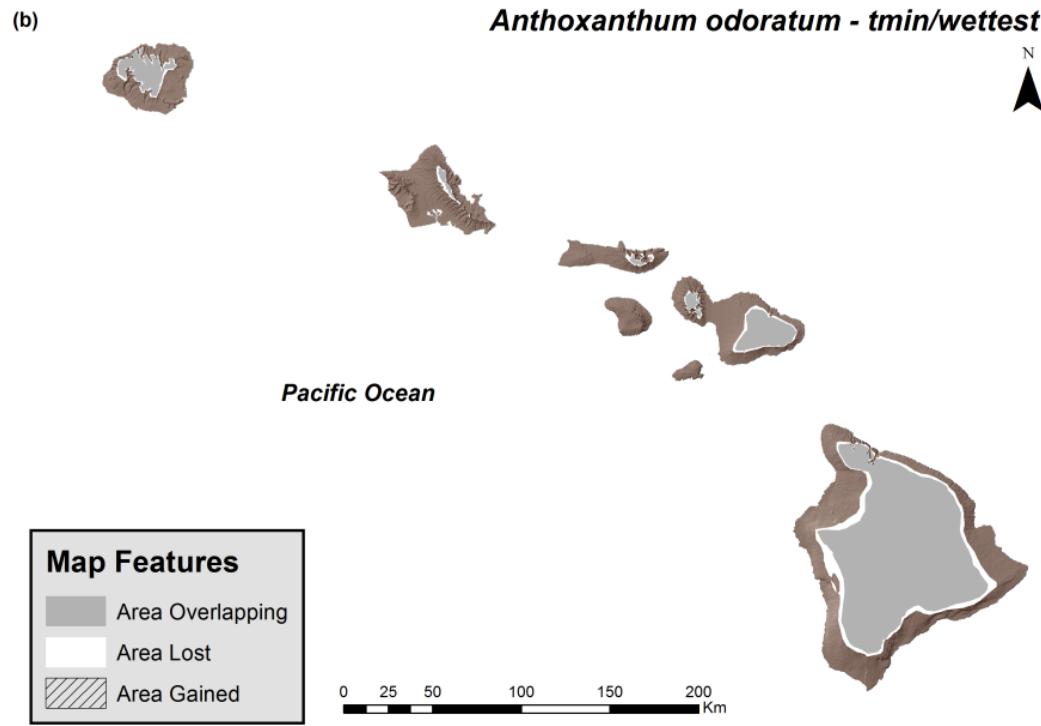


Figure 4.1 (b). Distribution projections for *Anthoxanthum odoratum* using *tmin/wettest* constraints. Distribution projections are made using PRISM model predictions.

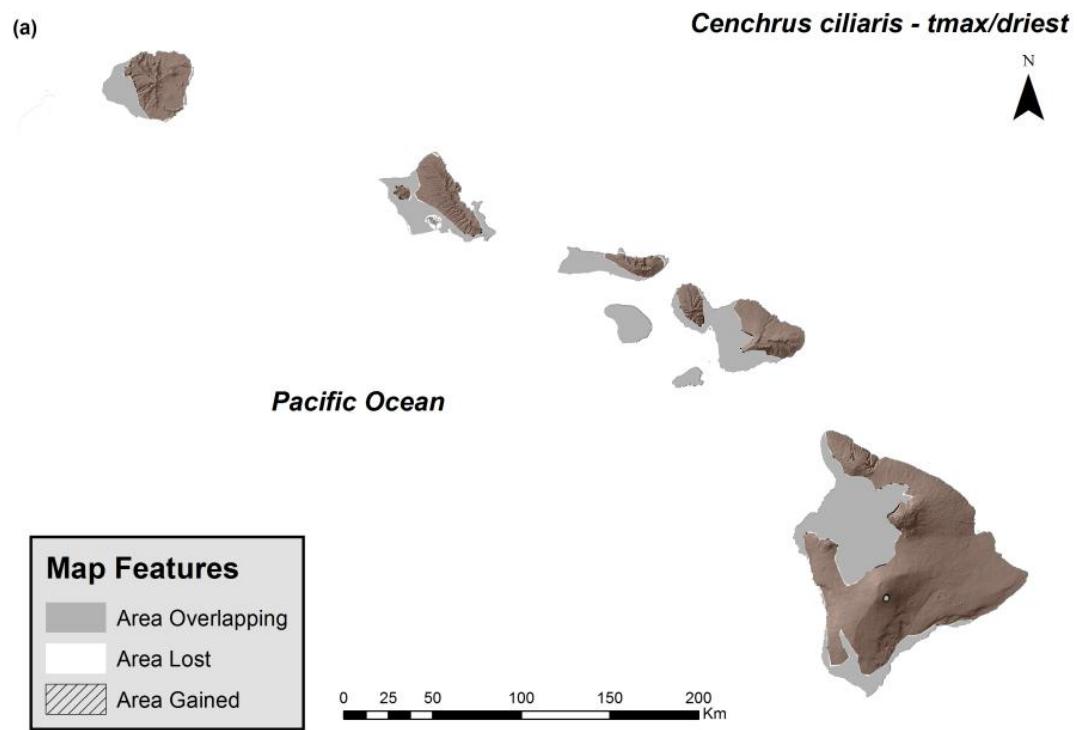


Figure 4.2 (a) Distribution projections for *Cenchrus ciliaris* using tmax/driest constraints. Distribution projections are made using PRISM model predictions.

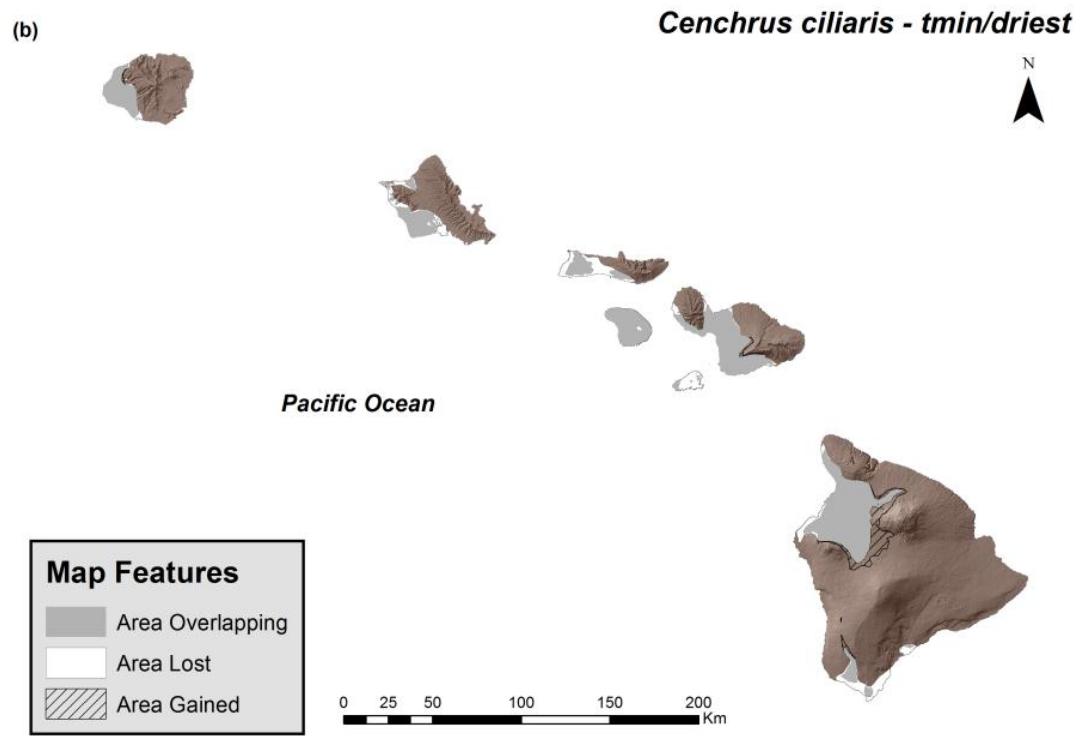


Figure 4.2 (b) Distribution projections for *Cenchrus ciliaris* using tmin/driest constraints. Distribution projections are made using PRISM model predictions.

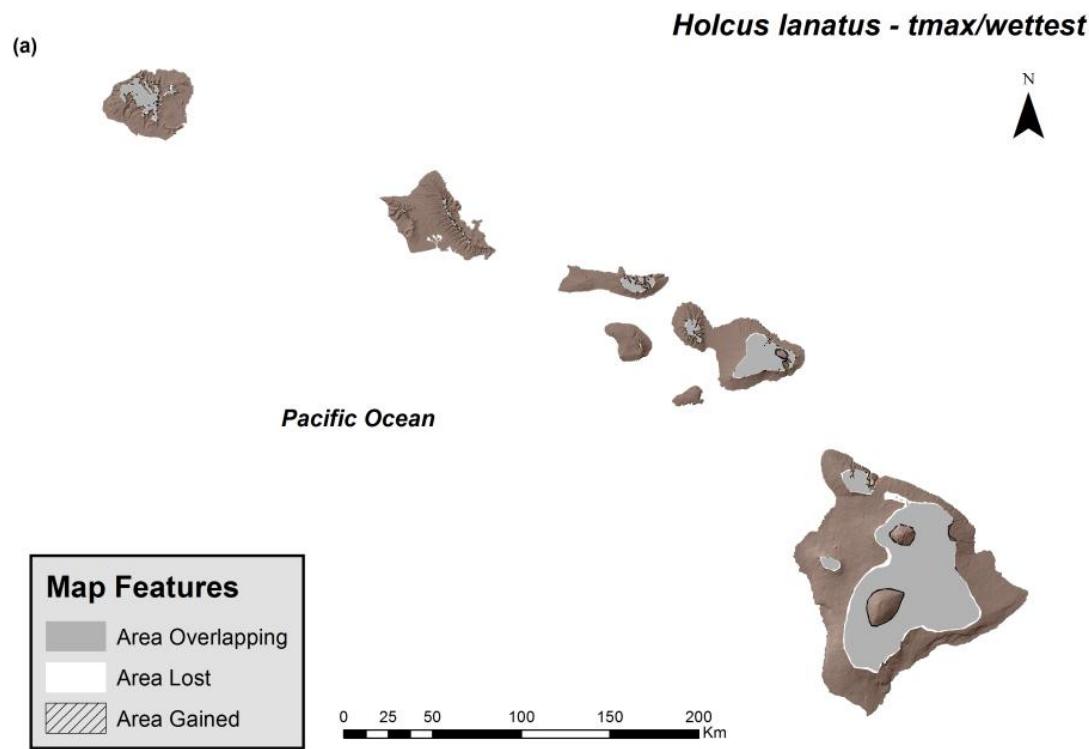


Figure 4.3 (a) Distribution projections for *Holcus lanatus* using tmax/wettest constraints. Distribution projections are made using PRISM model predictions.

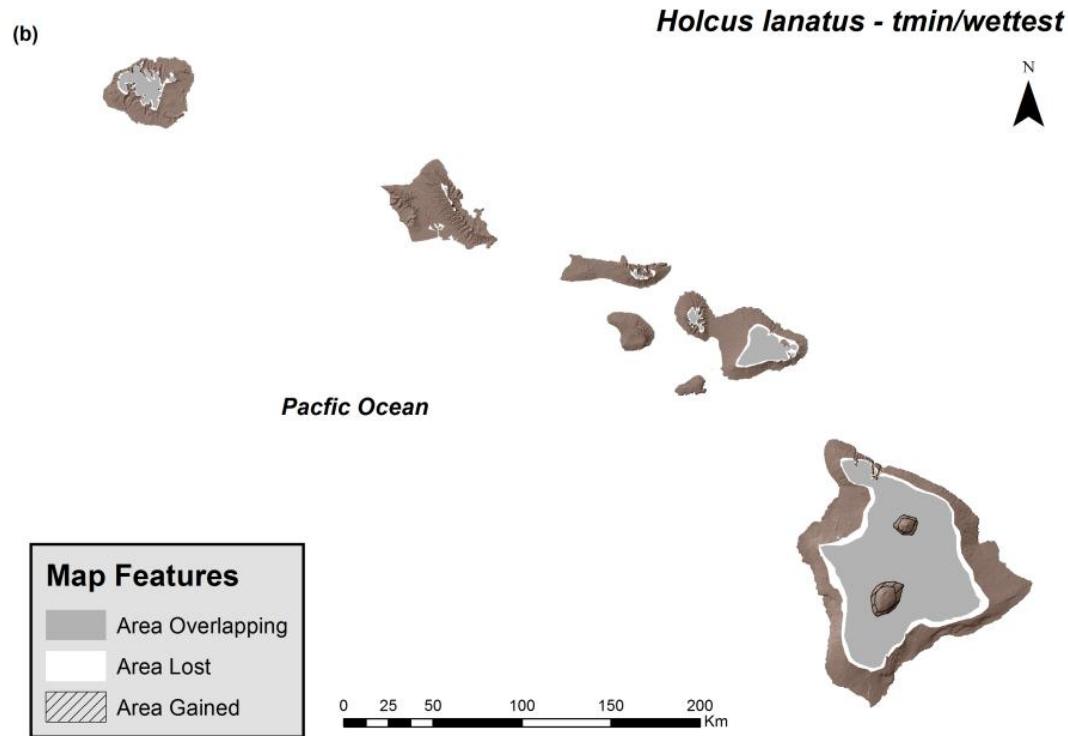


Figure 4.3 (b) Distribution projections for *Holcus lanatus* using tmin/wettest constraint. Distribution projections are made using PRISM model predictions.

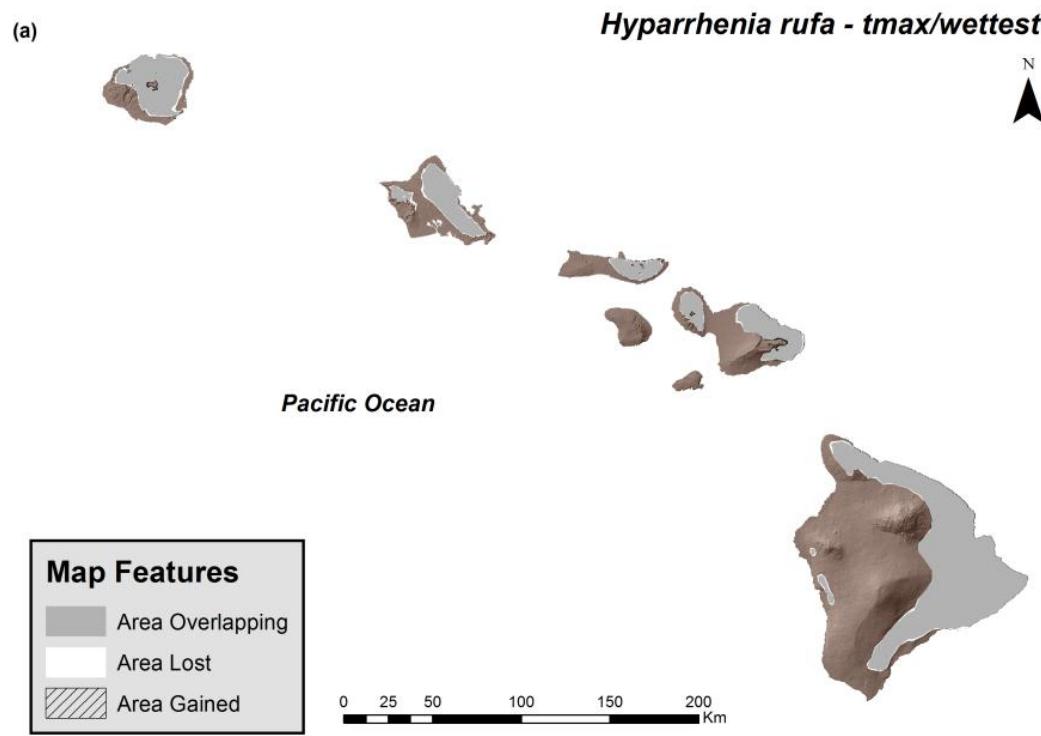


Figure 4.4 (a) Distribution projections for *Hyparrhenia rufa* using *tmax/wettest* constraints. Distribution projections are made using PRISM model predictions.

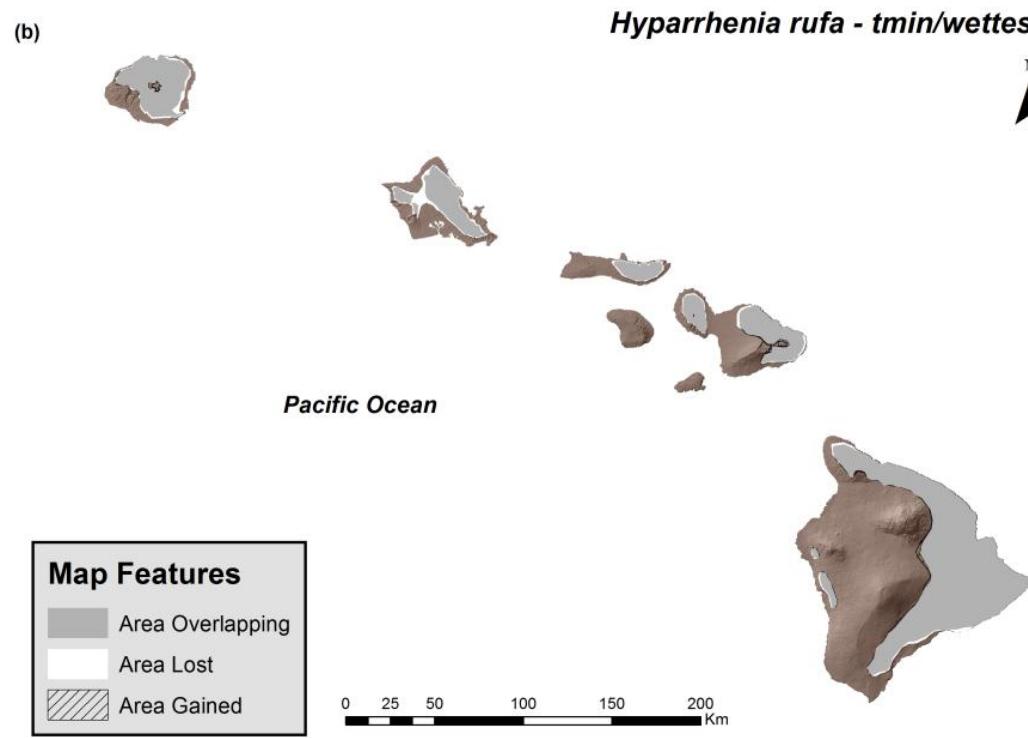


Figure 4.4 (b) Distribution projections for *Hyparrhenia rufa* using *tmin/wettest* constraints. Distribution projections are made using PRISM model predictions.

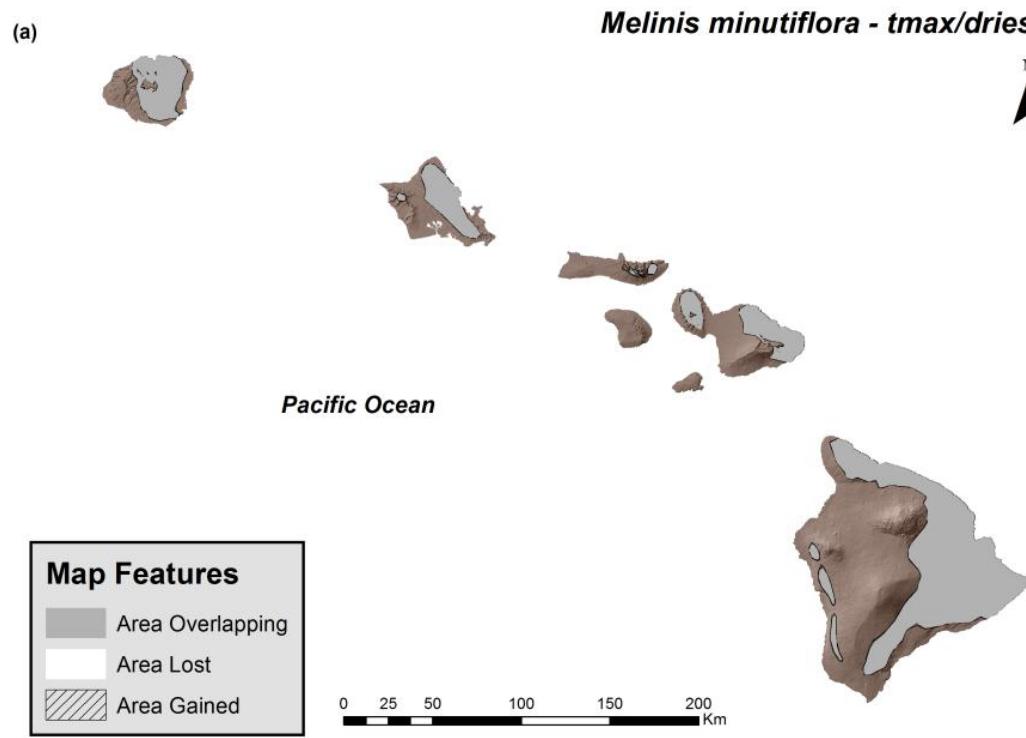


Figure 4.5 (a) Distribution projections for *Melinis minutiflora* using tmax/driest constraints. Distribution projections are made using PRISM model predictions.

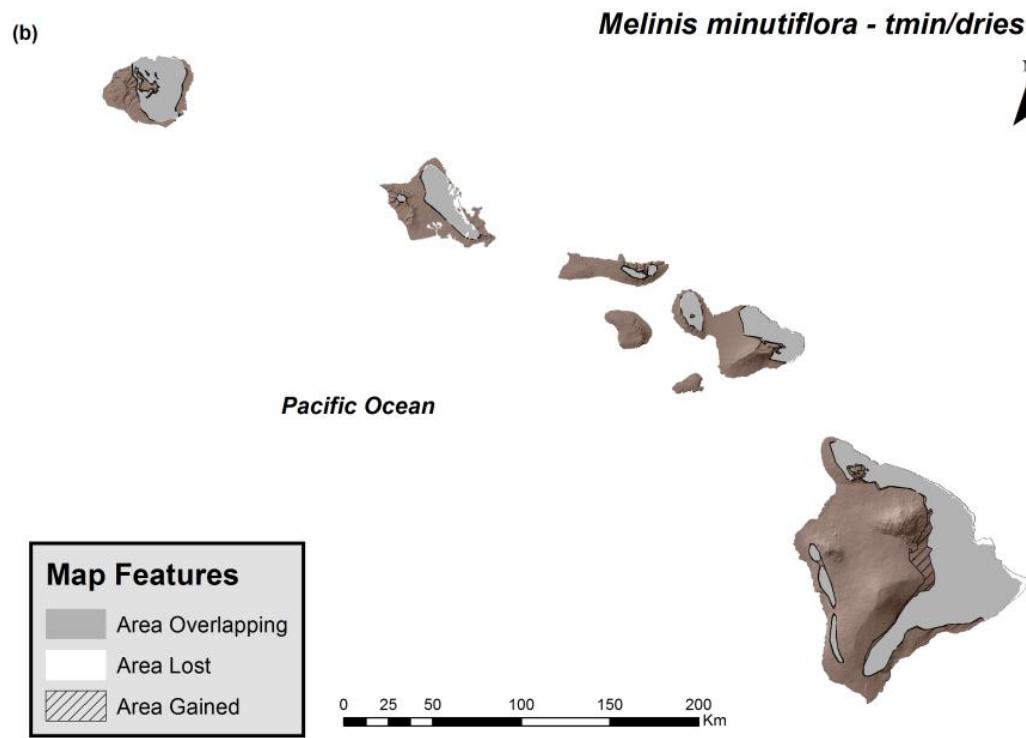


Figure 4.5 (b) Distribution projections for *Melinis minutiflora* using tmin/driest constraints. Distribution projections are made using PRISM model predictions.

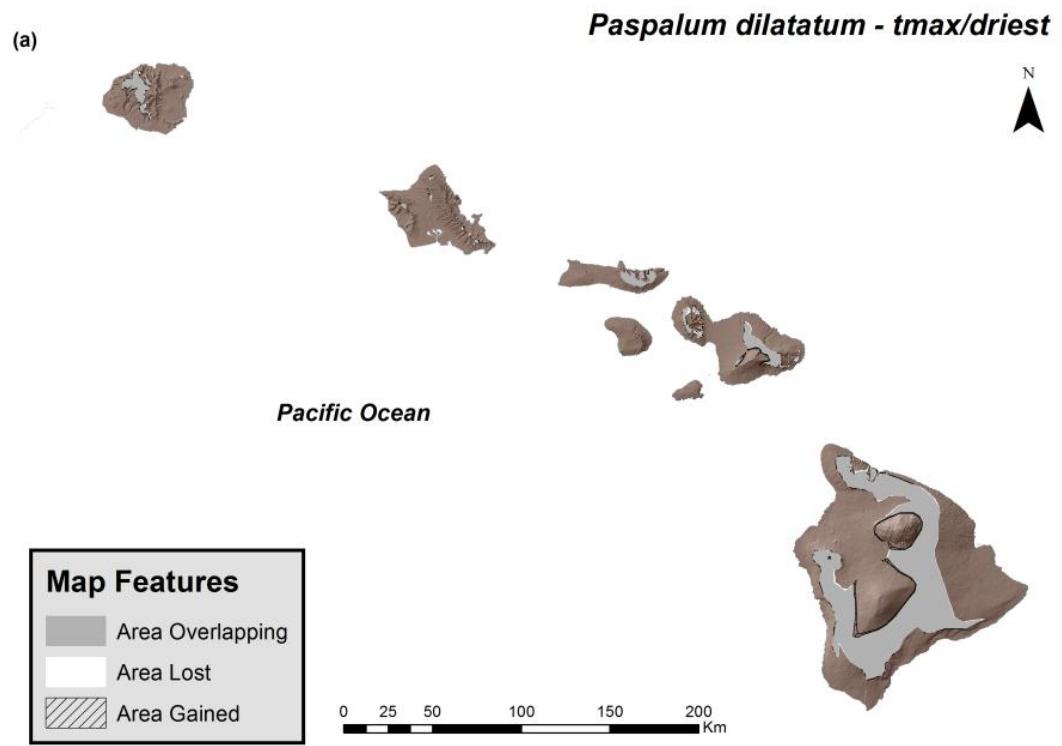


Figure 4.6 (a) Distribution projections for *Paspalum dilatatum* using tmax/driest constraints. Distribution projections are made using PRISM model predictions.

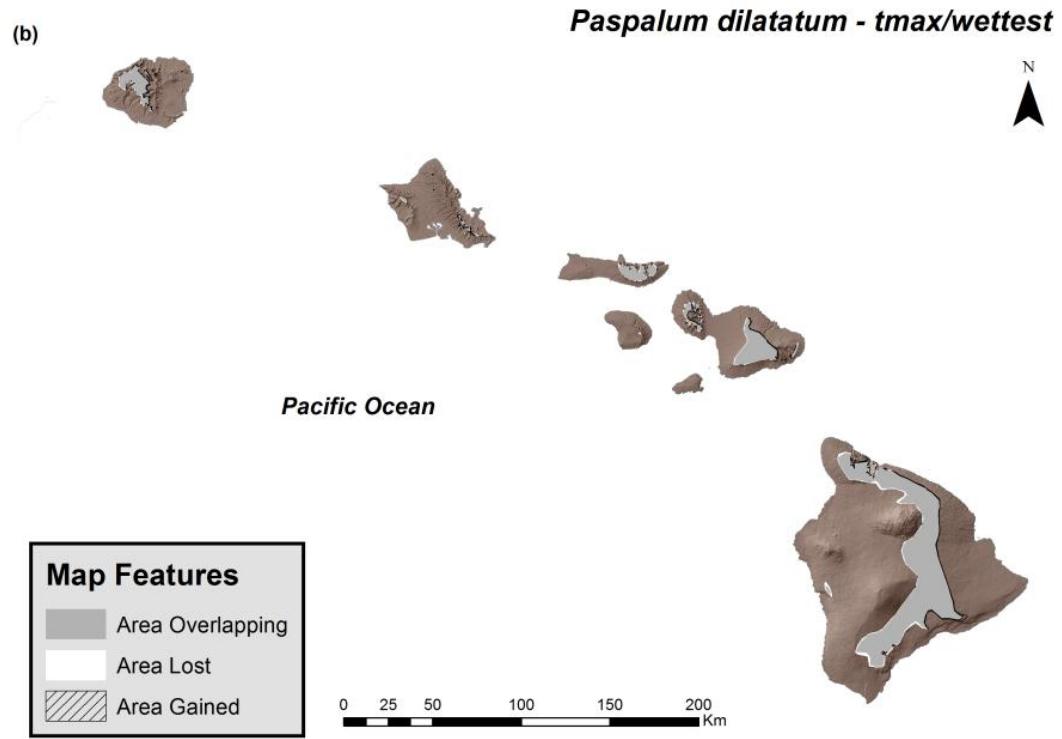


Figure 4.6 (b) Distribution projections for *Paspalum dilatatum* using tmax/wettest constraints. Distribution projections are made using PRISM model predictions.

