TO ESCAPE, AVOID, OR TOLERATE: PHYSIOLOGICAL RESPONSES OF PERENNIAL GRASSES TO EXPERIMENTAL CLIMATE CHANGE

by

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THESIS ABSTRACT

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Master of Science

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Title: To Escape, Avoid, or Tolerate: Physiological Responses of Perennial Grasses to Experimental Climate Change

I used an experimental warming and precipitation experiment in a restored Oregon, USA prairie with a Mediterranean climate to understand how a suite of leaf physiological traits allows two native perennial grasses (*Danthonia californica* and *Koeleria macrantha*) and one non-native perennial grass (*Agrostis capillaris*) to cope with projected changes in climate. I 1) identify shifts in resource-use strategies in relation to carbon and water from wet to dry seasons, 2) present the differential effects of temperature and soil moisture on each species' leaf physiology and fitness and their relationships by utilizing structural equation modeling, and 3) provide evidence for drought-coping mechanisms (dehydration tolerance and avoidance and drought escape). I demonstrate that plant species within the same functional group harbor differential sensitivities to environmental factors and utilize different resource-use strategies to cope with drought. Knowledge of these individualistic responses to projected climate change is imperative to accurately predict future vegetation dynamics.

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“Wolf is the Grand Teacher. Wolf is the sage, who after many winters upon
the sacred path and seeking the ways of wisdom, returns to
share new knowledge with the tribe.”
-*R.G.W.*

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CHAPTER I

INTRODUCTION

Natural History of Oregon's Willamette Valley

This body of research examines responses of leaf physiology and fitness of perennial grasses in a restored prairie to experimental climate change. The study site is located in the Willamette Valley, Oregon, USA. The valley is oriented north-south, bordered by the Coast and Cascade Mountain ranges. The central valley floor exhibits a low elevation gradient from 30-120 meters above sea level, and contains a variety of microenvironments, each with its own characteristic vegetation. It has been estimated prairies were the most extensive vegetation class (circa 1850s), encompassing 424,606 ha, and 2/3 of this area was upland prairie (Christy & Alverson, 2011). Presently, only 2% of prairies in the Willamette Valley remain (Hulse et al., 2002), and they are one of the most imperiled ecosystems in the United States due land-use change, habitat fragmentation, and species invasions (Noss et al., 1995; Sinclair et al., 2006). In the mid-nineteenth century, livestock was introduced to these prairies, and the burning regime practiced by the native Kalapuyans for 10,000 years prior was drastically reduced (Boyd, 1999). These factors instigated a shift in ecological structure, function, and composition of the prairie community, and much of the native vegetation was replaced by Eurasian grasses and herbs (Aschmann, 1991).

Willamette Valley upland prairies are dominated by perennial grasses and forbs. Spatial heterogeneity is imposed by the growth of bunchgrasses such as *Festuca roemeri* (Pavlick) Alexeev (Roemer's fescue), *Achnatherum lemmonii* (Vasey) Barkworth

(Lemmon's needlegrass), *Koeleria macrantha* (Ledeb.) Schult. (prairie junegrass), and *Danthonia californica* Bol. (California oatgrass) (Christy & Alverson, 2011). Bunched growth forms provide intervals of open soil, a unique microhabitat utilized by other plants for seedling establishment, and by ground-dwelling wildlife for nesting sites (Wilson, 1998). Non-native vegetation can significantly alter the spatial organization of prairies, and changes in the ecosystem's physiognomy influence important ecosystem processes such as patterns of resource acquisition, seedling establishment, rates of litter accumulation, and interactions with pollinators and herbivores (Facelli & Pickett, 1991; Wilson, 1998).

Local Restoration of Invaded Ecosystems

Invasive, non-native grasses may be sufficiently widespread to change regional and global aspects of ecosystem function, and have long been recognized as good competitors against many different plant functional groups (D'Antonio & Vitousek 1992). In California prairies, for instance, European annual grasses are one of the major inhibitors to oak seedling recruitment by modifying soil water and light availability (Davis & Mooney, 1985; Danielson & Halvorson, 1990). Colonization of an area by non-native plants often occurs following a disturbance in the ecosystem, and even intact prairies are subject to invasions due to the high occurrence of bare soil in between bunchgrass tussocks and gopher mounds (Facelli & Pickett, 1991). In the Pacific Northwest, non-native grasses pose a significant threat to protected prairies, and many invaded remnant sites still retain a desirable native biota, posing a challenge to designing ecological restoration projects that benefit one group over the other (Stanley et al., 2011).

Many non-native grasses have been introduced for agricultural seed production of cool season forage and turf in the Willamette Valley, which is one of the world's largest producers of grass seed because mild, moist winters coupled with dry summers provides an optimal growth environment. Economically valuable species include *Lolium multiflorum* Lam. and *Lolium perenne* L., (annual and perennial ryegrass, respectively), *Agrostis* sp. (bentgrass), *Poa pratensis* L. (Kentucky bluegrass), *Dactylis glomerata* L. (orchardgrass), and *Schedonerus arundinaceus* Roem. & Schult. (tall fescue). While none of these species appear on the Oregon State Noxious Weed List, local land managers have documented widespread and aggressive establishment of these species in prairie habitats (Stanley et al., 2008).

Ecological restoration is one of the primary approaches to repairing damaged ecosystems (Dobson et al., 1997; Hobbs & Harris, 2001, Cooke & Suski, 2008). One of the major strategies in restoring an ecosystem is controlling aggressive, non-native plants while maintaining or enhancing the abundance and diversity of native vegetation. In the Pacific Northwest, restorative treatments aimed at controlling non-native plants generally include spring and fall applications of herbicide to reduce the abundance of undesirable vegetation; and spring and fall mowing to eliminate seed set and reduce thatch accumulation. Following these treatments, a higher proportion of native species can be achieved by augmenting restoration areas with native seed. Much effort has been dedicated to quantifying the effects of combinations of these treatments to develop regional guidelines for ecological restoration, but the research driving these guidelines does not take into account climate change. An essential question for managers of prairies in the Pacific Northwest, and other endangered ecosystems, is how future climate change will impact the ability of native species to establish and persist within these habitats.

Climate Change in the Mediterranean Biome

The Willamette Valley eco-region of Oregon has a Mediterranean climate with mild, wet winters and hot, dry summers (Csb climate zone, dry-summer subtropical), based on the Köppen climate classification (Kottek et al., 2006). The Mediterranean biome is found on five continents, covers 2% of the Earth's land area, and harbors 20% of global vascular plant diversity (Cowling et al., 1996; Medail & Quezel, 1997). This biome includes the Mediterranean Basin, and regions in the western United States and Mexico, Chile, South Africa, and Australia. The mild climate and close proximity to the ocean attract human settlement and agriculture, making them highly susceptible to biological invasions and habitat fragmentation (Weber & Puissant, 2003; Gritti et al., 2006; Klausmeyer & Shaw, 2009). Mediterranean ecosystems are impacted by multiple global change drivers, and these ecosystems are predicted to experience larger proportional losses of biodiversity than other biomes by 2100, largely as a result of the interactive effects of land use and climate change (Sala et al., 2000).

General circulation models (GCMs), also known as global climate models, project an increase in global temperature by 3°C by the 2080's, along with increases in globally averaged annual precipitation from 1.5-1.9% (IPCC AR4, 2007), with substantial variations about these averages at regional and local scales. For the Pacific Northwest, GCM's predict similar increases in temperature from by the end of the 21st century with equal distribution across seasons, leading to an increase in summer soil moisture deficit up to 25% (National Assessment Synthesis Team, 2001; Millar et al., 2006; Mote & Salathe, 2010). Projected changes in annual precipitation of the region are small (+1% to +2%), but some models project an enhanced seasonal cycle with wetter autumns and winters (Mote & Salathe, 2010). Furthermore, observations of climate in the Mediterranean biomes are consistent with GCM projections of intensified summer drought as a result of an increased number of consecutive hot days (Mouillot et al., 2002).

In terrestrial ecosystems throughout the Northern hemisphere, widely observed responses to climate change include trends toward earlier leaf emergence, longer growing seasons (Menzel et al., 2001; Badeck et al., 2004; IPCC AR4, 2007), and shifts in phenology of plants and animals (Walther, 2004; Visser & Both, 2005; Menzel et al., 2006; Cleland et al., 2007). For example, long term observational studies have demonstrated that the amplification of the annual CO_2 cycle has been accompanied by a longer growing season and greater photosynthesis by terrestrial vegetation (Keeling et al., 1996). Analysis of satellite-sensed normalized difference vegetation index (NDVI) across Northern latitudes also showed accelerated leaf emergence and aboveground productivity, and an increasingly delayed autumn senescence, with correlated changes in NDVI and land surface temperature (Zhou et al., 2001). In natural and agricultural systems, climate warming experiments have significantly shifted timing and duration of flowering for the majority of species examined, where early season species often exhibit accelerated phenology (Price & Waser, 1998; Arft et al., 1999; Dunne et al., 2003; Estrella et al., 2007; Sherry et al., 2007; Sparks et al., 2011).

The temporal distribution of phenological events for a species is largely governed by the different developmental trajectories of species and their resource needs during reproduction. Plants monitor the prevailing environment and initiate reproduction during favorable conditions, and at this point, a series of physiological changes in plant meristems occur which are externally driven by temperature, water, nutrient availability, and light. These species-specific responses are likely to drive the direction, magnitude, and variability of the climate response across ecosystems, even among those subjected to similar climatic trends, due to differences in each species' physiological tolerances and life-history strategies (Parmesan & Yohe, 2003). Since global climate change has been found to affect both vegetative and reproductive phases of the plant life cycle, effective establishment and persistence of populations will be dependent on the individual's ability to coordinate metabolic processes to available resources, such as carbon and water.

The physiological capacity of dominant species in rare ecosystems to respond to warming and altered precipitation regimes is largely unknown, and to our knowledge, there is no literature on this topic regarding perennial grasses that inhabit the prairies of the Pacific Northwest. To understand the response of this functional group to climate change, we experimentally manipulated temperature and precipitation in an Oregon, USA restored prairie, and examined leaf physiological responses of perennial grasses. We selected two native bunchgrasses for our study, *D. californica* and *K. macrantha*, and one non-native grass, *Agrostis capillaris* L. Our objectives were to 1) identify seasonal shifts in resource-use strategies in relation to carbon and water, 2) determine how seasonal temperature and soil moisture differentially affect leaf physiology, performance (e.g. aboveground productivity and reproductive fitness), and their relationships, and 3) characterize drought-coping mechanisms of perennial grasses.

Background on Focal Species

Agrostis capillaris, colonial bentgrass, is a perennial, rhizomatous grass native to Europe and temperate Asia that has been naturalized throughout the eastern and western portions of the United States (USDA NGRP, 2008). The genus was introduced to the Willamette Valley following European settlement during the late nineteenth century. Plantings during the frontier days consisted of mixtures of several species, and stands today still contain a mixture of taxonomic forms (Cook, n.d.). The taxonomy of *Agrostis* sp. is complicated due to the existence of multiple species which are similar in morphological form and interspecies hybridization. The first mention of *A. capillaris* as a seed crop was in 1926 in Northwestern Oregon, and by 1930, this seed stock was planted in Klamath County, and soon after the Willamette Valley (Alderson, 1995). Bentgrasses are uniquely suited to the mild climate of the Pacific Northwest, performing best during the fall and spring. In addition, *Agrostis* sp. can readily colonize waste areas, and seed prolifically under un-mowed conditions. Members of this genus have become a major component of late-successional landscapes by persisting in the soil seed bank, and often are dominant species in old lawns and pastures. Due to its rhizomatous habit, a distinguishing trait of *A. capillaris*, this species is more apt to establish in landscapes composed of tall, erect plants, forming thick mats of vegetation that substantially contribute to thatch accumulation at the end of the growing season (Cook, n.d.). Another characteristic allowing *A. capillaris* to out-compete neighboring species is its low-nitrogen fertility requirements (Adams, 1977). Water-use of this species is similar to other cool-season grasses; its shallow root system prefers irrigation during the dry season (Cook, n.d.). Despite this preference, *A. capillaris* has been noted to be particularly prevalent in dry soils (Hubbard, 1984; Dixon, 1986), and drought resistance varies depending on the cultivar (Ruemmele, 2000).

Danthonia californica, California oatgrass, is a low-growing, long-lived, perennial bunchgrass with densely hairy vegetation, and a fibrous root system. The species naturally occurs from British Columbia to Southern California, and eastward toward the Rocky Mountains and it is considered a minor to dominant component of various woodland, shrubland, upland prairie, and transitional wetland habitats (USDA NGRP, 2000). Immature plants are favored by domesticated livestock, and protein content of vegetation is high, especially in the western portion of the species' range, making dense stands suitable for haying. Because of it's tolerance to fire, mowing, and trampling, it is used in natural lawns, green fire-breaks, and re-vegetation projects (USDA NRCS, 2008a). Healthy stands of *D. californica* can reduce invasions while exhibiting a spatial distribution that is compatible with native forbs (Maslovat, 2001), and provide habitat and food for songbirds and endemic insects, including the endangered Fender's blue butterfly, *Icaricia icarioides fenderi*, of the Willamette Valley (Oregon Department of Fish and Wildlife, 2000; Collins, 2006). Drought resistance in *D. californica* has been rated from low to high, depending on the region of inhabitance, but in the Willamette Valley, *D. californica* commonly inhabits xeric, south and west facing slopes where it comprises up to 70% of the vegetative cover at these sites (USDA NRCS, 2008a).

Koeleria macrantha, prairie junegrass, is a tall, perennial bunchgrass of medium longevity with densely hairy vegetation, and a fibrous root system. It is native to much of the United States, temperate Asia, and Europe, and in North America, colonizes in various open forest, coastal scrub, prairie, chapparal, and savanna habitats (USDA NGRP, 2007). In Ohio and Kentucky, *K. macrantha* is a listed endangered species, and is considered critically imperiled in Louisiana (USDA NRCS, 2008b). Active growth begins early in spring and provides good forage for livestock, deer, elk, small mammals, upland game birds, and insects (USDA NRCS, 2008b). Good cold, heat, drought, and fire tolerance of *K. macrantha* has spurred its usage in restoration projects, where it is often planted for erosion control in highly-degraded areas such as mine land, construction sites, and over septic systems. In the 1930s, this species also was used in re-vegetation projects following severe drought and dust storms (USDA NRCS, 2008b; Watkins, 2009). Until recently, this species has received little attention as a turf grass, but due to its broad distribution, and potential to withstand extreme environmental conditions, such as heat and cold, breeding projects for *K. macrantha* populations from the mid-western portions of the United States are now underway (Watkins, 2009).

Identifying Drought-Coping Phenotypes in Plants

Water deficits can result in significant declines in overall plant productivity, and can promote high rates of plant mortality (Touchette et al., 2007). Plants have evolved various physiological and morphological responses to endure periods of water stress. In arid habitats, plants have frequently been observed to avoid or tolerate dehydration, or to escape drought conditions all together. Each drought-coping mechanism requires coordination of a number of functional traits, emphasizing the importance of viewing the resulting phenotype as an integrated function of growth, morphology, and physiology. A large body of research provides hypotheses on how selection on these traits should depend on environmental water availability, and many of these adaptive hypotheses are based on leaf physiology (Givnish, 1986; Dudley, 1996).

