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SANTA CRUZ

**EXPLORING THE EFFECTS OF HEAT AND DROUGHT ON CONIFER
TREES: FROM SEMI-ARID WOODLANDS TO COAST REDWOODS**

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ENVIRONMENTAL STUDIES

by

Michael W. Jenkins

June 2016

The Dissertation of Name is approved:

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ABSTRACT

EXPLORING THE EFFECTS OF HEAT AND DROUGHT ON CONIFER TREES: FROM SEMI-ARID WOODLANDS TO COAST REDWOODS

By Michael W. Jenkins

Periods of low precipitation and increasing atmospheric temperature are having adverse effects on tree and forest growth and survival in part via limitations upon photosynthesis. Understanding how different species and plant functional types will physiologically respond to the combination of drought and heat is therefore critical for modeling and predicting the fate of trees and forests under future climate conditions. In addition, climate is changing at a faster pace than the slow natural adjustment rates of most species to their rapidly shifting habitat conditions, especially for long-lived tree species, which poses a major challenge for management, conservation, and preservation strategies and policies. Therefore the current traditional conservation/preservation methods, such as providing migration corridors and increasing suitable habitat at range margins will need to be supplemented with a more direct, innovative, and adaptive approach. One such approach is that of managed migration, which is the intentional translocation of species outside their current habitat in order to reduce anticipated loss of biodiversity caused by climate change related stress. This dissertation addresses these problems through the experimental examination of heat, drought, and the combination of heat and drought on two conifer species that have differing drought tolerances, which can serve as global models for a range of physiological mechanisms to deal with water and heat

stress, as well as a social science investigation into the preservation of an iconic conifer tree, the coast redwood into Oregon via managed migration.

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INTRODUCTION

A warmer and drier future is anticipated for many regions around the globe with longer and more frequent droughts (IPCC 2013), which will have profound implications on the functioning and structure of trees, forests, and ecosystems as well as biosphere-atmosphere interactions, land-surface stability, and ecosystem goods and services (Malhi et al. 2002, MA 2005, NRC 2007, Anderegg et al. 2013).

Understanding how different species and plant functional types will physiologically respond to the combination of drought and heat is therefore critical for modeling and predicting the fate of trees and forests under future climate conditions (Sitch et al. 2008, Jump et al. 2009). However, as Breshears et al. 2009 noted, “drought- induced tree mortality cannot be predicted with confidence, because long-term field observations of plant water stress prior to, and culminating in, mortality are rare, precluding the development and testing of mechanisms”. In addition, climate is changing at a faster pace than the slow natural adjustment rates of most species to their rapidly shifting habitat conditions (Davis and Shaw 2001, Hulme 2005, Peters and Darling 1985), especially for long-lived tree species, which poses a major challenge for management, conservation, and preservation strategies and policies.

Plant species have a very limited set of options to survive climate-induced potential extinction, which include plastic responses, such as changing their phenology or physiological responses, adapting to the new and changing climatic conditions via selection, or migration (Davis and Shaw 2001). However, these options

will not happen at the rate or to the extent needed to save many tree species. Therefore the current traditional conservation/preservation methods, such as providing migration corridors and increasing suitable habitat at range margins will need to be supplemented with a more direct, innovative, and adaptive approach (Hunter et al. 2010, Krosby et al. 2010). One such approach is that of managed migration (also called assisted migration/relocation and assisted colonization), which is the intentional translocation of species outside their current habitat in order to reduce anticipated loss of biodiversity caused by climate change related stress (Vitt et al. 2010).

Stress is characterized as any disturbing influence that results in physiological consequences (Rasmuson 2002). However, by the time plants display visible symptoms of stress, they can already be adversely affected (Omasa and Takayama 2002). Low water availability is considered the dominant environmental factor/stress limiting plant growth, health, and yield (Boyer 1982, Nemani et al. 2003), and drought is the primary factor limiting plant water availability and further reduces growth, survival, and distribution of trees around the globe (Boyer 1982, Allen and Breshears 1998, Engelbrecht et al. 2007). A report from Rehfeldt et al. (2006) suggests that 88% of the western United States will see a turnover in the kinds of tree communities it hosts by the end of the century. Models projecting vegetation cover change over the next 100 years suggest that in western North America needle-leaf evergreen trees will be reduced by approximately 15% and in southwestern North America most needleleaf evergreen trees will be lost (Jiang et al. 2013).

When trees suffer from water stress either through reduced soil moisture and/or enhanced evaporative demand i.e. increased vapor pressure deficit (VPD), they will minimize the risk of cavitation by reducing the opening of their stomata, which limits tension on the xylem and reduces water loss (Woodruff et al. 2015). However, when trees reduce the openness and/or close their stomata to reduce water loss, it also reduces the quantity of CO₂ that enters the leaves, and can lead to carbon starvation (McDowell et al. 2008a). Carbon starved trees end up utilizing carbon reserves (non-structural carbohydrates, NSC), which limits the available energy sources to defend against infestation of a long list of potential pests and pathogens (Woodruff et al. 2015, McDowell et al. 2008a).