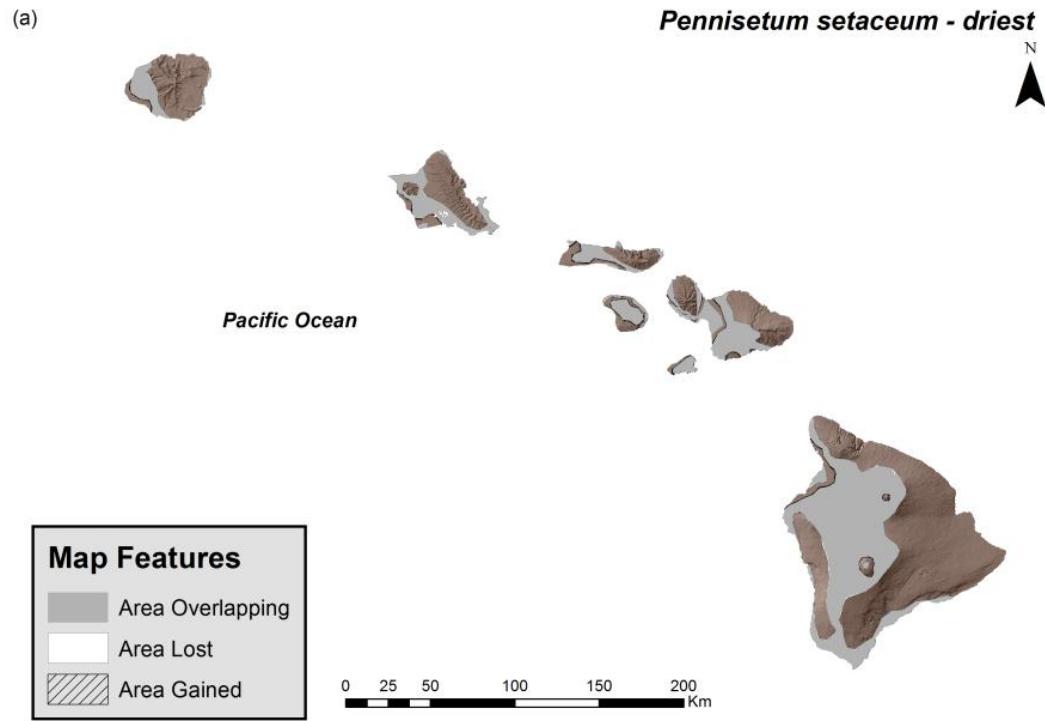


Figure 4.7 (a) Distribution projections for *Pennisetum setaceum* using the driest constraint. Distribution projections are made using PRISM model predictions.

(a)

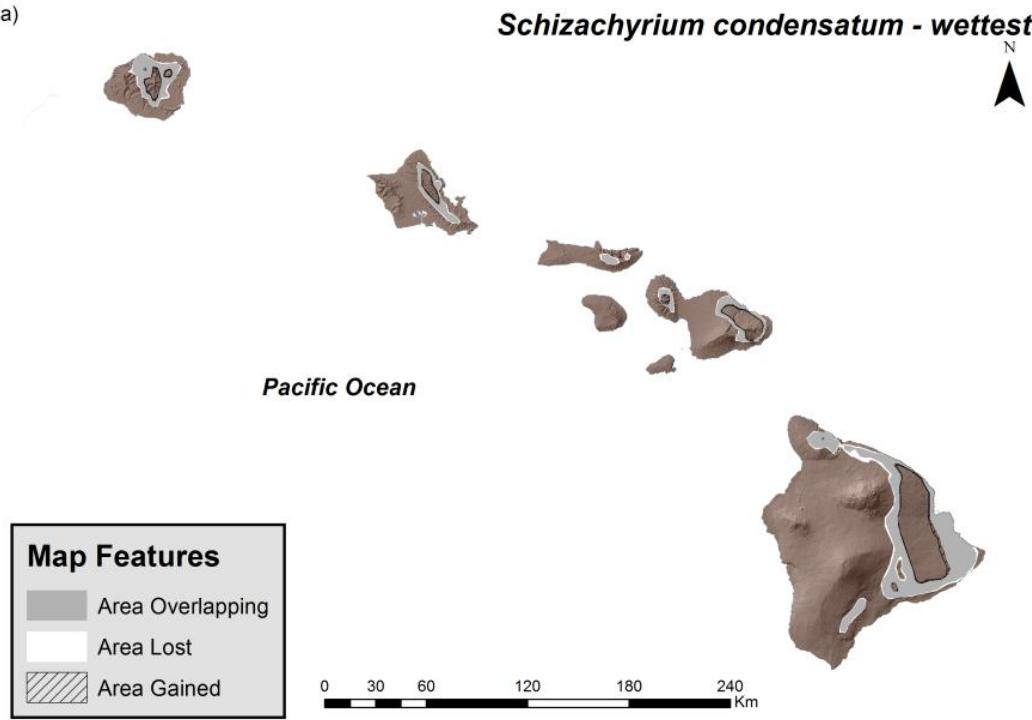


Figure 4.8 (a) Distribution projections for *Schizachyrium condensatum* using the wettest constraint. Distribution projections are made using PRISM model predictions.

APPENDIX

Appendix C. GPS Points for species' locations

Species Name	Island	Latitude	Longitude	GPS Point Source
<i>Anthoxanthum odoratum</i>	Hawaii	19.7483	-155.525	Bishop
<i>Anthoxanthum odoratum</i>	Hawaii	19.81166667	-155.4766667	Bishop
<i>Anthoxanthum odoratum</i>	Hawaii	19.83333333	-155.5933333	Bishop
<i>Anthoxanthum odoratum</i>	Hawaii	19.9367	-155.39	Bishop
<i>Anthoxanthum odoratum</i>	Hawaii	19.46333333	-155.35	Bishop
<i>Anthoxanthum odoratum</i>	Hawaii	19.46666667	-155.35	Bishop
<i>Anthoxanthum odoratum</i>	Hawaii	19.43666667	-155.3	Bishop
<i>Anthoxanthum odoratum</i>	Hawaii	19.4425	-155.3	Bishop
<i>Anthoxanthum odoratum</i>	Hawaii	19.43	-155.286667	Bishop
<i>Anthoxanthum odoratum</i>	Hawaii	19.46666667	-155.303333	Bishop
<i>Anthoxanthum odoratum</i>	Hawaii	19.48333333	-155.316667	Bishop
<i>Anthoxanthum odoratum</i>	Hawaii	19.48333333	-155.316667	Bishop
<i>Anthoxanthum odoratum</i>	Hawaii	19.4417	-155.2733	Bishop
<i>Anthoxanthum odoratum</i>	Hawaii	19.5	-155.316667	Bishop
<i>Anthoxanthum odoratum</i>	Hawaii	19.65	-155.366667	Bishop
<i>Anthoxanthum odoratum</i>	Hawaii	19.56833333	-155.216667	Bishop
<i>Anthoxanthum odoratum</i>	Hawaii	19.6	-155.116667	Bishop
<i>Anthoxanthum odoratum</i>	Hawaii	19.681511	-155.186842	Self
<i>Anthoxanthum odoratum</i>	Hawaii	19.694609	-155.218355	Self
<i>Anthoxanthum odoratum</i>	Hawaii	19.696043	-155.242462	Self
<i>Anthoxanthum odoratum</i>	Hawaii	19.691312	-155.259637	Self
<i>Anthoxanthum odoratum</i>	Hawaii	19.686644	-155.284506	Self
<i>Anthoxanthum odoratum</i>	Hawaii	19.677197	-155.312003	Self
<i>Anthoxanthum odoratum</i>	Hawaii	19.675367	-155.424068	Self

Appendix C. (Continued)

<i>Anthoxanthum odoratum</i>	Hawaii	19.670251	-155.366179	Self
<i>Anthoxanthum odoratum</i>	Hawaii	19.68119	-155.393274	Self
<i>Anthoxanthum odoratum</i>	Hawaii	19.685443	-155.429549	Self
<i>Anthoxanthum odoratum</i>	Hawaii	19.482443	-155.155508	Self
<i>Anthoxanthum odoratum</i>	Hawaii	19.452194	-155.186435	Self
<i>Anthoxanthum odoratum</i>	Hawaii	19.444103	-155.208654	Self
<i>Anthoxanthum odoratum</i>	Hawaii	19.864767	-155.653956	Self
<i>Anthoxanthum odoratum</i>	Hawaii	19.702191	-155.46102	Self
<i>Anthoxanthum odoratum</i>	Hawaii	19.716017	-155.445774	Self
<i>Anthoxanthum odoratum</i>	Hawaii	19.719349	-155.445834	Self
<i>Anthoxanthum odoratum</i>	Hawaii	19.726391	-155.447315	Self
<i>Anthoxanthum odoratum</i>	Hawaii	19.738887	-155.452741	Self
<i>Anthoxanthum odoratum</i>	Hawaii	19.747914	-155.453671	Self
<i>Anthoxanthum odoratum</i>	Hawaii	19.411935	-155.238557	Self
<i>Anthoxanthum odoratum</i>	Hawaii	19.408414	-155.248713	Self
<i>Anthoxanthum odoratum</i>	Hawaii	19.385682	-155.244955	Self
<i>Anthoxanthum odoratum</i>	Hawaii	19.437232	-155.303595	Self
<i>Anthoxanthum odoratum</i>	Hawaii	19.442117	-155.315003	Self
<i>Anthoxanthum odoratum</i>	Hawaii	19.449983	-155.33548	Self
<i>Anthoxanthum odoratum</i>	Hawaii	19.460393	-155.343389	Self
<i>Anthoxanthum odoratum</i>	Hawaii	19.462797	-155.348842	Self
<i>Anthoxanthum odoratum</i>	Hawaii	19.476553	-155.362666	Self
<i>Anthoxanthum odoratum</i>	Hawaii	19.9233	-155.3917	Smithsonian
<i>Anthoxanthum odoratum</i>	Maui	20.74166667	-156.216667	Bishop

Appendix C. (Continued)

<i>Anthoxanthum odoratum</i>	Maui	20.76923	-156.292591	Self
<i>Anthoxanthum odoratum</i>	Maui	20.765331	-156.290933	Self
<i>Anthoxanthum odoratum</i>	Maui	20.764387	-156.292908	Self
<i>Anthoxanthum odoratum</i>	Maui	20.764011	-156.288528	Self
<i>Anthoxanthum odoratum</i>	Maui	20.763477	-156.286771	Self
<i>Anthoxanthum odoratum</i>	Maui	20.761012	-156.283897	Self
<i>Anthoxanthum odoratum</i>	Maui	20.757872	-156.284577	Self
<i>Anthoxanthum odoratum</i>	Maui	20.756894	-156.280948	Self
<i>Anthoxanthum odoratum</i>	Maui	20.755894	-156.278787	Self
<i>Anthoxanthum odoratum</i>	Maui	20.754972	-156.270741	Self
<i>Anthoxanthum odoratum</i>	Maui	20.773414	-156.246862	Self
<i>Anthoxanthum odoratum</i>	Maui	20.758276	-156.247012	Self
<i>Anthoxanthum odoratum</i>	Maui	20.757016	-156.236534	Self
<i>Anthoxanthum odoratum</i>	Maui	20.75281	-156.229307	Self
<i>Anthoxanthum odoratum</i>	Maui	20.740327	-156.236195	Self
<i>Anthoxanthum odoratum</i>	Maui	20.715034	-156.251633	Self
<i>Anthoxanthum odoratum</i>	Molokai	21.15	-156.9433	Bishop
<i>Anthoxanthum odoratum</i>	Molokai	21.133	-156.9267	Bishop
<i>Cenchrus ciliaris</i>	Hawaii	20.027	-155.8167	Bishop
<i>Cenchrus ciliaris</i>	Hawaii	19.95	-155.816667	Bishop
<i>Cenchrus ciliaris</i>	Hawaii	19.925	-155.673333	Bishop
<i>Cenchrus ciliaris</i>	Hawaii	19.95	-155.633333	Bishop
<i>Cenchrus ciliaris</i>	Hawaii	18.972	-155.625	Bishop

Appendix C. (Continued)

<i>Cenchrus ciliaris</i>	Hawaii	20.022	-155.748722	Self
<i>Cenchrus ciliaris</i>	Hawaii	19.968	-155.679235	Self
<i>Cenchrus ciliaris</i>	Hawaii	20.176	-155.895637	Self
<i>Cenchrus ciliaris</i>	Hawaii	20.133	-155.885392	Self
<i>Cenchrus ciliaris</i>	Hawaii	20.08	-155.860992	Self
<i>Cenchrus ciliaris</i>	Hawaii	20.031	-155.821791	Self
<i>Cenchrus ciliaris</i>	Hawaii	19.949	-155.831422	Self
<i>Cenchrus ciliaris</i>	Hawaii	19.843	-155.751685	Self
<i>Cenchrus ciliaris</i>	Hawaii	20.025	-155.822678	Self
<i>Cenchrus ciliaris</i>	Hawaii	20.027	-155.817758	Self
<i>Cenchrus ciliaris</i>	Hawaii	20.02	-155.801195	Self
<i>Cenchrus ciliaris</i>	Hawaii	20.022	-155.781532	Self
<i>Cenchrus ciliaris</i>	Hawaii	20.024	-155.760713	Self
<i>Cenchrus ciliaris</i>	Hawaii	20.027	-155.705614	Self
<i>Cenchrus ciliaris</i>	Hawaii	20.027	-155.8167	Self
<i>Cenchrus ciliaris</i>	Hawaii	19.95	-155.816667	Self
<i>Cenchrus ciliaris</i>	Hawaii	19.925	-155.673333	Self
<i>Cenchrus ciliaris</i>	Hawaii	19.95	-155.633333	Self
<i>Cenchrus ciliaris</i>	Hawaii	18.972	-155.625	Self
<i>Cenchrus ciliaris</i>	Kahoolawe	20.515	-156.68	Smithsonian
<i>Cenchrus ciliaris</i>	Kahoolawe	20.512	-156.670833	Bishop
<i>Cenchrus ciliaris</i>	Kauai	21.967	-159.663333	Bishop
<i>Cenchrus ciliaris</i>	Kauai	21.9	-159.605	Bishop
<i>Cenchrus ciliaris</i>	Lanai	20.745	-156.895	Bishop

Appendix C. (Continued)

<i>Cenchrus ciliaris</i>	Maui	20.798	-156.471667	Bishop
<i>Cenchrus ciliaris</i>	Maui	20.837	-156.628333	Bishop
<i>Cenchrus ciliaris</i>	Maui	20.883	-156.416667	Smithsonian
<i>Cenchrus ciliaris</i>	Maui	20.9	-156.416667	Smithsonian
<i>Cenchrus ciliaris</i>	Molokai	21.2	-157.166667	Bishop
<i>Cenchrus ciliaris</i>	Molokai	21.2	-157.133333	Bishop
<i>Cenchrus ciliaris</i>	Oahu	21.347	-158	Smithsonian
<i>Cenchrus ciliaris</i>	Oahu	21.262	-157.81	Bishop
<i>Cenchrus ciliaris</i>	Oahu	21.382	-158.001667	Bishop
<i>Cenchrus ciliaris</i>	Oahu	21.573	-158.2706	Smithsonian
<i>Cenchrus ciliaris</i>	Oahu	21.571	-158.2662	Bishop
<i>Cenchrus ciliaris</i>	Oahu	21.358	-158.020767	Bishop
<i>Cenchrus ciliaris</i>	Oahu	21.303	-157.83	Bishop
<i>Holcus lanatus</i>	Hawaii	19.83333333	-155.5933333	Bishop
<i>Holcus lanatus</i>	Hawaii	19.6967	-155.4917	Bishop
<i>Holcus lanatus</i>	Hawaii	19.49666667	-155.3866667	Bishop
<i>Holcus lanatus</i>	Hawaii	19.4	-155.2833333	Bishop
<i>Holcus lanatus</i>	Hawaii	19.4	-155.2833333	Bishop
<i>Holcus lanatus</i>	Hawaii	19.46666667	-155.35	Bishop
<i>Holcus lanatus</i>	Hawaii	19.44	-155.3066667	Bishop
<i>Holcus lanatus</i>	Hawaii	19.44166667	-155.3033333	Bishop
<i>Holcus lanatus</i>	Hawaii	19.46666667	-155.3	Bishop
<i>Holcus lanatus</i>	Hawaii	19.5	-155.3166667	Bishop

Appendix C. (Continued)

<i>Holcus lanatus</i>	Hawaii	19.43333333	-155.235	Bishop
<i>Holcus lanatus</i>	Hawaii	19.44	-155.225	Bishop
<i>Holcus lanatus</i>	Hawaii	19.696043	-155.242462	Self
<i>Holcus lanatus</i>	Hawaii	19.691312	-155.259637	Self
<i>Holcus lanatus</i>	Hawaii	19.686644	-155.284506	Self
<i>Holcus lanatus</i>	Hawaii	19.677197	-155.312003	Self
<i>Holcus lanatus</i>	Hawaii	19.670251	-155.366179	Self
<i>Holcus lanatus</i>	Hawaii	19.68119	-155.393274	Self
<i>Holcus lanatus</i>	Hawaii	19.482443	-155.155508	Self
<i>Holcus lanatus</i>	Hawaii	19.452194	-155.186435	Self
<i>Holcus lanatus</i>	Hawaii	19.444103	-155.208654	Self
<i>Holcus lanatus</i>	Hawaii	19.829322	-155.63851	Self
<i>Holcus lanatus</i>	Hawaii	19.806624	-155.630971	Self
<i>Holcus lanatus</i>	Hawaii	19.816884	-155.619166	Self
<i>Holcus lanatus</i>	Hawaii	19.702191	-155.46102	Self
<i>Holcus lanatus</i>	Hawaii	19.715735	-155.445312	Self
<i>Holcus lanatus</i>	Hawaii	19.719349	-155.445834	Self
<i>Holcus lanatus</i>	Hawaii	19.726377	-155.447648	Self
<i>Holcus lanatus</i>	Hawaii	19.738887	-155.452741	Self
<i>Holcus lanatus</i>	Hawaii	19.747807	-155.454165	Self
<i>Holcus lanatus</i>	Hawaii	19.43721	-155.303862	Self
<i>Holcus lanatus</i>	Hawaii	19.439265	-155.30847	Self
<i>Holcus lanatus</i>	Hawaii	19.442117	-155.315003	Self
<i>Holcus lanatus</i>	Hawaii	19.449381	-155.332406	Self

Appendix C. (Continued)

<i>Holcus lanatus</i>	Hawaii	19.449983	-155.33548	Self
<i>Holcus lanatus</i>	Hawaii	19.45995	-155.343459	Self
<i>Holcus lanatus</i>	Hawaii	19.46304	-155.34894	Self
<i>Holcus lanatus</i>	Hawaii	19.476557	-155.363019	Self
<i>Holcus lanatus</i>	Hawaii	19.483613	-155.373882	Self
<i>Holcus lanatus</i>	Hawaii	19.491633	-155.385503	Self
<i>Holcus lanatus</i>	Hawaii	19.498038	-155.384673	Self
<i>Holcus lanatus</i>	Hawaii	19.411935	-155.238557	Self
<i>Holcus lanatus</i>	Hawaii	19.408414	-155.248713	Self
<i>Holcus lanatus</i>	Hawaii	19.385682	-155.244955	Self
<i>Holcus lanatus</i>	Hawaii	20.13833333	-155.7883333	Smithsonian
<i>Holcus lanatus</i>	Hawaii	19.55666667	-155.2966667	Smithsonian
<i>Holcus lanatus</i>	Hawaii	19.44	-155.225	Smithsonian
<i>Holcus lanatus</i>	Kauai	22.1	-159.6783333	Bishop
<i>Holcus lanatus</i>	Kauai	22.09833	-159.665	Bishop
<i>Holcus lanatus</i>	Kauai	22.129383	-159.658401	Self
<i>Holcus lanatus</i>	Kauai	22.11537	-159.669786	Self
<i>Holcus lanatus</i>	Kauai	22.13293	-159.654733	Self
<i>Holcus lanatus</i>	Kauai	22.141541	-159.647635	Self
<i>Holcus lanatus</i>	Kauai	22.148506	-159.636127	Self
<i>Holcus lanatus</i>	Kauai	22.147369	-159.631263	Self
<i>Holcus lanatus</i>	Maui	20.745	-156.2283	Bishop
<i>Holcus lanatus</i>	Maui	20.79166667	-156.255	Bishop
<i>Holcus lanatus</i>	Maui	20.73	-156.1533333	Bishop

Appendix C. (Continued)

<i>Holcus lanatus</i>	Maui	20.93333333	-156.6	Bishop
<i>Holcus lanatus</i>	Maui	20.768134	-156.303813	Self
<i>Holcus lanatus</i>	Maui	20.766839	-156.296109	Self
<i>Holcus lanatus</i>	Maui	20.76923	-156.292591	Self
<i>Holcus lanatus</i>	Maui	20.765331	-156.290933	Self
<i>Holcus lanatus</i>	Maui	20.764387	-156.292908	Self
<i>Holcus lanatus</i>	Maui	20.764011	-156.288528	Self
<i>Holcus lanatus</i>	Maui	20.763477	-156.286771	Self
<i>Holcus lanatus</i>	Maui	20.760862	-156.284073	Self
<i>Holcus lanatus</i>	Maui	20.757721	-156.284724	Self
<i>Holcus lanatus</i>	Maui	20.7568	-156.280709	Self
<i>Holcus lanatus</i>	Maui	20.755728	-156.278598	Self
<i>Holcus lanatus</i>	Maui	20.754972	-156.270741	Self
<i>Holcus lanatus</i>	Maui	20.773414	-156.246862	Self
<i>Holcus lanatus</i>	Maui	20.758817	-156.246973	Self
<i>Holcus lanatus</i>	Maui	20.757016	-156.236534	Self
<i>Holcus lanatus</i>	Maui	20.75281	-156.229307	Self
<i>Holcus lanatus</i>	Maui	20.739752	-156.244843	Self
<i>Holcus lanatus</i>	Maui	20.740327	-156.236195	Self
<i>Holcus lanatus</i>	Maui	20.755	-156.2683	Smithsonian
<i>Holcus lanatus</i>	Maui	20.74166667	-156.2	Smithsonian
<i>Holcus lanatus</i>	Maui	20.73666667	-156.1316667	Smithsonian
<i>Holcus lanatus</i>	Maui	20.8133	-156.2383	Smithsonian
<i>Holcus lanatus</i>	Molokai	21.14833333	-156.9433333	Bishop

Appendix C. (Continued)

<i>Holcus lanatus</i>	Oahu	21.40833333	-158.0983333	Bishop
<i>Hyparrhenia rufa</i>	Molokai	22.116667	-159.716667	Bishop
<i>Hyparrhenia rufa</i>	Oahu	21.111667	-156.976667	Bishop
<i>Hyparrhenia rufa</i>	Oahu	21.55	-158.1783	Bishop
<i>Hyparrhenia rufa</i>	Oahu	21.645	-158.0167	Bishop
<i>Hyparrhenia rufa</i>	Oahu	21.645991	-158.026408	Bishop
<i>Hyparrhenia rufa</i>	Oahu	21.593955	-158.008463	Bishop
<i>Hyparrhenia rufa</i>	Kauai	21.951851	-159.468364	Bishop
<i>Hyparrhenia rufa</i>	Kauai	22.122693	-159.714228	Bishop
<i>Hyparrhenia rufa</i>	Maui	20.868	-156.179	Bishop
<i>Hyparrhenia rufa</i>	Oahu	21.36678	-157.790596	Bishop
<i>Hyparrhenia rufa</i>	Kauai	22.037717	-159.665357	Bishop
<i>Hyparrhenia rufa</i>	Maui	21.441574	-157.875416	Bishop
<i>Hyparrhenia rufa</i>	Hawaii	19.57667	-155.065705	Self
<i>Hyparrhenia rufa</i>	Hawaii	19.23905	-155.44833	Self
<i>Hyparrhenia rufa</i>	Hawaii	19.323043	-155.40385	Self
<i>Hyparrhenia rufa</i>	Hawaii	19.35941	-155.377092	Self
<i>Hyparrhenia rufa</i>	Hawaii	19.353773	-155.222099	Self
<i>Hyparrhenia rufa</i>	Hawaii	19.338591	-155.207925	Self
<i>Hyparrhenia rufa</i>	Hawaii	19.319416	-155.174844	Self
<i>Hyparrhenia rufa</i>	Hawaii	19.314152	-155.151846	Self
<i>Hyparrhenia rufa</i>	Hawaii	19.308916	-155.140095	Self
<i>Hyparrhenia rufa</i>	Hawaii	19.297343	-155.151036	Self

Appendix C. (Continued)

<i>Hyparrhenia rufa</i>	Hawaii	19.288553	-155.130384	Self
<i>Hyparrhenia rufa</i>	Hawaii	19.293221	-155.102486	Self
<i>Hyparrhenia rufa</i>	Hawaii	19.682597	-155.150803	Self
<i>Hyparrhenia rufa</i>	Hawaii	19.68001	-155.161667	Self
<i>Hyparrhenia rufa</i>	Hawaii	19.681712	-155.142486	Self
<i>Hyparrhenia rufa</i>	Hawaii	19.680323	-155.124836	Self
<i>Hyparrhenia rufa</i>	Hawaii	19.553349	-154.985873	Self
<i>Hyparrhenia rufa</i>	Hawaii	19.427896	-154.947905	Self
<i>Hyparrhenia rufa</i>	Hawaii	19.432375	-154.937913	Self
<i>Hyparrhenia rufa</i>	Hawaii	19.379477	-155.356323	Self
<i>Hyparrhenia rufa</i>	Hawaii	19.420572	-155.304046	Self
<i>Hyparrhenia rufa</i>	Kauai	22.088641	-159.671434	Self
<i>Melinis minutiflora</i>	Hawaii	19.8	-155.85	Bishop
<i>Melinis minutiflora</i>	Hawaii	19.29666667	-155.315	Bishop
<i>Melinis minutiflora</i>	Hawaii	19.355	-155.3166667	Bishop
<i>Melinis minutiflora</i>	Hawaii	19.345	-155.3466667	Bishop
<i>Melinis minutiflora</i>	Hawaii	19.4	-155.2833333	Bishop
<i>Melinis minutiflora</i>	Hawaii	19.305	-155.1416667	Bishop
<i>Melinis minutiflora</i>	Hawaii	19.45	-155.3	Bishop
<i>Melinis minutiflora</i>	Hawaii	20.0375	-155.535	Bishop
<i>Melinis minutiflora</i>	Hawaii	19.45	-155.2833333	Bishop
<i>Melinis minutiflora</i>	Hawaii	19.51666667	-154.85	Bishop
<i>Melinis minutiflora</i>	Hawaii	19.51666667	-154.8666667	Bishop

Appendix C. (Continued)

<i>Melinis minutiflora</i>	Hawaii	19.6533	-155.07	Bishop
<i>Melinis minutiflora</i>	Hawaii	19.6833	-155.175	Bishop
<i>Melinis minutiflora</i>	Hawaii	19.682525	-155.150754	Self
<i>Melinis minutiflora</i>	Hawaii	19.681511	-155.186842	Self
<i>Melinis minutiflora</i>	Hawaii	19.694609	-155.218355	Self
<i>Melinis minutiflora</i>	Hawaii	19.696043	-155.242462	Self
<i>Melinis minutiflora</i>	Hawaii	19.691312	-155.259637	Self
<i>Melinis minutiflora</i>	Hawaii	19.57667	-155.065705	Self
<i>Melinis minutiflora</i>	Hawaii	19.556443	-155.101141	Self
<i>Melinis minutiflora</i>	Hawaii	19.23905	-155.44833	Self
<i>Melinis minutiflora</i>	Hawaii	19.532584	-155.129346	Self
<i>Melinis minutiflora</i>	Hawaii	19.282181	-155.426715	Self
<i>Melinis minutiflora</i>	Hawaii	19.323043	-155.40385	Self
<i>Melinis minutiflora</i>	Hawaii	19.35941	-155.377092	Self
<i>Melinis minutiflora</i>	Hawaii	19.407314	-155.328122	Self
<i>Melinis minutiflora</i>	Hawaii	19.437232	-155.303595	Self
<i>Melinis minutiflora</i>	Hawaii	19.441641	-155.314787	Self
<i>Melinis minutiflora</i>	Hawaii	19.442535	-155.323321	Self
<i>Melinis minutiflora</i>	Hawaii	19.462797	-155.348842	Self
<i>Melinis minutiflora</i>	Hawaii	19.476553	-155.362666	Self
<i>Melinis minutiflora</i>	Hawaii	19.408414	-155.248713	Self
<i>Melinis minutiflora</i>	Hawaii	19.385682	-155.244955	Self
<i>Melinis minutiflora</i>	Hawaii	19.353773	-155.222099	Self
<i>Melinis minutiflora</i>	Hawaii	19.338591	-155.207925	Self

Appendix C. (Continued)

<i>Melinis minutiflora</i>	Hawaii	19.319416	-155.174844	Self
<i>Melinis minutiflora</i>	Hawaii	19.314152	-155.151846	Self
<i>Melinis minutiflora</i>	Hawaii	20.061775	-155.532274	Self
<i>Melinis minutiflora</i>	Hawaii	20.172043	-155.824156	Self
<i>Melinis minutiflora</i>	Hawaii	19.963216	-155.201818	Self
<i>Melinis minutiflora</i>	Hawaii	19.953817	-155.18992	Self
<i>Melinis minutiflora</i>	Hawaii	19.906666	-155.135434	Self
<i>Melinis minutiflora</i>	Hawaii	19.878696	-155.11562	Self
<i>Melinis minutiflora</i>	Hawaii	19.771768	-155.093091	Self
<i>Melinis minutiflora</i>	Hawaii	19.68001	-155.161667	Self
<i>Melinis minutiflora</i>	Hawaii	19.631638	-155.035873	Self
<i>Melinis minutiflora</i>	Hawaii	19.553349	-154.985873	Self
<i>Melinis minutiflora</i>	Hawaii	19.361781	-154.976499	Self
<i>Melinis minutiflora</i>	Hawaii	19.363062	-154.966654	Self
<i>Melinis minutiflora</i>	Hawaii	19.398601	-154.920729	Self
<i>Melinis minutiflora</i>	Hawaii	19.432377	-154.937723	Self
<i>Melinis minutiflora</i>	Hawaii	19.379477	-155.356323	Self
<i>Melinis minutiflora</i>	Hawaii	19.420572	-155.304046	Self
<i>Melinis minutiflora</i>	Hawaii	20.010599	-155.289993	Self
<i>Melinis minutiflora</i>	Hawaii	20.0484	-155.479995	Self
<i>Melinis minutiflora</i>	Hawaii	19.6858	-155.973999	Self
<i>Melinis minutiflora</i>	Maui	20.675	-156.133333	Bishop
<i>Melinis minutiflora</i>	Maui	20.848307	-156.308485	Self
<i>Melinis minutiflora</i>	Maui	20.827267	-156.315764	Self