Gaining a predictive understanding of the complexity of relationships between leaf physiology and water stress requires placing the effect of one environmental factor in context of others operating simultaneously. Understanding the relative importance of each controlling factor, in addition to evaluating their interaction, is essential to identifying key environmental factors driving changes in leaf functional traits. To understand how projected climate change will affect correlated leaf physiological and morphological traits, and the resulting impact on the overall performance of the plant species, we utilized structural equation modeling (SEM).

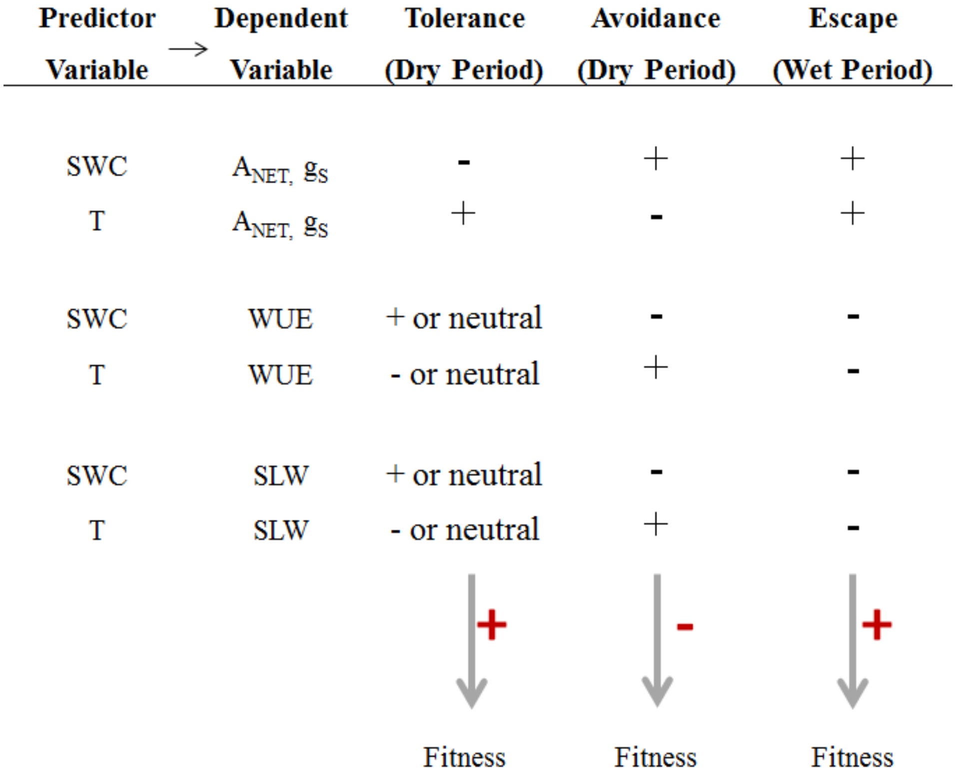
We formed SEMs (see Chapter 2, Fig. 2.1) to represent our multivariate hypothesis as a collection of causal relationships linking environmental factors (e.g. temperature and soil water content) and leaf physiological processes to plant performance. These networks are based upon *a priori* assumptions that our focal species will exhibit a spectrum of traits related to drought-coping mechanisms (Fig. 1.1). In SEM, model specification is the process by which hypotheses are translated into a statistical form (Iriondo et al., 2003; Grace, 2006; Grace et al., 2010). This process focuses on using available data to identify observed (measured) variables for the parameters in the conceptual model. To describe integrated phenotypes related to drought-coping mechanisms in our focal species, we selected several leaf gas exchange parameters: net photosynthesis (A_{NET}), stomatal conductance (g_s), and instantaneous water-use efficiency (photosynthesis divided by transpiration, WUE_{INST}). We also included specific leaf weight (SLW), a measure of leaf thickness. We measured environmental factors and leaf physiological traits over the course of the growing season, constructed separate conceptual models for the wet period (April-May), transitional period (June), and dry period (July-August), and determined the impact of seasonal environment and physiology on fitness. We also measured aboveground biomass (AGB) and leaf water potential (ψ) during each sampling period, in addition to leaf carbon : nitrogen ratio (C:N) and integrated water-use efficiency ($\delta^{13}C$) during the dry period, although these parameters were not included in the SEMs.

Open stomata facilitate gas-exchange, and since g_s is more sensitive to water vapor, the plant is able to partially close its pores to prevent high transpiration rates and control the balance of carbon gained versus water lost (WUE_{INST} and $\delta^{13}C$). Stomatal control of water loss allows plants to occupy habitats with fluctuating environmental conditions, and it is thought that this is an important predictor of speciation and evolutionary change (Hetherington & Woodward, 2003). The response of g_s to the environment can adapt to local and global changes in climate on the timescales of minutes to millennia, and exerts a major control on the balance of carbon and water cycles of ecosystems (Beerling & Woodward, 1997; Woodward, 1998; Royer, 2001).

The evolution of traits that affect photosynthesis may be constrained in dry habitats due to the potential cost of transpirational water loss. When a plant is not able to replenish the water diffusing from its leaves, ψ will decrease and the plant's permanent wilting point will eventually be reached. Habitats that experience great fluctuations in soil moisture are often dominated by dehydration tolerant plants that are able to maintain A_{NET} during low ψ without wilting (Pockman & Sperry, 2000; Bhaskar & Ackerly, 2006; Grime et al., 2008; McDowell et al., 2008). This may be a result of having higher optimal temperatures for metabolic processes, or by enhancing water uptake through adjustments in root morphology which allows stomata to remain open. High rates of photosynthesis in C_3 plants are associated with factors that increase intercellular CO_2 and consequently decrease WUE, such as high foliar N and high g_s (DeLucia & Schlesinger, 1991). These responses (e.g. high rates of leaf gas exchange, and low WUE) constitute dehydration tolerance (DeLucia & Schlesinger, 1991), a resource-use strategy that we expected to result in positive or neutral responses in terms of fitness to high temperature and low soil moisture throughout the growing season (Fig 1.1).

In contrast, we expected the collection of correlated traits representing the dehydration avoidance phenotype to decrease fitness in response to high temperatures and low soil moisture in the dry period of the growing season (Fig. 1.1). This response may be mediated by lowering A_{NET} and g_s to prevent water loss, resulting in higher WUE, but compromising growth and reproduction (Arntz & Delph, 2001; Brock & Galen, 2005). High SLW may also allow leaves to more efficiently assimilate internal CO_2 while limiting diffusion of water to the atmosphere (Wright & Westoby, 2002).

The third resource-use strategy, drought escape, is well documented for many annual and ephemeral species in arid ecosystems, whose performance during wet periods is thought to influence long-term persistence of populations (Beatley, 1974; Monson & Szarek, 1981). This strategy allows plants to escape soil moisture deficits by completing their life cycle prior to experiencing stressful drought conditions through increased metabolic activity and rapid growth (Bazzaz, 1979; Arntz & Delph, 2001). For perennial plants, escaping drought will restrict the majority of growth and resource acquisition needed for reproduction to wet periods of the growing season. In Mediterranean ecosystems, we expected drought escaping plants to exhibit a positive relationship between soil moisture and fitness, and may benefit from increased temperature during the rainy season. In addition to increasing gas exchange, high soil moisture and temperature are expected to lower WUE and SLW to promote faster growth (DeLucia & Schlesinger, 1991; Lambers & Poorter, 1992; Reich et al., 1997) (Fig. 1.1).



Predictor Variable	→	Dependent Variable	Tolerance (Dry Period)	Avoidance (Dry Period)	Escape (Wet Period)
SWC		A_{NET}, g_S	-	+	+
T		A_{NET}, g_S	+	-	+
SWC		WUE	+ or neutral	-	-
T		WUE	- or neutral	+	-
SWC		SLW	+ or neutral	-	-
T		SLW	- or neutral	+	-
			+	-	+
			Fitness	Fitness	Fitness

Figure 1.1. Hypothesized relationships between environmental factors and leaf physiological traits, and their effects on fitness for the drought-coping mechanisms-dehydration tolerance, dehydration avoidance, and drought escape. Environmental factors (predictor variables) are soil water content (SWC) and canopy temperature (T). Leaf physiological traits (dependent variables) include net photosynthesis (A_{NET}), stomatal conductance (g_s), water-use efficiency (WUE), and specific leaf weight (SLW). Signs (+ / - / neutral) indicate the direction of the relationship between parameters. Predictions are seasonally dependent, and we expected dehydration tolerance and avoidance strategies to be evident during the dry period of the growing season, whereas drought escape can only be identified in the wet period.

CHAPTER II

DIFFERENTIAL RESPONSES OF LEAF PHYSIOLOGY AND FITNESS TO EXPERIMENTALLY MANIPULATED TEMPERATURE AND PRECIPITATION

Introduction

Grasslands and Mediterranean ecosystems are sensitive to multiple factors driving global change, and are at risk of experiencing significant declines in biodiversity (Sala et al., 2000). Losses as a result of land-use and climate change are predicted to be proportionately larger than in any other terrestrial biome (Sala et al., 2000; Klausmeyer & Shaw, 2009). These ecosystems harbor 20% of global vascular plant diversity (Cowling et al., 1996; Medail & Quezel, 1997), and since moisture is the primary limitation to plant growth (Larcher et al., 2000), it is imperative that we understand how the vegetation will be impacted by the interactive effects of projected changes in temperature and precipitation.

Plant responses to climate change are regionally specific. In a meta-analysis of experimental ecosystem warming, elevated temperature increased aboveground productivity by 19%, but this positive response was greatest at northernmost sites (Rustad et al., 2001). In contrast, plants naturally experience temperatures close to their thermal optimum for photosynthesis in Mediterranean ecosystems, and warming can induce responses in the opposite direction, causing repressed rates of photosynthesis and decreased aboveground productivity (Tenhunen et al., 1990; Vallardes & Pearcy, 1997; ValPine & Harte, 2001; Llorens et al., 2003; Peñuelas et al., 2004). The response of plant communities to climate change will depend on the physiological tolerances and life history strategies of co-existing species (Parmesan & Yohe, 2003), which often have differential physiological responses to temperature and soil moisture (Silletti & Knapp, 2001; Swemmer et al., 2006; Nippert et al., 2009). Drought can decrease species' richness and aboveground productivity in grasslands (Tilman & Haddi, 1992), but the key environmental driver for changes in community composition in grasslands and Mediterranean ecosystems under projected climate change remains elusive.

Water availability drives selection on complex phenotypes related to leaf physiology (Givnish, 1986; Dudley, 1996), many of which confer the well-described strategies of dehydration tolerance, dehydration avoidance, or drought escape. Each strategy represents a different way for a plant to resist the potentially negative effects of drought. Habitats that experience large fluctuations in soil moisture are often dominated by deydration tolerant plants that are able to maintain photosynthesis during low leaf water potentials without wilting (Pockman & Sperry, 2000; Bhaskar & Ackerly, 2006; Grime et al., 2008; McDowell et al., 2008). This may be a result of having higher optimal temperatures for metabolic processes or of enhancing water uptake through adjustments in root morphology, which allows stomata to remain open. High rates of photosynthesis in C_3 plants are associated with factors related to high intercellular CO_2 and consequently decreased water-use efficiency (WUE), such as high foliar nitrogen and high stomatal conductance (DeLucia & Schlesinger, 1991). The dehydration tolerant phenotype is expected to be a collection of traits (e.g., high leaf gas exchange and low WUE) that we expected to result in positive or neutral responses in terms of fitness to high temperature and dry soils (Fig.1.1).

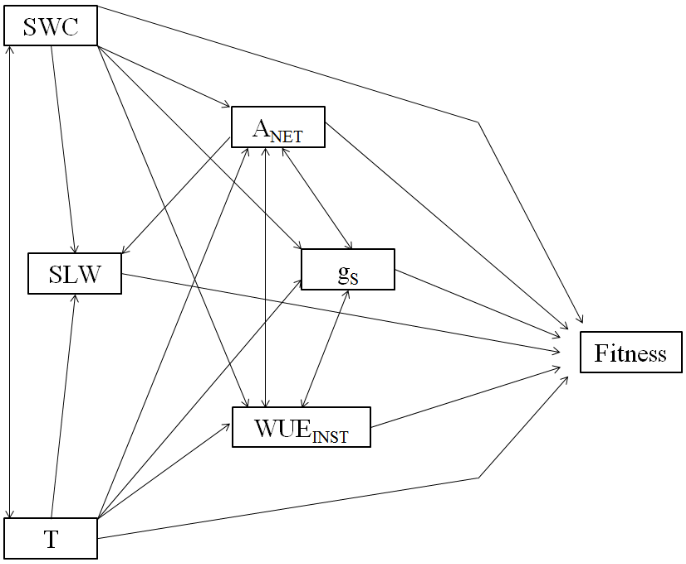
In contrast, we expected the dehydration avoidance phenotype to decrease fitness in response to high temperatures and low soil moisture in the dry period of the growing season (Fig. 1.1). This response may be mediated by lowering A_{NET} and g_s to prevent water loss, resulting in higher WUE, but compromising growth and reproduction (Arntz & Delph, 2001; Brock & Galen, 2005). High SLW may also allow leaves to more efficiently assimilate internal CO_2 while limiting diffusion of water to the atmosphere (Wright & Westoby, 2002).

The third resource-use strategy, drought escape, is well documented for many annual and ephemeral species in arid ecosystems, whose performance during wet periods is thought to influence long-term persistence of populations (Beatley, 1974; Monson & Szarek, 1981). This strategy allows plants to escape soil moisture deficits by completing their life cycle prior to experiencing stressful drought conditions through increased metabolic activity and rapid growth (Bazzaz, 1979; Arntz & Delph, 2001). For perennial plants, escaping drought will restrict the majority of growth and resource acquisition needed for reproduction to wet periods of the growing season. In Mediterranean ecosystems, we expected drought escaping plants to exhibit a positive relationship between soil moisture and fitness, and may benefit from increased temperature during the rainy season. In addition to increasing gas exchange, high soil moisture and temperature are expected to lower WUE and SLW to promote faster growth (DeLucia & Schlesinger, 1991; Lambers & Poorter, 1992; Reich et al., 1997) (Fig. 1.1).

We used an experimental warming and precipitation experiment in an Oregon, USA prairie with a Mediterranean climate to understand how a suite of physiological traits allows two native species, *Danthonia californica* Bol. and *Koeleria macrantha* (Ledeb.) Schult., and the non-native species, *Agrostis capillaris* L., within a single dominant functional group (perennial grasses) to cope with projected changes in climate. Our objectives were to 1) identify seasonal shifts in resource-use strategies in relation to carbon and water, 2) determine how seasonal temperature and soil moisture differentially affect leaf physiology, performance (e.g. aboveground productivity and fitness), and their relationships, and 3) characterize drought-coping strategies of perennial grasses.