The level understanding and willingness to put in place effective policies regarding the preservation of climate change threatened species is far from adequate. In addition, despite decades of research on plant drought tolerance, the current knowledge of physiological mechanisms and responses to drought and heat stress are still under debate (Sevanto et al. 2014, Woodruff et al. 2015). Recent assessments suggest conifers are particularly vulnerable to the combined stresses of heat and drought (Adams et al. 2009, Jiang et al. 2013, Williams et al. 2013); however, no experimental manipulations of both precipitation and temperature have yet been carried on mature trees in the field (Leuzinger et al. 2009). This dissertation addresses these problems through the experimental examination of heat, drought, and the combination of heat and drought on two conifer species that have differing drought tolerances, which can serve as global models for a range of physiological mechanisms

to deal with water and heat stress, as well as an investigation into the preservation of an iconic conifer tree, the coast redwood (*Sequoia sempervirens*) into Oregon via managed migration. Three questions guide the study:

1. What are the effects of drought and heat on gas-exchange of conifer species with different drought tolerances?
2. What effect do increases in leaf temperature in trees under water and heat stress have on the co-limitation and biochemical parameters of photosynthesis?
3. What is the subjectivity of stakeholders in Oregon's land use planning community regarding managed migration?

Dissertation Outline

This research explores these questions, beginning with an experimental examination (Chapter 1) of seasonal gas-exchange dynamics of heat and drought stress on two coexisting conifer species of Southwestern North America, piñon pine (*Pinus edulis*) and one-seed juniper (*Juniperus monosperma*), which represent trees on opposite ends of the isohdry-anisohdry spectrum (discussed below) (McDowell et al. 2008a). The cessation of leaf gas-exchange during drought is strongly associated with conifer mortality (Waring 1987, Martinez-Vilalta et al. 2002, McDowell et al. 2008a, 2010, Adams et al. 2013, Poyatos et al. 2013). A critical constraint in carbon uptake is at the interface of carbon gain and water loss through stomatal regulation. Multiple factors affect stomatal conductance (g_s), including strong hydraulic regulation in response to VPD and water potential (Ψ) of the hydraulic system (Brodrigg and Field 2000, Hubbard et al. 2001). These all serve to vary g_s in an adaptive manner that balances carbon uptake with water conservation.

The pine has recently experienced far more heat- and drought-induced mortality (up to 95%), throughout the region than juniper (up to 25%) (Breshears et al. 2005). The difference in mortality rates of *P. edulis* and *J. monosperma* in response to drought has been hypothesized to be related to their contrasting hydraulic strategies for the avoidance of hydraulic failure and tissue desiccation, and the subsequent impact of these strategies on their C balance (McDowell et al. 2008a). Plants that are relatively isohydric, such as *P. edulis*, respond quickly to declining water potential and increased VPD by closing their stomata in order to limit water loss that could lead to cavitation and, ultimately, hydraulic failure (Maherali et al. 2006, Meinzer et al. 2010). However, the consequence of this avoidance induces limited carbon assimilation due to reduced or limited gas-exchange. By contrast, plants that are considered to be more anisohydric, such as *J. monosperma*, spend more energy on the construction of embolism-resistant xylem to avoid hydraulic failure (Maherali et al. 2006, Meinzer et al. 2010), and show less strict stomatal regulation in response to water stress.

Accurate predictions of heat and drought stress on gas-exchange in plants also requires a detailed assessment of the different limitations imposed on leaf photosynthesis under naturally occurring variations in leaf temperature. Chapter 2 further examines gas-exchange dynamics of these two species under the same experimental treatments, but focused on stomatal and biochemical co-limitation of photosynthesis at different leaf temperatures. Photosynthetic limitations and constraints imposed by water stress have been studied in terms of co-limitation i.e.

‘stomatal’ and ‘non-stomatal’ limitations, with the former as a result of resistance imposed on the diffusion of CO₂ into intercellular leaf spaces and the later resulting from a combination of biochemical restraints i.e. enzyme and electron transport limitations. Most of the testing and models used to study and understand the effects of global climate change on plant function and growth utilize the Farquhar, von Caemmerer & Berry (1980) model of C₃ photosynthesis, which has two major parameters, the potential rate of RuBP limited electron transport (J_{MAX}) and the maximum rate of ribulose-1,5-*bis*phosphate carboxylase-oxygenase (Rubisco) activity (V_{CMAX}). This model has the potential to accurately represent the effects of the second major factor in global climate change that directly affects plant growth, that being elevated temperature (Medlyn et al. 2002).

Chapter 3 explores the idea of using managed migration to save the world-renowned coast redwood tree (*Sequoia sempervirens*) from climate change induced habitat loss, by managed migration it into Oregon. This chapter is focused on the subjective beliefs among stakeholder perspectives involved with land use regulation in Oregon and in particular regarding managed migration of coast redwood trees into suitable habitats in Oregon. The goal of this study is to identify and describe the current population of viewpoints held by stakeholders, which were identified using Q-methodology (Stephenson 1935), in Oregon’s land use planning community.

Case Selection: Chapter 1 and 2

The Southwest region of North America stretches from the southern Rocky Mountains to the Pacific coast with elevations ranging from among the highest in the country to the lowest, with climates ranging from some of the wettest to the driest (USGCRP 2009). The mean annual temperature in southwestern USA has increased by 0.8°C during the last century and is projected to rise by another 1.4-4.4°C by the end of the century (USGCRP 2009). Droughts are a common, natural, and long-standing feature of the Southwest's climate and climate change is projected to produce more severe droughts in the region and has already contributed to decreases in spring snowpack river flows (USGCRP 2009). My research in chapter 1 and 2 is focused on shifts in gas-exchange under increased heat and drought conditions of two dominant conifer tree species in the US southwest.