Appendix C. (Continued)

<i>Melinis minutiflora</i>	Maui	20.818417	-156.306405	Self
<i>Melinis minutiflora</i>	Maui	20.808308	-156.306556	Self
<i>Melinis minutiflora</i>	Maui	20.91334	-156.263223	Self
<i>Melinis minutiflora</i>	Maui	20.903446	-156.228009	Self
<i>Melinis minutiflora</i>	Maui	20.913299	-156.263	Self
<i>Melinis minutiflora</i>	Maui	20.9034	-156.227996	Self
<i>Melinis minutiflora</i>	Maui	20.805099	-156.328002	Self
<i>Melinis minutiflora</i>	Oahu	21.303304	-157.745057	Self
<i>Melinis minutiflora</i>	Oahu	21.304808	-157.762234	Self
<i>Melinis minutiflora</i>	Oahu	21.369546	-157.786267	Self
<i>Melinis minutiflora</i>	Oahu	21.401384	-157.895797	Self
<i>Melinis minutiflora</i>	Oahu	21.432137	-157.823453	Self
<i>Melinis minutiflora</i>	Oahu	21.440049	-157.914278	Self
<i>Melinis minutiflora</i>	Oahu	21.50155	-158.170488	Self
<i>Melinis minutiflora</i>	Oahu	21.502009	-158.149019	Self
<i>Melinis minutiflora</i>	Oahu	21.505823	-158.168192	Self
<i>Melinis minutiflora</i>	Oahu	21.396099	-157.901992	Self
<i>Megathyrsus maximus</i>	Haleakala	20.830649	-156.331655	Self
<i>Megathyrsus maximus</i>	Haleakala	20.829258	-156.322412	Self
<i>Megathyrsus maximus</i>	Haleakala	20.829292	-156.322825	Self
<i>Megathyrsus maximus</i>	Haleakala	20.818417	-156.306405	Self
<i>Megathyrsus maximus</i>	Haleakala	20.768134	-156.303813	Self
<i>Megathyrsus maximus</i>	Hana	20.911723	-156.391756	Self

Appendix C. (Continued)

<i>Megathyrsus maximus</i>	Hawaii	19.6	-155.966667	Bishop
<i>Megathyrsus maximus</i>	Hawaii	19.116667	-155.531667	Bishop
<i>Megathyrsus maximus</i>	Hawaii	19.425	-155.9	Bishop
<i>Megathyrsus maximus</i>	Hawaii	20.0375	-155.535	Bishop
<i>Megathyrsus maximus</i>	Hawaii	19.57667	-155.065705	Self
<i>Megathyrsus maximus</i>	Hawaii	19.23905	-155.44833	Self
<i>Megathyrsus maximus</i>	Hawaii	19.532584	-155.129346	Self
<i>Megathyrsus maximus</i>	Hawaii	19.282181	-155.426715	Self
<i>Megathyrsus maximus</i>	Hawaii	20.021901	-155.748722	Self
<i>Megathyrsus maximus</i>	Hawaii	20.026657	-155.719668	Self
<i>Megathyrsus maximus</i>	Hawaii	19.968287	-155.679235	Self
<i>Megathyrsus maximus</i>	Hawaii	19.7526	-155.091724	Self
<i>Megathyrsus maximus</i>	Hawaii	19.862977	-155.120452	Self
<i>Megathyrsus maximus</i>	Hawaii	20.159026	-155.815031	Self
<i>Megathyrsus maximus</i>	Hawaii	20.146078	-155.804378	Self
<i>Megathyrsus maximus</i>	Hawaii	19.973621	-155.216263	Self
<i>Megathyrsus maximus</i>	Hawaii	19.963216	-155.201818	Self
<i>Megathyrsus maximus</i>	Hawaii	19.953817	-155.18992	Self
<i>Megathyrsus maximus</i>	Hawaii	19.906666	-155.135434	Self
<i>Megathyrsus maximus</i>	Hawaii	19.878696	-155.11562	Self
<i>Megathyrsus maximus</i>	Hawaii	19.824119	-155.104608	Self
<i>Megathyrsus maximus</i>	Hawaii	19.771768	-155.093091	Self
<i>Megathyrsus maximus</i>	Hawaii	19.631638	-155.035873	Self
<i>Megathyrsus maximus</i>	Hawaii	19.553349	-154.985873	Self

Appendix C. (Continued)

<i>Megathyrsus maximus</i>	Hawaii	19.363062	-154.966654	Self
<i>Megathyrsus maximus</i>	Hawaii	19.370572	-154.954561	Self
<i>Megathyrsus maximus</i>	Hawaii	19.432377	-154.937723	Self
<i>Megathyrsus maximus</i>	Hawaii	19.806218	-155.842421	Self
<i>Megathyrsus maximus</i>	Hawaii	19.843439	-155.751685	Self
<i>Megathyrsus maximus</i>	Hawaii	19.887842	-155.714693	Self
<i>Megathyrsus maximus</i>	Hawaii	20.217199	-155.884994	Self
<i>Megathyrsus maximus</i>	Hawaii	20.2397	-155.848999	Self
<i>Megathyrsus maximus</i>	Hawaii	19.530599	-155.925994	Self
<i>Megathyrsus maximus</i>	Hawaii	19.63	-155.98085	Smithsonian
<i>Megathyrsus maximus</i>	Kauai	21.911667	-159.501667	Bishop
<i>Megathyrsus maximus</i>	Kauai	22.2	-159.583333	Bishop
<i>Megathyrsus maximus</i>	Kauai	21.958387	-159.671459	Self
<i>Megathyrsus maximus</i>	Kauai	21.952614	-159.662668	Self
<i>Megathyrsus maximus</i>	Kauai	21.980804	-159.717671	Self
<i>Megathyrsus maximus</i>	Kauai	21.90438	-159.568683	Self
<i>Megathyrsus maximus</i>	Kauai	21.967714	-159.664045	Self
<i>Megathyrsus maximus</i>	Kauai	21.993022	-159.710641	Self
<i>Megathyrsus maximus</i>	Kauai	21.968076	-159.663679	Self
<i>Megathyrsus maximus</i>	Kauai	21.946532	-159.475497	Self
<i>Megathyrsus maximus</i>	Kauai	21.978674	-159.665821	Self
<i>Megathyrsus maximus</i>	Kauai	22.002717	-159.706107	Self
<i>Megathyrsus maximus</i>	Kauai	21.994846	-159.676513	Self
<i>Megathyrsus maximus</i>	Kauai	22.011697	-159.699806	Self

Appendix C. (Continued)

<i>Megathyrsus maximus</i>	Kauai	22.010524	-159.675793	Self
<i>Megathyrsus maximus</i>	Kauai	22.021143	-159.687693	Self
<i>Megathyrsus maximus</i>	Kauai	22.026192	-159.672815	Self
<i>Megathyrsus maximus</i>	Kauai	22.026306	-159.67798	Self
<i>Megathyrsus maximus</i>	Kauai	22.033245	-159.671221	Self
<i>Megathyrsus maximus</i>	Kauai	21.91	-159.503333	Smithsonian
<i>Megathyrsus maximus</i>	Kula	20.818713	-156.327611	Self
<i>Megathyrsus maximus</i>	Kula	20.805052	-156.327516	Self
<i>Megathyrsus maximus</i>	Kula	20.787166	-156.326948	Self
<i>Megathyrsus maximus</i>	Kula	20.762881	-156.328777	Self
<i>Megathyrsus maximus</i>	Kula	20.73468	-156.334849	Self
<i>Megathyrsus maximus</i>	Kula	20.721824	-156.3442	Self
<i>Megathyrsus maximus</i>	Kula	20.702962	-156.362962	Self
<i>Megathyrsus maximus</i>	Kula	20.696199	-156.372328	Self
<i>Megathyrsus maximus</i>	Kula	20.68694	-156.382744	Self
<i>Megathyrsus maximus</i>	Kula	20.61432	-156.327255	Self
<i>Megathyrsus maximus</i>	Maui	20.608333	-156.425	Bishop
<i>Megathyrsus maximus</i>	Maui	20.939167	-156.511667	Bishop
<i>Megathyrsus maximus</i>	Maui	21.016667	-156.633333	Bishop
<i>Megathyrsus maximus</i>	Maui	20.848333	-156.608333	Bishop
<i>Megathyrsus maximus</i>	Maui	21.000278	-156.647778	Bishop
<i>Megathyrsus maximus</i>	Maui	20.757	-155.985	Bishop
<i>Megathyrsus maximus</i>	Maui	20.733333	-155.991667	Bishop
<i>Megathyrsus maximus</i>	Maui	20.911699	-156.391998	Self

Appendix C. (Continued)

<i>Megathyrsus maximus</i>	Maui	20.8187	-156.328002	Self
<i>Megathyrsus maximus</i>	Maui	20.805099	-156.328002	Self
<i>Megathyrsus maximus</i>	Maui	20.721799	-156.343994	Self
<i>Megathyrsus maximus</i>	Maui	20.702999	-156.363006	Self
<i>Megathyrsus maximus</i>	Maui	20.6145	-156.326995	Self
<i>Megathyrsus maximus</i>	Molokai	21.19667	-157.15	Bishop
<i>Megathyrsus maximus</i>	Molokai	21.15	-157.0833	Smithsonian
<i>Megathyrsus maximus</i>	Oahu	21.265	-157.805	Bishop
<i>Megathyrsus maximus</i>	Oahu	21.27	-157.82	Bishop
<i>Megathyrsus maximus</i>	Oahu	21.3	-157.85	Bishop
<i>Megathyrsus maximus</i>	Oahu	21.281667	-157.8	Bishop
<i>Megathyrsus maximus</i>	Oahu	21.5709	-158.2662	Bishop
<i>Megathyrsus maximus</i>	Oahu	21.3	-157.816667	Bishop
<i>Megathyrsus maximus</i>	Oahu	21.660278	-157.994444	Bishop
<i>Megathyrsus maximus</i>	Oahu	21.65	-158.0217	Bishop
<i>Megathyrsus maximus</i>	Oahu	21.583333	-157.9	Bishop
<i>Megathyrsus maximus</i>	Oahu	21.3658	-158.082	Self
<i>Megathyrsus maximus</i>	Oahu	21.371599	-158.089004	Self
<i>Megathyrsus maximus</i>	Oahu	21.3619	-158.087997	Self
<i>Megathyrsus maximus</i>	Oahu	21.4136	-158.046005	Self
<i>Megathyrsus maximus</i>	Oahu	21.422	-158.050994	Self
<i>Megathyrsus maximus</i>	Oahu	21.4451	-158.059997	Self
<i>Megathyrsus maximus</i>	Oahu	21.510299	-158.044006	Self
<i>Megathyrsus maximus</i>	Oahu	21.5363	-158.042007	Self

Appendix C. (Continued)

<i>Megathyrsus maximus</i>	Oahu	21.545	-158.044998	Self
<i>Megathyrsus maximus</i>	Oahu	21.552099	-158.052001	Self
<i>Megathyrsus maximus</i>	Oahu	21.5583	-158.065994	Self
<i>Megathyrsus maximus</i>	Oahu	21.5648	-158.076004	Self
<i>Megathyrsus maximus</i>	Oahu	21.5678	-158.083999	Self
<i>Megathyrsus maximus</i>	Oahu	21.572599	-158.098007	Self
<i>Megathyrsus maximus</i>	Oahu	21.3169	-157.830993	Self
<i>Megathyrsus maximus</i>	Oahu	21.3185	-157.830001	Self
<i>Megathyrsus maximus</i>	Oahu	21.3197	-157.830001	Self
<i>Megathyrsus maximus</i>	Oahu	21.330799	-157.817993	Self
<i>Megathyrsus maximus</i>	Oahu	21.3306	-157.815002	Self
<i>Megathyrsus maximus</i>	Oahu	21.3185	-157.817993	Self
<i>Megathyrsus maximus</i>	Oahu	21.311199	-157.822998	Self
<i>Paspalum dilatatum</i>	Hawaii	19.69	-155.865	Bishop
<i>Paspalum dilatatum</i>	Hawaii	19.19166667	-155.475	Bishop
<i>Paspalum dilatatum</i>	Hawaii	19.46666667	-155.35	Bishop
<i>Paspalum dilatatum</i>	Hawaii	19.46666667	-155.35	Bishop
<i>Paspalum dilatatum</i>	Hawaii	19.44	-155.30666667	Bishop
<i>Paspalum dilatatum</i>	Hawaii	19.46666667	-155.3	Bishop
<i>Paspalum dilatatum</i>	Hawaii	19.5	-155.31666667	Bishop
<i>Paspalum dilatatum</i>	Hawaii	19.53333333	-154.85	Bishop
<i>Paspalum dilatatum</i>	Hawaii	19.43	-155.23666667	Bishop
<i>Paspalum dilatatum</i>	Hawaii	19.829322	-155.63851	Self

Appendix C. (Continued)

<i>Paspalum dilatatum</i>	Hawaii	19.806624	-155.630971	Self
<i>Paspalum dilatatum</i>	Hawaii	19.442535	-155.323321	Self
<i>Paspalum dilatatum</i>	Hawaii	19.449381	-155.332406	Self
<i>Paspalum dilatatum</i>	Hawaii	19.449983	-155.33548	Self
<i>Paspalum dilatatum</i>	Hawaii	19.45995	-155.343459	Self
<i>Paspalum dilatatum</i>	Hawaii	19.462797	-155.348842	Self
<i>Paspalum dilatatum</i>	Hawaii	19.476553	-155.362666	Self
<i>Paspalum dilatatum</i>	Hawaii	19.483613	-155.373882	Self
<i>Paspalum dilatatum</i>	Hawaii	19.9667	-155.3833	Smithsonian
<i>Paspalum dilatatum</i>	Hawaii	19.98666667	-155.3883333	Smithsonian
<i>Paspalum dilatatum</i>	Hawaii	20.13833333	-155.7883333	Smithsonian
<i>Paspalum dilatatum</i>	Kauai	21.911667	-159.503333	Bishop
<i>Paspalum dilatatum</i>	Kauai	21.925	-159.528333	Bishop
<i>Paspalum dilatatum</i>	Kauai	22.125	-159.65	Bishop
<i>Paspalum dilatatum</i>	Kauai	22.026192	-159.672912	Self
<i>Paspalum dilatatum</i>	Kauai	22.026306	-159.67798	Self
<i>Paspalum dilatatum</i>	Kauai	22.088641	-159.671434	Self
<i>Paspalum dilatatum</i>	Kauai	22.129383	-159.658401	Self
<i>Paspalum dilatatum</i>	Kauai	22.109742	-159.669798	Self
<i>Paspalum dilatatum</i>	Kauai	22.13293	-159.654733	Self
<i>Paspalum dilatatum</i>	Kauai	22.141541	-159.647635	Self
<i>Paspalum dilatatum</i>	Kauai	22.147369	-159.631263	Self
<i>Paspalum dilatatum</i>	Kauai	22.021667	-159.405	Smithsonian
<i>Paspalum dilatatum</i>	Lanai	20.783333	-156.911667	Bishop

Appendix C. (Continued)

<i>Paspalum dilatatum</i>	Lanai	20.833333	-156.933333	Bishop
<i>Paspalum dilatatum</i>	Lanai	20.835	-156.918333	Bishop
<i>Paspalum dilatatum</i>	Maui	20.763333	-156.233333	Bishop
<i>Paspalum dilatatum</i>	Maui	20.703333	-156.145	Bishop
<i>Paspalum dilatatum</i>	Maui	20.7	-156.141667	Bishop
<i>Paspalum dilatatum</i>	Maui	20.76923	-156.292591	Self
<i>Paspalum dilatatum</i>	Maui	20.764011	-156.288528	Self
<i>Paspalum dilatatum</i>	Maui	20.761012	-156.283897	Self
<i>Paspalum dilatatum</i>	Maui	20.757872	-156.284577	Self
<i>Paspalum dilatatum</i>	Molokai	21.133	-156.92	Bishop
<i>Paspalum dilatatum</i>	Molokai	21.138333	-157.166667	Smithsonian
<i>Paspalum dilatatum</i>	Oahu	21.46	-158.0633	Bishop
<i>Paspalum dilatatum</i>	Oahu	21.65	-157.933333	Bishop
<i>Paspalum dilatatum</i>	Oahu	21.506667	-158.143333	Bishop
<i>Pennisetum setaceum</i>	Hawaii	19.95	-155.8166667	Bishop
<i>Pennisetum setaceum</i>	Hawaii	19.76	-155.6767	Bishop
<i>Pennisetum setaceum</i>	Hawaii	19.73333333	-155.7	Bishop
<i>Pennisetum setaceum</i>	Hawaii	19.71666667	-156.0333333	Bishop
<i>Pennisetum setaceum</i>	Hawaii	19.81666667	-155.85	Bishop
<i>Pennisetum setaceum</i>	Hawaii	19.8	-155.85	Bishop
<i>Pennisetum setaceum</i>	Hawaii	19.8	-155.85	Bishop
<i>Pennisetum setaceum</i>	Hawaii	19.71666667	-155.5	Bishop
<i>Pennisetum setaceum</i>	Hawaii	19.8	-155.9333333	Bishop

Appendix C. (Continued)

<i>Pennisetum setaceum</i>	Hawaii	19.68333333	-156.0166667	Bishop
<i>Pennisetum setaceum</i>	Hawaii	19.7	-155.4833333	Bishop
<i>Pennisetum setaceum</i>	Hawaii	19.78333333	-155.9166667	Bishop
<i>Pennisetum setaceum</i>	Hawaii	19.78333333	-155.9166667	Bishop
<i>Pennisetum setaceum</i>	Hawaii	19.15	-155.901	Bishop
<i>Pennisetum setaceum</i>	Hawaii	20.03333333	-155.6666667	Bishop
<i>Pennisetum setaceum</i>	Hawaii	20.03333333	-155.6666667	Bishop
<i>Pennisetum setaceum</i>	Hawaii	20.021901	-155.748722	Self
<i>Pennisetum setaceum</i>	Hawaii	20.026657	-155.719668	Self
<i>Pennisetum setaceum</i>	Hawaii	19.968287	-155.679235	Self
<i>Pennisetum setaceum</i>	Hawaii	20.003393	-155.67681	Self
<i>Pennisetum setaceum</i>	Hawaii	19.914149	-155.676803	Self
<i>Pennisetum setaceum</i>	Hawaii	19.949031	-155.831422	Self
<i>Pennisetum setaceum</i>	Hawaii	19.841223	-155.923234	Self
<i>Pennisetum setaceum</i>	Hawaii	19.793834	-150.005289	Self
<i>Pennisetum setaceum</i>	Hawaii	19.765	-155.946387	Self
<i>Pennisetum setaceum</i>	Hawaii	19.843439	-155.751685	Self
<i>Pennisetum setaceum</i>	Hawaii	19.836935	-155.771686	Self
<i>Pennisetum setaceum</i>	Hawaii	19.760929	-155.540793	Self
<i>Pennisetum setaceum</i>	Hawaii	19.769543	-155.585589	Self
<i>Pennisetum setaceum</i>	Hawaii	19.793619	-155.626245	Self
<i>Pennisetum setaceum</i>	Hawaii	19.893084	-155.67202	Self
<i>Pennisetum setaceum</i>	Hawaii	19.912581	-155.676023	Self
<i>Pennisetum setaceum</i>	Hawaii	19.993502	-155.676462	Self

Appendix C. (Continued)

<i>Pennisetum setaceum</i>	Hawaii	20.022246	-155.781532	Self
<i>Pennisetum setaceum</i>	Hawaii	20.023665	-155.760713	Self
<i>Pennisetum setaceum</i>	Hawaii	20.022748	-155.733691	Self
<i>Pennisetum setaceum</i>	Hawaii	20.026529	-155.705614	Self
<i>Pennisetum setaceum</i>	Hawaii	19.933254	-155.688792	Self
<i>Pennisetum setaceum</i>	Hawaii	19.91343	-155.702223	Self
<i>Pennisetum setaceum</i>	Hawaii	19.887842	-155.714693	Self
<i>Pennisetum setaceum</i>	Hawaii	19.833751	-155.792354	Self
<i>Pennisetum setaceum</i>	Hawaii	19.826049	-155.824513	Self
<i>Pennisetum setaceum</i>	Hawaii	19.806218	-155.842421	Self
<i>Pennisetum setaceum</i>	Hawaii	19.796552	-155.862556	Self
<i>Pennisetum setaceum</i>	Hawaii	19.948999	-155.830993	Self
<i>Pennisetum setaceum</i>	Hawaii	19.841199	-155.923004	Self
<i>Pennisetum setaceum</i>	Hawaii	19.764999	-155.945999	Self
<i>Pennisetum setaceum</i>	Kahoolawe	20.53888889	-156.63444444	Bishop
<i>Pennisetum setaceum</i>	Kauai	21.90166667	-159.60333333	Smithsonian
<i>Pennisetum setaceum</i>	Kauai	21.925	-159.52833333	Bishop
<i>Pennisetum setaceum</i>	Lanai	20.835	-156.91833333	Bishop
<i>Pennisetum setaceum</i>	Maui	20.88333333	-156.48333333	Smithsonian
<i>Pennisetum setaceum</i>	Maui	20.73888889	-156.3263889	Bishop
<i>Pennisetum setaceum</i>	Oahu	21.26166667	-157.81333333	Bishop
<i>Pennisetum setaceum</i>	Oahu	21.3	-157.83333333	Bishop
<i>Pennisetum setaceum</i>	Oahu	21.29	-157.79	Bishop
<i>Pennisetum setaceum</i>	Oahu	21.3117	-157.825	Bishop

Appendix C. (Continued)

<i>Pennisetum setaceum</i>	Oahu	21.389	-157.718	Self*
<i>Pennisetum setaceum</i>	Oahu	21.26	-157.809	Self*
<i>Schizachyrium condensatum</i>	Hawaii	19.29	-155.3	Smithsonian
<i>Schizachyrium condensatum</i>	Hawaii	19.29666667	-155.31	Bishop
<i>Schizachyrium condensatum</i>	Hawaii	19.4167	-155.3167	Bishop
<i>Schizachyrium condensatum</i>	Hawaii	19.37	-155.37	Bishop
<i>Schizachyrium condensatum</i>	Hawaii	19.43333333	-155.2666667	Bishop
<i>Schizachyrium condensatum</i>	Hawaii	19.40666667	-155.255	Bishop
<i>Schizachyrium condensatum</i>	Hawaii	20.06666667	-155.5166667	Smithsonian
<i>Schizachyrium condensatum</i>	Hawaii	19.53333333	-154.85	Bishop
<i>Schizachyrium condensatum</i>	Hawaii	19.53333333	-154.85	Bishop
<i>Schizachyrium condensatum</i>	Hawaii	19.3733	-155.21066	Bishop
<i>Schizachyrium condensatum</i>	Hawaii	19.44	-155.225	Bishop
<i>Schizachyrium condensatum</i>	Hawaii	19.64166667	-155.0833333	Smithsonian
<i>Schizachyrium condensatum</i>	Kauai	22.1267	-159.685	Smithsonian
<i>Schizachyrium condensatum</i>	Kauai	22.2	-159.4666667	Smithsonian
<i>Schizachyrium condensatum</i>	Oahu	21.4	-157.8333333	Bishop
<i>Schizachyrium condensatum</i>	Hawaii	19.362283	-154.967606	Self
<i>Schizachyrium condensatum</i>	Hawaii	19.398601	-154.920729	Self
<i>Schizachyrium condensatum</i>	Hawaii	19.432377	-154.937723	Self
<i>Schizachyrium condensatum</i>	Hawaii	19.361781	-154.976499	Self
<i>Schizachyrium condensatum</i>	Hawaii	19.369518	-154.96519	Self
<i>Schizachyrium condensatum</i>	Hawaii	19.288553	-155.130384	Self

Appendix C. (Continued)

<i>Schizachyrium condensatum</i>	Hawaii	19.631638	-155.035873	Self
<i>Schizachyrium condensatum</i>	Hawaii	19.553349	-154.985873	Self
<i>Schizachyrium condensatum</i>	Hawaii	19.399235	-154.955284	Self
<i>Schizachyrium condensatum</i>	Hawaii	19.583269	-155.0605	Self
<i>Schizachyrium condensatum</i>	Hawaii	19.427896	-154.947905	Self
<i>Schizachyrium condensatum</i>	Hawaii	19.680323	-155.124836	Self
<i>Schizachyrium condensatum</i>	Hawaii	19.436083	-154.945108	Self
<i>Schizachyrium condensatum</i>	Hawaii	19.681712	-155.142486	Self
<i>Schizachyrium condensatum</i>	Hawaii	19.68001	-155.161667	Self
<i>Schizachyrium condensatum</i>	Hawaii	19.23905	-155.44833	Self
<i>Schizachyrium condensatum</i>	Hawaii	19.532584	-155.129346	Self
<i>Schizachyrium condensatum</i>	Hawaii	19.482443	-155.155508	Self
<i>Schizachyrium condensatum</i>	Hawaii	19.45405	-155.177795	Self
<i>Schizachyrium condensatum</i>	Hawaii	19.35941	-155.377092	Self
<i>Schizachyrium condensatum</i>	Hawaii	19.353773	-155.222099	Self
<i>Schizachyrium condensatum</i>	Hawaii	19.385682	-155.244955	Self
<i>Schizachyrium condensatum</i>	Hawaii	19.407314	-155.328122	Self
<i>Schizachyrium condensatum</i>	Hawaii	19.420572	-155.304046	Self
<i>Schizachyrium condensatum</i>	Hawaii	19.43721	-155.303862	Self
<i>Schizachyrium condensatum</i>	Hawaii	19.434897	-155.27603	Self
<i>Schizachyrium condensatum</i>	Hawaii	19.441641	-155.314787	Self
<i>Schizachyrium condensatum</i>	Hawaii	19.45995	-155.343459	Self
<i>Schizachyrium condensatum</i>	Hawaii	19.462797	-155.348842	Self
<i>Schizachyrium condensatum</i>	Hawaii	19.476553	-155.362666	Self

CHAPTER 5

Growth, physiological and biochemical responses of C₄ and C₃ grasses to aspects of global change: Is there a true winner?

ABSTRACT

The grass family includes plants with C₄ (40%) and C₃ (60%) photosynthetic pathways. The two pathways vary in their response to temperature, light, and CO₂ concentrations. A rise in global atmospheric carbon dioxide concentration (CO₂) is estimated to reach concentrations of 600 ppm by the year 2050 ± 20 years and is expected to impact C₄ and C₃ grass distributions, since CO₂ is an important component of photosynthesis. However, differential responses to increases in CO₂ are expected for plants with either the C₃ or C₄ photosynthetic pathways due to differences in carbon uptake processes associated with each pathway. Studies have shown variation in C₄ grass species growth and physiological responses to elevated CO₂; in contrast, C₃ grasses have been relatively consistent with increased carbon uptake. Using growth chambers supplemented with either elevated CO₂ (600 ppm) or ambient CO₂ (390 ppm), four species of both C₄ and C₃ grasses were grown for 2 months. Half of the plants were also subjected to a drought treatment. I found that C₄ total plant biomass was significantly higher than C₃ total biomass for both ambient and elevated CO₂ conditions; however, under elevated CO₂ C₃ plants had a larger increase in total plant biomass (25%) compared with 12% for C₄ plants. Both C₃ and C₄ plants had higher carbon uptake (A_{max}) values under elevated CO₂ by 88% and 39%, respectively. Although, both C₃ and C₄ plants had comparable A_{max} values at elevated CO₂ conditions. C₃ plants subjected to drought conditions had reduced drought stress under elevated CO₂ conditions, whereas, C₄ plants

did not uniformly show evidence of reduced drought stress under increased CO₂. This reveals that both C₄ and C₃ grass species may be competitive in a world of rising CO₂ concentrations and that C₃ species may become more tolerant of drought.

INTRODUCTION

The atmospheric CO₂ concentration was stable at around 270 parts/million (ppm) for around 1000 years prior to the Industrial Revolution (Pearson and Palmer 2000). Since then the CO₂ concentration in the atmosphere has been increasing and has reached around 390 ppm today. This is 40% higher than at any time in the last 20 million years (Pearson and Palmer 2000). By 2050, CO₂ is expected to surpass 550 ppm (Prentice et al. 2001). Changes in temperature and precipitation will also be a product of increasing greenhouse gases of which atmospheric CO₂ is one of many (IPCC 2007).

The degree to which climate change impacts a particular area largely depends on latitude (IPCC 2007). High latitude areas have seen higher increases in temperature than low latitude, tropical areas (IPCC 2007). Nevertheless, changes in climate for tropical areas have been empirically shown (Giambelluca et al. 2008) and projected (Bradley et al. 2006; Timm and Diaz 2009). Previous studies have examined tropical plant growth in response to climate change and elevated CO₂ (Granados and Körner 2002; Hogan et al. 1991; Körner and Arnone 1992; Würth et al. 1998), however these studies mainly focused on tropical forest plants and only one study looked at differences between plants with different photosynthetic pathways (Ziska et al. 1991), although, Ziska et al. (1991) primarily studied plants with the C₃ photosynthetic pathway. Thus, more work needs to be done investigating the growth and physiological responses of tropical weeds.

Differences in the process of photosynthesis among vascular plant species can have important ecological consequences. The two most common photosynthetic pathways are C₄ and C₃ photosynthesis. There are anatomical and biochemical differences between C₄ and C₃ plants. Plants using the C₄ pathway have both mesophyll and bundle sheath cells and the enzyme PEP carboxylase to concentrate CO₂ at high concentrations as a substrate for Rubisco. In comparison, plants using the C₃ pathway undergo photosynthesis only in mesophyll cells and lower CO₂ concentrations in these cells means greater competition for Rubisco from O₂, resulting in an oxygenase reaction rather than carboxylation of RuBP, which in turn reduces the efficiency of carbon uptake or fixation (Sage 1999).