In previous climate manipulation studies, the direction and magnitude of changes in plant physiology and aboveground productivity were not only species specific, but were also dependent on seasonal dynamics (Loik et al., 2000; Zhou et al., 2007; Lambrecht et al., 2007; Shi et al., 2010). We hypothesized that physiological responses to increased temperature and precipitation vary in direction and magnitude with the contrasting wet and dry seasons of a Mediterranean climate. We formed structural equation models (SEMs) to represent our multivariate hypothesis as a collection of causal relationships linking environmental factors (e.g. temperature and soil water content) and leaf physiological processes to plant performance (Fig. 2.1). These networks are based upon *a priori* assumptions that our focal species will exhibit a spectrum of traits related to drought-coping mechanisms.

(a) Wet and Transitional Periods



(b) Dry period

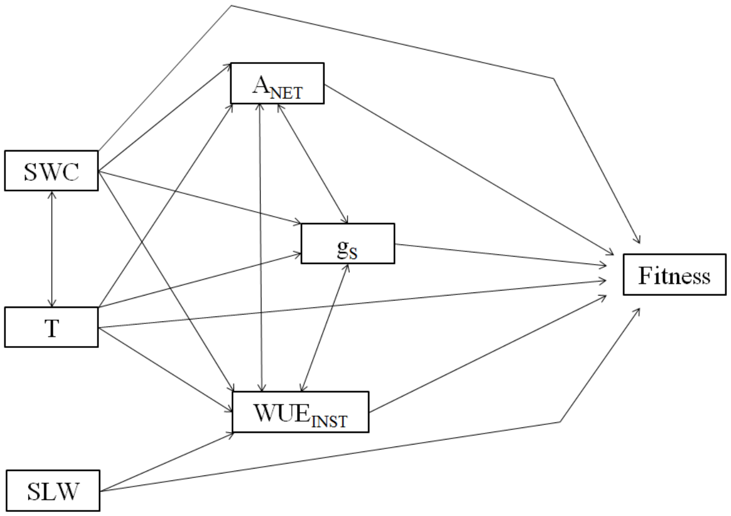


Figure 2.1. Path diagrams of hypothesized relationships for environmental controls over plant physiology and fitness in conceptual models for **(a)** wet and transitional periods and **(b)** dry period. Environmental factors include daytime canopy temperature (T) and soil water content (SWC). Physiological variables include net photosynthesis (A_{NET}), stomatal conductance (g_s), instantaneous water-use efficiency (WUE_{INST}), and specific leaf weight (SLW). Single headed arrows indicate directed paths, and double headed arrows represent correlations. Models are identical with the exception of the pathways involving SLW.

Methods

Site Description and Focal Species

This study was conducted in an upland prairie within the Willamette Valley eco-region at the Nature Conservancy's Willow Creek Preserve in Eugene, OR, USA (44°1'34"N/ 123°10'56"W). Presently, only 2% of prairies in the Willamette Valley remain (Hulse et al., 2002), and they are one of the most imperiled ecosystems in the United States due land-use change, habitat fragmentation, and invasions (Noss et al., 1995; Sinclair et al., 2006). The Willamette Valley has a Mediterranean climate (Kottek et al., 2006), characterized by mild, wet winters and warm, dry summers. For the Pacific Northwest, GCM's predict on average an increase in temperature of 3ºC by the 2080s, enhanced seasonal cycles producing warmer and wetter winters, and an increasing summer soil moisture deficit (Mote & Salathe 2010).

The soil at the experimental site is a silty clay loam Hazelair (very-fine, smetitic, mesic Vertic Haploxeroll) with a pH of 5.8. Prior to experimental manipulation, vegetation consisted primarily of grasses and forbs non-native to the region, with *Agrostis capillaris* L. (colonial bentgrass) being the dominant species. Perennial grasses are the dominant functional group in prairies of the Willamette Valley. Species within this functional group exhibit marked differences in growth form. We selected two native, bunchgrasses for our study, *Danthonia californica* Bol. and *Koeleria macrantha* (Ledeb.) Schult., which possess morphological traits characteristic of drought resistance, such as fibrous roots, and narrow, vertically oriented leaves with high densities of trichomes, and one non-native grass, *A. capillaris,* that forms rhizomatous root-systems. Despite commercial interest in *A. capillaris* and *D. californica* for turf and forage, reports of their drought resistance are conflicting, although a preference for dry soils has been observed for both species (Hubbard, 1984; Dixon, 1986; Ruemmele, 2000; USDA NRCS, 2008). *Koeleria macrantha* is known to tolerate extreme environmental conditions, such as heat, cold, and drought (Watkins, 2009).

Experimental Design

The experiment was designed as a fully crossed manipulation of temperature (+ 3ºC) and (+ 20%) precipitation with five replicate 3-m diameter (7.1 m^2) plots per treatment. Temperature was increased with six overhead 2000-W infrared heaters (Kalglo Electronics, Inc., Bethlehem, PA) angled at 45° to the surface (Kimball, 2005; Kimball et al., 2008), and were controlled for an increase in temperature by 3ºC above control plots. Heating of the plots was relatively uniform, and plant canopy temperatures were within 0.05ºC of the set temperature 88% of the time. A 20% increase in precipitation was achieved by pumping water from an on-site rain collection system, and hand watering plots using a gauged hose. Supplemental precipitation was added within two weeks of when it fell, and primarily increased wet season precipitation intensity with little addition during the dry season, thus mimicking GCM predictions for the region (Mote & Salathe, 2010). Dummy heaters were erected over ambient temperature plots to account for any shading from the infrared heaters. Treatments began in April 2010, and measurements described in this paper were performed from April to August in 2011.

Plots were restored in 2009 by spring and fall applications of the herbicide glyphosate followed by mowing and removal of thatch. In January 2010, plots were seeded with equal proportions of 31 native upland prairie graminoids and forbs. Seed mixtures contained local genotypes, and included the two native focal species, *K. macrantha* and *D. californica*. Following site restoration, *A. capillaris* continued to aggressively establish throughout the site and was hand-thinned in July 2010; however this species remained an important component of the plant communities in the plots in 2011.

Environmental Factors

Environmental factors, leaf gas exchange, and ψ were measured over the course of the growing season during the wet period (April and May), transitional period (June), and dry period (July and August). Volumetric soil water content (SWC) of the upper 30-cm in each plot was determined by time-domain reflectometry (TDR) probes (model CS616-L, Campbell Scientific, Logan, UT, USA). Canopy temperature was determined for each plot using infrared radiometers (model SI-121, Apogee Instruments Inc., Logan, UT, USA). One infrared probe was positioned over each plot at a height and angle to ensure integrated surface temperature measurements over a 1 m^2 plot area. Mean canopy surface temperature and SWC were recorded every 15 and 30-minutes, respectively, to a CR1000 data-logger. Average SWC and daytime canopy temperature from 9:00 – 17:00 during each 2 week sampling period were calculated for subsequent analyses. Sampling times also corresponded to pre-flowering, anthesis, and seed maturation periods of growth.

Physiology

We measured diurnal rates of photosynthesis (A_{NET}), stomatal conductance (g_s), and instantaneous water-use efficiency (photosynthesis divided by transpiration, WUE_{INST}) using a Li-Cor 6400 Portable Photosynthetic System (Li-Cor Biosciences, Lincoln, NE, USA) on two randomly selected individuals per plot for each species. Morning sampling (AM) took place between 9:00 and 12:30, and afternoon sampling from 13:30 to 17:00 (PM) during dry, clear to partly sunny days. Individuals of each species were randomly sampled during these periods. Prior to gas exchange measurements, each species' light saturation point was determined by measuring the photosynthetic response of five randomly selected individuals per treatment to a stepwise decrease in photosynthetic photon flux density (PPFD) using a red light sensor (400-700 nm). Light saturation points did not differ across treatments and were between 1400-1500 PPFD for all species. Leaf area based rates of A_{NET}, g_s, and WUE_{INST} were measured at each species' light saturation point to eliminate the effect of light on gas exchange.

The same newly expanded leaves were sampled for AM and PM gas exchange. To ensure that measurements reflected plot microclimatic conditions, temperature, relative humidity, and vapor pressure deficit were measured at canopy height in the center of each plot using external Li-Cor sensors prior to clamping leaves. Chamber conditions for sampling were then set to these ambient values. The CO_2 concentration within the cuvette was 390-400 ppm, and the flow was adjusted between 300-500 μmol s^1. Gas exchange parameters were logged every 30 seconds over a period of 2.5 minutes. A central portion of the leaf blade with parallel sides was enclosed in the cuvette, and area was estimated by measuring the length and width of leaves with digital calipers.

Leaf water potentials (ψ) were measured using a Scholander-type pressure chamber (PMS Inc., Corvallis, OR, USA) on days without rainfall. We excised 7 cm sections of leaf and petiole from plants, and immediately placed these in the pressure chamber. Predawn measurements occurred from 3:30 to 5:30 and midday measurements from 12:00 to 14:00. Due to the destructive nature of this measurement, we selected the nearest intraspecific neighbor ($\leq$ 20 cm) to each plant used for gas exchange measurements to obtain ψ.

During the transitional time period, leaves were harvested to determine specific leaf weight (SLW), a measure of leaf thickness (g/cm^2). Samples were dried for 48 hours at 60°C, weighed, and photographed to analyze leaf surface area using ImageJ 1.43 software (Abramoff et al., 2004). Additional leaves were harvested during the dry period from the same plants to determine total carbon (C) and nitrogen (N) and $\delta^{13}C$. Leaves were dried for 48 hours at 60°C, and ground plant material was pooled per plot. Samples were analyzed for nutrient content and $\delta^{13}C$ at the University of California at Berkeley's Center for Stable Isotope Biogeochemistry (Berkeley, CA, USA).

Plant Performance

For each species, aboveground biomass (AGB) was estimated during wet and transitional periods using allometric relationships. To develop allometric equations, we measured basal area and height of the tallest leaf of vegetative and flowering plants from wild, source populations of each species. Wild plants were harvested, dried for 48 hours at 60°C, and vegetative material was weighed. We performed a multiple regression for each species with AGB as the dependent variable, and basal area, height, and life history stage (vegetative or flowering) as the independent variables ($R^2 = 0.80\text{-}0.88$, $p \leq 0.001$). Dry period AGB was determined by harvesting plants directly from plots.

Aboveground competition was also estimated for individuals during the transitional period, which corresponded best to the peak growing season for most plant species in our plots. We centered a 50 cm^2 quadrat over each target plant and aligned each corner with the cardinal directions using a compass. In each direction, we measured a 10 cm distance from the edge of our target plant, and recorded canopy height to the nearest cm by dropping a pin to the ground. An average canopy height surrounding each plant was then calculated. We counted the total number of seeds produced per plant as a measure of fitness. Mature seeds were periodically collected, dried and weighed as above. For *D. californica*, we calculated fitness as the sum of cleistogamous (self-fertilized) seeds and open-pollinated seeds.

Statistical Analyses

Analysis of Variance (ANOVA)- Measurements from individuals within plots were averaged, and a two-way ANOVA using plot as the replicate unit was performed to analyze the effects of heating and precipitation on each of the dependent variables (n=5). Separate analyses were conducted for each species. To examine diurnal patterns in leaf physiology, we included time of day as a repeated measure in the ANOVAs. We also performed additional ANOVAs with season as a repeated measure for leaf physiological variables and AGB. Where there were significant time by treatment interactions (p <

0.10), we analyzed each time period separately in a univariate two-way ANOVA. This analysis was also used to examine differences between treatment means for leaf traits measured once during the study period. Data transformations (log and square root) were performed when necessary to meet the normality assumptions of the ANOVA. We chose not to make a correction for multiple comparisons because they are overly conservative in terms of inflating Type II errors, and we considered Type I and Type II errors to be equally problematic (Moran, 2003). However, we emphasize consistent results in both the ANOVAs and SEMs to control for the probability of spurious significant results. All diagnostic tests and ANOVAs were performed in PASW 18.0 Statistics software (SPSS Inc., Chicago IL, USA).

Structural equation modeling (SEM) was used to explore hypothesized relationships amongst environmental factors, leaf physiology, and fitness during the wet, transitional, and dry periods of the growing season. The SEM analysis consisted of three steps: 1) model specification, 2) model evaluation, and 3) selecting inferential models. For SEM, we used the individuals as our replicates rather than plots. All plants selected for sampling survived to the end of the growing season, except for three *A. capillaris* plants which were omitted from the data set. As the sample size is relatively small (n = 37 – 40), we attempted to meet the guideline of a 5:1 ratio of samples to free parameters (Bentler & Chou, 1987), and limited the number of selected variables within the confines of our hypothesis (Tanaka, 1987).

Model Specification- For each time period, daily averages for leaf gas exchange measurements were obtained. All other environmental factors (SWC and temperature) and dependent variables (SLW, AGB, and fitness) remained the same as described above.

We used bivariate scatter-plots, Pearson's correlations, and linear regression to evaluate whether these relationships met the normality and linearity assumptions for SEM (Grace, 2006). To avoid modeling non-linear relationships, we chose to analyze separate models for each period of the growing season, rather than utilizing a latent growth curve analysis that incorporates repeated measures into SEM (Grace, 2006). Selected variables within each model were log and square root transformed when necessary to satisfy distributional and linearity assumptions. Competition was eliminated from our conceptual model because we discovered a positive relationship between fitness and this construct, which is more indicative of a favorable microhabitat rather than inhibition of resource uptake from surrounding vegetation.

We chose to use fitness as a dependent variable and exclude AGB because of their high autocorrelation (r = 0.74 - 0.81). In addition, measurements of individual climate factors over the course of the growing season were highly correlated, solidifying our choice to analyze separate models for each time period. For other highly correlated variables (r = 0.60 - 0.80), we calculated variance inflation factors (VIFs) to further diagnose collinearity. VIFs for correlated independent variables never exceeded 2, and in many cases, they were even more highly correlated with dependent variables so we determined that our conceptual model could accurately identify significant relationships (Bishop & Schemske, 1998).

Model Estimation- The relationships amongst single, observed variables illustrated in Fig. 2.1 were modeled as path coefficients, representing the magnitude and direction of the effect of each predictor on a dependent variable, with the other predictors statistically held constant. All SEM analyses were conducted using Amos 18.0 SEM software (SPSS Inc., Chicago IL, USA), and utilized maximum likelihood procedures for model evaluation and parameter estimation. Model fit was evaluated by using the χ^2 goodness-of-fit statistic and associated p-values (larger p-values indicate a good fit between the model and the data), Bentler-Bonnett Normed Fit Index (NFI), and Goodness of Fit Index (GFI). Both NFI and GFI range between 0 and 1 with values > 0.90 indicating a good model fit (Bentler, 1989), and tend to underestimate model fit when sample sizes are small (Bishop & Schemske, 1998).