My field site is located in New Mexico utilizing a set of mature juniper and piñon trees ($n=63$) that have been experimentally heated and droughted. Manipulations of precipitation were designed to mimic historic precipitation conditions during mortality-inducing drought during 2002-2003 in piñon-juniper woodlands (~50% below the multi-decadal mean) (Breshears et al. 2005). Manipulations of temperature (~5°C above ambient) were designed to mimic the worst-case emissions scenario (business-as-usual) by 2100 (IPCC 2013).

Piñon-juniper woodlands are widespread throughout southwestern United States. However, these species future coexistence, and relative dominance of piñon-

juniper woodlands in the region is likely to be substantially impacted by current conditions and future climate change projections. In addition, these species serve well as a research focus and case selection due to their range of physiologies in regards to gas-exchange, their distinct hydraulic strategies, as well as their drought tolerance levels.

Chapter 3

Coast redwoods and their many associated species are impacted by a variety of stressors, including climate change and a variety of land use practices, which threatens their continued persistence on the landscape. The response of species to past (Overpeck et al. 2002, Benton and Twitchett 2003) and recent (Pounds 1999, Parmesan and Yohe 2003, Root 2003) climate change and the fact that the Earth is set to become warmer than any period in the last 1-40 million years (Houghton et al. 2001) raises the concern that anthropogenic climate change could act as a major cause of mass extinctions in the near future (Thomas et al. 2004). Many ecosystems are rapidly being transformed into non-historical configurations that differ in composition and/or function from present and past systems, which is increasingly being recognized as an almost inevitable consequence of environmental alteration and changing species distributions through climate and land use change (Root and Schneider 2006, Harris et al. 2006). *S. sempervirens* has a much-reduced current distribution and now naturally only occurs within a narrow coastal belt from southernmost Oregon to the south of Monterey County, California (Watt 2009). In

addition, the state of Oregon has areas on its coast that encompass the conditions of the small climactic envelope required by *S. sempervirens*.

Oregon has what is arguably the most well-developed and progressive state land use planning system in the United States. In 1973 Oregon passed the country's first state wide land use regulations Senate Bill 100 (SB 100), with the initial intention to limit sprawl and protect Oregon's farmlands, open spaces, and beautiful landscapes (Walker and Hurley 2011). The mission of Oregon's land use planning system is:

[T]o conserve farm land, forest land, coastal resources, and other important natural resources; encourage efficient development; coordinate the planning activities of local governments and state and federal agencies; enhance the state's economy; and reduce the public cost that result from poorly planned development.

—Oregon Blue Book

One of the most important and complex social questions regarding assisted migration is that of land use policies and regulations in the area being considered. This chapter looks at subjective beliefs among stakeholder perspectives involved with land use regulation in Oregon and in particular regarding managed migration of coastal redwood trees into the Oregon Coastal Zone. The combination of the threat climate change is imposing on coastal redwood trees, the fact that Oregon has suitable habitat for the managed migration of redwood trees, and the history of land use regulations in Oregon make this an excellent case study.

The goal of this dissertation is to provide a greater understanding of the physiological responses of gas-exchange in two co-occurring conifer trees that have very different drought tolerances and hydraulic strategies, to heat, drought, and the combination of heat and drought stress, which can provide important, but as of now lacking, empirical data to increase the accuracy on global vegetation models. Another major goal and focus of this research is to provide the extremely important first step towards achieving successful managed migration policies and strategy, which is to develop an understanding of the current beliefs, thoughts, and subjectivity of stakeholders in the land use planning community.

CHAPTER 1

THE EFFECTS OF DROUGHT AND HEAT ON GAS-EXCHANGE OF CO-OCCURRING ISOHYDRIC AND ANISOHYDRIC TREE SPECIES

Abstract

Periods of low precipitation and increasing atmospheric temperature are having adverse effects on tree and forest growth and survival in part via limitations upon photosynthesis. Variation among co-occurring species in gas-exchange tolerance to low precipitation and heat may explain species differences in survival during drought. We examined the effects of chronic warming (ambient +~5°C), drought (~45% precipitation reduction below ambient), and their combination on leaf gas-exchange in a mature piñon pine-juniper (*Pinus edulis-Juniperus monosperma*) woodland. In this ecosystem, isohydric piñon pine has suffered extensive mortality over the last decade, while juniper has not, a survival difference potentially related to species' gas-exchange tolerance. Drought had a greater effect on gas-exchange of both species than heat, but heat had a greater effect on gas-exchange in pine than juniper. Across large treatment effects, the soil to leaf water potential gradient explained 68 and 58% of the variation in stomatal conductance, and 76 and 60% of the variation in photosynthesis for juniper and piñon, respectively. Surprisingly, increased atmospheric temperature resulted in higher species-specific leaf water potential thresholds at which net photosynthesis reached zero.