The variation in anatomical and biochemical structure between plants having C₃ and C₄ photosynthetic pathways causes unique responses to environmental variables. In C₄ plants, the photosynthetic response or carbon uptake (A) to intercellular CO₂ (C_i) concentrations consists of a steep slope of A versus rising CO₂, and a plateau where carbon uptake is saturated under relatively low intercellular CO₂ concentrations. In contrast, C₃ plants have a lower initial slope and a relatively high CO₂ saturation point. These differences help explain why C₄ plants often seem to show lower photosynthetic responses to elevated CO₂ compared to C₃ plants (Sage 1994). Furthermore, C₄ plants generally are characterized by having a high optimum temperature range (25°-30°C), a high light saturation point, minimal photorespiration and a higher nitrogen-use efficiency; while C₃ plants have a lower optimum temperature range

(usually < 20°C), a much lower light saturation point, susceptibility to photorespiration, and lower nitrogen-use efficiency (Sage and Kubien 2003). The physiological characteristics of C₄ plants give them an advantage in warm and arid environments compared to C₃ species.

Grass species are important for primary productivity, ecosystem function, and food security. Grasslands cover approximately one-fifth of the world's land area (Hadley 1993), with tropical grasslands storing about 26% of the carbon sequestered by terrestrial ecosystems (Long and Jones 1992) and C₄ grasses accounting for about 18% of the total global productivity (Ehleringer et al. 1997). In addition, some C₄ grasses have become invasive in the tropics and are known to alter ecosystem processes, including changing fire frequencies and intensities (D'Antonio and Vitousek 1992). Furthermore, C₃ and C₄ grasses are also the most important agricultural crops. For example, the most important grain crop is maize (*Zea mays*, C₄), which is grown in over 160 countries (Markelz et al. 2011). Many of the current and potential biofuels are also C₄ grass species (Somerville et al. 2010).

Despite the fact that about half of the world's grass species possess the C₄ photosynthetic pathway, most early studies focused solely on C₄ crop species (reviewed in Ghannoum et al. 2000), while fewer studies have tested the responses of either wild temperate or tropical C₄ grass species to elevated CO₂ (Wand et al. 1999). The proportion of land covered by grasslands, especially the savannas, is expected to increase with rising atmospheric CO₂ levels (Archer 1993). Thus, understanding how C₃ and C₄ grass species respond to aspects of

global change is vital for food and energy security, along with ecosystem health where these grasses have overlapping distributions.

Previous research using growth chambers and field studies have found that for C₃ plants, elevated CO₂ increases total biomass and water use efficiency (WUE), reduces stomatal conductance (g_s), and increases carbon uptake (A) (Ainsworth and Long 2005; Anderson et al. 2001; Leakey et al. 2009; Poorter 1993; Wand et al. 2001). C₃ grasses are expected to have less water-limitation in response to increasing CO₂ because of reduced stomatal conductance and leaf transpiration (Volk et al. 2000), with C₃ grasses having higher A under drought conditions when grown in elevated CO₂ chambers (Lecain et al. 2003). In C₃ plants, a down regulation or reduction of A through adjustments in photosynthetic enzymes has occurred in plants grown at elevated CO₂ (Sage 1994; Stitt 1991). A down regulation in C₃ plants is largely controlled by regulatory signals that reduce enzymes such as Rubisco in response to higher carbohydrate accumulation (Sage and Kubien 2003). However, a recent meta-analysis has shown that carbon uptake (A) remains the same with elevated CO₂ despite reductions in photosynthetic enzymes (Ainsworth and Rogers 2007).

The growth and physiological responses of C₄ grasses to elevated CO₂ are less consistent than in C₃ grass species (Ainsworth and Long 2005; Wand et al. 1999). A few studies have shown that C₄ plants do respond to elevated CO₂ with higher A (Anderson et al. 2001; Wand et al. 2001; Wand et al. 1999; Ziska and Bunce 1997). Increases in total plant biomass and water use efficiency have also been observed, along with decreases in stomatal conductance in C₄ grasses

at elevated CO₂ concentrations. In addition, photosynthetic down regulation or lower A at elevated CO₂ can also occur in C₄ plants, but there are numerous exceptions (Sage 1994). Leakey et al. (2009) and Markelz et al. (2011) have found that C₄ plants only respond to elevated CO₂ when the plants were experiencing drought stress and there was no CO₂ effect of carbon uptake (A) at any other time. Furthermore, a review reported that C₄ plants exhibit only a limited number of consistent changes with elevated CO₂, such as reduced stomatal conductance and increased leaf area, while, effects on leaf tissue N concentration varied among studies (Ghannoum et al. 2000).

C₄ plants can be divided into three biochemical subtypes, and there is a close relationship between the amount of precipitation and the distribution of grasses representing two of the three C₄ biochemical subtypes (Hattersley 1992; Schulze et al. 1996). The NADP-ME subtype has higher relative abundance in regions with higher rainfall, whereas the NAD-ME subtype occurs predominately in areas with low rainfall. The relative abundance of the PCK subtype has been shown to vary with precipitation depending on site (Cabido et al. 2008; Taub 2000).

Taub (2000) and Cabido et al. (2008) found that phylogenetic relationships such as C₄ grass subfamilies may have a closer relationship with precipitation than C₄ biochemical subtypes. Increases in atmospheric CO₂ concentrations could potentially alter the distributions of C₄ grasses if these subtypes or subfamilies respond differently to changes in the greenhouse gas (Fravolini et al. 2002). Variation in C₄ biochemical subtype and/or ancestral subfamily responses

to elevated CO₂ may be complicating the growth and physiological responses seen by C₄ grass species. Wand et al. (2001) found differences in growth responses of C₄ grass biochemical subtypes to elevated CO₂ with the NADP-ME subtype often responding more favorably. However, not all NADP-ME species respond favorably to elevated CO₂, suggesting species-specific growth and physiological responses to elevated CO₂ (Wand et al. 2001). In addition, Ziska and Bunce (1997) found inconsistencies in the growth responses of NAD-ME and NADP-ME C₄ subtypes to high CO₂ concentrations, however, the authors found that the more weedy species (fast growing, non-crop species) responded favorably to elevated CO₂. In addition, Kellogg et al. (1999), found that not all C₄ grasses responded in the same way to elevated CO₂. The study showed that variation among species within a genus in response to elevated CO₂ was as great as the variation between genera within a subfamily and between subfamilies within the Poaceae.

Based on the inconsistencies from previous studies, some authors have suggested that no general conclusions can be made about C₄ species' responses to elevated CO₂ based on subtype (LeCain and Morgan 1998; Ziska and Bunce 1997). Due to the inconsistently in C₄ species' responses to elevated CO₂, careful species selections must be made for physiological investigations in order to reach useful conclusions regarding the responses of the pathway (Christin et al. 2009).

In Hawai'i, the grass family is represented by 39 endemic species and 8 indigenous species in 19 genera (Wagner et al. 1999). Over the last 200 hundred

years, over 400 grass species having both the C₄ and C₃ photosynthetic pathways have been introduced into the Hawaiian Islands (Rotar 1968), with around 100 of these species becoming naturalized (Wagner et al. 1999). Most nonnative grasses that have altered the grass-fire cycle, which perpetuates the spread of nonnative grasses and increases the intensity and frequency of fire in Hawai'i, are C₄ grasses. These grasses are also outcompete native grasses and thus threaten native plant communities (D'Antonio and Vitousek 1992). Therefore, it is important to understand the potential ranges and limitations of C₄ grasses in Hawai'i, and how they may interact with C₃ grasses under aspects of global change such as elevated CO₂ and drought conditions. By understanding the factors that promote dominance of C₄ or C₃ grasses in the tropics, predictions about future invasions and impacts can be made. I hypothesized that NADP-ME (Panicoideae subfamily) C₄ grass species and C₃ grass species will both have growth, physiological, and biochemical responses to elevated CO₂ under well-watered and drought conditions. I also hypothesized that the effects of drought will be reduced for both C₄ and C₃ grass species under elevated CO₂.

METHODS

CO₂ and Drought Treatments

Eight grass species were grown for the experiment, four C₄ and four C₃ (Table 5.1). Grass species were selected based on their broad distributions and weedy growth characteristics (naturalized, fast growing, and common). Grass seeds for all species were collected on the island of Hawai'i at multiple sites. Seeds were hand sorted and germinated in trays in a Percival incubator at 25/16 °C. After 10 days, 32 seedlings of each species (16 seedlings/chamber) were transplanted individually into containers in a 2:1:1 mixture of potting soil, volcanic rock, and perlite to mimic natural soil conditions and grown in growth chambers (94.3 x 72.4 x 45.7 cm) built following the design of Jahren et al. (2008). The chambers were calibrated to either ambient atmospheric CO₂ levels (390 ppm ± 30 ppm) or elevated atmospheric CO₂ levels (600 ppm ± 30 ppm), with CO₂ supplied from a pressurized gas tank. The elevated CO₂ level was chosen based on predictions for atmospheric CO₂ concentrations for the year 2050 (Prentice et al. 2001). The plants were grown with Super HPS EN Enhanced Spectrum grow lights (Eye Lighting International of North America, Inc., Mentor, OH) on a 12hr/12hr light/dark cycle at circa 600 to 800 µmol m⁻²s⁻¹ of photosynthetic active radiation (PAR). Plants were moved within the chambers every other day to diminish effects of potential spatial variations in PAR or other variables within the chambers. Plants were watered every other day with 30 ml of water for four weeks before beginning drought treatments. Plants were watered with 30 ml of water because this amount of water was observed to saturate the

soil and drain out the bottom of the cone pots. At 4 weeks, half of the plants (8 plants/species/chamber) were randomly assigned to a drought treatment in both growth chambers. Plants in the drought treatment were only watered once a week for four weeks with 30 ml of water. The experimental design was replicated twice; once in the fall from September to November 2010 and again in the spring from February to April 2011, swapping chambers for the CO₂ treatments.

Temperature and humidity were monitored in the chambers using HOBO loggers (Onset Computer Corporation, Bourne, MA) and CO₂ was monitored using a Telaire temperature/CO₂ monitor (General Electric, Wilton, CT). All plants were harvested after gas exchange, leaf water relations, and chlorophyll a measurements were made at the end of the experiment. Plants were dried at 45°C for 1 week. Plant biomass was then measured and recorded.

Gas Exchange Measurements

Leaf level gas exchange measurements were made on all grass species and treatments during the last 7 days of the experiment for both experiment periods (fall and spring). Four individual plants per species per treatment were measured. Leaf-level gas exchange measurements were made at the CO₂ levels the plants were grown at (either 390 ppm or 600 ppm). Measurements were made on the youngest, fully expanded leaves using a CID Photosynthesis monitor (CID Bio-science Inc., Camas, WA) between 9am and 3pm local time at a PAR of 1500 µmol m⁻²s⁻¹ and air temperature of 28.0°C. Leaves were left at these environmental conditions for ten minutes before photosynthetic carbon uptake maximum (A_{max}) was recorded. Concurrent stomatal conductance (g_s)

measurements were also made. Instantaneous water use efficiency (WUE) values were subsequently calculated from A_{max}/g_s .

Chlorophyll a fluorescence measurements

Chlorophyll a measurements were made using a CID Photosynthesis monitor with a modulated fluorometer (CID Bio-science Inc., Camas, WA). Light-adapted quantum yield of photosystem II (Φ_{PSII}) was calculated as $(F_m' - F_s)/F_m'$ (F_m' = maximal fluorescence of a light-adapted leaf with all PSII reaction centers closed following a saturating light pulse; F_s = fluorescence during steady state of photosynthesis). Φ_{PSII} measurements were made at the same time as leaf gas exchange measurements. Dark-adapted photochemical efficiency (F_v/F_m) was calculated as $F_v = F_m - F_0$ (F_0 = fluorescence of dark-adapted leaf with al PSII reaction centers open; F_m = maximal fluorescence of a dark-adapted leaf with all PSII reaction centers closed following a saturating light pulse (Ghannoum et al. 2003)). F_v/F_m measurements were made on leaves after plants had been dark-adapted for 12 hours.

Leaf water relations

At the end of the experiment, relative water content (RWC) measurements were made on all plants. Freshly-cut leaf sections were immediately weighed, then put in petri-dishes with distilled water overnight at room temperature. Turgid leaf sections were then weighed and allowed to dry at 45°C for 24 hours. Oven dried biomass was then determined. The leaf relative water content (RWC) of each sample was calculated following Carmo-Silva et al. (2007), by the equation

RWC = 100* (FW-DW)/(TW-DW), where FW, DW, and TW are the fresh, dry, and turgid weight, respectively.

Nitrogen Concentration

Half of the plants both C₄ and C₃ species were randomly chosen for nitrogen content analysis. Plants were analyzed at the Isotope Biogeochemistry Lab at the University of Hawai'i at Manoa using mass spectrometers. Leaf N percent (N%) was then subsequently calculated based on N mg/mg of leaf.

A/C_i Response Curves

CO₂ uptake (*A*) versus intercellular CO₂ concentration (C_i) curves (A/C_i response curves) were performed at the end of the experiment (8 weeks) using a LI-COR 6400 (LI-COR Biosciences, Lincoln, NE). Due to time limitations, A/C_i response curves were performed on a subset of 2 species per photosynthetic pathway with 3 replicates per species per treatment. A/C_i responses were determined at 10 different cuvette CO₂ concentrations (50, 100, 125, 150, 250, 350, 500, 700, 900, 1200) for C₃ plants and 9 different cuvette CO₂ concentrations (35, 50, 80, 110, 150, 250, 350, 700, 1000) for C₄ plants. Leaf temperatures were ~28°C and the light level was 1500 μmol m⁻²s⁻¹.

A/c_i response curves for C₃ plants were analyzed using the A/C_i curve fitting utility version 1.1 by Sharkey et al. (2007). The maximum carboxylation rate of rubisco (V_{cmax}) and the maximum electron transport rate leading to ribulose-1,5-bisphosphate (RuBP) regeneration (J_{max}) were calculated using Sharkey et al. (2007). C₄ plants were analyzed using the function $y=a(1-e^{-bx})^c$ in SigmaPlot version 12. The efficiency of the PEP carboxylase CO₂ pump (V_{pmax})

was determined using the linear slope of the portion of the A/C_i curve in the vicinity of 50 ppm and the equation $V_{p\max} = (\text{slope} * g_i * K_p) / (g_i - \text{slope})$; where $g_i = 2 \text{ mol m}^{-2}\text{s}^{-2}$ and $K_p = 80 \mu\text{bar}$ (von Caemmerer and Furbank 1999).

Data Analysis

Total plant biomass (g), aboveground biomass (g), belowground biomass (g), photosynthetic carbon uptake maximum (A_{\max}), stomatal conductance (g_s), instantaneous water use efficiency (WUE or A_{\max}/g_s), relative water content (RWC) and light-adapted quantum yield of photosystem II (Φ_{PSII}) were analyzed using a mixed model analysis of variance (ANOVA) in Systat 13 (Systat Software, Inc., Chicago, IL). The fixed effects of CO_2 , water, and photosynthetic pathway, along with the random effects of block (either fall or spring) and species nested within photosynthetic pathway were analyzed. Species was considered a random effect because species were selected to be representative of the broader group of naturalized grasses on the island of Hawai'i, thus different combinations of species could have been used in this experiment. Dark-adapted photochemical efficiency (F_v/F_m), leaf nitrogen percent (N%) were analyzed using the same model as above, but since they were only measured during the spring experiment, there was no block variable in the model. Maximum rate of rubisco carboxylation ($V_{c\max}$), maximum electron transport rate of RuBP regeneration (J_{\max}), and maximum rate of phosphoenolpyruvate carboxylase (PEPC) ($V_{p\max}$) were analyzed by photosynthetic pathway using a mixed model analysis of variance (ANOVA) in Systat 13 (Systat Software, Inc., Chicago, IL) with CO_2 and water as fixed effects and species as a random factor. Three-way interactions

were analyzed for all variables, but removed from the model if they were not significant.

RESULTS

Experimental Growth Chamber Conditions

Temperature and relative humidity conditions for chambers and experimental periods (fall versus spring) were relatively similar (Figure 5.1). There was no clear difference for temperature or relative humidity between fall or spring experimental periods.

Plant Biomass

On average the biomass of C₃ and C₄ plants increased significantly (by 25% and 12%, respectively) under elevated CO₂, compared to ambient conditions (Figure 5.2); there was no CO₂ by photosynthetic pathway interaction (Figure 5.2; Table 5.2). Across all treatments, C₄ plants had significantly higher biomass than C₃ plants (Figure 5.2; Table 5.2). Across both photosynthetic pathways, the well-watered treatment had significantly higher total biomass (mean = 0.652 g, ± SE = 0.015 g) than drought treatments (mean = 0.552 g, ± SE = 0.012 g) (Table 5.2). C₄ species had higher total biomass under drought conditions compared with C₃ species. The magnitude of biomass decrease under drought conditions varied by species within photosynthetic pathway, as indicated by a significant water by species within photosynthetic pathway (species(PP)) interaction. *Dactylis glomerata* and *Holcus lanatus* were more negatively impacted by drought than the other two C₃ species (*Bromus diandrus* and *Ehrharta calycina*) while *Digitaria insularis* and *Setaria parviflora* were more negatively impacted by drought than the other C₄ species (*Cenchrus ciliaris* and *Paspalum dilatatum*) (Figure 5.3; Table 5.2).

Aboveground and Belowground Biomass

On average the aboveground biomass of C₃ and C₄ plants increased significantly (by 25% and 12%, respectively) under elevated CO₂, compared to ambient conditions (Figure 5.2; Table 5.2). Again, across all treatments, C₄ plants had significantly higher aboveground biomass than C₃ plants (Figure 5.2; Table 5.2). Across both photosynthetic pathways, well-watered plants had 19% more aboveground biomass than drought plants (Table 5.2). On average the belowground biomass of C₃ and C₄ plants increased significantly (by 27% and 12%, respectively) under elevated CO₂, compared to ambient conditions (Figure 5.2; Table 5.2). Under elevated CO₂, C₃ and C₄ plants did not have significant differences in belowground biomass, suggesting that belowground C₃ plants may be more competitive with C₄ plants under elevated CO₂ (Figure 5.2; Table 5.2). The percent increases in belowground biomass for C₃ and C₄ plants, respectively, are similar to those determined for both total and aboveground biomass revealing that both aboveground and belowground biomass for C₃ and C₄ plants responded in the same proportions to the effects of elevated CO₂. There was also a significant water by species within photosynthetic pathway (species(PP)) interaction for both above and belowground biomass. C₄ plants tended to have higher aboveground biomass for well-watered and drought conditions compared with C₃ plants, however, for below ground biomass this trend was not seen and the growth response to water treatments depended more on species (Figure 5.3; Table 5.2). For both photosynthetic pathways, species that had higher aboveground biomass tended to contribute less to belowground

biomass. However, the relative differences between well-watered and drought treatments for each species were similar for both above and belowground biomass (Figure 5.3). This suggests that C₃ plants may be more competitive underground with C₄ plants under elevated CO₂.

Carbon Uptake (A_{max})

Across both photosynthetic pathways, carbon uptake rates (A_{max}) were on average 60% higher under the elevated CO₂ treatment compared with ambient CO₂ conditions (Figure 5.4; Table 5.2). Carbon uptake rates also had a significant photosynthetic pathway (PP) by CO₂ interaction (Table 5.2). C₃ plants had on average A_{max} rates that were 88% higher under elevated CO₂ than under ambient CO₂ concentrations, while, C₄ plants had A_{max} rates only 39% higher than ambient conditions (Figure 5.4). The magnitude of increase in A_{max} in response to increased CO₂ was larger for C₃ species than C₄ species, but both pathways had species that responded differently to elevated CO₂, as indicated by a significant CO₂ by species(PP) interaction (Figure 5.5; Table 2). Overall, carbon uptake rates at elevated CO₂ were comparable between C₃ and C₄ photosynthetic pathways (mean = 13.98 ± SE = 0.5 versus 13.44 ± SE = 0.38, respectively). I also found a significant water by species(PP) interaction (Figure 5.6). Three out of the four C₄ species had higher A_{max} values under drought conditions. C₄ A_{max} values under drought conditions were more consistent than C₃ A_{max} values under drought (Figure 5.6). Across both photosynthetic pathways, drought significantly reduced A_{max} rates by 42% (well-watered plants A_{max} mean = 13.06 ± SE = 0.34 versus 9.19 ± SE = 0.33 for drought plants).

Stomatal Conductance (g_s)

Across photosynthetic pathways, stomatal conductance (g_s) was not significantly different under elevated CO₂ (mean = 59.55, ± SE = 4.41) compared to ambient conditions (mean = 58.77 ± SE = 4.03). However, C₃ plants had significantly larger stomatal conductance (mean = 87.16 ± SE = 4.55) compared with C₄ plants (mean = 31.16 ± SE = 1.61) (Figure 5.4; Table 5.2). Water had a significant effect on C₃ and C₄ plants stomatal conductance (Table 5.2). The stomatal conductance of C₃ plants was reduced 159% when grown under drought treatments compared to well-watered treatments. While C₄ plants had reduced stomatal conductance of 96% when grown under drought treatment. A significant water by CO₂ by species(PP) interaction was found, indicating a wide range of responses, especially within C₃ species (Figure 5.7, Table 5.2). C₃ species had consistently larger stomatal conductance under elevated CO₂ and drought compared to ambient CO₂ and drought. This may have contributed to overall non-significant effects of CO₂ on stomatal conductance (Figure 5.4; Table 5.2).

Instantaneous Water Use Efficiency (WUE)

Across photosynthetic pathways and water treatments, WUE was significantly lower in the ambient CO₂ treatment (mean = 0.33 ± SE = 0.05) in comparison to the elevated CO₂ treatment (mean = 0.42 ± SE = 0.05) (Figure 5.4; Table 5.2). C₃ plants had 32% higher WUE under elevated CO₂, while C₄ plants had 25% higher WUE under elevated CO₂ relative to the ambient CO₂ treatment. However, overall WUE was significantly higher for C₄ plants in both

ambient and elevated CO₂ conditions (Figure 5.4; Table 5.2). There was a significant water by species(PP) interaction (Figure 5.6; Table 5.2). The C₄ plant *Paspalum dilatatum* had the highest increase in WUE, whereas the C₃ plant, *Bromus diandrus*, barely increased in WUE under drought conditions. Across photosynthetic pathways and CO₂ treatments, WUE was significantly higher when grown under drought treatments (mean = 0.52 ± SE = 0.07) compared with well-watered treatments (mean = 0.24 ± SE = 0.07). C₄ plants increased in WUE under drought by 124% compared to ambient conditions, whereas C₃ plants increased in WUE by 100% when exposed to drought conditions.

Relative Water Content (RWC)

A significant water by CO₂ by species(PP) interaction was found, reflecting variability in response of RWC to CO₂ and drought at the species level (Figure 5.7, Table 5.2). Drought treatments significantly reduced RWC on average by 188 % compared with well-watered treatments (Table 5.2). There was no overall influence of CO₂ or photosynthetic pathway (PP) on RWC (Table 2).

Leaf Nitrogen

There was a significant reduction in leaf percent nitrogen between the ambient CO₂ treatment (mean = 0.015 ± SE = 0.001) and the elevated CO₂ treatment (mean = 0.012 ± SE = 0.001). C₃ plants experienced a 31% reduction in leaf percent nitrogen under elevated CO₂ conditions compared with plants grown under ambient conditions. C₄ plants experienced only an 18% reduction when exposed to elevated CO₂ compared with plants grown in ambient CO₂ concentrations (Figure 5.8; Table 5.3). There was a significant water by

photosynthetic pathway (PP) interaction (Figure 5.8; Table 5.3); with C₃ plants losing 35% of their leaf nitrogen under drought conditions compared to well-watered conditions, while C₄ plants lost only 6% under drought conditions. Across photosynthetic pathways, the well-watered treatment significantly increased leaf percent nitrogen (mean = 0.015 ± SE = 0.001) compared to drought treatments (mean = 0.012 ± SE = 0.001) (Figure 5.8; Table 5.3).

Light-adapted quantum yield of photosystem II (Φ_{PSII})

Significant PP by water, CO₂ by water and PP by CO₂ by water interactions were found for Φ_{PSII} , indicating complex responses of Φ_{PSII} to CO₂ and water (Figure 5.9; Table 5.2). For C₄ plants, Φ_{PSII} was reduced by drought, but not affected by CO₂, whereas for C₃ plants, Φ_{PSII} was reduced in the drought treatment at ambient CO₂ but not at elevated CO₂.

Dark-adapted photochemical efficiency (F_v/F_m)

A water by CO₂ interaction was significant for F_v/F_m , indicating that treatment responses to CO₂ depended on the water treatment (Figure 5.10; Table 5.3). A significant effect of species(PP) and water by species(PP) interaction was also found for F_v/F_m (Figure 5.6; Table 5.3), indicating variability among species. F_v/F_m had significantly higher values for well-watered and elevated CO₂ treatments compared to drought and ambient CO₂ treatments (Table 5.3).

A/C_i Response Curves

For the C₃ grass species, I found that there was both a down and up regulation of photosynthetic capacity with elevated CO₂ depending on C₃ species

(Figure 5.11). *Bromus diandrus* had a lower carbon uptake saturation (A_{sat}) at higher CO₂ compared with ambient CO₂, while *Ehrharta calycina* had a higher A_{sat} at elevated CO₂. For *E. calycina*, I found that under combined drought and elevated CO₂ conditions there was an up regulation of A_{sat} . *E. calycina* had higher A_{sat} under drought and elevated CO₂ conditions compared with drought and ambient CO₂ conditions, however *B. diandrus* had comparable A_{sat} in drought conditions grown under both elevated and ambient CO₂ (Figure 5.12). Both C₃ species had a higher operating internal CO₂ when grown at elevated CO₂ compared with ambient CO₂ conditions in both well-watered and drought conditions (Figures 5.11 -12).

For C₄ grass species, there was an up regulation of A_{sat} under combined elevated CO₂ and well-water conditions (Figure 5.13). Under combined elevated CO₂ and drought conditions, C₄ species had different responses. *Cenchrus ciliaris* had an up regulation of A_{sat} , while *Paspalum dilatatum* had a down regulation of A_{sat} (Figure 5.14). For both C₄ species, the operating C_i concentrations were in the responsive part of the A/c_i curve when grown under ambient CO₂ concentrations for both well-watered and drought treatments (Figures 5.13-14).

V_{cmax} and J_{max} for C₃ species

For V_{cmax} , responses of both C₃ species were consistent with A/c_i curves (Figures 5.11-12). There were no significant differences found for V_{cmax} (Figure 5.15), however, both C₃ species had higher V_{cmax} activity under elevated CO₂ and drought.

For J_{\max} , there was a significant species by CO_2 by water interaction ($p = 0.036$; Figure 5.16). J_{\max} increased or decreased with elevated CO_2 depending on if there was an up or down regulation of photosynthetic carbon uptake (A) under elevated CO_2 (Figures 5.11-12). In *B. diandrus*, J_{\max} was higher under combined elevated CO_2 and drought conditions compared to ambient CO_2 and drought conditions, whereas in *E. calycina*, J_{\max} had similar values for these treatments (Figure 5.16).

V_{pmax} for C₄ species

For V_{pmax} , there was a significant species by CO_2 by water interaction ($p = 0.019$; Figure 5.17). The response of V_{pmax} was higher for *P. dilatatum* under combined elevated CO_2 and well-watered conditions, but was decreased under combined elevated CO_2 and drought conditions, whereas for *C. ciliaris* V_{pmax} was substantially higher under combined elevated CO_2 and drought conditions (Figure 5.17).

DISCUSSION

There is a clear mechanistic basis for the stimulation of carbon uptake (A) by CO₂ in C₃ plants that is lacking in C₄ plants (Leakey et al. 2009). Photosynthetic theory indicates that C₄ plants should be saturated at ambient CO₂ concentrations and should not be stimulated by elevated CO₂ due to their CO₂-concentrating mechanism in their bundle sheath cells (Ghannoum et al 2000; Wand et al. 1999). However, under experimental conditions, it has been shown that C₄ plants do respond to elevated CO₂ (Anderson et al. 2001; Wand et al. 1999; Wand et al. 2001; Ziska and Bunce 1997). In a meta-analysis by Wand et al. (1999), both C₃ and C₄ biomass and carbon uptake rates increased under elevated CO₂, biomass by 44% and 33% respectively, carbon uptake rates (A) by 33% and 25%, respectively. However, the magnitude of response to elevated CO₂ has varied by study (Ainsworth and Long 2005). In my study, I found that both C₃ and C₄ grasses responded to elevated CO₂ with changes in total plant biomass, aboveground biomass, underground biomass, A_{max} and changes in their A/c_i curves. For A_{max} , C₃ grasses had a larger relative increase than C₄ grasses which is expected from photosynthetic theory. Although, there appeared to be a down-regulation of the C₃ grass, *Bromus diandrus*, under elevated CO₂ based on evidence from A/c_i curves, this down-regulation of *B. diandrus* may be due to root restriction in my experiment. I found that on average *B. diandrus* had almost twice as much root biomass as *Ehrharta calycina* for both ambient (mean = 0.223 ± SE = 0.015 versus mean = 0.108 ± SE = 0.007; respectively) and elevated CO₂ conditions (0.256 ± SE = 0.014 versus 0.134 ± SE = 0.015;

respectively). Down regulation of A_{sat} at elevated CO₂ is not common in the field (Ainsworth and Rogers 2007), but may be seen in greenhouse studies due root restrictions in pots (Sage 1994), thus *Bromus diandrus* might not experience a down regulation of A_{sat} under elevated CO₂ in the field. Furthermore, C₃ plants had comparable underground biomass to C₄ plants under elevated CO₂, suggesting that C₃ plants may be competitive belowground under elevated CO₂. In contrast, Wand et al. (1999) showed that C₃ grasses had higher underground biomass under elevated CO₂ compared with C₄ plants.