Inferential models for each species include significant standardized path coefficients (by standard deviation units) and squared multiple correlations. Path coefficients are displayed and discussed when path p-values were ≤ 0.10. We also report all standardized total effects for the final inferential models which describe the influences that variables have on one another through direct and indirect paths (Grace, 2006).

Results

Seasonal Treatment Effects on Soil Moisture

The precipitation and heating treatments differentially affected soil moisture depending on season and whether they were combined (Fig. 2.2). Heating had only a modest soil drying effect during the wet season and transitional period (April through mid-June). During the dry season (mid-June through August), soil moisture was typically very similar across all heated plots, regardless if precipitation was supplemented, indicating the lesser amounts of water applied in the precipitation treatment and the drying effect of the heating treatment. In the absence of heating, the precipitation plots consistently had higher soil moisture than the control plots until August.

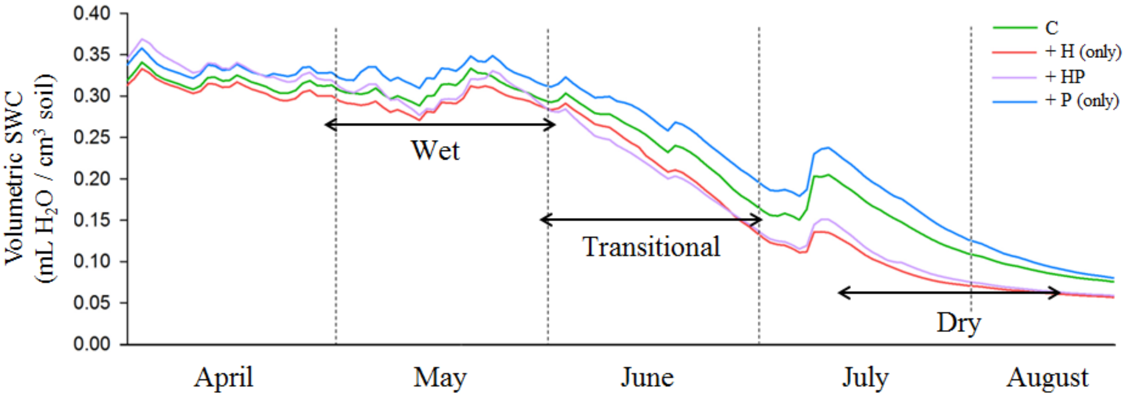


Figure 2.2. Daily average volumetric soil water content across the growing season for each experimental treatment. Wet, transitional, and dry sampling periods correspond to pre-flowering, anthesis, and seed maturation life-history stages for all focal species. *Treatment Key:* C = control, + P (only) = +20% precipitation (only), + H (only) = +3°C (only), + HP = +20% precipitation and +3°C.

Seasonal Responses of Diurnal Leaf Physiology to Treatments

Time of day had significant effects on each physiological response during one or more of the seasonal periods ($p < 0.10$, Appendix A) with the exception of A_{NET} in *A. capillaris*. Season was also an important determinant of leaf physiological responses ($p < 0.10$, Appendix B), with the exception of WUE_{INST} (AM) in *K. macrantha*. Across species, A_{NET}, g_s, WUE_{INST}, and ψ decreased over the course of the day and from the wet to dry season.

The photosynthetic response to the manipulative climate treatments varied across species (Fig. 2.3a, $p < 0.10$). *Agrostis capillaris* exhibited a seasonal interaction with precipitation, with A_{NET} (PM) decreasing with additional rainfall during the wet period, but increasing with added precipitation during the dry period. Warming increased A_{NET} (AM) in *D. californica*, but decreased A_{NET} (AM) in *K. macrantha*, regardless of season. In addition, warming caused a decrease in g_s (AM) in *K. macrantha* and *A. capillaris* (Fig 2.3b, $p < 0.10$).

Only the native species had a treatment response in WUE_{INST} (Fig. 2.4). For *K. macrantha*, WUE_{INST} (AM) was higher in the combined heat and precipitation treatment ($p = 0.08$). For *D. californica*, WUE_{INST} (PM) depended on season and treatment. The heat and precipitation treatments alone caused higher values during the wet and dry periods, but these effects were dampened by the combined treatment. During the transitional period, however, warming substantially lowered WUE_{INST} (PM).

For all species, the heating treatments consistently increased plant water stress (lowered ψ) across all seasonal and diurnal periods (Fig. 2.5a-b). Across species, *K. macrantha* showed the highest levels of midday water stress in the heated treatment during the dry period, as indicated by the pre-dawn measurements, water stress was not alleviated overnight. Warming lowered leaf C:N in *D. californica*, a response driven by N content of the leaves (Fig. 2.6a). Precipitation increased $\delta^{13}C$ in *K. macrantha*, which corresponds to a higher integrated WUE (Fig. 2.6b) (Lambers et al., 2008).

Seasonal Responses of Plant Performance to Treatments

Across species, AGB increased from the wet to dry season. Aboveground biomass of native species was not affected by our treatments, but *A. capillaris* had greater AGB in the heat treatments (Fig. 2.7). There were no fitness responses to treatments for any of our focal species ($p > 0.10$, Appendix C), although for *K. macrantha* and *A. capillaris*, high variance may have prevented detection significant results (Table 2.1). *Danthonia californica* produced the least number of seeds of all species, and results for cleistogamous and open-pollinated seed sets (data not shown) did not differ significantly from those for the total seed set (Table 2.1).

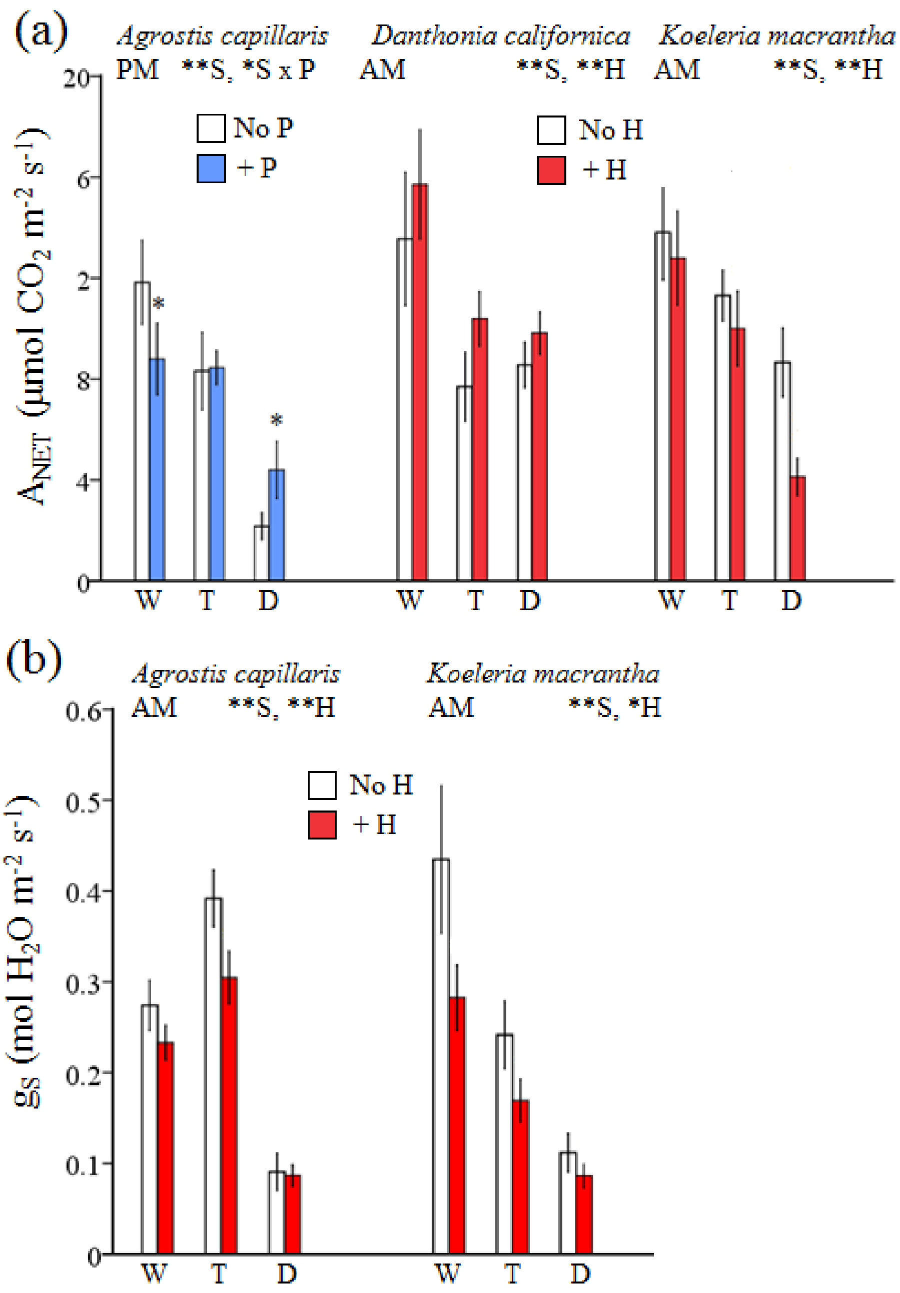


Figure 2.3. Responses of **(a)** photosynthesis and **(b)** conductance to treatments. Mean values ± 1 S.E. during wet (W), transitional (T), and dry (D) periods are shown for significant effects of season (S), heated treatment (H), and precipitation treatment (P), and interactions from two-way repeated measures ANOVAs. Species, time of day (AM or PM), and significant effects are listed above panels of graphs.

*denotes $0.05 < p < 0.10$, **denotes $p \leq 0.05$

Treatment Key: + H = +3°C, No H = ambient temperature, + P = +20% precipitation, No P = ambient precipitation

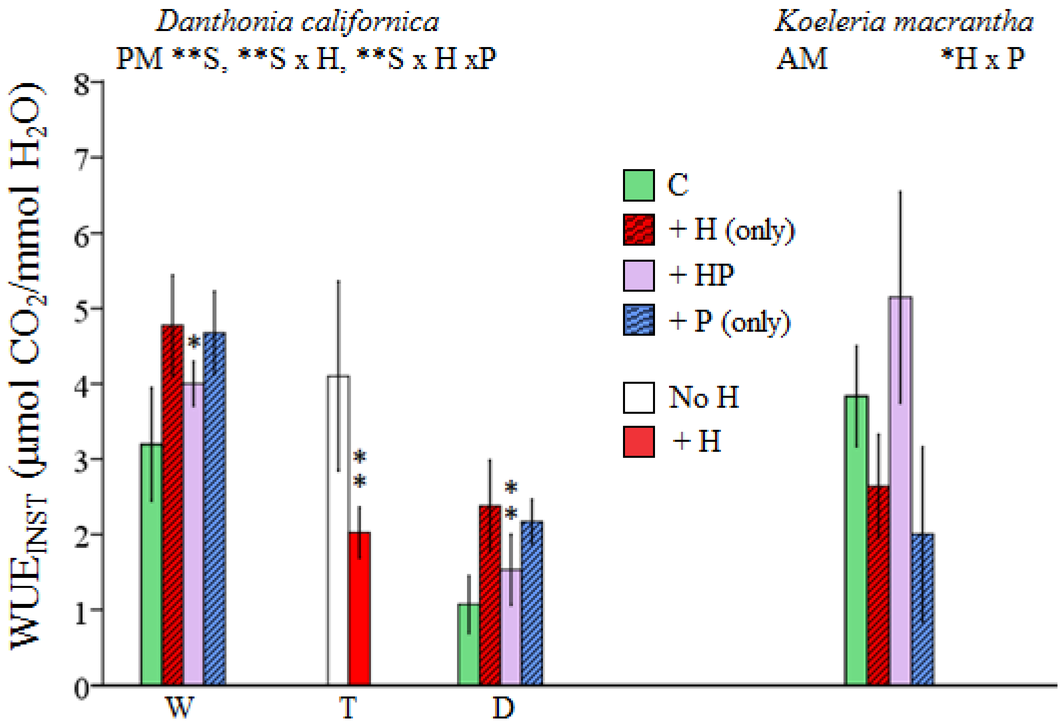


Figure 2.4. Response of instantaneous water-use efficiency to treatments. See Figure 2.3. for description of statistics and data reported. For *K. macrantha*, season was not significant, and mean values ± 1 S.E. were pooled across the growing season.
Treatment Key (Danthonia californica): C = control, + H (only) = +3°C (only), + P (only) = +20% precipitation (only), + HP = + 20% precipitation and +3°C
Treatment key (Koeleria macrantha): + H = +3°C, No H = ambient temperature

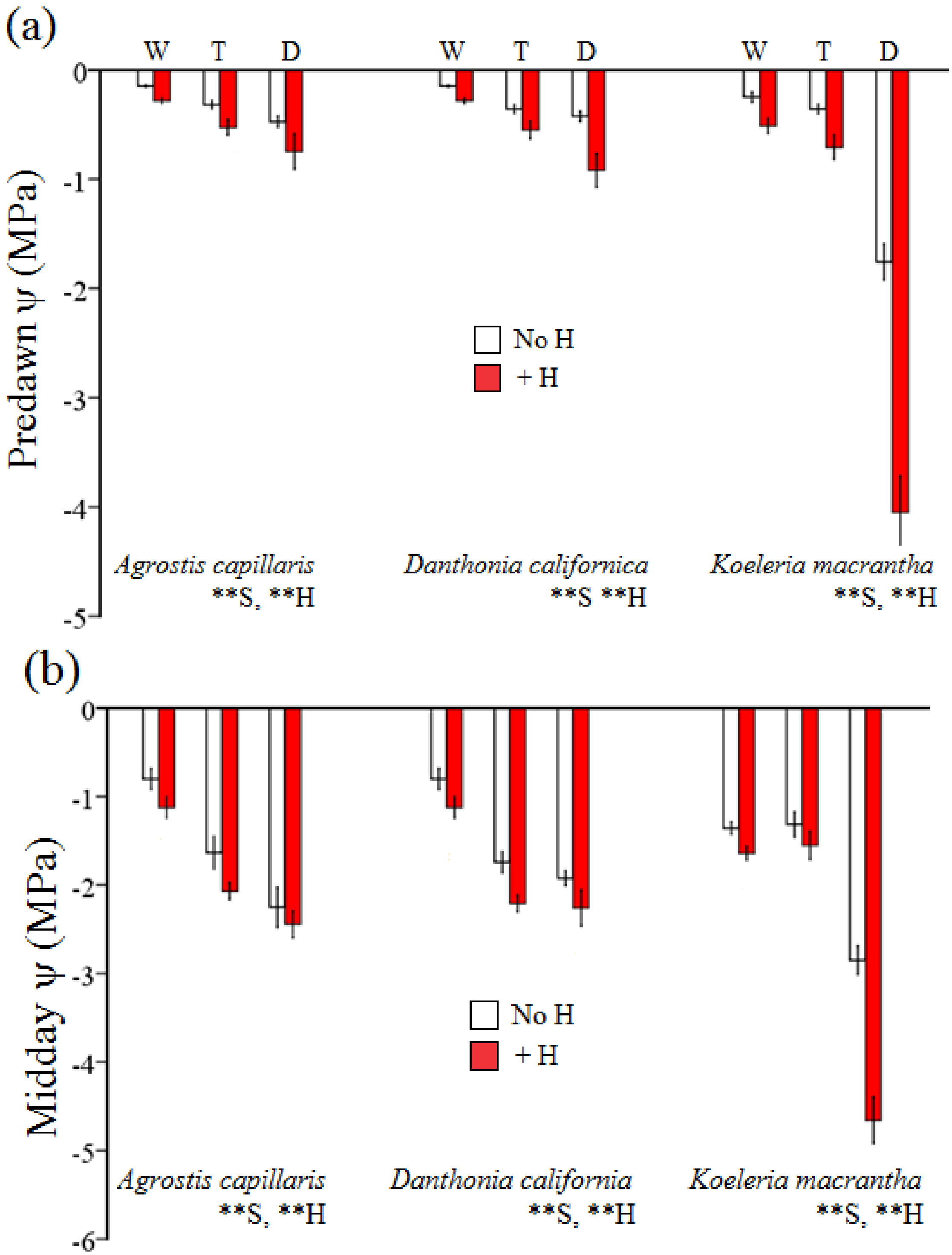


Figure 2.5. Responses of **(a)** predawn and **(b)** midday water potential to treatments. See Figure 2.3. for description of statistics and data reported.