Key words: light-saturated carbon assimilation, global-change-type drought, increased temperature, stomatal response, piñon-juniper woodland

Introduction

Anthropogenic emissions of greenhouse gases are causing changes in the Earth's surface temperatures and altering regional and global precipitation patterns (Weltzin et al. 2003). Temperatures during recent droughts have been higher than in historical drought events (e.g. Breshears et al. 2005, Williams et al. 2013), exacerbating vegetation drought stress in multiple ways including changes in carbon budgets, hydraulic systems and susceptibility to biotic agents (McDowell et al. 2008a, 2011, Breshears et al. 2013). Recent assessments suggest conifers are particularly vulnerable to the combined stresses of heat and drought (Adams et al. 2009, Jiang et al. 2013, Williams et al. 2013); however, no experimental manipulations of both precipitation and temperature have yet been carried on mature trees in the field (Leuzinger et al. 2009).

The cessation of leaf gas-exchange during drought is strongly associated with conifer mortality (Waring 1987, Martinez-Vilalta et al. 2002, McDowell et al. 2008a, 2010, Adams et al. 2013, Poyatos et al. 2013). A critical constraint in carbon uptake is at the interface of carbon gain and water loss through stomatal regulation. Multiple factors affect stomatal conductance (g_s), including strong hydraulic regulation in response to vapour pressure deficit (VPD, kPa) and water potential (Ψ , MPa) of the hydraulic system (Brodribb and Feild 2000, Hubbard et al. 2001). These all serve to vary g_s in an adaptive manner that balances carbon uptake with water conservation.

Hydraulic regulation of gas exchange by leaf water potential (Ψ_l , MPa) changes in response to soil water potential (Ψ_s , MPa), and VPD varies with plants' strategies of stomatal control within the iso-anisohydry continuum (Klein 2014). The plants' stomatal regulation over the iso-anisohydry continuum varies with genetics, site, and age (Tardieu et al. 1993, Yoder et al. 1994, Hubbard et al. 2001, Franks et al. 2007, McDowell et al. 2008a).

Predictions of the influence of drought and elevated temperature on g_s can be represented as follows based on the assumption that water loss from the leaf equals water uptake from the soil based on Darcy's law:

$$g_s = \frac{K_L(\Delta\Psi)}{hD} \quad \text{Equation (1-1)}$$

in which K_L is leaf specific hydraulic conductance, $\Delta\Psi$ is the Ψ_s to Ψ_l gradient and h is tree height (m). Refer to Whitehead et al. (1984), Whitehead and Hinckley (1991), Whitehead (1998), Oren et al. (1999) and McDowell et al. (2002, 2005, 2008b) for other versions and empirical evaluation of the model.

We can predict how plants will respond to low precipitation, which reduces $\Delta\Psi$ via more negative Ψ_s and correspondingly lower Ψ_s to Ψ_l gradient, and elevated VPD using equation (1-1) (Figure 1-6). Specifically, we hypothesize that 1) drought reduces g_s via reducing $\Delta\Psi$, 2) increasing heat reduces g_s by raising D , and 3) the combination of drought and heat causes the largest reductions in g_s (predicted by McDowell et al. 2011, Figure 1a).

Piñon pine (*Pinus edulis*) and one-seed juniper (*Juniperus monosperma*) are two sympatric tree species of Southwestern North America that represent relatively isohydric and anisohydric, hydraulic strategies (McDowell et al. 2008a); and the pine has recently experienced far more heat- and drought-induced mortality throughout the region than juniper (Breshears et al. 2005). Using our hydraulic framework (Eq. 1-1), we predict that the relatively isohydric pine maintains g_s at lower levels than anisohydric juniper (Figure 1-6), predisposing it to lower overall A during periods of heat and drought. We tested the hypotheses from the hydraulic model (Eq. 1, Figure 1-6) using a precipitation reduction and temperature increase experiment located in a piñon-pine juniper woodland in northern New Mexico. Notably, our experiment is the first manipulation of both drought and temperature on mature trees growing in the field to examine the physiological responses of two co-occurring species with contrasting hydraulic strategies.

Materials and Methods

Study site and experimental design

The experimental site is located at Los Alamos National Laboratory Earth and Environmental Science Division's SURvival-MOrtality (SUMO) experimental site (35.8180°, -106.3053°, elevation 2180 m). Soil texture is sandy loam or loam at the surface grading to a clay loam with depth (Davenport et al. 1996, Breshears et al. 2009), shallow (.3 to 1m) and well-drained, derived from a volcanic tuff substrate, and described as the Hackroy series (Nyhan et al. 1978). The site is located in an

upland topographic position near the ecotone between piñon-juniper woodland and ponderosa pine forest. *Pinus edulis* and *Juniperus monosperma* are the dominant tree species. Gambel oak (*Quercus gambelii*) is also present. The understory is composed of grasses, including blue grama (*Bouteloua gracilis*), and some forbs and cacti.