In contrast to photosynthetic theory, C₄ grasses did substantially respond to elevated CO₂ with increases in total plant biomass of 12%, A_{max} of 39% and an up regulation of A_{sat} in A/c_i curves. These increases in A_{max} and total biomass are comparable to findings from Poorter (1993) and Wand et al. (1999), but are higher than results from Ainsworth and Long (2005). Furthermore, my A/c_i curves for C₄ species showed that the operational CO₂ concentration was below the saturation portion of the A/c_i curve for ambient CO₂ conditions. This contrasts with photosynthetic theory that states that the operational CO₂ concentration should be in the saturated portion of A/c_i curve under ambient CO₂ concentrations(Ghannoum 2009; Sage and Kubien 2003), although, Wand et al. (2001) also found that C₄ species may have an up regulation of A_{sat} with elevated CO₂.

Reductions in leaf percent nitrogen (N%; gN/gleaf) were found for both C₄ and C₃ grasses that are consistent with responses from other studies (Ainsworth

and Long 2005; Wand et al. 1999). However, Lee et al. (2001) and Lee et al. (2011) found that decreased leaf N concentrations and elevated CO₂ could result in substantial down regulation of *A* over time. These responses may not have been seen in my study due to the shorter period of the experiment. Although, the lower leaf percent nitrogen in C₄ plants may have profound impacts under global change in the Hawaiian Islands. Large areas of the Hawaiian Islands and conservation areas have already become dominated with invasive C₄ grasses. Invasive grasses have been shown to reduce soil N availability (Reich et al. 2001) which perpetuates the replacement of C₃ vegetation (Sage and Kubien 2003). Furthermore, the establishment of C₄ grasses also increases fire frequency as has happened in the Hawaiian Islands. Fire volatizes N and reduces site N availability (Kauffman et al. 1995). In tropical soils, the reduction in soil nitrogen availability that follows the C₄ grass invasion reduces reestablishment of woody C₃ plants (Aide and Cavelier 1994). This phenomenon may become exacerbated under elevated CO₂. In grassland soils of limited N, elevated CO₂ can cause a reduction in site N availability due to higher plant tissue C:N ratios which makes leaf litter decompose more slowly. A meta-analysis by DeGraff et al. (2006) found a significant increase in soil C:N ratios under elevated CO₂ and suggests a potential decrease in soil N availability. This in turn should favor C₄ grasses over C₃ grasses due to their lower nitrogen requirement (Sage and Kubien 2003). Additionally, net N mineralization has been shown not to change under elevated CO₂ (DeGraff et al. 2006), but has been shown to increase under a warming climate in temperate areas (Rustad et al.

2001; Shaw and Harte 2001). Higher soil N should favor C₃ species over ecologically similar C₄ species in temperate latitude. However, weedy tropical C₄ grasses have shown positive growth responses to additional soil N enrichment in tropical areas, thus temperate latitude patterns may not apply at low latitude (Knapp and Medina 1999; Wedin and Tilman 1993). Furthermore, Shaw and Harte (2001) showed that increases in net mineralization did not occur in xeric soils with higher temperatures. Understanding N-dynamics may be critical in predicting changes in plant relative competitive abilities especially in grasslands (Tilman 1990) due to differences in nitrogen requirements for C₃ and C₄ plants. C₃ plants typically have to invest more nitrogen into photosynthetic enzymes compared with C₄ plants (Sage et al. 1987), thus they need more nitrogen to grow which limits their distributions in areas with low soil nitrogen.

My results reveal that elevated CO₂ may help to reduce some of the stresses of drought in C₃ species. A reduction in stomatal conductance (g_s) is one of the most ubiquitous responses to elevated CO₂ for both C₄ and C₃ species (Ainsworth and Long 2005; Anderson et al. 2001; Wand et al. 1999; Wand et al. 2001); while increases in WUE in response to elevated CO₂ has varied for C₄ and C₃ grasses depending on the study (Ainsworth and Long 2004; Anderson et al. 2001; Wand et al. 1999; Wand et al. 2001). These physiological responses to elevated CO₂ should have significant positive effects on the plant's water relations. In this study, I found that biomass, A_{max} , and WUE increased significantly with elevated CO₂ for both C₄ and C₃ plants. I also found that all C₃ species had values of g_s , Φ_{PSII} , and F_v/F_m comparable to non-drought values

when grown under drought combined with elevated CO₂ conditions. Data from A/c_i curves for C₃ plants also shows that there was an up regulation of A_{sat} , V_{cmax} and J_{max} under elevated CO₂ and drought compared to drought conditions at ambient CO₂. Many studies have suggested that stomatal limitations are primarily responsible for decreased A_{max} or A_{sat} in C₃ plants under moderate water stress due to decreases in internal CO₂ concentrations (Carmo-Silva et al. 2007; Ghannoum 2009; Lawlor and Cornic 2002). In my study, I found that physiological variables, Φ_{PSII} , F_v/F_m , V_{cmax}, and J_{max} increased with the combined effects of CO₂ and drought conditions, thus suggesting that stomatal limitations at ambient CO₂ reduced efficiency in these plants under drought conditions, and these limitations are alleviated by increased CO₂.

While C₄ plants had similar A_{max} , total biomass, and WUE responses when exposed to CO₂ and water, I did not see overall increases in g_s under combined elevated CO₂ and drought conditions. The stomatal limitations to photosynthesis in C₄ plants may be less important than in C₃ plants due to the specialized C₄ plant anatomy that concentrates CO₂ around Rubisco (Carmo-Silva et al. 2007). It is worth noting that due to the operation of a CO₂-concentrating mechanism, C₄ compared with C₃, photosynthesis is less affected by the initial reduction in g_s and internal CO₂ concentrations (Ghannoum et al. 2003), thus the plant is still up taking carbon (A) at high rates despite low g_s and does not need to increase g_s as substantially as in C₃ plants to maintain high A_{max} . This could partially explain why I did not see increases in stomatal conductance across all C₄ species as was seen with the C₃ species with combined elevated CO₂ and drought conditions.

However, I found that Φ_{PSII} was not improved with increased CO₂ under drought conditions for C₄ plants as was seen with the C₃ plants. Based on A/c_i curves, elevated CO₂ did not reduce the stress of drought seen in *Paspalum dilatatum* and a down regulation of A_{sat} and V_{pmax} occurred in this species. Due to the reductions in g_s, Φ_{PSII} , and the down regulation of *P. dilatatum* under drought stress, my study suggests that NADP-ME C₄ grasses may be inhibited under drought conditions by both stomatal and nonstomatal limitations. Ghannoum et al. (2003) also found that Φ_{PSII} in C₄ wild grass species were not responsive to elevated CO₂ under drought conditions and suggested that (A) inhibition may partially be independent of internal CO₂ concentrations and that water stress caused some biochemical (nonstomatal) inhibition of (A).

Ghannoum et al. (2003) found that Φ_{PSII} was affected at RWC below 80%, while Carmo-Silva et al. (2007) found that Φ_{PSII} and F_v/F_m were affected at RWC below 70%. Plants in this study had RWC below 70% in the drought treatment. However, in my study, F_v/F_m appeared to increase in efficiency with combined elevated CO₂ and drought conditions. Mixed responses of F_v/F_m to water stress in C₄ plants was seen in previous studies (Carmo-Silva et al. 2007; Ghannoum et al. 2003). Ripley et al. (2007) found a loss of the C₄ photosynthesis advantage over the C₃ type during drought conditions caused by reductions in biochemical limitations. The C₄ species used in my study are of the biochemical subtype NADP-ME and Ripley et al. (2007) suggested that these limitations may be more pronounced in this C₄ biochemical subtype due to its high prevalence in areas with high precipitation and may partially explain the paradox of decreasing C₄

NADP-ME species abundance in low precipitation areas, despite high WUE. Thus, the NADP-ME biochemical subtype may be more sensitive to reductions in precipitation due to biochemical limitations compared with the other two C₄ biochemical subtypes limiting its occurrence in areas with low precipitation. In a literature review, Ghannoum et al. (2009) found that biochemical limitations of C₄ photosynthesis may be caused by water stress and suggested that the biochemistry of C₄ photosynthesis is as or even more sensitive to water stress as that of C₃ photosynthesis, although the reasons for this biochemical inhibition are not clear (Ghannoum et al. 2009).

Many authors have found that inconsistencies in responses to elevated CO₂ within the C₄ biochemical subtype (Wand et al. 2001), within genera (Kellogg et al. 1999), or within subfamily (Kellogg et al. 1999), and weedy species (fast growing, non-crop species) may respond more than crop species (Ziska and Bunce 1997). This study used weedy species that are found throughout the Hawaiian Islands and used C₄ species from the same biochemical subtype and the same subfamily (Panicoideae) to minimize cofounding effects. I found that there was more variation in C₄ species response to water than CO₂, even though NADP-ME species should respond similarly to changes in precipitation or watering patterns. *Digitaria insularis* and *Setaria parviflora* are two C₄ species that are typically found on the windward side of the island of Hawai‘i, an area that receives high amounts of precipitation, while *Cenchrus ciliaris* and *Paspalum dilatatum* are typically found on the leeward side the island of Hawai‘i based on GPS points. *D. insularis* and *S. parviflora* had larger

reductions in total plant biomass and smaller increases in WUE under drought conditions compared to the other two C₄ species. They also contributed less to underground biomass for both well-watered and drought conditions compared to the other two species that are usually grown in drier areas in Hawai'i. This suggests that *D. insularis* and *S. parviflora* typically do not contribute large amounts of biomass to underground growth due to sufficient water supply in their natural habitats. However, these patterns were not translated in the response of A_{max} .

The NADP-ME subtype may have arose three times in different ancestral lines, thus there could be considerable genetic variation even within this subtype (Hattersley et al. 1992), which may give differential responses of species within the subtype to water availability or CO₂. However, all of my species were from the same subfamily (Panicoideae) and species responses to water appear to vary even within this relatively narrow phylogenetic grouping. Furthermore, Kellogg et al. (1999) found that species-specific diversity in internal growth regulation to elevated CO₂ was more important than phylogenetic origin. This may also apply to a plant's response to water. Where a species is located in an environment may be a better predictor of water stress tolerance than biochemical subtype or subfamily. In addition, Roumet and Roy (1996) concluded that life form and selective pressures were more important in determining CO₂ responses than generic affiliation. Ziska and Bunce (1997) found that weedy C₄ species responded more to elevated CO₂ than C₄ crop species. My data show that only A_{max} had a species(PP) by CO₂ interaction and for C₄ plants; the rest of the

variables I measured had more universally similar responses to elevated CO₂ for the photosynthetic pathway. Thus, this could be due to the fact that all the species in my study are weedy species in the Hawaiian Islands.

The results from this study contradict previous research that found that C₄ plants only responded to elevated CO₂ when exposed to drought treatments (Leakey et al. 2004; Leakey et al. 2006; Markelz et al. 2011), however previous studies were done with C₄ domesticated crop plants in the field. In early CO₂ research, C₄ crops showed smaller responses to elevated CO₂ than weedy C₄ species (Ziska and Bunce 1997). In addition, these studies found that reduced stomatal conductance through lower leaf transpiration under elevated CO₂ indirectly led to soil water conservation and increased performance of C₄ crop grasses under drought conditions. Ghannoum et al. (2009) suggested that during field studies such as FACE (Free-Air CO₂ Enrichment and enclosure studies), plants experience water stress at more natural rates than in pot studies. The pots in my study may have experienced an unnatural reduction in water availability that may have caused some of the observed biochemical inhibition such as low Φ_{PSII} and V_{pmax} in the C₄ plants.

Differences in methodologies have been suggested to explain why some studies show favorable A_{max}, A_{sat}, and biomass responses for C₄ species to elevated CO₂ while others do not (Leakey et al. 2009). Leakey et al. (2009) proposed that rooting volume is an important factor. Even when plants are well-watered in pots, the roots may not be able to absorb enough water to fully meet the requirements of the above ground biomass if pots limit root growth. Thus,

under elevated CO₂, water requirements of the plant could be reduced and alleviate the water stress of the plant giving the perception that elevated CO₂ directly stimulates carbon gain (Leakey et al. 2009). Pot volume was relatively small (346 cm³) in this study and may have contributed to the positive CO₂ response in C₄ biomass and carbon uptake that was observed. But at the same time, plant size was generally small (averaging 0.602 g total plant dry mass) due to the short-term nature of the experiment, and in most cases, roots did not seem to be crowded in the pots. A meta-analysis by Wand et al. (1999) concluded that pot size or exposure method (chamber type) did not determine the response of C₄ plants to elevated CO₂. Pots smaller less than <10 dm³ and plants grown in the ground did not have significant differences for total biomass or carbon uptake responses to elevated CO₂. Furthermore Wand et al. (1999) found no significant difference in C₄ A_{max} response under elevated CO₂ for indoor controlled growth chambers, outdoor enclosed greenhouse, or open-top chambers in the field or greenhouse. However, Wand et al. (1999) state that sample size was small for the C₄ plants.

This study had further light and temperature limitations that could have altered the growth and physiological responses of C₄ plants. Due to the relatively low light conditions in my chambers (600-800 $\mu\text{mol m}^{-2}\text{s}^{-1}$), PEP and RuBP regeneration rates may have been decreased, limiting carbon uptake rates for C₄ plants. Peisker and Henderson (1992) showed this at light conditions of < 500 $\mu\text{mol m}^{-2}\text{s}^{-1}$. Fravolini et al. (2002) also suggested that low light ($600 \pm 50 \mu\text{mol m}^{-2}\text{s}^{-1}$) conditions may have contributed to large increases in carbon isotope

discrimination (Δ) and bundle sheath leakiness (Φ) under elevated CO₂ conditions. However, Wand et al. (1999) showed that low light conditions did not significantly influence the response of C₄ or C₃ grasses to elevated CO₂ for total biomass or above ground biomass, respectively.

Along with increases in atmospheric CO₂, temperature will also increase in the future. Temperature was ~4°C above the transition temperature for C₄ and C₃ plants (Figure 5.1) in Hawai'i (Rundel 1980) suggesting that C₃ plants in this study were exposed to temperatures that they would experience under climate warming. C₄ plants may not have experienced high enough temperatures to reflect temperature increases in the future at sea level where temperatures may be around 30°C by around year 2050. However, *Paspalum dilatatum* and *Setaria parviflora* can be found at high elevations (around 1600-1700 m), while *Digitaria insularis* can be found at elevations up to 350 m suggesting that only *Cenchrus ciliaris*, a species that is found at low elevations, did not experience temperatures in the chambers that would be expected in the field with elevated CO₂ conditions in the year 2050. C₃ species in this study experienced higher temperatures in the chambers relative to where they are most commonly found in the field, but greater temperature changes are expected at higher elevations in Hawai'i, where C₃ grasses are most common (Giambelluca et al. 2008), and C₃ grasses can certainly be found growing in the field at mean monthly temperatures of 26-27 °C, which was around the mean temperature of the chambers.

My study complements other studies that have found that C₄ species respond to elevated CO₂ (Ainsworth and Long 2005; Anderson et al. 2001;

Kellogg et al. 1999; Morgan et al. 2011; Wand et al. 2001; Wand et al. 1999; Ziska and Bunce 1997). These results suggest that it may be incorrect to predict that C₄ plant species will lose their competitive edge in the future with elevated CO₂, especially in areas with low nitrogen. However, whether a species has weedy growth characteristics may impact the response of the photosynthetic pathway to global change. It is widely known that C₄ species, with their CO₂ concentrating mechanism, have increased efficiency of carboxylation in their bundle sheath cells, reducing photorespiration and stomatal conductance, while increasing overall water use efficiency. In contrast, C₃ plants are widely viewed as being at a disadvantage because of their lack of a CO₂ concentrating mechanism. In this study, I found that elevated CO₂ aided in a reduction of drought stress in C₃ plants. Some of the variables measured for C₄ plants had similar responses, while other variables were mixed showing evidence of interacting effects of CO₂ and drought. My results reveal that there may not be a consistent winner between C₄ grass and C₃ grass species under global change and that species selection and location of the studied area (area with low nitrogen content and/or low precipitation), may be more important in determining how an area will be impacted. These conclusions have implications for the Hawaiian Islands, which are now dominated by over 100 naturalized non-native grass species and many invasive C₄ grass species that have already altered ecosystems throughout the islands. Reductions in N tissue content with increased CO₂ and C₄ tolerance of low N could mean that high relative

abundances of invasive C₄ grasses could expand in degraded areas under global change impacts in the Hawaiian Islands.

My study contributes to previous research that has tried to untangle the multifaceted responses of C₄ plants to aspects of global change. It further draws attention to the gap in research in tropical areas examining plant responses to aspects of global change, such as elevated CO₂ and drought, and the need for future research.

LITERATURE CITED

- Aide TM, Cavelier J (1994) Barriers to lowland tropical forest restoration in the Sierra Nevada de Santa Marta, Colombia. *Restoration ecology* 2:219-229
- Ainsworth EA, Long SP (2005) What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO₂. *New phytologist* 165:351-372
- Ainsworth EA, Rogers A (2007) The response of photosynthesis and stomatal conductance to rising [CO₂]: mechanisms and environmental interactions. *Plant, cell & environment* 30:258-270
- Anderson LJ, Maherli H, Johnson HB, et al. (2001) Gas exchange and photosynthetic acclimation over subambient to elevated CO₂ in a C₃-C₄ grassland. *Glob. change biol.* 7:693-707
- Archer S (1993) Climate change and grasslands: a life-zone and biota perspective. In: Barker, MJ (ed) *Grasslands for Our World*. SIR Publishing, Wellington. pp. 396-402
- Bradley RS, Vuille M, Diaz HF, et al. (2006) Threats to water supplies in the tropical Andes. *Science* 312:1755
- Cabido M, Pons E, Cantero JJ, et al. (2008) Photosynthetic pathway variation among C₄ grasses along a precipitation gradient in Argentina. *J. biogeogr.* 35:131-140
- Carmo-Silva AE, Soares AS, da Silva JM, et al. (2007) Photosynthetic responses of three C₄ grasses of different metabolic subtypes to water deficit. *Functional plant biology* 34:204-213
- Christin PA, Salamin N, Kellogg EA, et al. (2009) Integrating phylogeny into studies of C₄ variation in the grasses. *Plant physiology* 149:82-87
- D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. rev. ecol. syst.* 23:63-87
- De Graaff MA, Van Groenigen KJ, Six J, et al. (2006) Interactions between plant growth and soil nutrient cycling under elevated CO₂: a metaanalysis. *Glob. change biol.* 12:2077-2091
- Ehleringer JR, Cerling TE, Helliker BR (1997) C₄ photosynthesis, atmospheric CO₂, and climate. *Oecologia* 112:285-299

Fravolini A, Williams D, Thompson T (2002) Carbon isotope discrimination and bundle sheath leakiness in three C₄ subtypes grown under variable nitrogen, water and atmospheric CO₂ supply. *Journal of experimental botany* 53:2261

Ghannoum O (2009) C₄ photosynthesis and water stress. *Annals of botany* 103:635-644

Ghannoum O, Caemmerer SV, Ziska L, et al. (2000) The growth response of C₄ plants to rising atmospheric CO₂ partial pressure: a reassessment. *Plant, cell & environment* 23:931-942

Ghannoum O, Conroy JP, Driscoll SP, et al. (2003) Nonstomatal limitations are responsible for drought-induced photosynthetic inhibition in four C₄ grasses. *New phytologist* 159:599-608

Giambelluca TW, Diaz HF, Luke MSA (2008) Secular temperature changes in Hawaii. *Geophys. res. lett.* 35

Granados J, Körner C (2002) In deep shade, elevated CO₂ increases the vigor of tropical climbing plants. *Glob. change biol.* 8:1109-1117

Hadley M (1993) Grasslands for sustainable ecosystems. In: Baker MJ, Crush JR, Humphreys LR (eds) *Proceedings of the 17th International Grassland Congress*, Hamilton, New Zealand, 21-27

Hattersley P (1992) C₄ photosynthetic pathway variation in grasses (Poaceae): its significance for arid and semi-arid lands. In: Chapman, GP (ed) *Desertified grasslands: their biology and management*. Linn. Soc. Symp. No. 13. Academic Press: London, UK, pp. 181-212

Hattersley P, Watson L (1992) Diversification of photosynthesis. In: Chapman GP (ed) *Grass evolution and domestication*. Cambridge University Press, Cambridge, UK, pp. 38-116

Hogan K, Smith A, Ziska L (1991) Potential effects of elevated CO₂ and changes in temperature on tropical plants. *Plant, cell & environment* 14:763-778

IPCC (2007) *Climate Change 2007: The Physical Science Basis: Working Group I Contribution to the Fourth Assessment Report of the IPCC*. Cambridge University Press, UK

Jahren AH, Crystal Arens N, Harbeson SA (2008) Prediction of atmospheric ¹³CO₂ using fossil plant tissues. *Reviews of Geophysics* 46

Kauffman JB, Cummings D, Ward D, et al. (1995) Fire in the Brazilian Amazon: 1. Biomass, nutrient pools, and losses in slashed primary forests. *Oecologia* 104:397-408

Kellogg EA, Farnsworth EJ, Russo ET, et al. (1999) Growth Responses of C₄ Grasses of Contrasting Origin to Elevated CO₂. *Annals of botany* 84:279

Knapp AK, Medina E (1999) Success of C₄ Photosynthesis in the Field: Lessons from Communities Dominated by. C₄ plant biology. pp. 251

Körner C, Arnone JA (1992) Responses to elevated carbon dioxide in artificial tropical ecosystems. *Science* 257:1672

Lawlor D, Cornic G (2002) Photosynthetic carbon assimilation and associated metabolism in relation to water deficits in higher plants. *Plant, cell & environment* 25:275-294

Leakey A, Bernacchi C, Dohleman F, et al. (2004) Will photosynthesis of maize (*Zea mays*) in the US Corn Belt increase in future [CO₂] rich atmospheres? An analysis of diurnal courses of CO₂ uptake under free-air concentration enrichment (FACE). *Glob. change biol.* 10:951-962

Leakey ADB, Ainsworth EA, Bernacchi CJ, et al. (2009) Elevated CO₂ effects on plant carbon, nitrogen, and water relations: six important lessons from FACE. *Journal of experimental botany* 60:2859

Leakey ADB, Uribe Larrea M, Ainsworth EA, et al. (2006) Photosynthesis, productivity, and yield of maize are not affected by open-air elevation of CO₂ concentration in the absence of drought. *Plant physiology* 140:779-790

LeCain DR, Morgan JA (1998) Growth, gas exchange, leaf nitrogen and carbohydrate concentrations in NAD-ME and NADP-ME C₄ grasses grown in elevated CO₂. *Physiologia Plantarum* 102:297-306

Lecain DR, Morgan JA, Mosier AR, et al. (2003) Soil and Plant Water Relations Determine Photosynthetic Responses of C3 and C4 Grasses in a Semi-arid Ecosystem under Elevated CO₂. *Annals of Botany* 92:41-52

Lee TD, Barrott SH, Reich PB (2011) Photosynthetic responses of 13 grassland species across 11 years of free-air CO₂ enrichment is modest, consistent and independent of N supply. *Glob. change biol.*

Lee TD, Tjoelker MG, Ellsworth DS, et al. (2001) Leaf gas exchange responses of 13 prairie grassland species to elevated CO₂ and increased nitrogen supply. *New phytologist* 150:405-418

Long S, Jones M (1992) Introduction, aims, goals and general methods. Primary Productivity of Grass Ecosystems of the Tropics and Sub-Tropics:1-24

Markelz R, Strellner RS, Leakey ADB (2011) Impairment of C₄ photosynthesis by drought is exacerbated by limiting nitrogen and ameliorated by elevated CO₂ in maize. Journal of experimental botany 62:3235

Morgan JA, LeCain DR, Pendall E, et al. (2011) C₄ grasses prosper as carbon dioxide eliminates desiccation in warmed semi-arid grassland. Nature 476:202-205

Pearson PN, Palmer MR (2000) Atmospheric carbon dioxide concentrations over the past 60 million years. Nature 406:695-699

Peisker M, Henderson S (1992) Carbon: terrestrial C₄ plants. Plant, cell & environment 15:987-1004

Poorter H (1993) Interspecific variation in the growth response of plants to an elevated ambient CO₂ concentration. Plant ecology 104:77-97

Prentice IC, Farquhar G, Fasham M, et al. (2001) The carbon cycle and atmospheric carbon dioxide. In:Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Dai X, Maskell K, Johnson CA (eds) Climate change 2001: the scientific basis. Cambridge University Press, Cambridge, UK, pp. 183–237

Reich PB, Tilman D, Craine J, et al. (2001) Do species and functional groups differ in acquisition and use of C, N and water under varying atmospheric CO₂ and N availability regimes? A field test with 16 grassland species. New phytologist 150:435-448

Ripley BS, Gilbert ME, Ibrahim DG, et al. (2007) Drought constraints on C₄ photosynthesis: stomatal and metabolic limitations in C₃ and C₄ subspecies of *Alloteropsis semialata*. Journal of experimental botany 58:1351-1363

Rotar P (1968) Grasses of Hawaii. University of Hawaii Press, Honolulu, HI,

Roumet C, Roy J (1996) Prediction of the growth response to elevated CO₂: a search for physiological criteria in closely related grass species. New Phytologist:615-621

Rundel PW (1980) The ecological distribution of C₄ and C₃ grasses in the Hawaiian Islands. Oecologia 45:354-359

Rustad L, Campbell J, Marion G, et al. (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* 126:543-562

Sage RF (1994) Acclimation of photosynthesis to increasing atmospheric CO₂: the gas exchange perspective. *Photosynthesis research* 39:351-368

Sage RF (1999) Why C₄ photosynthesis. In: Sage RF, Monson RK (eds) C₄ plant biology. Academic Press, San Diego, CA, pp. 3-16

Sage RF, Kubien DS (2003) Quo vadis C₄? An ecophysiological perspective on global change and the future of C₄ plants. *Photosynthesis research* 77:209-225

Sage RF, Pearcy RW, Seemann JR (1987) The nitrogen use efficiency of C₃ and C₄ plants: III. Leaf nitrogen effects on the activity of carboxylating enzymes in *Chenopodium album* (L.) and *Amaranthus retroflexus* (L.). *Plant physiology* 85:355

Schulze ED, Ellis R, Schulze W, et al. (1996) Diversity, metabolic types and δ 13 C carbon isotope ratios in the grass flora of Namibia in relation to growth form, precipitation and habitat conditions. *Oecologia* 106:352-369

Sharkey TD, Bernacchi CJ, Farquhar GD, et al. (2007) Fitting photosynthetic carbon dioxide response curves for C₃ leaves. *Plant, cell & environment* 30:1035-1040

Shaw MR, Harte J (2001) Response of nitrogen cycling to simulated climate change: differential responses along a subalpine ecotone. *Glob. change biol.* 7:193-210

Somerville C, Youngs H, Taylor C, et al. (2010) Feedstocks for lignocellulosic biofuels. *Science* 329:790

Stitt M (1991) Rising CO₂ levels and their potential significance for carbon flow in photosynthetic cells. *Plant, cell & environment* 14:741-762

Taub DR (2000) Climate and the US distribution of C4 grass subfamilies and decarboxylation variants of C₄ photosynthesis. *American journal of botany* 87:1211-1215

Tilman D (1990) Constraints and tradeoffs: toward a predictive theory of competition and succession. *Oikos*:3-15

Timm O, Diaz HF (2009) Synoptic-statistical approach to regional downscaling of IPCC Twenty-first-century climate projections: seasonal rainfall over the Hawaiian Islands. *Journal of climate* 22:4261-4280

Volk M, Niklaus PA, Körner C (2000) Soil moisture effects determine CO₂ responses of grassland species. *Oecologia* 125:380-388

von Caemmerer S, Furbank RT (1999) Modeling C₄ photosynthesis. In: Sage RF, Monson RK (eds) C₄ plant biology. Academic Press, San Diego, CA, pp. 173-211

Wagner WL, Herbst DR, Sohmer SH (1999) Manual of the Flowering Plants of Hawai'i, Vols. 1 and 2. University of Hawai'i and Bishop Museum Press, Honolulu, HI

Wand SJE, Midgley GF, Stock WD (2001) Growth responses to elevated CO₂ in NADP-ME, NAD-ME and PCK C₄ grasses and a C₃ grass from South Africa. *functional plant biology* 28:13-25

Wand SJE, Midgley GYF, Jones MH, et al. (1999) Responses of wild C₄ and C₃ grass (Poaceae) species to elevated atmospheric CO₂ concentration: a meta-analytic test of current theories and perceptions. *Glob. change biol.* 5:723-741

Wedin D, Tilman D (1993) Competition among grasses along a nitrogen gradient: initial conditions and mechanisms of competition. *Ecological monographs* 63:199-229

Würth M, Winter K, Körner C (1998) In situ responses to elevated CO₂ in tropical forest understorey plants. *Functional ecology* 12:886-895

Ziska L, Hogan K, Smith A, et al. (1991) Growth and photosynthetic response of nine tropical species with long-term exposure to elevated carbon dioxide. *Oecologia* 86:383-389

Ziska LH, Bunce JA (1997) Influence of increasing carbon dioxide concentration on the photosynthetic and growth stimulation of selected C₄ crops and weeds. *Photosynthesis research* 54:199-208

TABLES

Table 5.1. C₄ and C₃ species used in the experiment, and their subtype in the case of C₄ species (NADP-ME indicates NADP-malic enzyme)

Species	Photosynthetic Pathway	C ₄ subtype
<i>Bromus diandrus</i>	C ₃	-
<i>Dactylis glomerata</i>	C ₃	-
<i>Ehrharta calycina</i>	C ₃	-
<i>Holcus lanatus</i>	C ₃	-
<i>Cenchrus ciliaris</i>	C ₄	NADP-ME
<i>Digitaria insularis</i>	C ₄	NADP-ME
<i>Paspalum dilatatum</i>	C ₄	NADP-ME
<i>Setaria parviflora</i>	C ₄	NADP-ME

Table 5.2. Mixed model of analysis of variance for CO₂, Water, Photosynthetic Pathway (PP), Block and Species within Photosynthetic Pathway (Species(PP)) for total biomass (TB), aboveground biomass (AGB), belowground biomass (BGB), photosynthetic assimilation (A), stomatal conductance (g_s), instantaneous water use efficiency, relative water content, Φ_{PSII}

	TB	AGB	BGB	A	g_s	WUE	RWC	Φ_{PSII}
<i>Fixed Effects</i>								
CO ₂	**	**	**	**	ns	**	ns	ns
Water	**	*	ns	**	**	**	**	**
PP	**	**	ns	ns	**	**	ns	ns
CO ₂ *Water	ns	ns	ns	ns	**	Ns	ns	**
CO ₂ *PP	ns	ns	ns	**	ns	Ns	ns	ns
PP*Water	ns	ns	ns	ns	ns	Ns	ns	**
CO ₂ *Water*PP	rm	rm	rm	rm	rm	Rm	rm	**
<i>Random Effects</i>								
Block	ns	ns	ns	ns	ns	Ns	ns	ns
Species(PP)	ns	*	**	ns	ns	Ns	ns	**
Species(PP)*CO ₂	ns	ns	ns	**	ns	Ns	ns	ns
Species(PP)*Water	**	**	**	**	ns	**	ns	ns
Species(PP)*Water*CO ₂	rm	rm	rm	rm	**	Rm	**	rm

**, *, ns, rm for P ≤ 0.01, P ≤ 0.05, not significant, and removed from model respectively.

Table 5.3. Mixed model of analysis of variance for CO₂, Water, Photosynthetic Pathway (PP), and Species within Photosynthetic Pathway (Species(PP)) on F_v/F_m and Leaf Nitrogen Percent (N%).