Treatment key: + H = +3°C, No H = ambient temperature

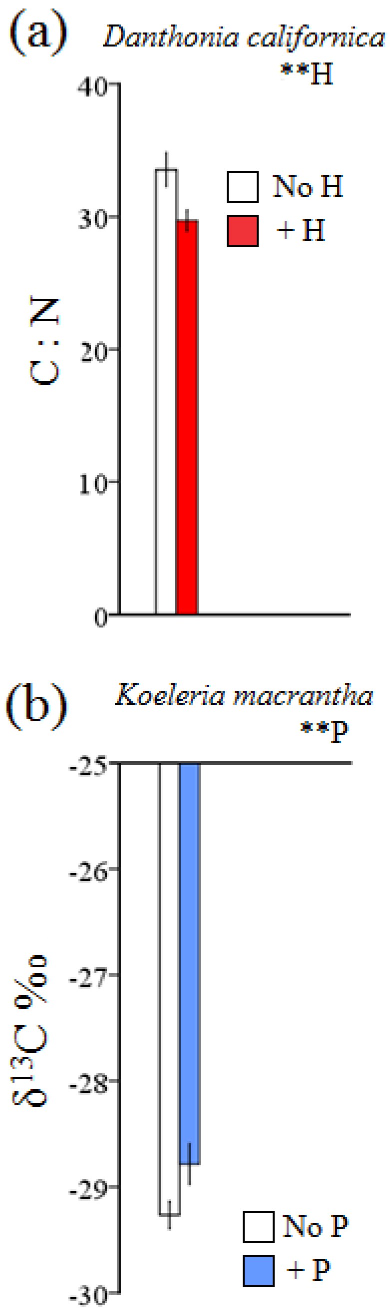


Figure 2.6. Responses of (**a**) leaf carbon : nitrogen and **(b)** carbon isotope ratio to treatments. Mean values ± 1 S.E. are shown for significant effects of heating treatment (H), and precipitation treatment (P), and interactions from two-way univariate ANOVAs.
* denotes $0.05 < p < 0.10$ **denotes $p \leq 0.05$

Treatment Key: + H = +3°C, No H = ambient temperature, + P = +20% precipitation, No P = ambient precipitation

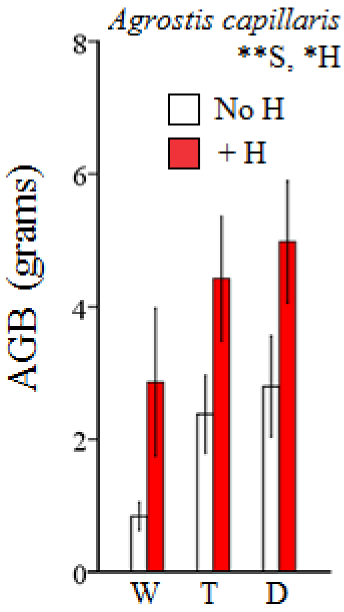


Figure 2.7. Response of aboveground biomass to treatments. See Figure 2.3. for description of statistics and data reported.

Table 2.1. Mean values ± 1 S.E of fitness per treatment for each species. No significant main effects or interactions were detected in two-way univariate ANOVA with heating and precipitation as fixed effects (p > 0.10, Appendix C).

	Mean	**± 1 S.E**
Agrostis capillaris		
Control	2650	1638
Heat	4891	1478
Heat + Precipitation	3060	713
Precipitation	1907	374
Danthonia californica		
Control	30	25
Heat	22	11
Heat + Precipitation	4	3
Precipitation	41	12
Koeleria macrantha		
Control	1297	1088
Heat	1511	514
Heat + Precipitation	864	547
Precipitation	3093	1600

Structural Equation Modeling

Aside from the transitional period for *A. capillaris*, all proposed SEMs had non-significant χ^2 values (p > 0.10), and Bentler-Bonett GFIs and NFIs > 0.90, indicating moderate to excellent model fit (Table 2.2). Squared multiple correlations (R^2) indicated that the relationships between environmental factors and physiological traits could explain 19 – 42 % of the variation in fitness depending on the species and model (Figs. 2.8-2.10).

Table 2.2. Model fit of hypothesized relationships. Model fit was evaluated by the Bentler-Bonnett Normed Fit Index (NFI), Goodness of Fit Index (GFI), and χ^2 goodness-of-fit statistics and associated p-values.

WET PERIOD

Species	NFI	GFI	df	$\chi 2$	P
Agrostis capillaris	0.96	0.98	2	2.10	0.35
Danthonia californica	0.98	0.99	2	1.34	0.51
Koeleria macrantha	0.98	0.99	2	1.71	0.43

TRANSITIONAL PERIOD

Species	NFI	GFI	df	$\chi 2$	P
Agrostis capillaris	0.93	0.96	2	5.52	0.06
Danthonia californica	0.97	0.99	2	1.25	0.54
Koeleria macrantha	0.98	0.99	2	1.88	0.39

DRY PERIOD

Species	NFI	GFI	df	$\chi 2$	P
Agrostis capillaris	0.95	0.97	4	3.86	0.43
Danthonia californica	0.92	0.96	4	6.60	0.16
Koeleria macrantha	0.95	0.98	4	3.51	0.48

Environmental factors had few effects on leaf gas exchange in *A. capillaris*, with the exception of higher soil moisture increasing g_s in the dry period, a relationship that we observed for all focal species (Figs. 2.8-2.10). Fitness was, however, directly affected by environmental factors, and their total effects on fitness during the dry period were the greatest in magnitude of all species (Figs. 2.8-2.10, Table 2.3). The total effects of SWC on fitness of *A. capillaris* were consistently larger than any other variables during the wet and dry periods of the growing season (Table 2.3). Drier soils during these time periods increased fitness, while higher temperature during the dry period decreased fitness. Fitness was not largely affected by leaf gas exchange, although high WUE_{INST} in the dry period negatively impacted fitness, a relationship that we observed for all focal species (Figs. 2.8-2.10).

Soil moisture had several direct effects on different leaf physiological traits over the course of the growing season in *D. californica*. Plants with drier soils in the wet period achieved higher A_{NET}, while drier soils in the transitional and dry periods diminished g_s, and in the transitional model, g_s accounted for the largest total effect on fitness (Fig. 2.9, Table 2.3). In contrast to *A. capillaris*, environmental factors had no significant, direct effects on the fitness of *D. californica* (Fig. 2.9), but influenced fitness indirectly through leaf physiology. The relationship between g_s and fitness displayed a seasonal switch. During the wet period, g_s had a direct, positive effect, and the largest total effect on fitness of all variables. In the dry period, however, achieving high A_{NET} with low g_s directly increased fitness, and both leaf gas exchange parameters had the largest total effects on fitness identified in this model (Fig. 2.9, Table 2.3).

For *K. macrantha*, the total effects of environmental factors on fitness were weak in magnitude throughout the growing season, despite wet period temperature having a marginally positive, direct effect on fitness (Table 2.3, Fig. 2.10). High temperatures promoted stomatal closure during the wet and transitional periods, and decreased WUE_{INST} during the dry period. Similar to our observations for *D. californica*, low SWC during the dry period repressed g_s, but in this case, was also accompanied by lower A_{NET}, and these leaf gas exchange parameter did not directly impact fitness (Fig. 2.10). While we observed a direct, negative effect of dry period WUE_{INST} on fitness for all species, this relationship was also observed for *K. macrantha* in the transitional period, and the total effect of WUE_{INST} on fitness was stronger in magnitude than for any other species or seasonal time period (Fig. 2.10, Table 2.3).

We observed additional similarities between the native species. For example, wet period g_s had large, positive total effects on fitness (Table 2.3). As the growing season progressed, fitness directly benefited from high A_{NET}, an effect identified in the transitional period for *K. macrantha* and the dry period for *D. californica*. In addition, repressed A_{NET} in the wet period promoted the production of leaves with high SLW, which ultimately compromised the fitness of both native species. Environmental factors, however, directly affected SLW in only *D. californica*, where high temperature and dry soils increased leaf thickness (Figs. 2.9-2.10). Furthermore, it is worth noting that the model for the wet period best explained the variation in fitness for *D. californica* and *K. macrantha* (R^2 = 0.36 and 0.44), while the model for the dry period explained the greatest variation in fitness for *A. capillaris*, (R^2 = 0.42), although we did not statistically compare models for each time period within each species (Figs. 2.8-2.10).

Agrostis capillaris

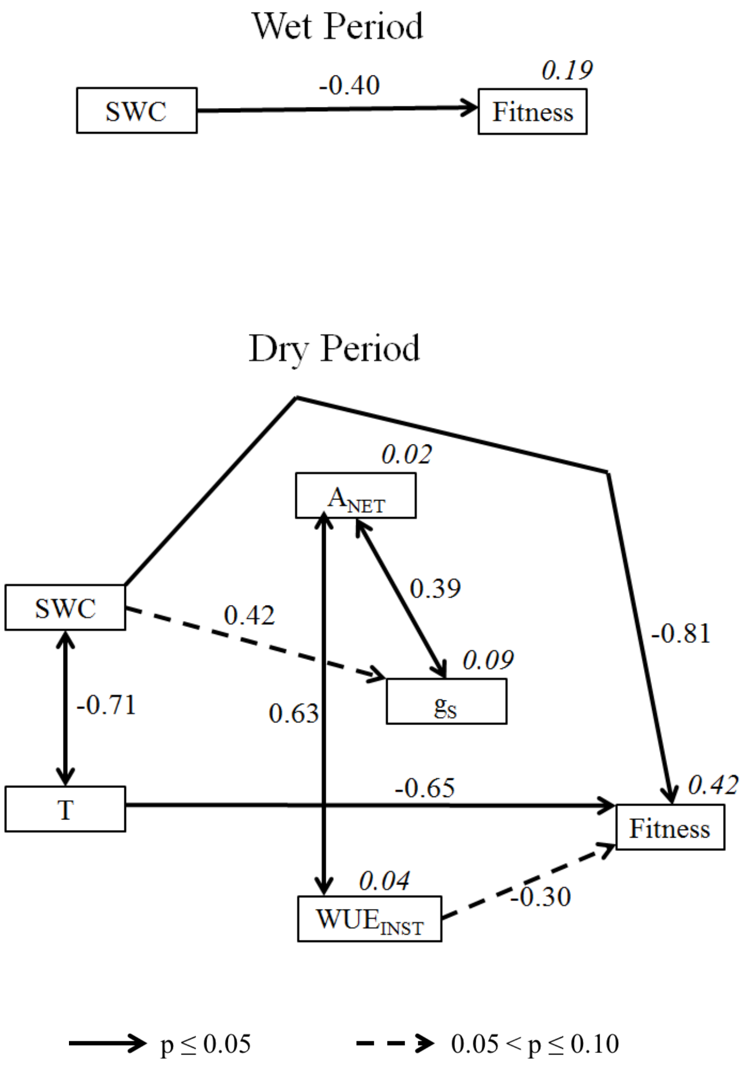


Figure 2.8. Final inferential model for *Agrostis capillaris* during wet and dry periods. Models include significant relationships between parameters. The transitional period for *A. capillaris* is not shown because of poor model fit. Single headed arrows indicate directed paths, and double headed arrows represent correlations. Values corresponding to each path are standardized path coefficients, and values in italics represent squared multiple correlations.

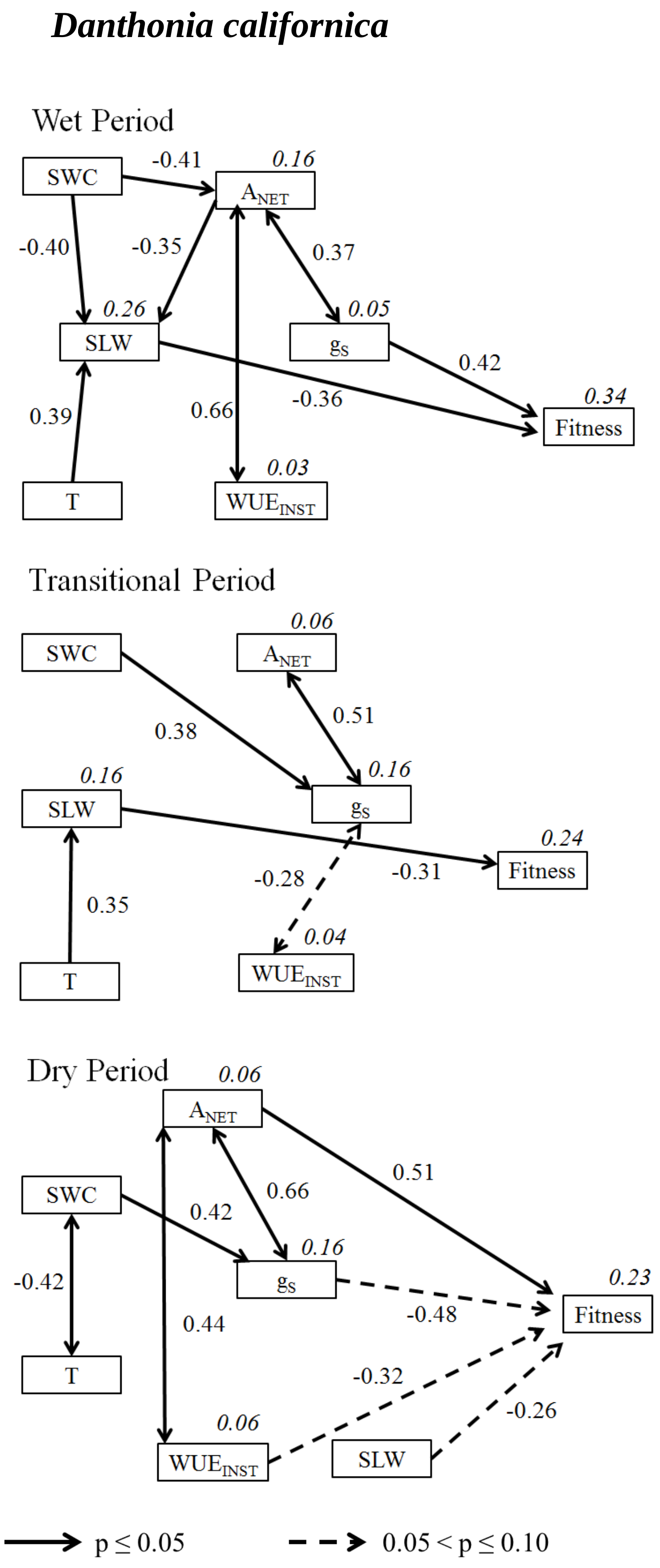


Figure 2.9. Final inferential model for *Danthonia californica* during wet, transitional, and dry periods. See Figure 2.8 for description of statistics and data reported.