The 30 year mean annual temperature and total precipitation at a meteorological tower located ~1km distant are 9.2 °C and 470 mm. Roughly half of the annual total precipitation falls from July to September during the North American Monsoon, with the remainder falling primarily as snow in the winter. Manipulations of precipitation and temperature were designed to mimic historic precipitation conditions during mortality-inducing drought in piñon-juniper woodlands (~50% below the multi-decadal mean) (Breshears *et al.* 2005) and extreme heat waves occurring on top of the predicted temperature in 2050 (~5°C above ambient) (IPCC 2013). The experimental design includes treatments to both piñon pine and juniper trees, and includes: 1) control tree (C; ambient temperature and precipitation), 2) control chamber (CC; open top chambers, with temperature maintained at ambient values (measured at the mean canopy height in an adjacent clearing), 3) heated chamber (H; ~5°C above ambient), 4) drought (D; ~50% precipitation reduction), and 5) combined drought and heat (HD). The below-canopy drought structure is nearly identical to that described in Pangle *et al.* (2012). Chamber air temperature was maintained at ambient for CC treatment or set to +5 °C above ambient for H treatment using heating-air conditioning units, and resulting in a +4.4°C heat treatment over the study period. The drought structure was installed on June 1, 2012

and heat treatments were operational on June 11, 2012 (Julian day 163). The sample sizes for juniper trees were N = 7 (C), 6 (CC), 9 (D), 5 (H), and 5 (HD). Sample sizes for piñon trees were N = 6 (C), 5 (CC), 9 (D), 6 (H), and 5 (HD).

Meteorological measurements

Two micrometeorological stations located 100m apart collected a data record of ambient temperature, humidity, wind speed, wind direction, and precipitation (see Garcia-Forner et al. 2015 for more detail). Temperature and relative humidity within both the CC and H open-top chambers were also recorded at both 1/3rd and 2/3rd tree height (CS215, Campbell Scientific) and the averages used to represent the temperature in the chambers.

Climate

In 2012 the annual average temperature was 10.9 °C compared to the long-term annual average of 9.11 °C. Daily mean heated treatment temperatures ranged from 6.5 to 30.7 °C after initiation of the heat treatment (Figure 1-1a). Annual ambient precipitation was 244 mm, compared to long-term average (482 mm). Ambient treatment VPD ranged from 0.19 to 3.38 kPa (Figure 1-1b). Heated treatment VPD ranged from 0.46 to 4.21 kPa (Figure 1-1b). Winter months had no precipitation events greater than 5 mm, with 2 spring days where precipitation reached greater than 10 mm (Figure 1-1c). Although 2012 was a dry year 61% of the precipitation did occur during the monsoon season from late July to early October

(Figure 1-1c), with the drought plot receiving an estimated 91 mm (55% of ambient, Figure 1-1c).

Gas exchange measurements

Gas-exchange and predawn and midday stem water potentials (assumed to be equivalent to Ψ_s and Ψ_l , respectively) were collected from 63 target trees seven times throughout the 2012-growing season. Leaf level gas-exchange measurements were conducted using five portable gas-exchange systems (model LI-6400, Li-Cor, Nebraska, USA) coupled to a 2 x 3 cm light source chamber (6400-02B LED, Li-Cor Inc.) and an external CO₂ source. Field measurements were limited to morning hours (7:00-11:00 h local time) on south-facing twigs supporting green, turgid foliage. The five Li-Cor 6400 systems were inter-calibrated each day, for days 95 (pre-monsoon), 135 (pre-monsoon), 178 (pre-monsoon), 205 (monsoon), 240 (monsoon), 269 (post-monsoon) and 312 (post-monsoon). The environment inside the chamber was set using the CO₂ mixer at 380 ppm. Photosynthetically active photon flux density (PPFD) of 1500 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ was used to assure light saturation. An airflow rate of 300 $\mu\text{mol s}^{-1}$, and no lower than 200 $\mu\text{mol s}^{-1}$, was used to maintain a significant differential of CO₂ and H₂O concentration between the two IRGAs of the system. To assure no leaks contaminated the measurement the chambers were sealed with G35 Qubitac Sealant (Qubit Systems Inc., Kingston, ON, Canada) and tested until CO₂ leaks were less than 0.01 ($\mu\text{mol mol}^{-1}$). The chamber air was dried to achieve similar conditions among the five LiCor's and limit condensation issues.

Measurements were only recorded after both CO₂ and water flux parameters were stable for at least two minutes and before stomatal response to any changes in humidity (Vico et al. 2011); thus these are considered representative of light-saturated photosynthetic capacity. Carbon assimilation rate (A), was calculated by the LI-6400 software (OPEN versions 6.1.4) based on equations presented by von Caemmerer & Farquhar (1981). Foliage was collected after measurements and projected leaf area obtained using a leaf area meter (model LI-3100, Li-Cor, Nebraska, USA). Values of A were corrected for projected leaf area.

Stem water potential

Predawn and midday stem water potentials were measured as surrogates for Ψ_s and Ψ_l , respectively, using Scholander-type pressure chambers (PMS Instruments, Corvallis, OR, USA), on twigs supporting green, turgid foliage. Two twigs per tree were collected before sunrise and again at midday, stored in sealed plastic bags in a refrigerator, and measured within two hours. The difference between Ψ_s and Ψ_l is defined as the water potential gradient ($\Delta\Psi$). Correction of water potential for the hydrostatic gradient was not done because all twigs were sampled within two meters of the ground (maximum tree height at this site is ~ six meters).

Data analyses

Initial two-way ANOVA tests were performed to determine significant differences gas-exchange parameters and water potentials among species or treatments at different measurement days. Then unpaired Student's t -tests with

Welch's correction were used to discriminate differences among species or treatments when the ANOVA revealed a significant effect. We used the general additive model with R software SemiParrametric Regression Package 1.0 (Ruppert *et al.* 2003) to test whether there is significant difference in the nonlinear relationships between g_s and D for different treatments and species. Statistical analyses were performed using GraphPad Prism software (version 6.0a 2012) and R software (version 2.15.0, R-Development-Core-Team 2012).