	F _v /F _m	N%
<i>Fixed Effects</i>		
CO ₂	**	**
Water	**	**
PP	ns	Ns
CO ₂ *Water	**	Ns
CO ₂ *PP	ns	Ns
PP*Water	ns	*
CO ₂ *Water*PP	rm	Rm
<i>Random Effects</i>		
Species(PP)	**	Ns
Species(PP)*CO ₂	ns	Ns
Species(PP)*Water	**	Ns
Species(PP)*Water*CO ₂	rm	Rm

**, *, ns, rm for P ≤ 0.01, P ≤ 0.05, not significant, and removed from model respectively.

FIGURES

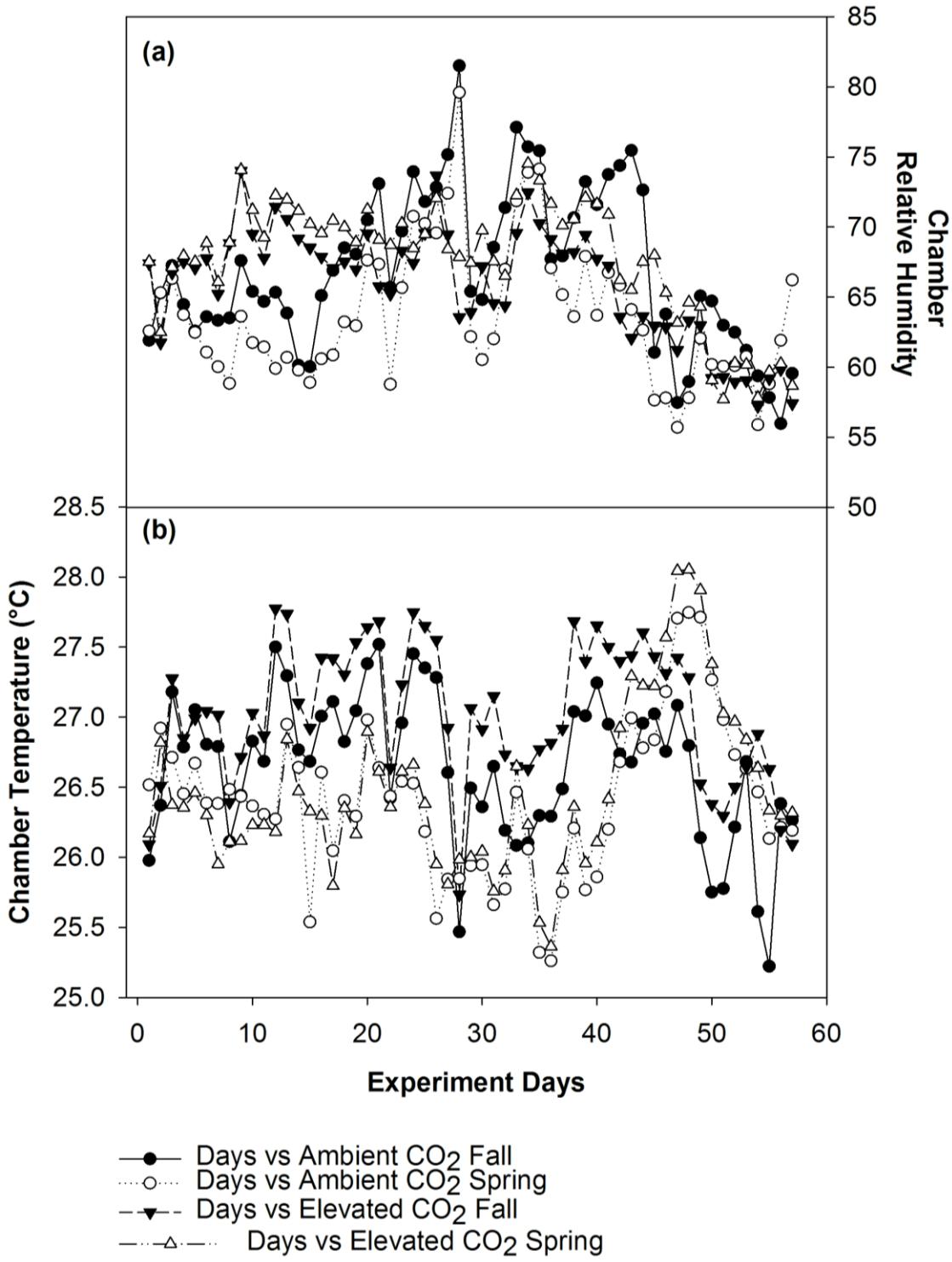


Figure 5.1. Mean daily relative humidity (a) and chamber temperatures (b) for ambient and elevated CO₂ chambers in the fall and spring experiments

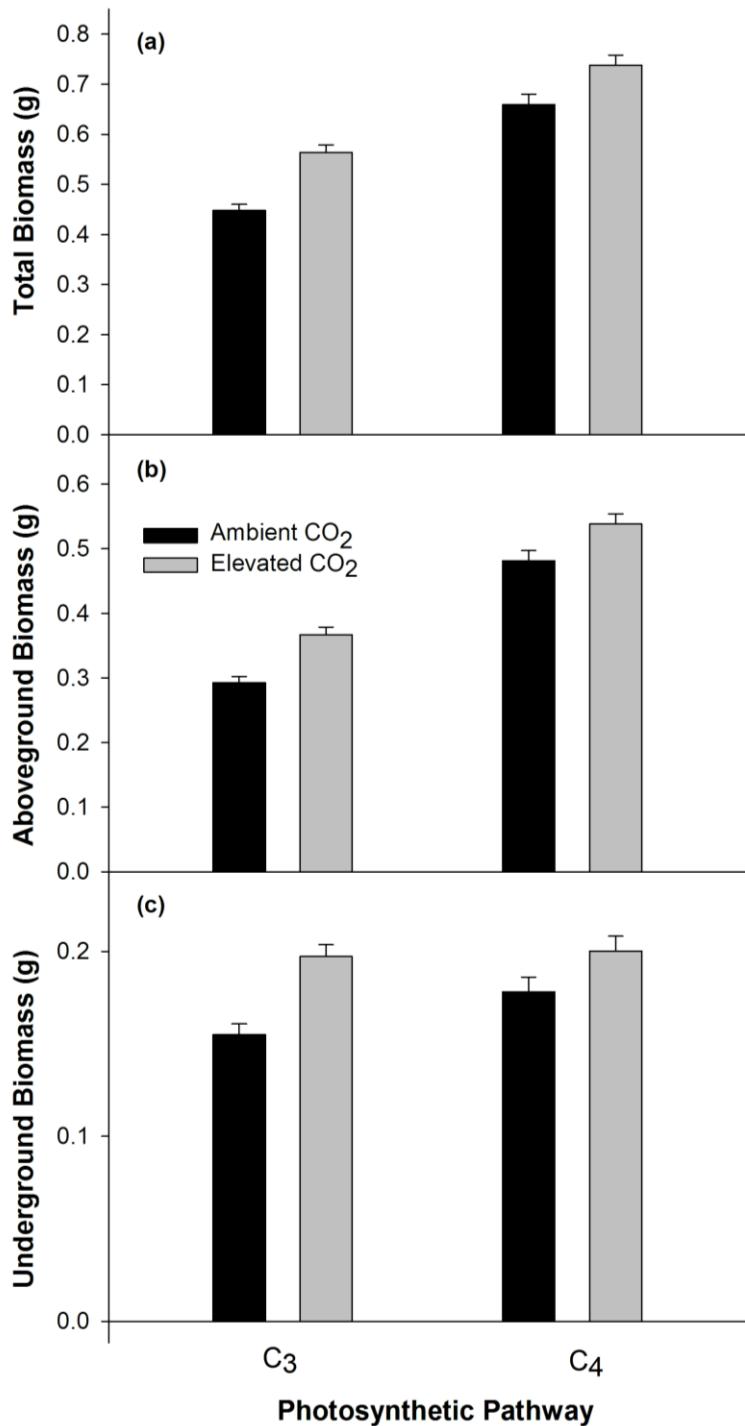


Figure 5.2. Mean values for the effects of CO₂ and Photosynthetic Pathway (PP) for the variables (a) total plant biomass, (b) aboveground biomass, and (c) underground biomass (+/- SE). All CO₂ effects are significant. All photosynthetic pathway effects are significant except for underground biomass.

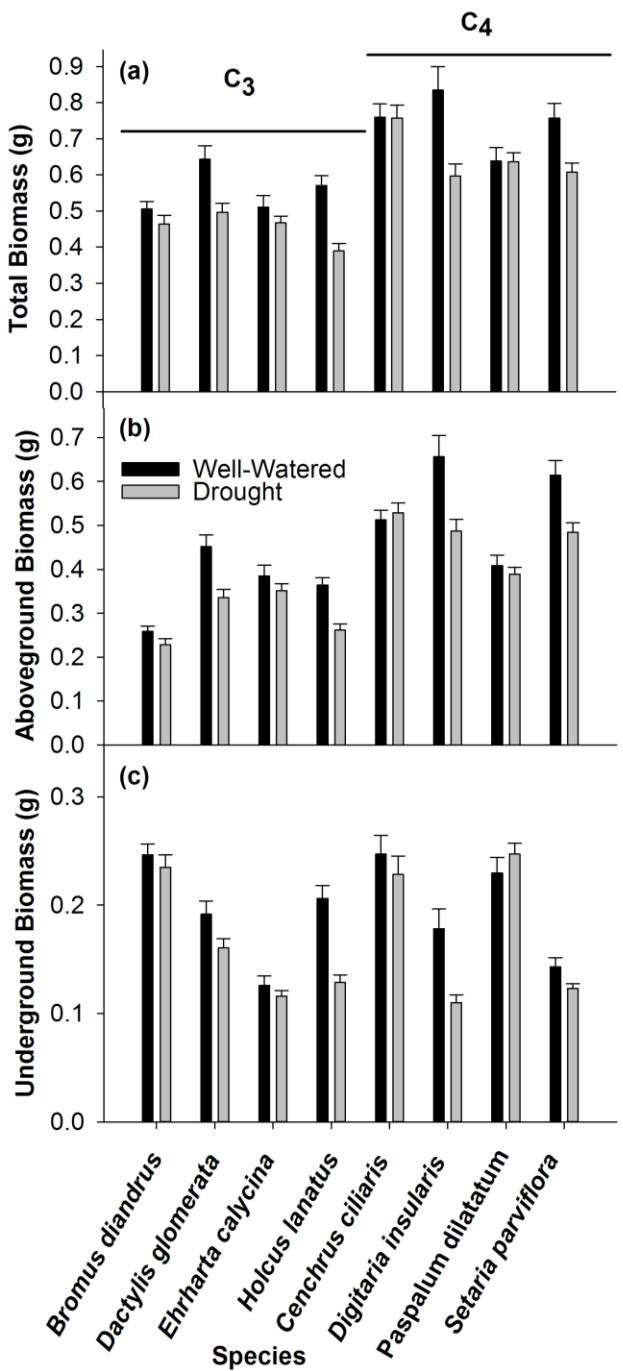


Figure 5.3. Mean values for the effects of water treatment on C₃ and C₄ grass species for the variables (a) total plant biomass, (b) aboveground biomass, and (c) underground biomass (+/- SE). Water treatment by species within photosynthetic pathway interactions are significant for all variables listed.

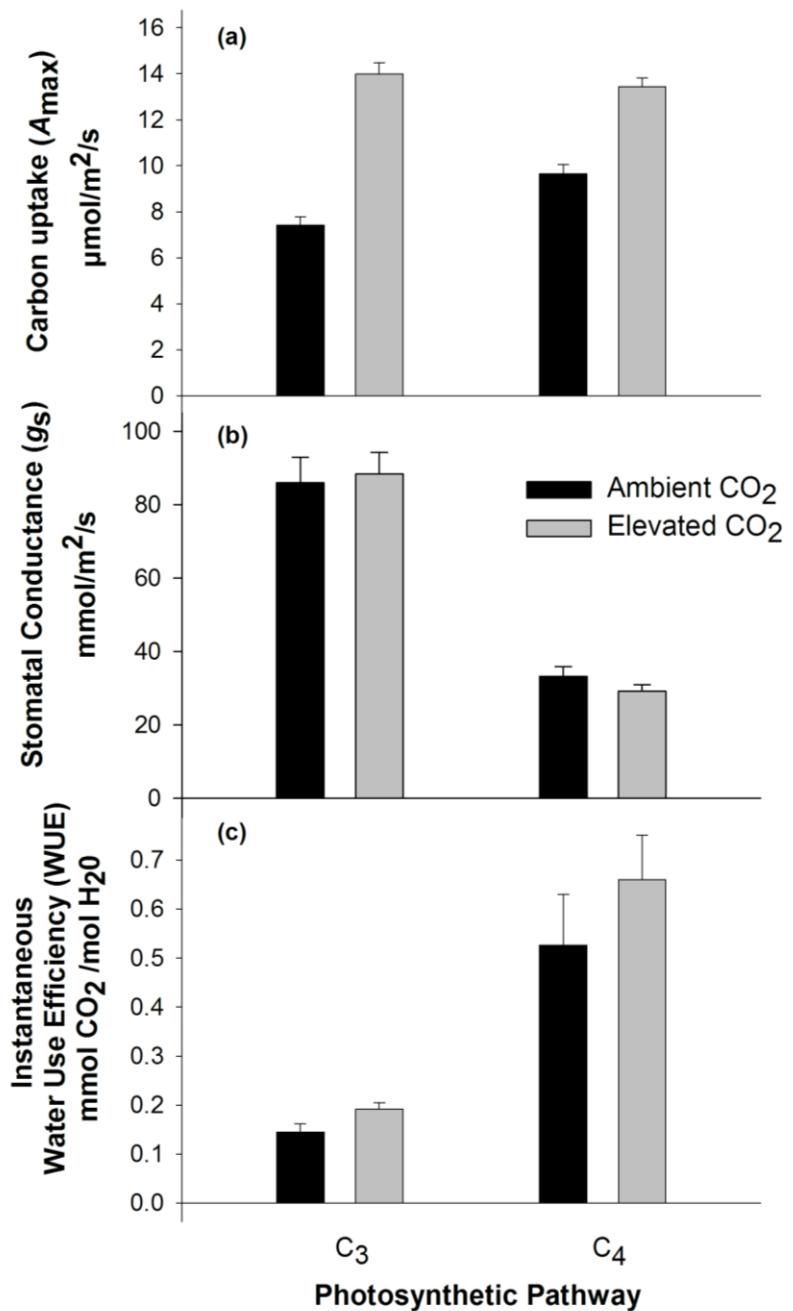


Figure 5.4. Mean values for the effects of CO₂ and Photosynthetic Pathway (PP) for the variables (a) A_{\max} , (b) g_s , and (c) WUE (+/- SE). All CO₂ effects are significant except g_s . All photosynthetic pathway effects are significant except A_{\max} .

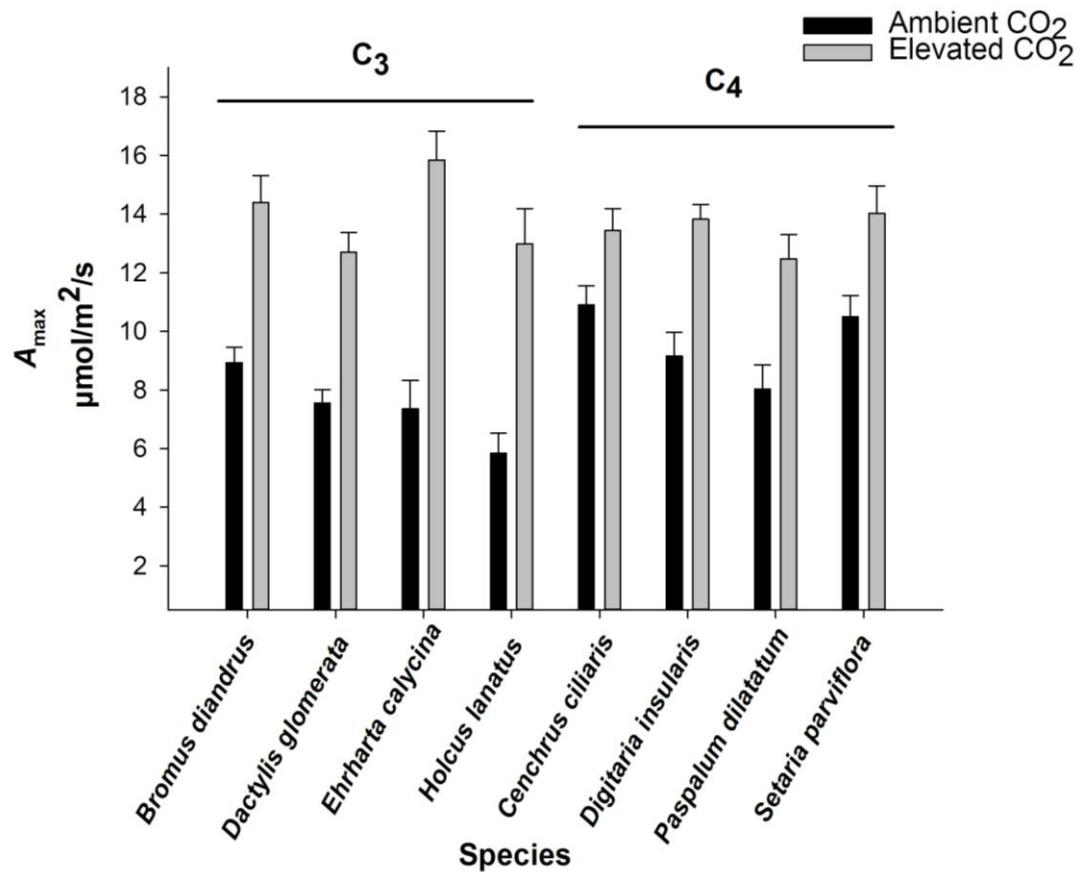


Figure 5.5. Mean values among species variation in A_{\max} (+/- SE) in response to CO_2 levels. There is a significant interaction of CO_2 by photosynthetic pathway and a significant interaction of CO_2 by species within photosynthetic pathway for A_{\max} .

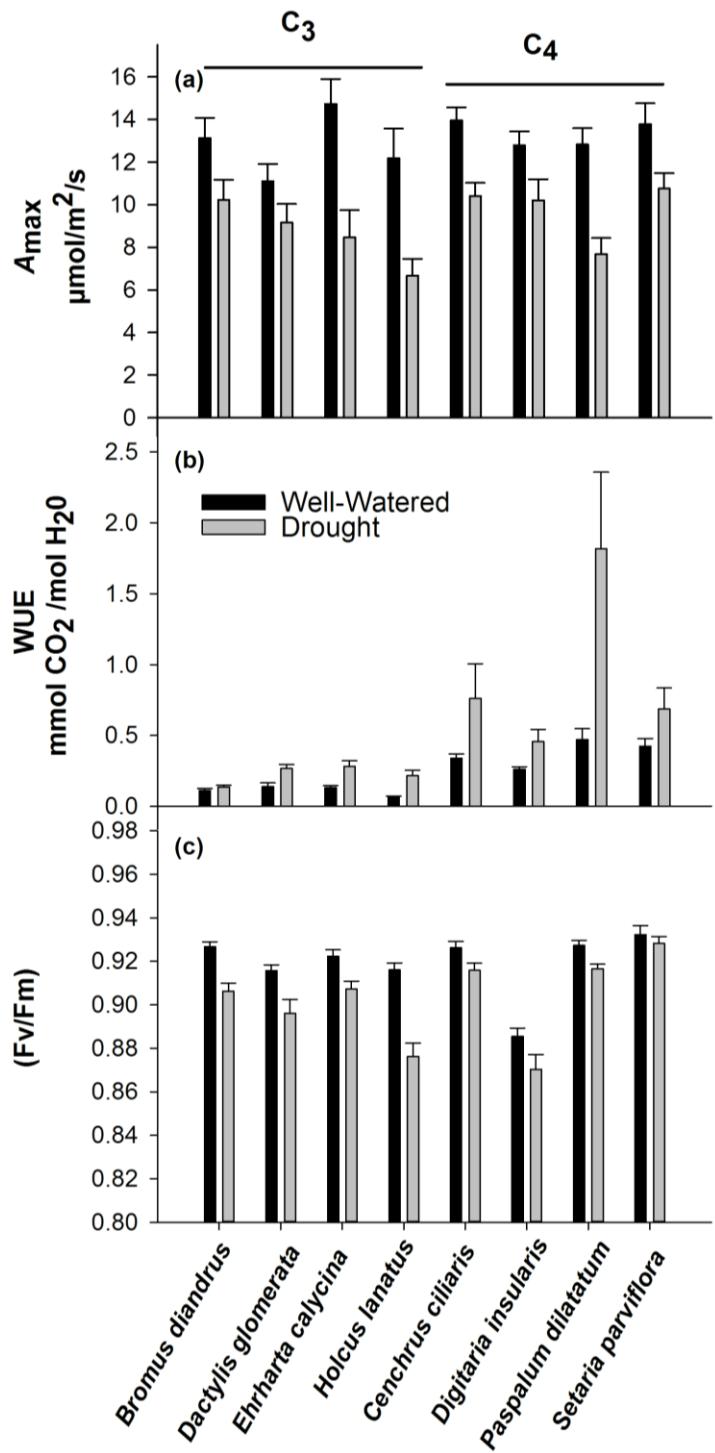


Figure 5.6. Mean values for the effects of water treatment on C₃ and C₄ grass species for the variables (a) A_{max} , (b) WUE, and (c) F_v/F_m (+/- SE). Water treatment by species within photosynthetic pathway interactions are significant for all variables listed.

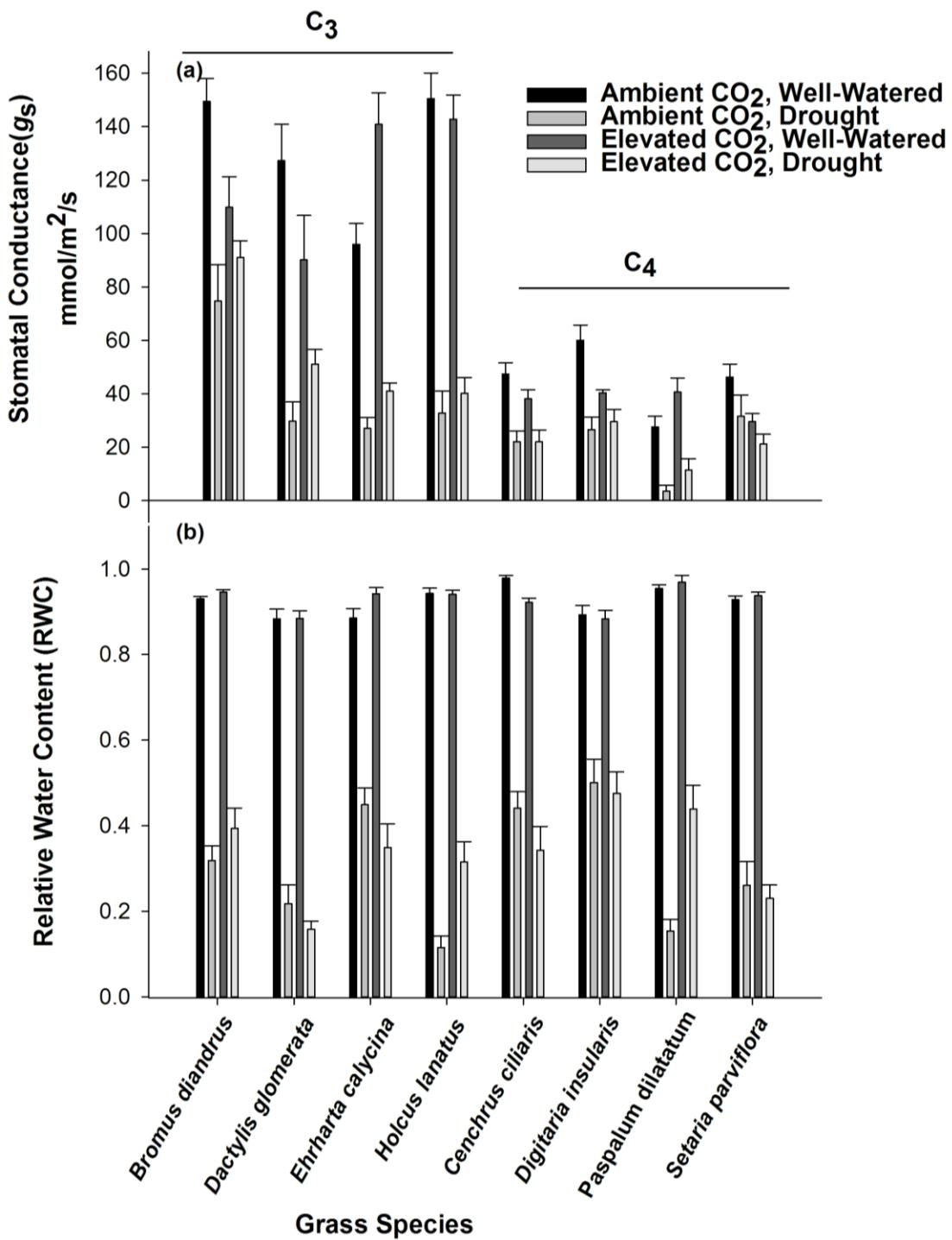


Figure 5.7. Mean values for the effects of CO₂ and water treatment on (a) stomatal conductance (g_s) and (b) relative water content (RWC) (+/- SE). There is a significant interaction for species within photosynthetic pathway by CO₂ by water for both g_s and RWC.

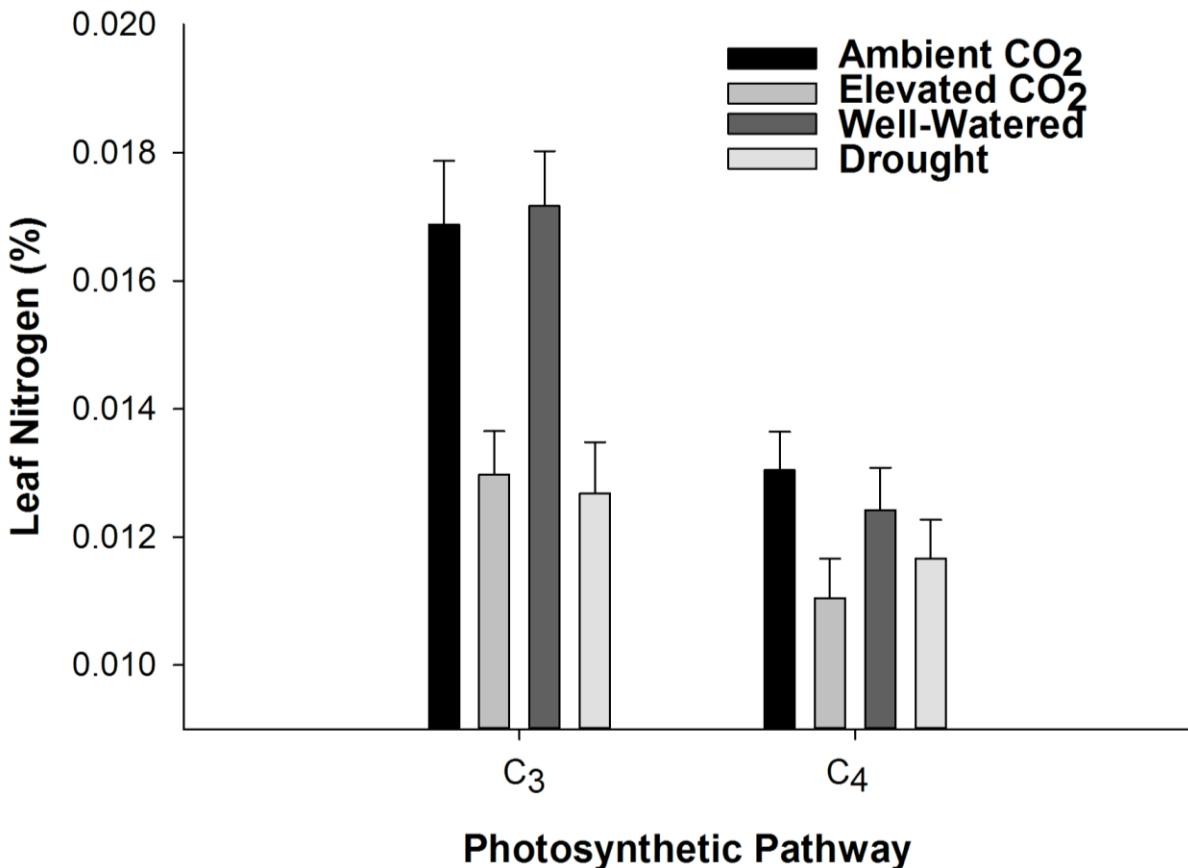


Figure 5.8. Mean Values for leaf Nitrogen (%) for CO₂ and water treatments, by photosynthetic pathway (+/- SE). There is a significant effect of CO₂ and a significant effect of water on leaf percent nitrogen. There is also a significant interaction between photosynthetic pathway and water treatments on leaf percent nitrogen.