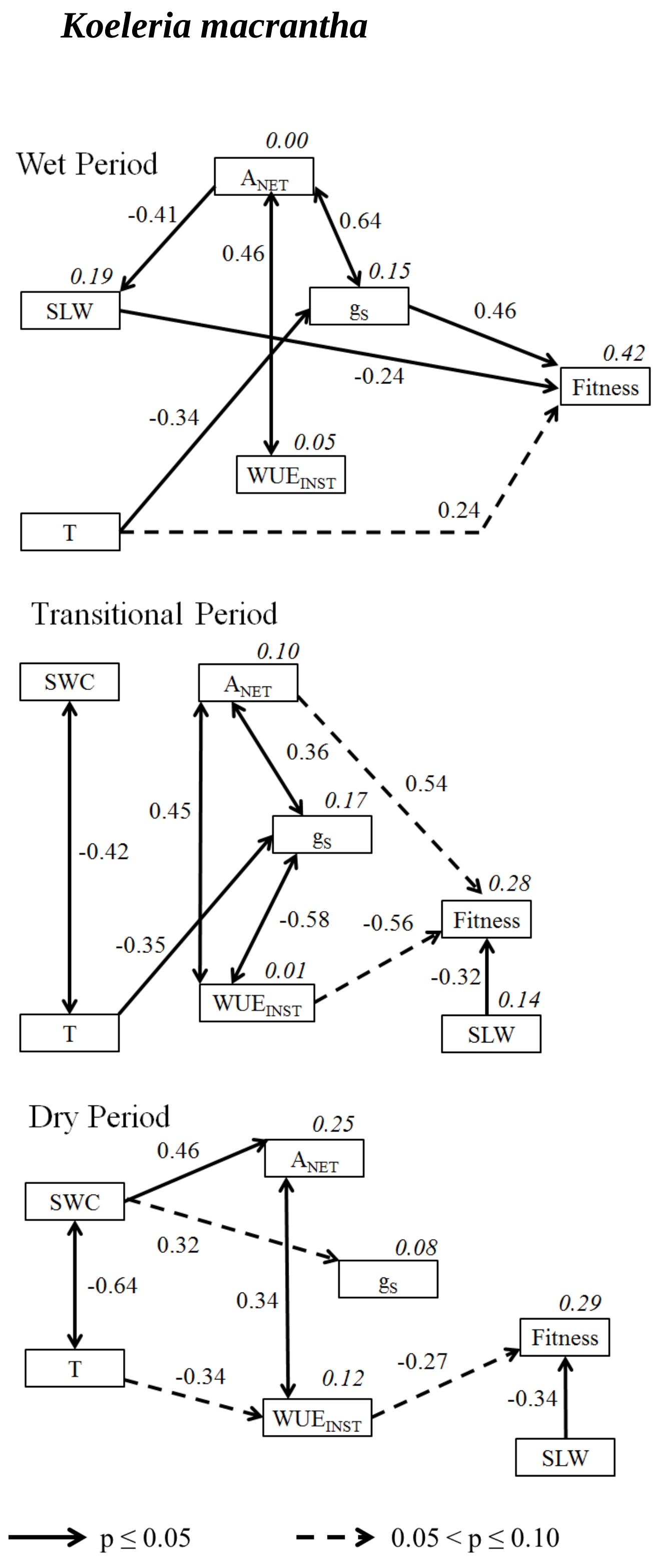


Figure 2.10. Final inferential model for *Koeleria macrantha* during wet, transitional, and dry periods. See Figure 2.8 for description of statistics and data reported.

Table 2.3. Standardized total effects describing both indirect and direct influences of variables on one another. Dashes represent instances where we predicted no relationship in the original SEM model (see Fig. 1.1), where a variable is compared to itself, or where we predicted correlated variables. The transitional period for *Agrostis capillaris* is not shown because of poor model fit.

WET PERIOD

	SWC	T	A_{NET}	SLW	WUE_{INST}	g_S
Agrostis capillaris						
A_{NET}	0.05	-0.10	-	-	-	-
SLW	0.10	-0.01	0.14	-	-	-
WUE_{INST}	0.11	0.12	-	-	-	-
g_S	-0.05	-0.16	-	-	-	-
Fitness	-0.41	0.09	0.06	-0.11	-0.11	-0.05
Danthonia californica						
A_{NET}	-0.41	0.06	-	-	-	-
SLW	-0.26	0.36	-0.35	-	-	-
WUE_{INST}	-0.17	0.03	-	-	-	-
g_S	-0.24	0.05	-	-	-	-
Fitness	0.14	-0.18	-0.05	-0.36	0.23	0.42
Koeleria macrantha						
A_{NET}	-0.01	-0.04	-	-	-	-
SLW	-0.14	0.12	-0.41	-	-	-
WUE_{INST}	0.22	0.03	-	-	-	-
g_S	-0.15	-0.34	-	-	-	-
Fitness	-0.01	0.04	0.25	-0.24	-0.15	0.46

TRANSITIONAL PERIOD

	SWC	T	A_{NET}	SLW	WUE_{INST}	g_S
Danthonia californica						
A_{NET}	-0.22	0.09	-	-	-	-
SLW	-0.16	0.33	-0.12	-	-	-
WUE_{INST}	-0.19	0.06	-	-	-	-
g_S	0.38	-0.09	-	-	-	-
Fitness	0.23	-0.25	0.20	-0.31	-0.12	-0.15
Koeleria macrantha						
A_{NET}	0.13	-0.25	-	-	-	-
SLW	-0.25	0.13	-0.19	-	-	-
WUE_{INST}	-0.09	-0.07	-	-	-	-
g_S	0.12	-0.35	-	-	-	-
Fitness	0.18	-0.07	0.60	-0.32	-0.56	-0.27

Table 2.3. (continued)

DRY PERIOD

	SWC	T	A_{NET}	SLW	WUE_{INST}	g_s
Agrostis capillaris						
A_{NET}	0.17	0.11	-	-	-	-
WUE_{INST}	-0.08	-0.23	-	-0.04	-	-
g_s	0.42	0.24	-	-	-	-
Fitness	-0.75	-0.56	-0.03	-0.18	-0.30	0.11
Danthonia californica						
A_{NET}	0.23	0.21	-	-	-	-
WUE_{INST}	-0.22	-0.06	-	0.14	-	-
g_s	0.42	0.08	-	-	-	-
Fitness	0.14	-0.10	0.51	-0.31	-0.32	-0.48
Koeleria macrantha						
A_{NET}	0.46	-0.07	-	-	-	-
WUE_{INST}	-0.30	-0.34	-	0.21	-	-
g_s	0.32	0.06	-	-	-	-
Fitness	0.02	-0.09	0.22	-0.40	-0.27	0.17

Discussion

For all species, we identified seasonal shifts in resource-use strategies of carbon and water, although the impacts of environmental factors and leaf physiology on fitness were variable. These relationships acted in opposing directions, yielding insignificant ANOVA effects of the climate treatments on fitness despite reasonable explanatory power of the SEMs on this variable. The lack of a fitness response to leaf physiology in the non-native species, *A. capillaris*, may result from its ability to rapidly acclimatize to the distinct seasonal environment of a Mediterranean climate. For the natives, *D.*

californica and *K. macrantha*, seasonally dependent leaf physiological responses had substantial impacts on fitness. Environmental factors (temperature and SWC) had differential effects on each species' leaf physiology and performance. Responses of *A. capillaris* and *D. californica* were largely driven by soil moisture throughout the growing season, but *K. macrantha* was sensitive to both environmental factors and their interaction. Furthermore, these perennial grasses provided evidence for all three drought-coping mechanisms- dehydration tolerance, dehydration avoidance, and drought escape.

Seasonal Shifts in Resource-use Strategies

For *A. capillaris*, we observed that A_{NET} is lowered under high moisture in the wet period and low moisture in the dry period (Fig. 2.3a). It is generally thought that greater CO_2 assimilation is beneficial to reproduction (Arntz et al., 1998; Arntz & Delph, 2001), but we saw no direct relationship between the two in *A. capillaris* (Fig. 2.8), and we have no evidence that A_{NET} drives the performance (i.e., fitness and biomass) of this species. A plausible explanation for this lies in the level of plasticity of this species, which is known to be high (Rapson & Wilson, 1988). Phenotypic plasticity may allow *A. capillaris* to rapidly acclimatize to the distinct seasonality of a Mediterranean climate, and for other invasive, non-native species, high plasticity can promote colonization in a broad range of environments prior to, or in the absence of adaptation (Rapson & Wilson, 1992; Daehler, 2003; Helmuth et al., 2005).

We did not detect shifts in leaf physiology or fitness directly in response to environmental factors over the course of the growing season for *D. californica*, but we did observe opposite responses of fitness to wet and dry period g_s, where high rates were initially favorable, but inhibitory during the dry period (Fig. 2.9). Stomatal closure reduces transpiration more than photosynthesis (Maherali et al., 2003), and conservation of water through low g_s can be beneficial during drought. Stomatal closure causes a drop in intercellular CO_2, and under these conditions, increasing the activity of ribulose 1, 5 bisphosphate carboxylase-oxygenase (rubisco) can allow for the maintenance of photosynthesis (Flexas & Medrano, 2002). The greater A_{NET} we observed in heating treatments (Fig. 2.3a) may have been abtained by these plants incorporating a high % N in their leaves (Fig. 2.6a), a major component of the enzyme rubisco.

For *K. macrantha*, high temperature caused plants to lower WUE_{INST}, but this response was only apparent during the dry period (Fig. 2.10). If water conservation mechanisms allow neighboring competitors to use available soil moisture, or if it is otherwise lost via evaporation or percolation, it may be favorable to use water to grow and reproduce quickly, even if WUE is reduced (Donovan & Ehleringer, 1992; Sandquist et al., 1993, Donovan et al., 2007). Our findings also indicated a higher WUE integrated over the entire growing season ($\delta^{13}C$) in precipitation treatments (Fig. 2.6b). Although these results may seem puzzling, a comparison of WUE in wet and dry environments revealed below average WUE of water-limited plants (Dudley, 1996). *Koeleria macrantha* may forgo water conservation during drought to hasten seed maturation and senescence, a “live hard, die young” strategy that promotes long-term survival of perennial plants at the cost of short-term fitness (Aragón et al., 2009).

Differential Effects of Temperature and Soil Moisture on Each Species' Leaf Physiology and Fitness

The extent to which plant performance (AGB and fitness) was affected by environmental factors and leaf physiology was variable across species, with few significant effects identified for *A. capillaris* (Fig. 2.8). Infrared heaters promoted drying of soils (Fig. 2.2), and other studies using similar heating technology have observed this effect (Harte et al., 1995; Loik et al., 2000; Aronson & McNulty, 2005). The increase in AGB we observed for *A. capillaris* in response to warming may have been driven by reduced soil moisture, canopy air temperature and relative humidity, or their interaction. We conclude that AGB and fitness (which are highly correlated, $r = 0.81$) in *A. capillaris* are strongly driven by soil moisture because this species had consistent, positive responses to heating (Fig. 2.7) and low SWC (Fig. 2.8).

The total effects of soil moisture on leaf physiology of *D. californica* were generally stronger in magnitude than the total effects of environmental factors on fitness (Table 2.3). Similar to the photosynthetic response of *A. capillaris*, dry soils during the wet period increased A_{NET} in *D. califonica*, and since we saw no direct effects of temperature on leaf gas exchange in the SEMs (Fig. 2.9), the elevated A_{NET} we observed in the heated treatments was likely from the drying effect on the soil (Fig. 2.3a). For *D. californica*, maintenance of high A_{NET} into the dry period had strong, positive direct and total effects on fitness (Fig. 2.9, Table 2.3). High photosynthetic capacity has been found to be adaptive under drought (Dudley, 1996), and strong selection has been observed on A_{NET} after flowering, possibly as a result of the need for increased carbon allocation for seed maturation (Sherrard & Maherali, 2006). While both *A. capillaris* and *D. californica* are impacted primarily by soil moisture, fitness of *D. californica* is indirectly impacted by environmental factors through their effects on leaf physiology.

During leaf construction in the wet period, high temperature and low SWC produced thicker leaves in *D. californica* (Fig. 2.9), a response accompanied by a reduced leaf surface area (per unit mass) from which water is transpired. Plants with thick leaves may have a diminished capacity to assimilate CO_2 and grow slower because fewer leaves are produced for a given mass of carbon invested in photosynthetic tissues (Lambers & Poorter, 1992; Reich et al., 1997). These individuals may increase water conservation, but compromise their effort to reach reproductive maturity before drought, and in both native species, high SLW had a negative effect on fitness (Figs. 2.9-2.10).

The total effects of environmental factors on fitness of *K. macrantha* were weak and similar in magnitude throughout the growing season (Table 2.3). Although canopy warming had a positive, direct effect on fitness in the wet period, the total effect of temperature was dampened by the fact that warming also decreased g_s (Fig. 2.10, Table 2.3). Consistent with this response, *K. macrantha* had lower rates of A_{NET} and g_s in the heated treatment (Figs. 2.3a-b). We did not identify a connection between repressed metabolic activity and fitness during drought, but low g_s and A_{NET} had large negative total effects on fitness in the wet and transitional periods, respectively (Table 2.3). These responses indicate that the consequences of sacrificing carbon gain under hotter, drier conditions are seasonally dependent, and when these traits are exhibited during summer drought, there is little reproductive cost. On the other hand, the response of WUE_{INST} in the latter half of the growing season does impact this species' performance.

Drought-Coping Mechanisms

Based on the large total effects of environmental factors on fitness of *A. capillaris* (Table 2.2), this species is sensitive to projected changes in climate, and with its preference for dry soils throughout the growing season, increasing intensity of wet season precipitation may have a negative impact on overall performance. Although we cannot suggest a drought-coping mechanism involving leaf physiology, we posit that if dry soils increase A_{NET} and AGB during the wet period, it is possible that greater proportional biomass is allocated belowground (Hamblin et al., 1990; Huang & Fu, 2000; Wang et al., 2008), which may have a long-lasting effect of relieving stress during summer drought by maximizing water uptake.