Results

Water potentials

Our results did not reveal statistically significant within species treatment differences in pre-dawn, midday or $\Delta\Psi$ until day 179, which generally yielded minimum water status for all water potential measurements in both species (Figure 1-2). Seasonal shifts in pre-dawn and midday water potentials were much greater in amplitude for juniper than piñon (Figure 1-2a-e). Pre-dawn stem water potential for juniper fell below -5 while piñon never fell to -3 (Figure 1-2, Figure 1-4). During monsoon, shifts in $\Delta\Psi$ varied across species and among treatments with treatments having little impact on juniper, but a significant effect with the combination heat and drought treatment in piñon $\Delta\Psi$ (Figure 1-2).

Gas-exchange

No significant differences in leaf gas-exchange between C and CC treatments were observed for any measurement day for either species, with the exception of day 135 for juniper (Figure 1-3). Therefore, statistical testing for treatment effects was performed using CC data as the control. Neither juniper nor piñon displayed gas-exchange differences between the CC and the various treatments until the monsoon arrived (before measurement day 240; Figure 1-3). A and g_s were significantly lower in juniper D and piñon HD treatments than all other treatments on day 240 (Figure 1-3). All treatments exhibited significant lower A rates than CC by day 269 (Figure 1-3). H, D, and HD treatment effects were similar across species, with higher A and g_s in C and CC after treatments were implemented (Julian day 159, Figure 1-3). In every treatment, maximum gas-exchange rates were higher in juniper than in piñon after treatments were implemented (Figure 1-3). Gas-exchange rates were strongly correlated with pre-dawn, midday and $\Delta\Psi$ for juniper and piñon, with the exception of piñon midday leaf water potentials (Table 1-1).

Water potential effect on gas-exchange

The seasonal shifts of leaf gas-exchange in both species followed water potential values with minimum rates during the driest seasons and enhanced physiological performance with monsoon precipitation (Figure 1-2, Figure 1-3). Zero assimilation was observed at predawn water potentials of -4.92 and -2.47 for control, -4.67 and -2.34 for heat, -5.10 and -2.48 for drought, -4.96 and -2.38 for heat and

drought (MPa), in juniper and piñon, respectively (Table 1-1, Figure 1-4). Linear regression lines of predawn and midday water potentials and A displayed a much sharper decline in gas-exchange under increased water stress for piñon than juniper (Table 1-1, Figure 1-4). There was no statistical treatment difference within species of linear regression slopes or Y-intercepts of A and pre-dawn, midday or $\Delta\Psi$ for juniper or piñon (Table 1-1). Slopes of linear regression lines of A and pre-dawn, varied significantly across species in CC, H and HD treatments, but no significant differences were observed across species for midday or $\Delta\Psi$ (Table 1-1).

Vapour pressure deficit impacts on gas-exchange

As expected based on Eq. (1-1), our results showed that g_s declined in response to increasing VPD (Figure 1-5). Juniper and piñon exhibited significant differences between g_s and VPD (using semi-parametric regression using a general additive model, $P < 0.001$). Within species, gas-exchange was significantly lower in D relative to all other treatments for both juniper and piñon (using semi-parametric regression using a general additive model, $P < 0.01$), however H and HD treatments did not have much effect on the gas-exchange to VPD relationships for either species.

Predicted and observed stomatal results

Stomatal sensitivity to atmospheric and soil water availability was predicted using Equation 1-1 (Figure 1-6a, c) which generally matched trends in observed data (Figure 1-6b, d). Darcy's law equation (1) succeeded in predicting g_s in juniper ($R^2 = 0.73$, $P < 0.0001$) and piñon ($R^2 = 0.86$, $P < 0.0001$) (Figure 1-7). The linear

regression line for modeled vs. observed g_s in juniper was determined to be statistically different than the 1:1 line ($P = 0.033$). However no statistical difference was determined between the linear regression line for modeled vs. observed g_s in piñon and the 1:1 line (Figure 1-7).

Discussion

In this paper, we have tested the hypotheses that 1) drought reduces g_s by reducing $\Delta\Psi$, 2) increasing heat reduces g_s by raising VPD, and 3) the combination of drought and heat causes the largest reductions in g_s . Results of this experiment do not fully support our hypotheses. g_s and $\Delta\Psi$ were positively correlated, as predicted, however this relationship did not differ between species or treatments (Figure 1-4c,f). Similarly, g_s and VPD were negatively correlated, however the heat treatment did not modify this relationship (Figure 1-5). The addition of increased temperature and corresponding impacts on physiological processes are novel, and advance the knowledge of these model global species representing iso and anisohydric water strategies. Our anisohydric model tree (juniper) and our isohydric model tree (piñon) did not differ in the relationship between gas-exchange rates and $\Delta\Psi$ (Figure 1-4c and f). Furthermore, no difference was determined between species for gas-exchange rates vs. $\Delta\Psi$ when separated by treatments (Table 1-1). The relationship between g_s and VPD only differed significantly in the drought treatment for both species (Figure 1-5). Our third hypothesis that heat would exacerbate reductions in g_s was only supported during the monsoon period in piñon HD trees (Figure 1-3).