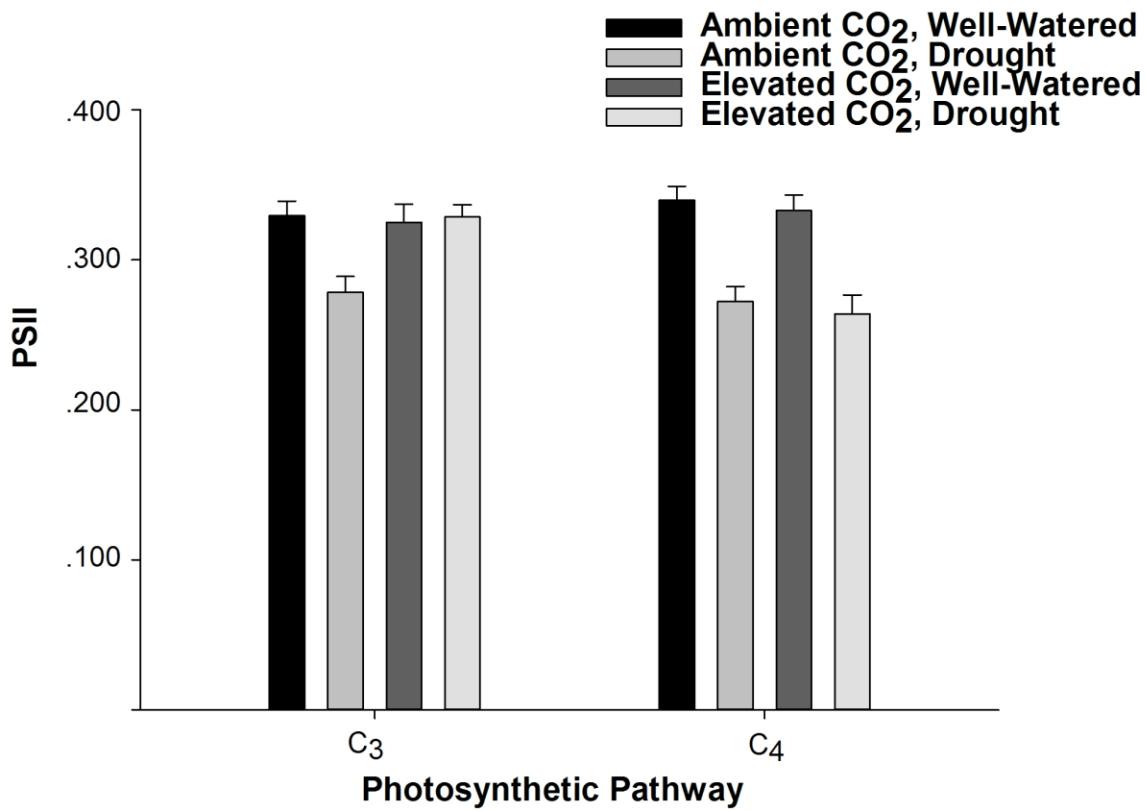


Figure 5.9. Mean values for light-adapted quantum yield of photosystem II (Φ_{PSII}) in response to CO₂ and water treatments (+/- SE). There is a significant CO₂ by water by photosynthetic pathway interaction for Φ_{PSII} .

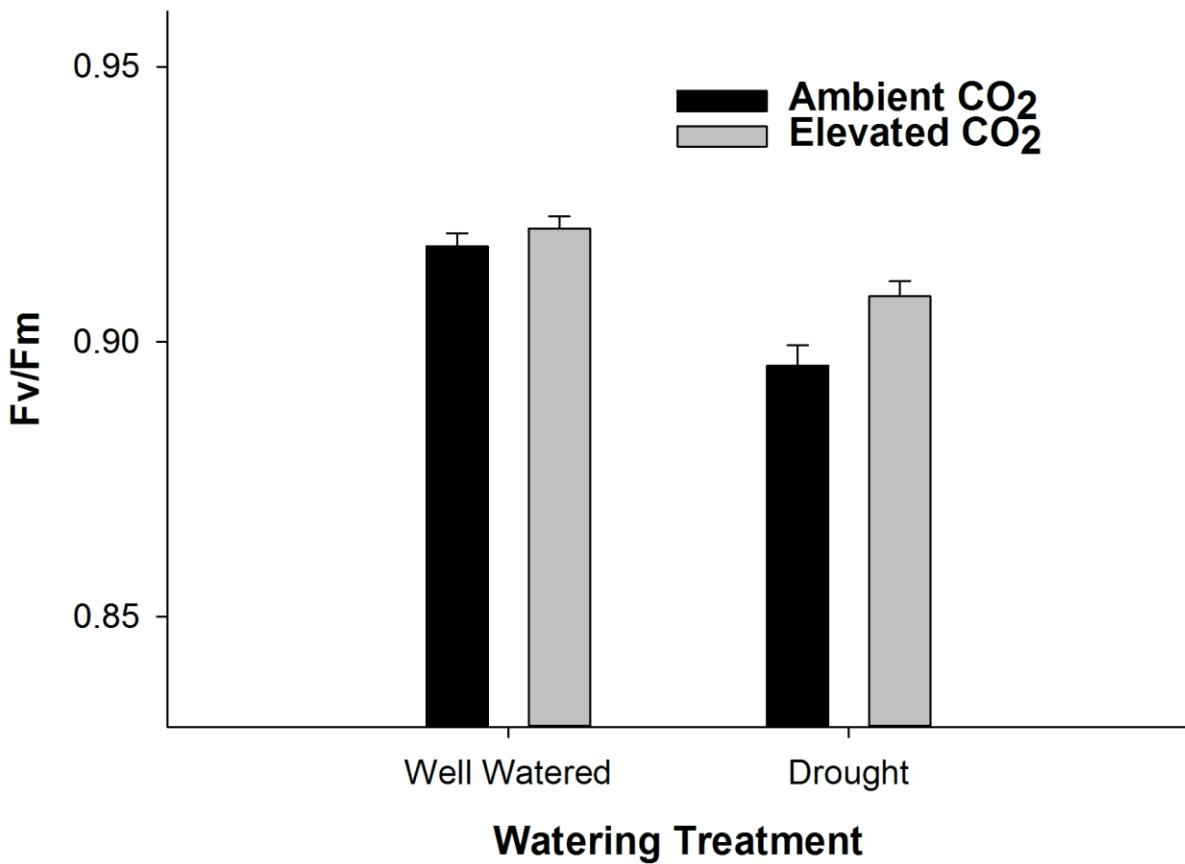


Figure 5.10. Mean values for dark-adapted photochemical efficiency (F_v/F_m) in response to CO_2 by water treatments (+/- SE). C_3 and C_4 species are combined due to lack of statistically significant differences. There is a significant interaction between CO_2 and water.

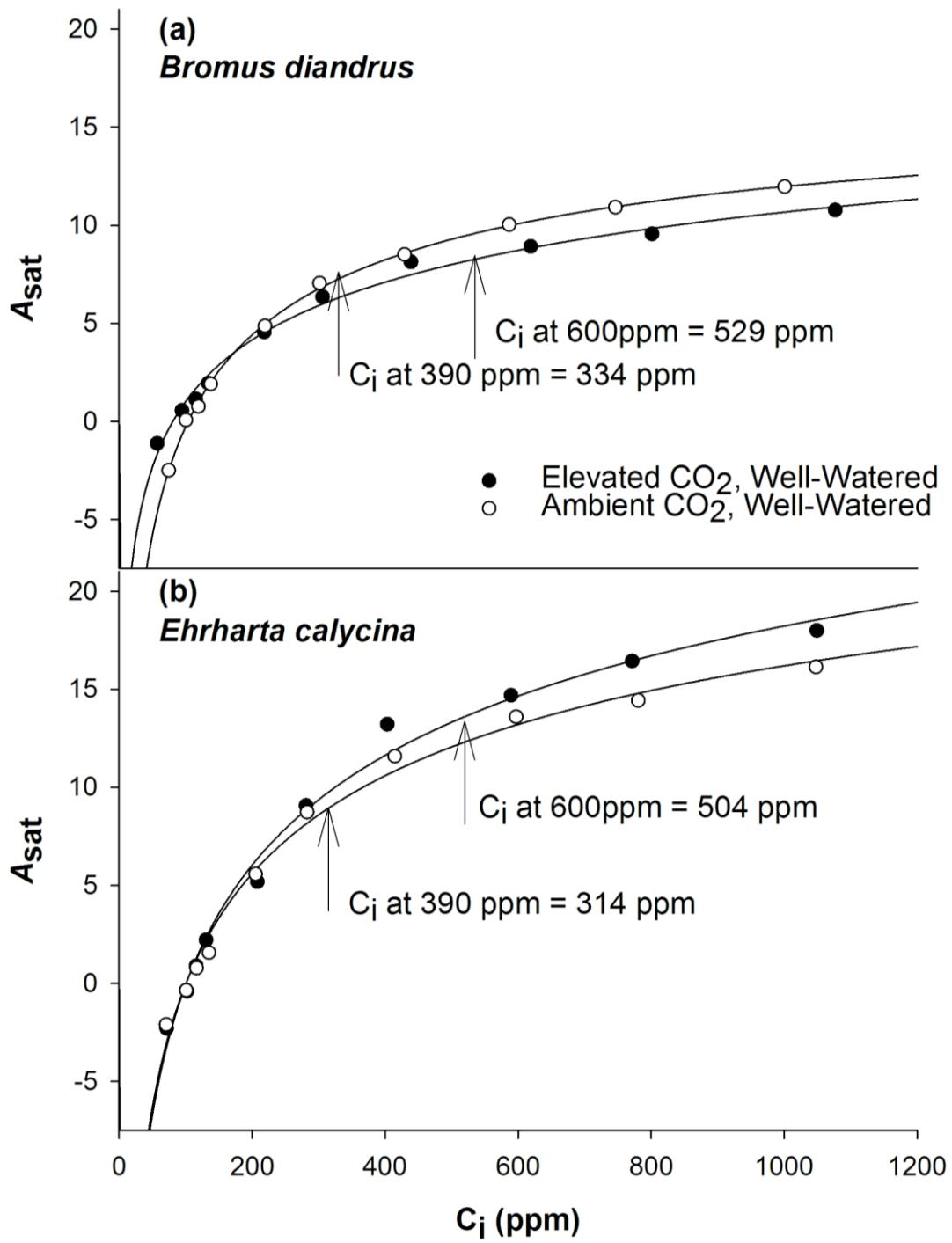


Figure 5.11. Mean values for C_3 A/c_i curves for (a) *Bromus diandrus* and (b) *Ehrharta calycina* for ambient and elevated CO_2 , well-watered conditions

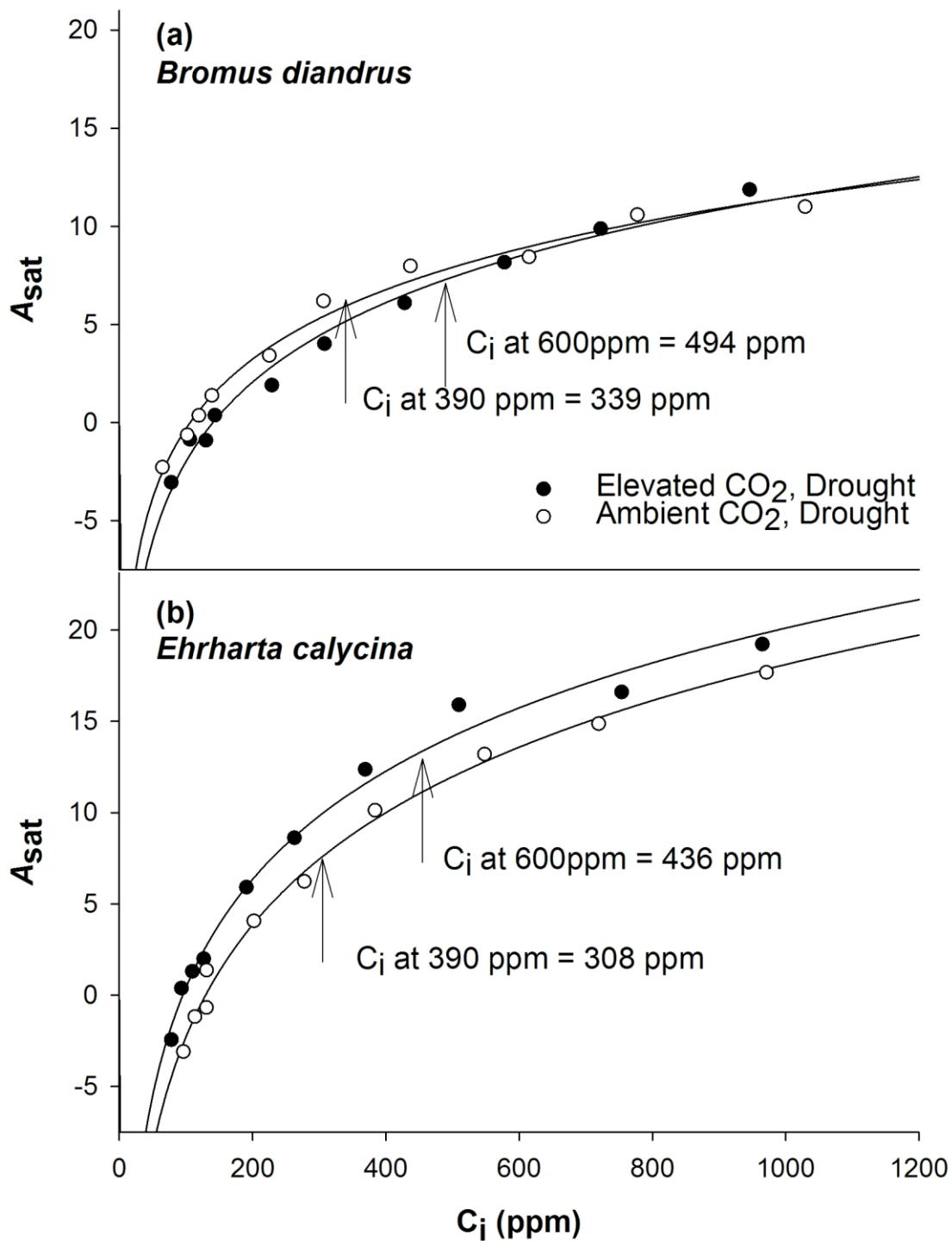


Figure 5.12. Mean values for C₃ A/c_i curves for (a) *Bromus diandrus* and (b) *Ehrharta calycina* for ambient and elevated CO₂, drought conditions

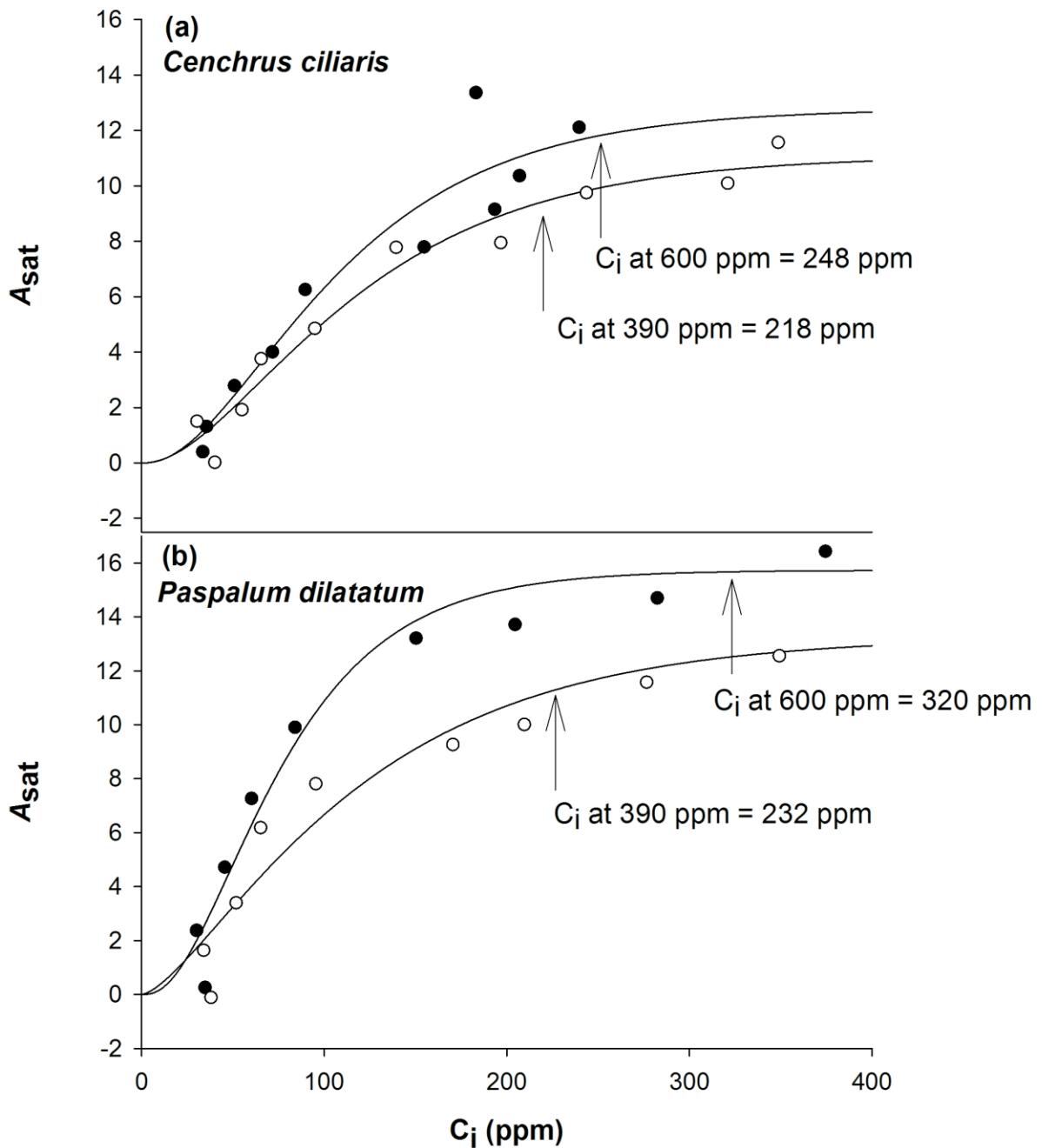


Figure 5.13. Mean values for C_4 A/c_i curves for (a) *Cenchrus ciliaris* and (b) *Paspalum dilatatum* for ambient and elevated CO_2 , well-watered conditions

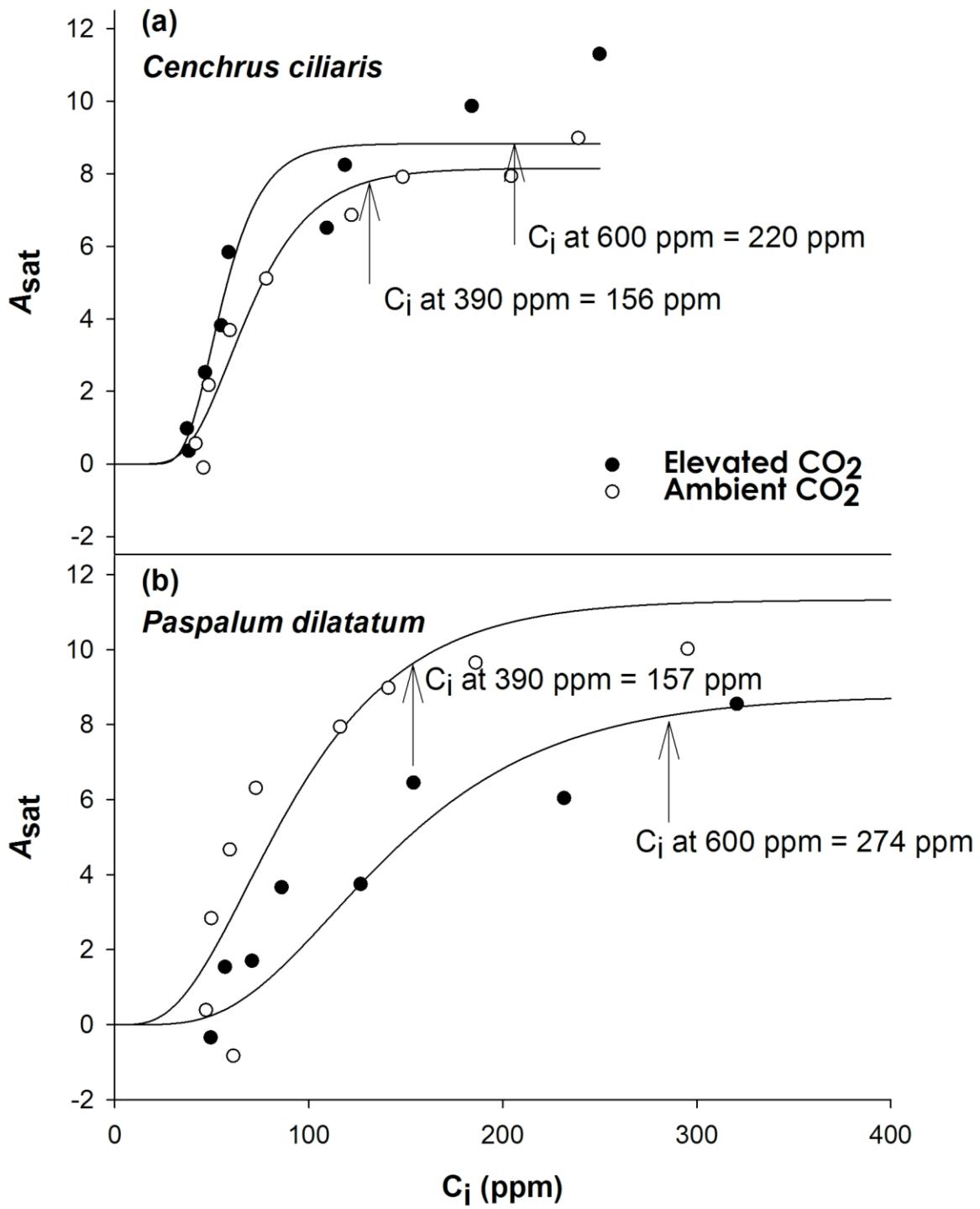


Figure 5.14. Mean values for C_4 A/c_i curves for (a) *Cenchrus ciliaris* and (b) *Paspalum dilatatum* for ambient and elevated CO_2 , drought conditions

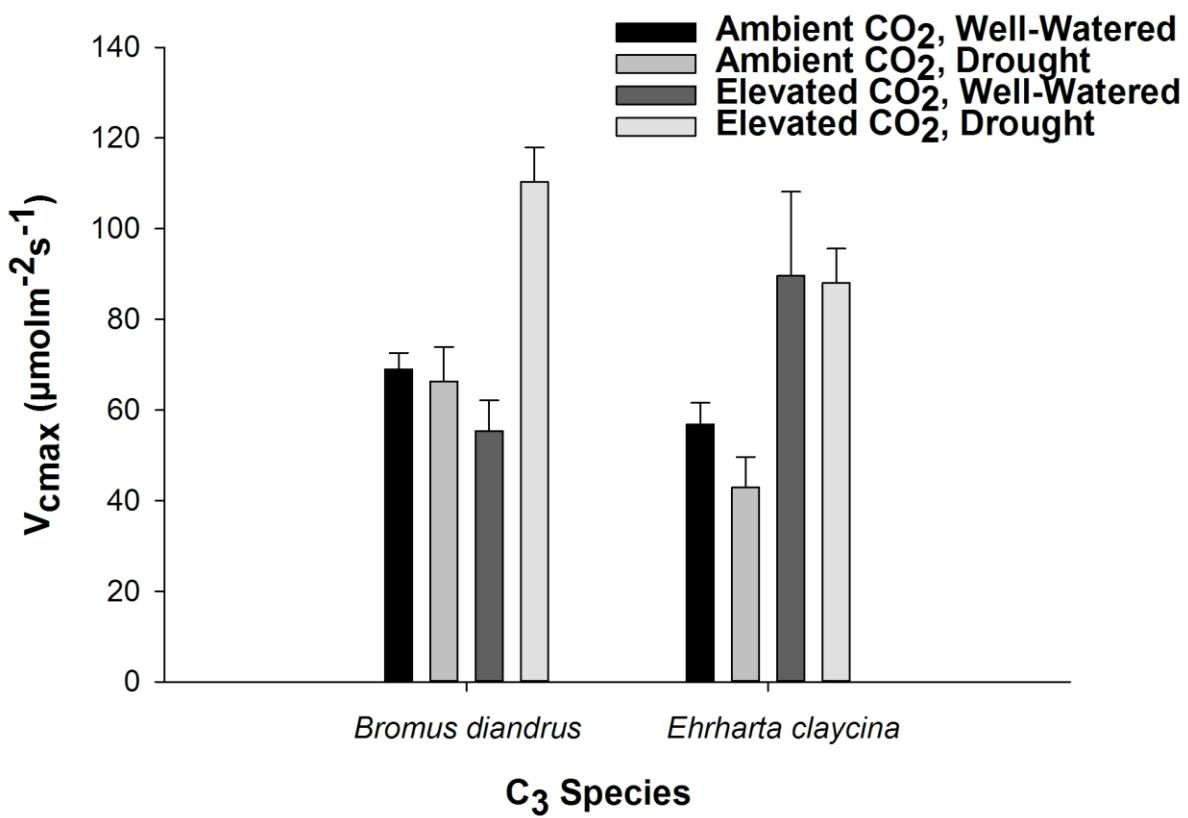


Figure 5.15. Mean values for $V_{c\max}$ for C_3 species in response to CO₂ and water treatments (+/- SE). There are no significant differences for $V_{c\max}$.

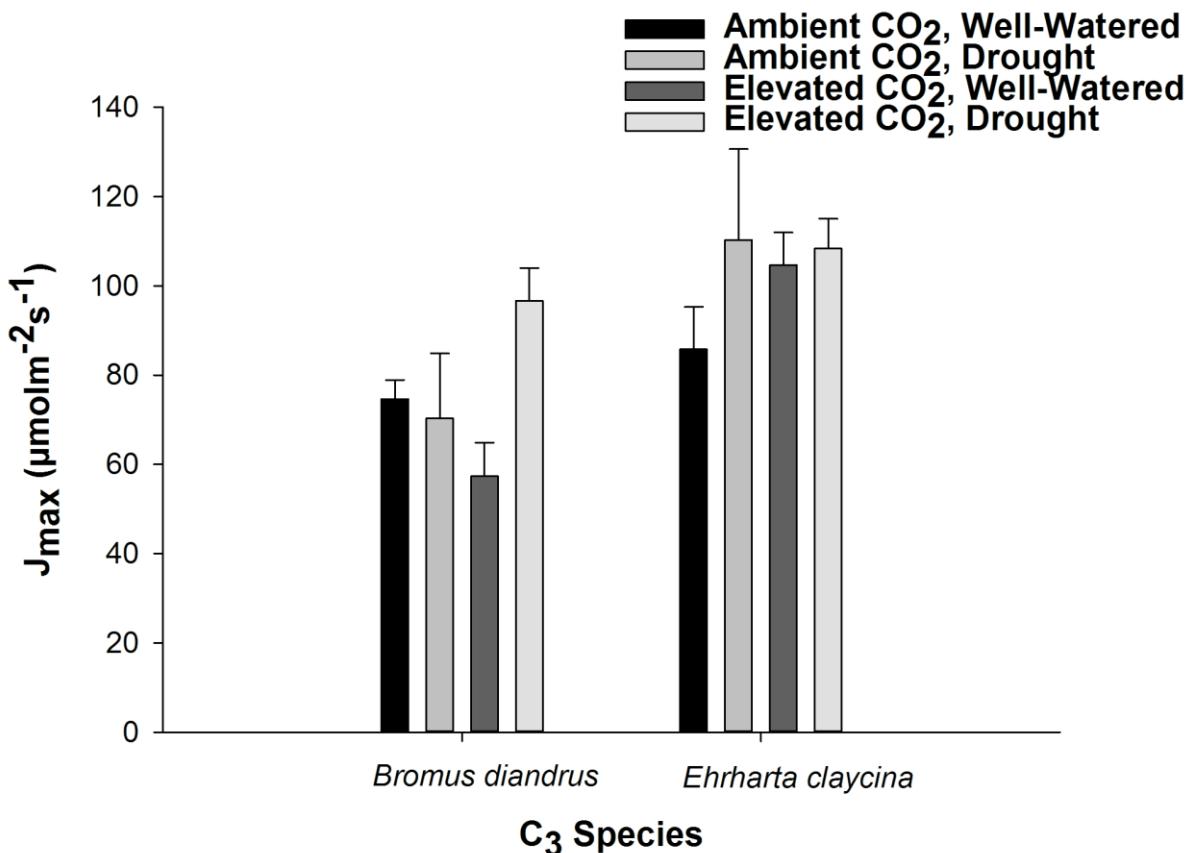


Figure 5.16. Mean values for J_{\max} for C₃ species in response to CO₂ and water treatments (+/- SE). There is a significant CO₂ by water by species interaction for J_{\max} .