Agrostis capillaris and *D. californica* exhibited high midday ψ during the dry period (mean values > -2.35 MPa), and subsequently recovered from internal water deficits overnight, displaying predawn (mean) values > -0.06 MPa (Fig. 2.5a-b), which are well above the threshold for mortality in plants as a result of dessication (Oliver et al., 2010). Since the increased performance of *A. capillaris* in dry soils was independent of leaf physiology, relief of internal water deficits was likely facilitated by osmotic adjustments that maximize extraction of soil water, such as increased root growth (Lilley & Ludlow, 1996; Subbarao et al., 2000).

The ψ responses of *D. californica* represent probable concomitant adjustments in leaf physiology and belowground biomass or root morphology that lower this species' susceptibility to drought. Despite greater water stress in heated treatments (Fig. 2.5a-b), these same individuals maintained high A_{NET} (Fig. 2.3a), a response of dehydration tolerant plants (Pockman & Sperry, 2000; Bhaskar & Ackerly, 2006; Grime et al., 2008;

McDowell et al., 2008). Persistence of *D. californica* in increasingly dry and hot summers will be reliant on this species ability to maintain photosynthesis during the dry period of the summer when seeds are maturing, while simultaneously preventing water loss through adjustments of g_s. The strength of the correlation between A_{NET} and g_s may be reliant on the leaf N content, which is generally greater in perennial plants of drier regions (Cunningham et al., 1999; Reich et al. 1999).

In heated treatments, mean values for predawn and midday ψ were similar in *K. macrantha* (Fig. 2.5a-b), and plants were unable to recover from severe internal water deficits when midday ψ plummeted to -3.75 MPa (mean value, Fig. 2.5b), a common threshold for survival of many plant species (Oliver et al., 2010). Contrary to our hypothesis that traits conferring drought escape in perennial plants of Mediterranean ecosystems could be identified early in the growing season, we found evidence for this drought-coping mechanism in *K. macrantha* during the dry period. Widely observed responses to climate change in terrestrial ecosystems include shifts in phenology (Walther, 2004; Visser & Both, 2005; Menzel et al., 2006; Cleland et al., 2007), and the absence of recovery from greater water stress in heated treatments, in addition to sacrificing water conservation in drier, hotter conditions, are responses indicative of earlier senescence. The drought escape strategy utilized *K. macrantha* demonstrates that this species' has the capability of "tracking" seasonal environmental conditions by coordinating metabolic processes to water availability, and the onset of senescence may be an important phenological indicator for its sensitivity to climate change. Throughout the growing season, *K. macrantha* also displayed repressed rates of A_{NET} and g_s in response to hotter, drier conditions, responses that allow plants to avoid dehydration.

Since we did not observe mortality of any plants of this species during the course of this experiment, and there were no treatment effects on AGB or fitness (Fig. 2.7, Table 2.2), we attribute this proportional success across a range of environmental conditions to drought escape and dehydration avoidance strategies.

Conclusions

The responses of leaf physiology and fitness to environmental factors were both season and species-specific. Wet period environmental factors and leaf physiology explained the greatest variation in fitness for the native species (34 - 42%, Figs. 2.9-2.10). Despite the dry period model having greater explanatory power for the fitness of *A. capillaris* (42%, Fig. 2.8), this species is a cool season grass (Ruemmele, 2003), and it is reasonable to suspect the trajectory for greater AGB in heated plots may have set prior to our sampling scheme (May – August). This would account for the lack of significant physiological responses we identified (Fig. 2.8). The ecological implications of more extreme rainfall regimes has received less attention from the scientific community than warming (Jentsch et al., 2007; Knapp et al., 2008) although patterns of precipitation are predicted to have an impact on terrestrial ecosystems proportional to other global-change drivers (Easterling et al., 2000; Parmesan, 2006). Our study suggests that in a Mediterranean climate, responses of perennial vegetation to climate change may be greatest during their initial period of growth during the cool, wet season.

The inherently different physiological tolerances between species within a dominant functional group pose a challenge to predicting future alterations in ecosystem function and structure (Nippert et al., 2009). For many plant species, responses to shifting climate are likely to depend on the relative responses of agressive competitors (Dukes, 2010). In this experiment, we were only able to qualitatively compare the responses of the two native and one non-native species due to the unavailability of other exotic grasses in the plots, and future research should examine larger numbers of these groups to determine the generality of our results. Many studies support the hypothesis that invasive, non-native species are more plastic for physiological and morphological traits than their native counterparts (Williams & Black, 1994; Pattison et al., 1998; Daehler, 2003). Phenotypic plasticity, which can expand ecological niches and allow species to persist in a wide range of environmental conditions (Donahue et al., 2001; Sultan, 2001; Sultan et al., 2009), might increase the potential for successful establishment and persistence throughout a range of climate conditions, and may be an important driver of the contrasting leaf physiological responses during wet and dry seasons that we observed within each species.

As we have demonstrated, plant species within the same functional group harbor differential sensitivities to environmental factors and utilize different resource-use strategies to cope with drought. When empirical information about the physiological limits constraining species' geographical distributions is available, modelers have the option of limiting predictor and physiological variables through an *a priori* selection of those which have previously been found to be meaningful. While SEM is not used to model spatial dynamics due to difficulties with modeling non-linear relationships (Austin, 2007), SEM offers a promising framework to assess causality, and provides readily interpretable results that climate change modelers can use to improve their analyses and predictions.

CHAPTER III

CONCLUSIONS

Seasonal and Species Specific Responses to Climate Change

The direction and magnitude of changes in aboveground productivity and physiological responses have been documented as both season and species specific in climate warming experiments (Loik et al., 2000; Zhou et al. 2007; Lambrecht et al., 2007; Shi et al., 2010). Experimental ecosystem warming for consecutive years has substantially increased aboveground productivity in northern latitudes, a response that may be directly mediated by lengthening the growing season and increasing photosynthesis (Rustad et al., 2001). Warming can, however, induce a response in the opposite direction, particularly when a plant species naturally experiences temperatures close to their thermal optimum for photosynthesis (ValPine & Harte, 2001; Llorens et al., 2003; Peñuelas et al., 2004). Research in Mediterranean climates has unveiled lower photosynthetic rates during periods of drought (Tenhunen et al., 1990; Vallardes & Pearcy, 1997; Llorens et al., 2003), with declines occurring during maximum summer air temperatures from 35-40°C (Tenhunen et al., 1990).

Amplified dry season temperatures may lead to changes in foliar water stress, and if prolonged, this can reduce the pool of available carbon allocated aboveground for vegetative growth and reproduction, leading to diminished fitness. During the 2011 growing season, the Pacific Northwest experienced moderate La Niña conditions, and dry period temperatures during leaf gas exchange and ψ sampling did not exceed 34°C (data not shown). While the temperature optimum for photosynthesis in our focal species is unknown, it is possible that temperatures during our study period did not exceed their threshold for metabolic processes, and therefore, we did not observe a drastic switch in the photosynthetic response from the wet to dry periods that affected overall plant performance. We did, however, find that seasonal environment and physiology have differential effects on fitness. Although these responses were dependent on species, our study suggests that in a Mediterranean climate, responses of perennial vegetation to climate change may be greatest during their initial period of growth during the cool, wet season.

To understand responses of vegetation to climate change in Mediterranean ecosystems, the distinct seasonality of the region must be taken into account, in addition to the inter-annual variability of temperature and precipitation, which is largely affected by the El Niño/La Niña-Southern Oscillation (ENSO). The frequency of ENSO events are predicted to change with climate, which may lead to major regional changes in biodiversity and ecosystem function through changes in drought and fire (Trenberth & Hoar, 1997). Grasslands outside of the Mediterranean biome are also commonly limited by seasonal water availability, and intra- and interannual variability in precipitation has been found to drive their diversity and productivity (Knapp et al., 2001).

In mesic North American habitats, aboveground productivity generally increases with annual rainfall (Sala et al., 1988; Köchy & Wilson, 2004), and in addition, species composition shifts from shortgrass to tallgrass prairies (Küchler, 1974). Dominant species within these habitats respond differentially in terms of physiology and productivity to changes in temperature and precipitation, with some species being more sensitive to temperature, and others to patterns of precipitation (Silletti & Knapp, 2001; Nippert et al. 2009), and the magnitude of responses to climate manipulation is variable amongst dominant species (Swemmer et al., 2006). In our study of perennial grasses, we found that fitness of *A. capillaris* and leaf physiology of *D. californica* were largely driven by soil moisture, while the interactive effect of temperature and precipitation is more important to the performance and physiology of *K. macrantha.*

Dynamic global vegetation models (DVGMs) use first principles of photosynthesis, carbon processing, and plant physiology to predict future changes in plant functional types (Cramer et al., 2000), but do not yield species-specific results (Woodward & Beerling, 1997). For producing species-specific information, bioclimatic envelope models are the best available tool (Hannah et al., 2002), allowing for the identification of key relationships between individual species and the governing factors of their distributions (Iverson & Prasad, 2001; Gavin & Hu, 2005). When empirical information about the physiological limits constraining species' geographical distributions is available, modelers have the option of limiting predictor and physiological variables through an *a priori* selection of those which have previously been found to be meaningful. As we have demonstrated, plant species within the same functional group harbor differential sensitivities to environmental factors and utilize different resource-use strategies to cope with drought. These individualistic responses to projected climate change are imperative to accurately predict future vegetation dynamics. While SEM is not used to model spatial dynamics due to difficulties with modeling non-linear relationships (Austin, 2007), SEM offers a promising framework to assess causality, and provides readily interpretable results that climate change modelers can use to improve their analyses and predictions.

Trait-based Restoration Ecology

Invasive, non-native species have attracted attention because of their huge economic costs (Pimentel, 2005), and because they may reduce native biodiversity (Wilcove et al., 1998). Much effort has been focused on understanding the mechanisms that make some species agressive. Some studies have suggest that evolution of plasticity may happen after a species is introduced to a new area, and this increase in plasticity may contribute to successful colonization (Parker et al., 2003; Bossford et al., 2005). Phenotypic plasticity, which can expand ecological niches and allow species to persist in a wide range of environmental conditions (Donahue et al., 2001; Sultan, 2001; Sultan et al., 2009), might increase the potential for a species to successfully establish and persist throughout a range of climate conditions. Plasticity can play a role in both the short term response of plant populations to global change, as well as their long-term persistence through the maintenance of genetic variation, and should be recognized as a factor which may contribute to shifts in the range over which a species colonizes. While many studies support the hypothesis that invasive, non-native species are more plastic for physiological and morphological traits which affect fitness than their native counterparts (Williams & Black, 1994; Pattison et al., 1998; Daehler, 2003), our results demonstrate that this may not always the case, and that native biota also exhibit this strategy of success. *Danthonia californica,* for example, was able to seasonally adjust g_s to cope with drought, a short-term response that may be adaptive due to its direct, positive effects on fitness. *Koeleria* *macrantha*, also appeared to display sufficient physiological plasticity in response to seasonal environmental factors, and utilized drought escape and dehydration avoidance strategies to cope with dry conditions.

The concept of the "physiology/life-history nexus" was introduced by Ricklefs and Wikelski (2002), wherein physiology is the key response mechanism linking organisms and populations to their environment. Since physiology can both drive and constrain an organism's metabolism, nutrition, thermal relationships, and reproduction, associated traits govern an individual's ability to maintain homeostasis in a changing climate. Soil moisture availability has been found to affect the competitive dynamics of plants in Pacific Northwest prairies (Pfeifer-Meister et al., 2008). Due to the distinct seasonality of the region, niche partitioning is based on a temporal scale of resource use, which may be altered with changing patterns in temperature and precipitation, and could shift the structure and function of this ecosystem depending on the strategies which prove most successful over consecutive growing seasons.

Our experimental design allowed us to capture contrasting patterns of success by determining how short term (instantaneous), seasonal responses to climate manipulation shaped fitness. While we did not directly compare strategies of carbon and water use between each species, it is evident that *D. californica* is robust to a range of environmental conditions, and will likely perform well under predicted climate change due to its tolerance of dehydration. *Koeleria macrantha* also displays significant ability to cope with projected climate change, but longer term studies are needed to assess the impact of traits associated with dehydration avoidance on plant performance over consecutive growing seasons. Functional trait variation across taxonomic groups has been proposed as a mechanism to elucidate patterns of organization, and have received much attention recently. Restoration ecology can benefit greatly from developments in trait-based ecology that enable the identification of phenotypes that are suitable for a changing climate (Sandel et al., 2011). For instance, if dehydration tolerant phenotypes lead to heightened performance of perennial grasses in Mediterranean regions, and if highly plastic species are better able to take advantage of a wide range of conditions (Funk, 2008; Berg & Ellers, 2010), monitoring these traits in native populations could allow restoration ecologists to prioritize populations and genotypes for cultivation of propagules and seeds. This knowledge would ensure persistence of native biota well into the future by assisting with identification and preservation of at-risk species, and providing a case for the utilization robust, native species to reclaim invaded habitats.

Restoration of degraded communities has mixed success across systems, even when similar treatments are applied, due to the important control over the restoration outcome exerted by each unique plant community (Hendrickson & Lund, 2010). Where native and invasive, non-native species are functionally similar, it may be difficult to design restoration treatments that benefit one group over the other (Corbin & D'Antonio, 2010), but even if these groups do differ in particular traits, restoration treatments may not benefit all native species equally. Functional traits and knowledge of integrated phenotypes can not only assist with selecting plant materials for restoration, but may also be incorporated with monitoring the success of restoration projects. For example, in a restored California grassland, establishment and survival of the invasive, non-native annual grass, *Holcus lanatus* L. (velvetgrass), was increased by summer water addition, whereas native species (such as *D. californica*) were able to prevent invasion under ambient, drier conditions late in the growing season (Thomsen et al., 2005). A stress associated with a mismatch between an individual's physiology and its abiotic environment can limit the spread of invasive, non-native species (Alpert et al., 2000), as we have demonstrated for *A. capillaris*, where increased wet season precipitation inhibits this species' performance. On the other hand, since we provided evidence for a positive response by *A. capillaris* to dry soils, management of this non-native species in the Willamette Valley may be a priority where it inhabits dry microsites.

In ecological restoration, knowledge of the environmental factors causing degradation or inhibiting successful restoration is essential to regulating and managing ecosystems. Since physiological regulation is directly responsible for the ability of an organism to adapt to new environmental conditions, tools to measure leaf gas-exchange, WUE, nutrient content, and morphology are well-suited for the short term monitoring periods typical of restoration projects (Cooke & Suski, 2008). These parameters allow for the ability to detect subtle changes in the health of populations that is otherwise difficult to assess with population demography, community structure, and other classical ecological techniques. If other studies can express physiology as a measurable phenotype with direct connections to fitness, as we have done using SEM, there may be a greater opportunity for integrating these causal networks into models of population dynamics, which would not only improve our understanding of how vegetation will respond to future climate change, but will also provide more opportunities for adaptive management in ecological restoration, and the creation of successful projects aimed to restore and preserve native biota and biodiversity.