Effectiveness of treatment structures

Our experimental structures and corresponding meteorological treatment results proved to be an excellent system for measuring the effects of drought, heat and their combination on gas-exchange for two species that are ideal global models for isohydric and anisohydric tree species (Figure 1-1). Similar to results from multi-year experiments on the same species using an almost identical drought structure (Pangle et al. 2012, Plaut et al. 2012, Plaut et al. 2013, Limousin et al. 2013), water potentials were significantly affected by precipitation manipulation in both species (Figure 1-2). Moreover, the heat treatments successfully altered atmospheric temperature and vapor pressure deficits for the H and HD treatments (Figure 1-1).

Seasonality of leaf level gas-exchange

The decline in rates of gas-exchange in C and CC treatments of both isohydric and anisohydric species during seasonal reductions in precipitation and corresponding pre-dawn water potentials clearly demonstrate the physiological ability of these co-occurring species to adjust gas-exchange rates and stomatal regulation during water stress conditions (Figure 1-3). Both species exhibited a clear gas-exchange response to all treatments with significantly lower average A than trees under control chamber conditions once monsoon precipitation ceased (Figure 1-3).

Iso vs. anisohydric differential responses to environmental drivers on water potentials and gas-exchange

Our analyses of the gas-exchange response to water potential fluxes under drought treatments are consistent with prior studies of the same species (Plaut et al. 2012, Plaut et al. 2013, Limousin et al. 2013), and support the isohydric nature of piñon and anisohydric nature of juniper. In particular, our findings indicate that juniper is less sensitive to heat than piñon, which has important climate change implications. In this study, we observed heat having little impact on $\Delta\Psi$ in our anisohydric tree during monsoon and a significant effect on our isohydric HD trees (Figure 1-2c and f). While monsoon gas-exchange rates in our anisohydric tree were significantly reduced in D, the heated treatments (H and HD) did not differ significantly from control treatments (Figure 1-3).

Previous analysis of leaf level gas-exchange in piñon and juniper has demonstrated that juniper can conduct photosynthesis at much lower Ψ than piñon, and demonstrates far more hydraulic acclimation to experimental reduction in precipitation (Limousin et al. 2013, McDowell et al. 2008, Williams and Ehleringer 2000, Lajtha and Barnes 1991), less vulnerability to drought-induced xylem cavitation and embolism (Linton et al. 1998, Willson et al. 2008, Delzon et al. 2010, Plaut et al. 2012), and enhanced drought stress recovery through potential refilling of embolized root xylem (Plaut et al. 2013). Breshears et al. 2005, observed the 2000's drought in this region was hotter, which resulted in extensive *Pinus edulis* mortality across the region, than the cooler but drier 1950's drought. The effects of warmer

temperatures accompanied with longer and more intense droughts in this region, has the potential for a forest ecotone shift.

Darcy's Law

A key strength in the use and strong correlation found between modeled and observed g_s using Darcy's Law (eq. 1-1 and Figure 1-7) is the ability to predict how plants will respond to this ecosystem's modeled future climactic shift of low precipitation and elevated VPD. The correlation between modeled vs. observed stomatal conductance rates in relation to $\Delta\Psi$ and VPD was stronger for piñon than juniper with the regression line of juniper below the 1:1 line and statistically different, while the regression line of piñon was not statistically different than the 1:1 line. These results suggest stomatal conductance in anisohydric trees may be more hindered by reductions in $\Delta\Psi$ and VPD than isohydric trees.

Table 1-1. Coefficients \pm SE of linear regression lines and 95% confidence intervals of zero assimilation between A ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and predawn stem water potential, midday stem water potential, and predawn - midday stem water potential (MPa), for each species and treatment. No statistical difference within species was determined at $P < 0.05$ between A and Ψ control and treatment slopes and Y-intercepts. * Denotes across species significant differences between slopes of linear regressions of A and Ψ at $P < 0.05$.