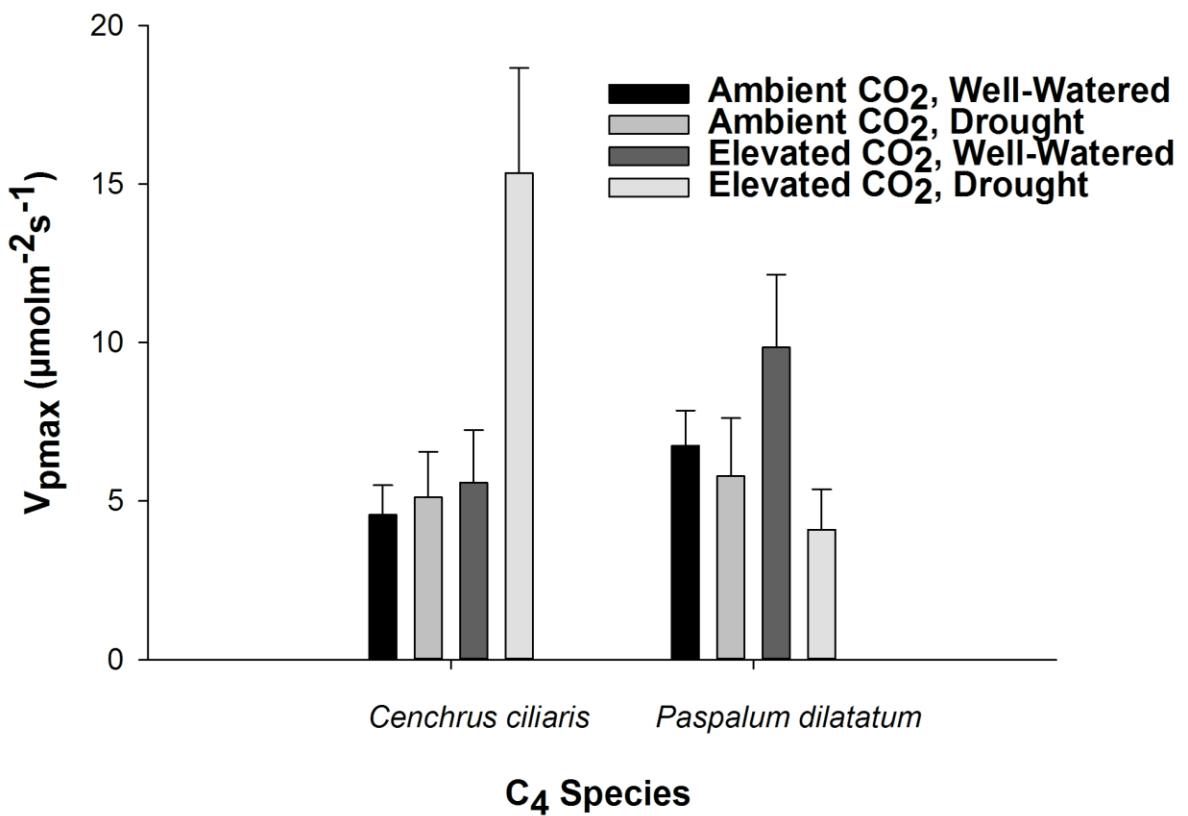


Figure 5.17. Mean values for $V_{p\max}$ values C₄ species in response to CO₂ and water treatments (+/- SE). There is a significant CO₂ by water by species interaction for $V_{p\max}$.

CHAPTER 6

Past, current, and future distributions of C₄ and C₃ grasses in
the Hawaiian Islands: What we know now, limitations, and
future directions.

In Hawai'i, the grass family is represented by 47 native species (Wagner et al. 1999). However, many nonnative grass species have been introduced to the islands (Rotar 1968), and around 100 of these species have become naturalized (Wagner et al. 1999). The grass species found in the Hawaiian Islands have either the C₄ or C₃ photosynthetic pathway. Ecological characteristics associated with the C₄ and C₃ photosynthetic pathways vary, with C₄ plants typically found in warm arid locations, whereas C₃ plants are typically found in cooler moist environments (Long 1999). The physiological characteristics of C₄ plants give them an advantage in warm and dry environments. Thus, grass species can respond differently to environmental conditions depending on which photosynthetic pathway they possess, giving them unique distributional patterns. In the Hawaiian Islands, extreme elevation gradients occur over short distances, with tropical conditions at low elevations and cold alpine conditions at mountain summits. Along these elevation gradients, C₄ grasses tend to be found at low to mid elevations while C₃ grasses are found at mid to high elevations (Rundel 1980). The transition point is the place with 50% cover of both C₄ and C₃ grasses. In theory, the transition point occurs where climatic conditions are such that both grasses have equal quantum yields and photosynthesize at similar rates, giving them similar competitive abilities (Ehleringer 1978).

The invasion of certain C₄ and C₃ grasses can have major implications for ecosystem function and structure (D'Antonio and Vitousek 1992). In Hawai'i, most nonnative grasses that have altered the grass fire-cycle and threaten native

plant communities are C₄ grasses. Therefore, it is important to understand the distributional ranges and limitations of C₄ grasses in Hawai‘i and how they may interact with C₃ grasses. In Hawai‘i, high mountain systems appear to be more strongly affected by climate change than low elevation sites, based on empirical data (Giambelluca et al. 2008). Specifically, high elevation sites have warmed three times more than low elevation sites during the last 30 years in the Hawaiian Islands. Furthermore, future changes in precipitation have been predicted for the Hawaiian Islands, in both the wet and dry seasons. Wet season precipitation is predicted to decrease by 5 - 10%, while dry season precipitation is expected to increase by 5% (Timm and Diaz 2009). Thus, there is a need to understand the mechanisms and drivers that promote dominance of C₄ and C₃ grasses currently in Hawai‘i to facilitate management and prediction of future invasions and impacts.

In temperate localities, temperature has been shown to be the most critical climatic factor driving C₄ and C₃ grass distributions (Teeri and Stowe 1976); while research findings in the tropics have varied (Chazdon 1978; Livingstone and Clayton 1980; Rundel 1980). Importantly, only one study has used statistics to determine climatic drivers of grass distributions in the tropics (Young and Young 1983). The second chapter of my dissertation examined the climatic drivers of PACCMAID C₄ and mainly BEP C₃ grass distributional patterns in the Hawaiian Islands across five elevation gradients. I used correlations to examine whether temperature or rainfall were associated with distributions of these grasses. Due to the unique rainfall patterns found along elevation gradients in Hawai‘i (PRISM

Climate Group 2010), I was able to determine that temperature was the most critical factor driving C₄ and C₃ grass distributions in Hawai‘i. Rainfall was only correlated with C₄ and C₃ grass distributional patterns when it was also correlated with temperature. This is the first study in the tropics to show statistically that temperature drives grass distributional patterns. Using previous studies from both temperate and tropical locations, I was also able to show that the transition temperatures of C₄ and C₃ grasses in the Hawaiian Islands are lower than those in temperate locations but comparable to other tropical locations. Determining that temperature is the key climatic factor influencing distributional patterns of the principle C₄ and C₃ grasses has implications for understanding how these grass distributions in Hawai‘i may shift in the future with climate change. Furthermore, knowing that C₄ grasses are established at higher elevations in the tropics than expected based on temperature-elevation relationships in temperate areas, we can expect that with small changes in temperature, high elevation mountains will become suitable habitat for invasive C₄ species. This finding may be applicable to other tropical locations such as those in Australia and South America where invasive grasses have also become a conservation concern.

One way that plants can respond to climate change is by shifting their distributions to new areas where the climate meets their physiological requirements. Previous studies have investigated how plant distributions shift upwards in elevation in response to climate change in temperate locations (Kelly and Goulden 2008; Kullman 2002; Lenoir et al. 2008; Parolo and Rossi 2008; Penuelas and Boada 2003), although, studies documenting tropical range shifts

in response to climate change have been minimal (Feeley 2012; Feeley et al. 2011; Juvik et al. 2011). Furthermore, no study has compared distributional shifts between C₄ and C₃ species in response to climate change, even though these species have been shown to have unique distributional patterns in response to climate (Cabido et al. 1997; Mo et al. 2004; Wan and Sage 2001)

The third chapter of my dissertation compares distributional patterns of C₄ and C₃ grasses in Hawai'i Volcanoes National Park over a 40 year period (Newell 1968). I also used temperature data from Hawai'i Volcanoes National Park headquarters to confirm temperature increases at the study location. I found that the transition elevation, marking a shift in dominance between C₄ and C₃ grasses based on relative cover, shifted upward over the 40 year period. Although maximum elevations for C₄ or C₃ grasses grouped together were not significantly greater in 2008 than in the 1960's, a subset of C₄ (and fewer C₃) grasses moved to substantially higher elevations, and these were the species adapted to fire. Thus, my study showed that C₄ grasses are now established at higher elevations compared to their ranges in the 1960's, and that these expanding species are mainly fire-adapted grasses.

This is the first study to show that transition elevations between C₄ and C₃ grasses are moving upward in elevation and that an expansion of fire-adapted grasses will pose a threat to Hawaiian montane ecosystems. Similar grass expansion patterns are expected for montane ecosystems elsewhere in the tropics, where invasion by fire-adapted grasses at lower elevations is already well documented. This work makes a contribution to the few studies looking at

distributional shifts in response to climate change in the tropics and supports results found by Juvik et al. (2011). If historical data exists for other elevational gradients in Hawai‘i, future studies could be done to examine changes along different elevation gradients and changes for other plant species and/or functional groups.

Bioclimatic envelope models (BEMs) can be used to statistically describe a species' climatic habitat (Pearson and Dawson 2003; Phillips et al. 2006). These models have proven useful tools to predict invasive species distributions under current climates (Thuiller et al. 2005); and under climate change (Colwell et al. 2008; Hijmans and Graham 2006; Pearson and Dawson 2003; Thomas et al. 2004; Thuiller 2004). However, the studies that have tried to determine how current plant distributions may change in the future with climate change in the tropics (Colwell et al. 2008; Feeley and Silman 2010a; Feeley and Silman 2010b; Kriticos et al. 2003a, b; Thomas et al. 2004) are from outside of Hawai‘i. For invasive species, climate change can create an expansion or a reduction of the area at risk of invasion (Bradley et al. 2009). In addition, predicting how invasive species will impact protected areas with climate change would provide important information for land managers and conservation planners (Bradley 2009).

Due to the increase in species range size for fire-adapted grasses seen in my third chapter, I decided to use bioclimatic models to predict how important fire-promoting grasses in Hawai‘i will shift under climate change for the year 2050. I found that mean temperature of both the warmest (T_{max}) and coldest (T_{min}) months was the principle climatic constraint for the C₃ grass species with

precipitation being secondary. Temperature was also the climatic variable of most importance in models described in Parker-Allie et al. (2009) for C₃ grasses. In contrast, temperature and precipitation were found to be key climatic constraints for C₄ species, depending on the species. Again, these results support previous studies that have shown temperature and precipitation as factors driving grass distributional patterns (Chazdon 1978; Teeri and Stowe 1976). However, in my second chapter, I found that temperature was the most important climatic factor driving distributions of C₄ and C₃ grasses in Hawai'i. This shows that temperature may contribute to the overall distributions of these grasses, but that due to the complexities of the C₄ pathway, precipitation is also an important climatic variable. My study suggests that characteristics other than biochemical subtype may be responsible for the variance in climatic constraints for the C₄ species. C₄ species range changes under climate change may be hard to predict than for C₃ species, and lumping C₄ species together to predict range changes as a functional group may be misleading.

The percent range change of species distributions under climate change was smaller in my study compared with temperate studies (Bradley 2009; Bradley et al. 2009; Parker-Allie et al. 2009) and even in comparison to other tropical studies (Feeley and Silman 2010a; Feeley and Silman 2010b; Thomas et al. 2004). Differences between my study and other studies in the tropics could be due to the differences in projected increases in temperature and projected year under study (Colwell et al. 2008; Feeley and Silman 2010a; Feeley and Silman 2010b; Kriticos et al. 2003a, Kriticos et al. 2003b; Thomas et al. 2004).

Furthermore, it has been shown that temperature in Hawai‘i is not increasing at the same rate across the Hawaiian Islands, but is increasing faster at higher elevations (Giambelluca et al. 2008). Thus, smaller climate changes were expected for low elevations compared to higher elevations. This may also have reduced the predicted range changes seen in my study compared to other tropical studies.

The magnitudes of range changes presented in my study are smaller for C₄ species than for C₃ species under climate change. A reduction in range size for C₃ grass species was expected due to a loss of habitat area as these species are forced up in elevation. While a large expansion in range size was expected for C₄ grasses as more area at mid to high elevations becomes climatically suitable due to increases in temperature. However, this was not seen in my study. More than half of the C₄ species in my study had a precipitation constraint contributing more than 50% to the species climate niche model, which likely reduced increases in range size due to small static increases or decreases that were modeled for precipitation. Contrasting responses of C₄ grasses were also seen by Parker-Allie et al. (2009), who found C₄ species responses were species-specific in South Africa.

While the impact of invasive plants on protected areas in the Hawaiian Islands has been documented (Ainsworth and Kauffman 2010; D’Antonio et al. 2000; Smith and Tunison 1992), understanding the potential changes in invasive species within natural areas in response to climate change has received little attention. Among major nature reserves in Hawai‘i, I found that not all of them

contained suitable habitat for all of the fire-promoting grass species in my study and that species responses to potential future climate change within the natural areas varied. Thus, each reserve should be evaluated individually for potential risks of expansion and contractions of invasive fire-promoting grasses. The differences in species responses within each reserve are likely due to the broad differences in temperature and precipitation gradients, along with the elevation span of each reserve. Since not all fire-promoting grass species responded to climate change in the same manner, species-specific risk assessments appear critical for land management and conservation planning in Hawai'i.

This study had limitations and could have been improved with better climate projections or a broader range of climate projections for the year 2050. Precipitation layers were also uniformly altered based on precipitation predictions for the Hawaiian Islands, while spatially variable changes in rainfall may be more realistic. This study could have also been improved if multiple BEMs were used to obtain a consensus model. Bradley et al. (2010) suggested that multiple BEM approaches should be used when predicting future projections since these projections are only an estimate, and having multiple projections will more likely define the area that may be occupied in the future.

Along with changes in temperature and precipitation, the global atmospheric carbon dioxide concentration (CO_2) is expected to reach concentrations of 600 ppm by the year 2050 ± 20 years (Hogan et al. 1991). C_3 plant responses to elevated CO_2 have been shown to be more consistent compared with responses by C_4 plants (Ainsworth and Long 2005; Wand et al.

1999). Previous studies have shown inconsistencies in C₄ grass responses to elevated CO₂ at levels of genus, subfamily (Kellogg et al. 1999), and biochemical subtype (Ziska and Bunce 1997). In addition, weedy (fast-growing, non-crop species) versus non-weedy C₄ species have also shown contrasting responses. Furthermore, Leakey et al. (2009) found that C₄ plants only respond to elevated CO₂ when experiencing drought stress. The fifth chapter of my dissertation evaluated the effects of elevated CO₂ and drought conditions on C₄ and C₃ growth, physiological, and biochemical responses in order to determine how weedy grass species in Hawai'i will respond to these aspects of global change.

In this study, I found that both C₄ and C₃ grasses responded to elevated CO₂ for A_{\max} (maximum carbon uptake rate), A_{sat} (CO₂ saturated carbon uptake rate), and plant biomass, and these findings are consistent with previous work (Ainsworth and Long 2005; Wand et al. 1999). For C₃ species, I found that growth, physiological, and biochemical responses were all improved in drought exposed plants when grown in elevated CO₂ conditions. This study supports previous work that found that the effects of drought were improved for C₃ plants when grown in elevated CO₂ conditions (Leakey et al. 2009; Volk et al. 2000). These results also suggest that drought stress in C₃ grasses may be due to stomatal limitations, which has been previously proposed (Carmo-Silva et al. 2007; Ghannoum 2009; Lawlor and Cornic 2002). Furthermore, I found that C₄ plants grown in drought and elevated CO₂ conditions had both stomatal and biochemical limitations under these conditions. Ghannoum et al. (2003) found that biochemical processes in C₄ wild grass species were not responsive to

elevated CO₂ under drought conditions and suggested that water stress caused some biochemical (nonstomatal) inhibition of photosynthesis. Ripley et al. (2007) also found a loss of the C₄ photosynthesis advantage over the C₃ type during drought conditions caused by reductions in biochemical limitations and suggested that these limitations may be more pronounced in the NADP-ME C₄ subtype. These results and those of Ghannoum et al. (2003) suggest that water-relation advantages in C₄ plants (Long 1999) may be smaller under drought conditions than previously thought due to biochemical limitations. Thus, elevated CO₂ may not alleviate drought stress in C₄ plants. These results also contradict previous studies that showed that C₄ plants only responded to elevated CO₂ when exposed to drought treatments (Leakey et al. 2004; Leakey et al. 2006; Markelz et al. 2011).

I found that there was more variation in C₄ species responses to water than CO₂, even though I expected NADP-ME species to respond similarly to changes in precipitation patterns. Kellogg et al. (1999), Roumet and Roy (1996), and Ziska and Bunce (1997) all found that species-specific growth regulation may be more important in determining a C₄ grass species response to elevated CO₂ than any other type of species grouping. My data show that among C₄ plants, only A_{max} had a species-specific response to CO₂. The rest of the measured variables had more consistent responses to elevated CO₂ for the plants with the C₄ photosynthetic pathway. The consistent response of C₄ species to elevated CO₂ could be because all the C₄ grasses in my study are

known to be weedy (fast-growing, naturalized, non-crop species) in the Hawaiian Islands.

Overall, my results reveal that there may not be a real winner between C₄ and C₃ grass species under global change, and that species selection and location of the studied area (areas with low nitrogen content and/or low precipitation), may be more important in determining how an area will be impacted. These conclusions have land management and conservation implications for the Hawaiian Islands, where many pervasive C₄ grass species have already changed ecosystems throughout the islands.

This CO₂ and drought experiment had limitations because it was conducted in growth chambers rather than under field conditions. Ghannoum et al. (2009) suggested that in field studies such as FACE (Free Air carbon Dioxide Enrichment and enclosure studies) plants experience water stress at more natural rates than in pot studies. Differences in methodologies have been suggested to explain why some studies show favorable responses for C₄ species while others do not (Leakey et al. 2009). Leakey et al. (2009) proposed that even when plants are in well-watered pots, the roots may not be able to absorb enough water to fully meet the requirements of their aboveground biomass. Thus, under elevated CO₂, water requirements of the plant could be reduced and alleviate the water stress of the plant giving the appearance that elevated CO₂ directly stimulates carbon gain (Leakey et al. 2009). In my study, pot volume was small (346 cm³) and may have contributed to the positive CO₂ response in C₄ biomass and carbon uptake (*A*). However, in a meta-analysis by Wand et al.

(1999), pot size and exposure method did not determine the response of C₄ plants to elevated CO₂. Other limitations in this study included low light conditions for C₄ plants and a growing temperature that was not as high as expected future temperatures at low elevations. Thus, the next step in understanding the complex growth, physiological, and biochemical dynamics of C₄ and C₃ grasses found in Hawai'i in response to aspects of global change would be to conduct a field experiment where rooting volume, low light, and temperature reflect natural field conditions. Since this study only used one biochemical subtype (NADP-ME), and other FACE studies typically use maize or sorghum which are also the NADP-ME subtype, it would be informative to look at weedy C₄ species with all three biochemical subtypes (NADP-ME, NAD-ME, and PCK) in field conditions.

Overall results from my dissertation reveal that in Hawai'i, C₄ and C₃ grass distributional patterns are driven by temperature and suggests that the C₄ to C₃ transition point will shift upward in elevation in the future with continued climate warming. However, this work also shows that individual C₄ grass distributions in Hawai'i may also be influenced by precipitation. Furthermore, my dissertation found that determining distributional shifts for C₄ species in Hawai'i is complex and requires species-specific evaluation. Throughout all of my research, C₃ species responded as predicted with climate warming and elevated CO₂ revealing that these species will likely have smaller distributions in the future at higher elevations in Hawai'i and may be competitive in drought conditions with increased atmospheric CO₂ due to reductions in drought stress. However, for C₄

species in Hawai'i under the combined conditions of increased atmospheric CO₂ and drought, some species may have physiological limitations that cannot be overcome with increased CO₂, giving way to increased C₃ grass distributions. Furthermore, in degraded areas in Hawai'i, C₄ species may continue to spread in the future due to their low nitrogen requirement compared with C₃ species. As a final point, future research still needs to be done to evaluate C₄ species responses to aspects of global change in Hawai'i due to differential species responses seen in this work.

In conclusion, my dissertation contributed to the global knowledge of C₄ and C₃ grass distributional patterns and the drivers of these distributions in Hawai'i. It also added to the limited research to date in the tropics, evaluating plant distributional changes in response to climate change in current and future climates. Hopefully, it also highlights the need for more research to be done in the tropics investigating species responses to aspects of climate change. My research further contributes to the many studies that have tried to untangle the complexities of C₄ and C₃ grass responses to elevated CO₂ and drought. My dissertation revealed that C₄ grass responses under climate change may be harder to predict than C₃ grass species and that there is still a need for more research investigating the multifaceted responses of these species to aspects of global change. This work can further be applied in natural resource and land management decisions in areas where C₄ and C₃ grasses pose ecological problems in the Hawaiian Islands and other tropical localities.

LITERATURE CITED

- Ainsworth A, Kauffman JB (2010) Interactions of fire and nonnative species across an elevation/plant community gradient in Hawaii Volcanoes National Park. *Biotropica* 42:647-655
- Ainsworth EA, Long SP (2005) What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO₂. *New phytologist* 165:351-372
- Bradley BA (2009) Regional analysis of the impacts of climate change on cheatgrass invasion shows potential risk and opportunity. *Glob. change biol.* 15:196-208
- Bradley BA, Oppenheimer M, Wilcove DS (2009) Climate change and plant invasions: restoration opportunities ahead? *Glob. change biol.* 15:1511-1521
- Bradley BA, Wilcove DS, Oppenheimer M (2010) Climate change increases risk of plant invasion in the Eastern United States. *Biol. invasions* 12:1855-1872
- Cabido M, Ateca N, Astegiano M, et al. (1997) Distribution of C₃ and C₄ grasses along an altitudinal gradient in Central Argentina. *J. biogeogr.* 24:197-204
- Carmo-Silva AE, Soares AS, da Silva JM, et al. (2007) Photosynthetic responses of three C4 grasses of different metabolic subtypes to water deficit. *Functional plant biology* 34:204-213
- Chazdon RL (1978) Ecological aspects of the distribution of C₄ grasses in selected habitats of Costa Rica. *Biotropica*:265-269
- Colwell RK, Brehm G, Cardelus CL, et al. (2008) Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322:258-261
- D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. rev. ecol. syst.* 23:63-87
- D'Antonio CM, Tunison JT, Loh RK (2000) Variation in the impact of exotic grasses on native plant composition in relation to fire across an elevation gradient in Hawaii. *Austral ecology* 25:507-522
- Ehleringer JR (1978) Implications of quantum yield differences on the distributions of C₃ and C₄ grasses. *Oecologia* 31:255-267

Feeley KJ (2012) Distributional migrations, expansions, and contractions of tropical plant species as revealed in dated herbarium records. *Glob. change biol.*

Feeley KJ, Silman MR (2010a) Land-use and climate change effects on population size and extinction risk of Andean plants. *Glob. change biol.* 16:3215-3222

Feeley KJ, Silman MR (2010b) Modelling the responses of Andean and Amazonian plant species to climate change: the effects of georeferencing errors and the importance of data filtering. *J. biogeogr.* 37:733-740

Feeley KJ, Silman MR, Bush MB, et al. (2011) Upslope migration of Andean trees. *J. biogeogr.* 38:783-791

Ghannoum O (2009) C₄ photosynthesis and water stress. *Annals of botany* 103:635-644

Ghannoum O, Conroy JP, Driscoll SP, et al. (2003) Nonstomatal limitations are responsible for drought-induced photosynthetic inhibition in four C₄ grasses. *New phytologist* 159:599-608

Giambelluca TW, Diaz HF, Luke MSA (2008) Secular temperature changes in Hawaii. *Geophys. res. lett.* 35

Hijmans RJ, Graham CH (2006) The ability of climate envelope models to predict the effect of climate change on species distributions. *Glob. change biol.* 12:2272-2281

Hogan K, Smith A, Ziska L (1991) Potential effects of elevated CO₂ and changes in temperature on tropical plants. *Plant, cell & environment* 14:763-778

Juvik JO, Rodomsky BT, Price JP, et al. (2011) "The upper limits of vegetation on Mauna Loa, Hawaii": a 50th-anniversary reassessment. *Ecology* 92:518-525

Kellogg EA, Farnsworth EJ, Russo ET, et al. (1999) Growth Responses of C₄ Grasses of Contrasting Origin to Elevated CO₂. *Annals of botany* 84:279

Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent climate change. *Proc. Natl. Acad. Sci. U. S. A.* 105:11823-11826

Kriticos D, Sutherst R, Brown J, et al. (2003a) Climate change and biotic invasions: a case history of a tropical woody vine. *Biol. invasions* 5:147-165

Kriticos D, Sutherst R, Brown J, et al. (2003b) Climate change and the potential distribution of an invasive alien plant: *Acacia nilotica* ssp. *indica* in Australia. *J. appl. ecol.* 40:111-124

Kullman L (2002) Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *J. ecol.* 90:68-77

Lawlor D, Cornic G (2002) Photosynthetic carbon assimilation and associated metabolism in relation to water deficits in higher plants. *Plant, cell & Environment* 25:275-294

Leakey A, Bernacchi C, Dohleman F, et al. (2004) Will photosynthesis of maize (*Zea mays*) in the US Corn Belt increase in future [CO₂] rich atmospheres? An analysis of diurnal courses of CO₂ uptake under free-air concentration enrichment (FACE). *Glob. change biol.* 10:951-962

Leakey ADB, Ainsworth EA, Bernacchi CJ, et al. (2009) Elevated CO₂ effects on plant carbon, nitrogen, and water relations: six important lessons from FACE. *Journal of experimental botany* 60:2859

Leakey ADB, Uribe Larrea M, Ainsworth EA, et al. (2006) Photosynthesis, productivity, and yield of maize are not affected by open-air elevation of CO₂ concentration in the absence of drought. *Plant physiology* 140:779-790

Lenoir J, Gegout JC, Marquet PA, et al. (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science* 320:1768-1771

Livingstone D, Clayton W (1980) An altitudinal cline in tropical African grass floras and its paleoecological significance. *Quaternary research* 13:392-402

Long SP (1999) Environmental responses. In: Sage RM, Monson RK (eds) C₄ Plant Biology. Academic Press, San Diego, CA, pp. 215-249

Markelz R, Strellner RS, Leakey ADB (2011) Impairment of C₄ photosynthesis by drought is exacerbated by limiting nitrogen and ameliorated by elevated CO₂ in maize. *Journal of experimental botany* 62:3235

Mo W, Nishimura N, Soga Y, et al. (2004) Distribution of C₃ and C₄ plants and changes in plant and soil carbon isotope ratios with altitude in the Kirigamine Grassland, Japan. *Grassland science* 50:243-254

Newell C (1968) A phytosociological study of the major vegetation types in Hawaii Volcanoes National Park, Hawaii. MS Thesis, Honolulu: Univ. of Hawaii,

Parker-Allie F, Musil C, Thuiller W (2009) Effects of climate warming on the distributions of invasive Eurasian annual grasses: a South African perspective. *Climatic change* 94:87-103

Parolo G, Rossi G (2008) Upward migration of vascular plants following a climate warming trend in the Alps. *Basic appl. ecol.* 9:100-107

Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global ecology and biogeography* 12:361-371

Penuelas J, Boada M (2003) A global change-induced biome shift in the Montseny mountains (NE Spain). *Glob. change biol.* 9:131-140

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. *Ecological modelling* 190:231-259

Ripley BS, Gilbert ME, Ibrahim DG, et al. (2007) Drought constraints on C₄ photosynthesis: stomatal and metabolic limitations in C₃ and C₄ subspecies of *Alloteropsis semialata*. *Journal of experimental botany* 58:1351-1363

Rotar P (1968) Grasses of Hawaii. University of Hawaii Press, Honolulu, HI,

Roumet C, Roy J (1996) Prediction of the growth response to elevated CO₂: a search for physiological criteria in closely related grass species. *New phytologist*:615-621

Rundel PW (1980) The ecological distribution of C₄ and C₃ grasses in the Hawaiian Islands. *Oecologia* 45:354-359

Smith CW, Tunison JT (1992) Fire and alien plants in Hawaii: research and management implications for native ecosystems. University of Hawaii Press, Honolulu

Teeri J, Stowe L (1976) Climatic patterns and the distribution of C₄ grasses in North America. *Oecologia* 23:1-12

Thomas CD, Cameron A, Green RE, et al. (2004) Extinction risk from climate change. *Nature* 427:145-148

Thuiller W (2004) Patterns and uncertainties of species' range shifts under climate change. *Glob. change biol.* 10:2020-2027

Thuiller W, Richardson DM, Pysek P, et al. (2005) Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Glob. change biol.* 11:2234-2250

Timm O, Diaz HF (2009) Synoptic-statistical approach to regional downscaling of IPCC Twenty-first-century climate projections: Seasonal rainfall over the Hawaiian Islands. *Journal of climate* 22:4261-4280

Volk M, Niklaus PA, Körner C (2000) Soil moisture effects determine CO₂ responses of grassland species. *Oecologia* 125:380-388

Wagner WL, Herbst DR, Sohmer SH (1999) Manual of the Flowering Plants of Hawai'i, Vols. 1 and 2. University of Hawai'i and Bishop Museum Press, Honolulu, HI

Wan CSM, Sage RF (2001) Climate and the distribution of C₄ grasses along the Atlantic and Pacific coasts of North America. *Canadian Journal of botany* 79:474-486

Wand SJE, Midgley GYF, Jones MH, et al. (1999) Responses of wild C₄ and C₃ grass (Poaceae) species to elevated atmospheric CO₂ concentration: a meta-analytic test of current theories and perceptions. *Glob. change biol.* 5:723-741

Young HJ, Young TP (1983) Local distribution of C₃ and C₄ grasses in sites of overlap on Mount Kenya. *Oecologia* 58:373-377

Ziska LH, Bunce JA (1997) Influence of increasing carbon dioxide concentration on the photosynthetic and growth stimulation of selected C₄ crops and weeds. *Photosynthesis research* 54:199-208