APPENDIX A

TWO-WAY ANOVAS WITH TIME OF DAY AS REPEATED MEASURE

Appendix A. Significant main effects and interactions ($p < 0.10$) from two-way repeated measures ANOVAs, where heating (H) and precipitation (P) are fixed effects and time of day is the repeated measure. Wet, transitional, and dry period measurements were analyzed separately for net photosynthesis (A_{NET}), stomatal conductance (g_s), instantaneous water-use efficiency (WUE_{INST}), water potential (ψ), and aboveground biomass (AGB).

WET PERIOD					**TRANSITIONAL PERIOD**			
	A_{NET}	g_s	WUE_{INST}	ψ	A_{NET}	g_s	WUE_{INST}	ψ
Agrostis capillaris								
Time of day	ns	0.04	ns	<0.01	ns	<0.01	ns	<0.01
Time of day x H	ns	ns	ns	ns	ns	ns	ns	ns
Time of day x P	ns	ns	ns	ns	ns	ns	ns	ns
Time of day x H x P	ns	ns	ns	ns	ns	ns	ns	ns
H	ns	ns	ns	0.02	ns	0.03	ns	<0.01
H x P	ns	ns	ns	ns	ns	ns	ns	ns
P	ns	ns	ns	ns	ns	ns	ns	0.01
Danthonia californica								
Time of day	ns	0.02	ns	<0.01	ns	ns	0.02	<0.01
Time of day x H	ns	ns	ns	ns	0.08	ns	0.03	0.09
Time of day x P	ns	ns	ns	ns	ns	ns	ns	ns
Time of day x H x P	ns	ns	ns	ns	ns	ns	ns	ns
H	ns	ns	ns	0.02	ns	ns	ns	<0.01
H x P	ns	ns	ns	ns	0.09	ns	ns	ns
P	ns	ns	ns	ns	ns	ns	ns	ns
Koeleria macrantha								
Time of day	0.02	<0.01	< 0.01	<0.01	<0.01	ns	0.04	<0.01
Time of day x H	ns	ns	ns	ns	ns	ns	ns	ns
Time of day x P	0.07	ns	ns	ns	ns	0.02	0.08	ns
Time of day x H x P	ns	ns	ns	ns	ns	ns	0.09	ns
H	ns	ns	ns	<0.01	ns	ns	ns	0.06
H x P	ns	ns	ns	ns	ns	ns	ns	ns
P	ns	ns	ns	ns	ns	ns	ns	ns

Appendix A (continued)

DRY PERIOD

	A_{NET}	g_s	WUE_{INST}	ψ
Agrostis capillaris				
Time of day	ns	ns	0.06	<0.01
Time of day x H	ns	ns	ns	ns
Time of day x P	ns	ns	ns	ns
Time of day x H x P	ns	ns	ns	ns
H	ns	ns	ns	ns
H x P	ns	ns	ns	ns
P	ns	ns	ns	ns
Danthonia californica				
Time of day	<0.01	ns	0.02	<0.01
Time of day x H	ns	ns	ns	ns
Time of day x P	ns	ns	ns	ns
Time of day x H x P	ns	ns	ns	ns
H	ns	ns	ns	0.04
H x P	ns	ns	ns	ns
P	ns	ns	ns	ns
Koeleria macrantha				
Time of day	< 0.01	0.04	ns	<0.01
Time of day x H	ns	ns	ns	ns
Time of day x P	ns	ns	ns	ns
Time of day x H x P	ns	ns	ns	ns
H	ns	ns	ns	<0.01
H x P	ns	ns	ns	ns
P	ns	ns	ns	ns

APPENDIX B

TWO-WAY ANOVAS WITH SEASON AS REPEATED MEASURE

Appendix B. Significant main effects and interactions ($p < 0.10$) from two-way repeated measures ANOVAs, where heating (H) and precipitation (P) are fixed effects and season is the repeated measure. Morning (AM) and afternoon (PM) measurements were analyzed separately for net photosynthesis (A_{NET}), stomatal conductance (g_s), instantaneous water-use efficiency (WUE_{INST}), water potential (ψ), and aboveground biomass (AGB).

	A_{NET} AM	**A_{NET} PM**	**g_s AM**	**g_s PM**	**WUE_{INST} AM**	**WUE_{INST} PM**	**ψ AM**	**ψ PM**	**AGB**
Agrostis capillaris									
Season	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Season x H	ns	ns	ns	ns	ns	ns	ns	ns	ns
Season x P	ns	0.08	ns	ns	ns	ns	ns	ns	ns
Season x H x P	ns	ns	ns	ns	ns	ns	ns	ns	ns
H	ns	ns	0.09	ns	ns	ns	<0.01	0.01	0.06
H x P	ns	ns	ns	ns	ns	ns	ns	ns	ns
P	ns	ns	ns	ns	ns	ns	ns	ns	ns
Danthonia californica									
Season	0.02	<0.01	<0.01	<0.01	0.04	<0.01	<0.01	<0.01	<0.01
Season x H	ns	ns	ns	ns	ns	0.02	ns	ns	ns
Season x P	ns	ns	ns	ns	ns	ns	ns	ns	ns
Season x H x P	ns	ns	ns	ns	ns	0.01	ns	ns	ns
H	0.04	ns	ns	ns	ns	ns	<0.01	0.02	ns
H x P	ns	ns	ns	ns	ns	ns	ns	ns	ns
P	ns	ns	ns	ns	ns	ns	ns	ns	ns
Koeleria macrantha									
Season	<0.01	<0.01	<0.01	<0.01	ns	0.04	<0.01	<0.01	<0.01
Season x H	ns	ns	ns	ns	ns	ns	ns	0.10	ns
Season x P	ns	ns	ns	ns	ns	ns	ns	ns	ns
Season x H x P	ns	ns	ns	ns	ns	ns	ns	ns	ns
H	0.05	ns	0.08	ns	ns	ns	<0.01	<0.01	ns
H x P	ns	ns	ns	ns	0.08	ns	ns	ns	ns
P	ns	ns	ns	ns	ns	ns	ns	ns	ns

APPENDIX C

UNIVARIATE TWO-WAY ANOVAS

Appendix C. Significant main effects and interactions ($p \leq 0.10$) from univariate two-way ANOVAs with heating (H) and precipitation (P) as fixed effects. Specific leaf weight (SLW), leaf carbon : nitrogen (C:N), integrated water-use efficiency ($\delta^{13}C$), and fitness were measured once over the growing season. Season x treatment interactions were identified for afternoon, net photosynthesis (A_{NET} PM) in *Agrostis capillaris*, and instantaneous water-use efficiency (WUE_{INST} PM) in *Danthonia californica* (see Appendix C).

	SLW	C:N	$\delta^{13}C$	Fitness
Agrostis capillaris				
H	ns	ns	ns	ns
P	ns	ns	ns	ns
H x P.	ns	ns	ns	ns
Danthonia californica				
H	ns	0.02	ns	ns
P	ns	ns	ns	ns
H x P	ns	ns	ns	ns
Koeleria macrantha				
H	ns	ns	ns	ns
P	ns	ns	0.05	ns
H x P	ns	ns	ns	ns

Agrostis capillaris

A_{NET} PM

	Wet	Transitional	Dry
H	ns	ns	ns
P	0.10	ns	0.10
H x P	ns	ns	ns

Danthonia californica

WUE_{INST} PM

	Wet	Transitional	Dry
H	ns	0.05	0.00
P	ns	ns	ns
H x P.	0.08	ns	0.01

APPENDIX D

STANDARDIZED AND UNSTANDARDIZED PATH COEFFICIENTS

Appendix D. Standardized and unstandardized path coefficients, and associated p-values for direct relationships between predictors (X) and independent variables (Y) in structural equation models. * denotes $0.05 < p \leq 0.10$ **denotes $p \leq 0.05$

WETPERIOD

Agrostis capillaris

		Path Coefficients	
X	Y	Unstandardized	Standardized
SWC	A_{NET}	5.73	0.05
SWC	g_s	-0.11	-0.05
SWC	WUE_{INST}	3.16	0.11
SWC	SLW	0.97	0.09
SWC	Fitness	-5.30**	-0.40**
T	A_{NET}	-0.26	-0.10
T	g_s	0.09	0.12
T	WUE_{INST}	-0.01	-0.16
T	SLW	0.00	0.01
T	Fitness	0.03	0.10
SLW	Fitness	-0.14	-0.11
A_{NET}	SLW	0.01	0.14
A_{NET}	Fitness	0.01	0.07
g_s	Fitness	-0.33	-0.05
WUE_{INST}	Fitness	-0.05	-0.11

Danthonia californica

		Path Coefficients	
X	Y	Unstandardized	Standardized
SWC	A_{NET}	-64.84**	-0.41**
SWC	g_s	-1.33	-0.24
SWC	WUE_{INST}	-6.67	-0.17
SWC	SLW	-2.07**	-0.40**
SWC	Fitness	2.74	0.12
T	A_{NET}	0.79	0.06
T	g_s	0.08	0.03
T	WUE_{INST}	0.02	0.05
T	SLW	0.15**	0.39**
T	Fitness	-0.11	-0.06
SLW	Fitness	-1.68**	-0.36**
A_{NET}	SLW	-0.01**	-0.35**
A_{NET}	Fitness	-0.03	-0.18
g_s	Fitness	1.78**	0.42**
WUE_{INST}	Fitness	0.14	0.23

Koeleria macrantha

		Path Coefficients	
X	Y	Unstandardized	Standardized
SWC	A_{NET}	-0.85	-0.01
SWC	g_s	-0.86	-0.15
SWC	WUE_{INST}	9.77	0.22
SWC	SLW	-0.04	-0.14
SWC	Fitness	2.62	0.06
T	A_{NET}	-0.13	-0.04
T	g_s	-0.05**	-0.34**
T	WUE_{INST}	0.03	0.03
T	SLW	0.00	0.10
T	Fitness	0.26*	0.24*
SLW	Fitness	-40.40*	-0.24*
A_{NET}	SLW	0.00**	-0.41**
A_{NET}	Fitness	0.05	0.16
g_s	Fitness	3.77**	0.46**
WUE_{INST}	Fitness	-0.15	-0.15

Appendix D (continued)

TRANSITIONAL PERIOD

Agrostis capillaris

		Path Coefficients	
X	Y	Unstandardized	Standardized
SWC	A_{NET}	-4.18	-0.07
SWC	g_s	-0.12	-0.07
SWC	WUE_{INST}	1.64	0.08
SWC	SLW	0.79	0.10
SWC	Fitness	-3.60**	-0.38**
T	A_{NET}	-0.45	-0.24
T	g_s	-0.02**	-0.41**
T	WUE_{INST}	0.00	-0.01
T	SLW	0.02	0.08
T	Fitness	-0.08*	-0.27*
SLW	Fitness	-0.11	-0.09
A_{NET}	SLW	0.01	0.04
A_{NET}	Fitness	0.02	0.12
g_s	Fitness	-2.18*	-0.42*
WUE_{INST}	Fitness	-0.09	-0.19

Danthonia californica

		Path Coefficients	
X	Y	Unstandardized	Standardized
SWC	A_{NET}	-12.41	-0.22
SWC	g_s	0.85**	0.38**
SWC	WUE_{INST}	-1.03	-0.19
SWC	SLW	-0.71	-0.19
SWC	Fitness	4.32	0.26
T	A_{NET}	0.15	0.09
T	g_s	0.01	0.06
T	WUE_{INST}	-0.01	-0.09
T	SLW	0.04**	0.35**
T	Fitness	-0.08	-0.17
SLW	Fitness	-1.43**	-0.31**
A_{NET}	SLW	-0.01	-0.12
A_{NET}	Fitness	0.05	0.16
g_s	Fitness	-1.17	-0.15
WUE_{INST}	Fitness	-0.37	-0.12

Koeleria macrantha

		Path Coefficients	
X	Y	Unstandardized	Standardized
SWC	A_{NET}	9.40	0.13
SWC	g_s	0.23	0.12
SWC	WUE_{INST}	-0.48	-0.09
SWC	SLW	-0.05	-0.22
SWC	Fitness	0.43	0.01
T	A_{NET}	-0.47	-0.25
T	g_s	-0.02**	-0.35**
T	WUE_{INST}	-0.01	-0.07
T	SLW	0.00	0.08
T	Fitness	-0.03	-0.03
SLW	Fitness	-53.06**	-0.32**
A_{NET}	SLW	0.00	-0.19
A_{NET}	Fitness	0.26*	0.54*
g_s	Fitness	-4.95	-0.27
WUE_{INST}	Fitness	-3.94*	-0.56*

Appendix D (continued)

DRY PERIOD

Agrostis capillaris

		Path Coefficients	
X	Y	Unstandardized	Standardized
SWC	A_{NET}	11.59	0.17
SWC	g_s	2.31^{*}	0.42^{*}
SWC	WUE_{INST}	-0.59	-0.08
SWC	Fitness	-9.97^{**}	-0.81^{**}
T	A_{NET}	0.03	0.24
T	g_s	0.14	0.11
T	WUE_{INST}	-0.04	-0.23
T	Fitness	-0.16^{**}	-0.65^{**}
SLW	WUE_{INST}	-0.03	-0.04
SLW	Fitness	-0.24	-0.19
A_{NET}	Fitness	-0.01	-0.03
g_s	Fitness	0.24	0.11
WUE_{INST}	Fitness	-0.47^{*}	-0.30^{*}

Danthonia californica

		Path Coefficients	
X	Y	Unstandardized	Standardized
SWC	A_{NET}	17.75	0.23
SWC	g_s	0.79^{**}	0.42^{**}
SWC	WUE_{INST}	-5.40	-0.22
SWC	Fitness	2.57	0.15
T	A_{NET}	0.41	0.21
T	g_s	0.00	0.08
T	WUE_{INST}	-0.04	-0.06
T	Fitness	-0.08	-0.19
SLW	WUE_{INST}	0.92	0.14
SLW	Fitness	-1.15^{*}	-0.26^{*}
A_{NET}	Fitness	0.11^{**}	0.51^{**}
g_s	Fitness	-4.31^{**}	-0.48^{**}
WUE_{INST}	Fitness	-0.21^{*}	-0.32^{*}

Koeleria macrantha

		Path Coefficients	
X	Y	Unstandardized	Standardized
SWC	A_{NET}	56.98^{**}	0.46^{**}
SWC	g_s	0.46^{*}	0.32^{*}
SWC	WUE_{INST}	-41.69	-0.30
SWC	Fitness	-12.88	-0.22
T	A_{NET}	-0.11	-0.07
T	g_s	0.00	0.06
T	WUE_{INST}	-0.65^{*}	-0.34^{*}
T	Fitness	-0.15	-0.18
SLW	WUE_{INST}	82.52	0.21
SLW	Fitness	-57.47^{**}	-0.34^{**}
A_{NET}	Fitness	0.11	0.22
g_s	Fitness	6.95	0.17
WUE_{INST}	Fitness	-0.12^{*}	-0.27^{*}

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