Species	Regression	Treatment	Slope	R ²	Y-Intercept	X-Intercept	95% CI of zero A
Piñon	Ψ_{pd} and A	CC	3.62 \pm 0.85*	0.35	9.72 \pm 1.45	-2.69	-3.75 to -2.27
		H	5.36 \pm 0.68*	0.63	12.59 \pm 1.25	-2.35	-2.62 to -2.17
		D	3.33 \pm 0.54	0.43	8.72 \pm 1.03	-2.62	-3.04 to -2.38
		HD	4.61 \pm 0.85*	0.51	11.48 \pm 1.62	-2.49	-2.95 to -2.25
Piñon	Ψ_{md} and A	CC	0.53 \pm 1.87	0.00	5.19 \pm 4.61	-9.84	NA to -3.30
		H	2.69 \pm 2.27	0.03	9.63 \pm 5.63	-3.58	NA to -2.83
		D	1.14 \pm 0.87	0.03	5.57 \pm 2.23	-4.89	NA to -3.39
		HD	3.50 \pm 1.40	0.16	11.53 \pm 3.49	-3.29	-7.01 to -2.85
Piñon	$\Delta\Psi$ and A	CC	3.24 \pm 0.86	0.3	1.19 \pm 0.87	-0.37	-1.86 to 0.13
		H	5.09 \pm 0.76	0.56	-0.31 \pm 0.67	0.06	-0.27 to 0.27
		D	3.23 \pm 0.70	0.30	0.44 \pm 0.57	-0.14	0.81 to 0.16
		HD	3.35 \pm 1.18	0.22	0.95 \pm 0.90	-0.28	-2.66 to 0.17
Juniper	Ψ_{pd} and A	CC	1.81 \pm 0.14*	0.81	8.88 \pm 0.39	-4.92	-5.50 to -4.48
		H	1.99 \pm 0.16*	0.84	9.44 \pm 0.45	-4.75	-5.26 to -4.37
		D	1.55 \pm 0.13	0.70	8.14 \pm 0.46	-5.25	-5.80 to -4.84
		HD	1.92 \pm 0.19*	0.76	9.52 \pm 0.60	-4.95	-5.57 to -4.50
Juniper	Ψ_{md} and A	CC	2.30 \pm 0.50	0.69	11.65 \pm 0.81	-5.33	-5.97 to -4.89
		H	2.51 \pm 0.22	0.80	12.86 \pm 0.79	-5.12	-5.57 to -4.79
		D	1.83 \pm 0.19	0.60	10.10 \pm 0.74	-5.52	-6.12 to -5.10
		HD	2.45 \pm 0.30	0.67	12.59 \pm 1.11	-5.15	-5.80 to -4.73
Juniper	$\Delta\Psi$ and A	CC	5.56 \pm 0.40	0.84	-0.01 \pm 0.40	0.00	-0.16 to 0.13
		H	4.37 \pm 0.87	0.45	0.76 \pm 0.86	-0.17	-0.92 to 0.17
		D	3.89 \pm 0.58	0.45	1.23 \pm 0.48	-0.32	-0.76 to 0.06
		HD	4.82 \pm 0.86	0.50	0.63 \pm 0.76	-0.13	-0.67 to 0.15

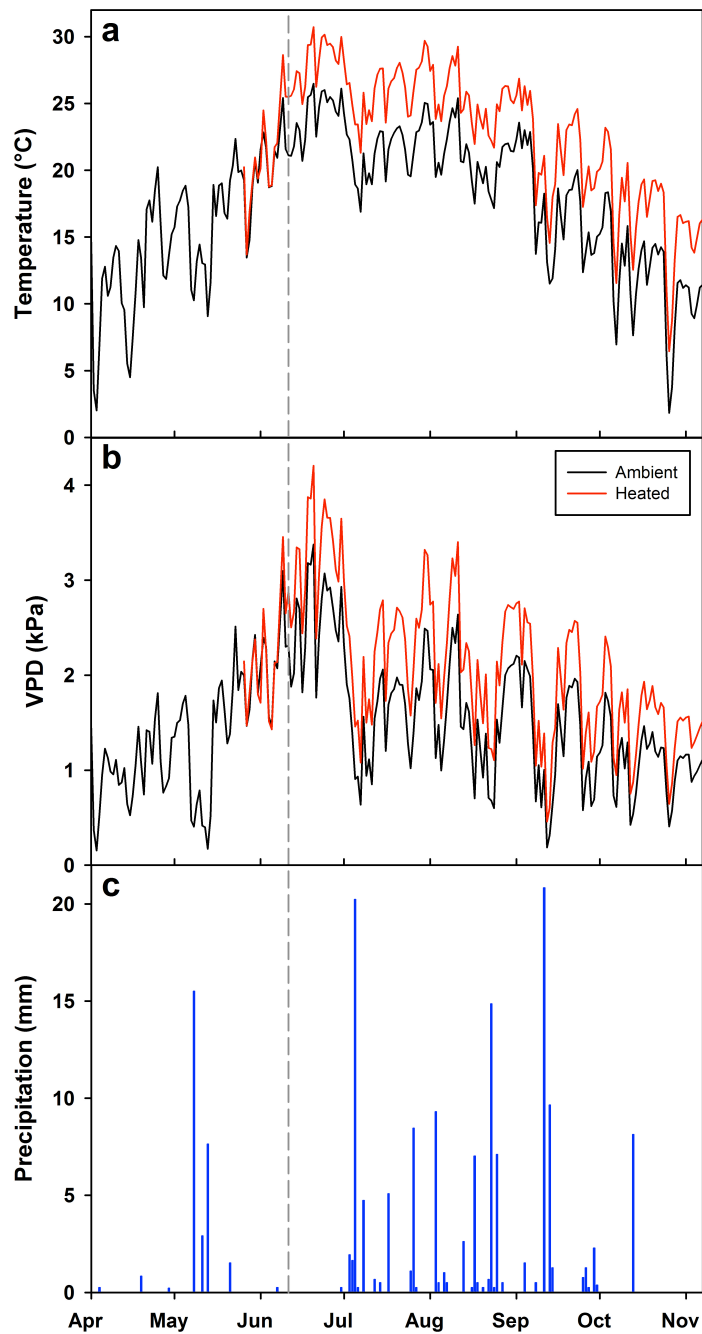


Figure 1-1. Climate data over the study period. (a) Mean daily temperature, (b) mean atmospheric daily vapour pressure deficit (VPD) and (c) daily precipitation totals. Vertical dashed grey line indicates when treatments were operational. Lines in a and b represent ambient (black) and mean heated chamber (red) temperatures and vapour pressure deficits.

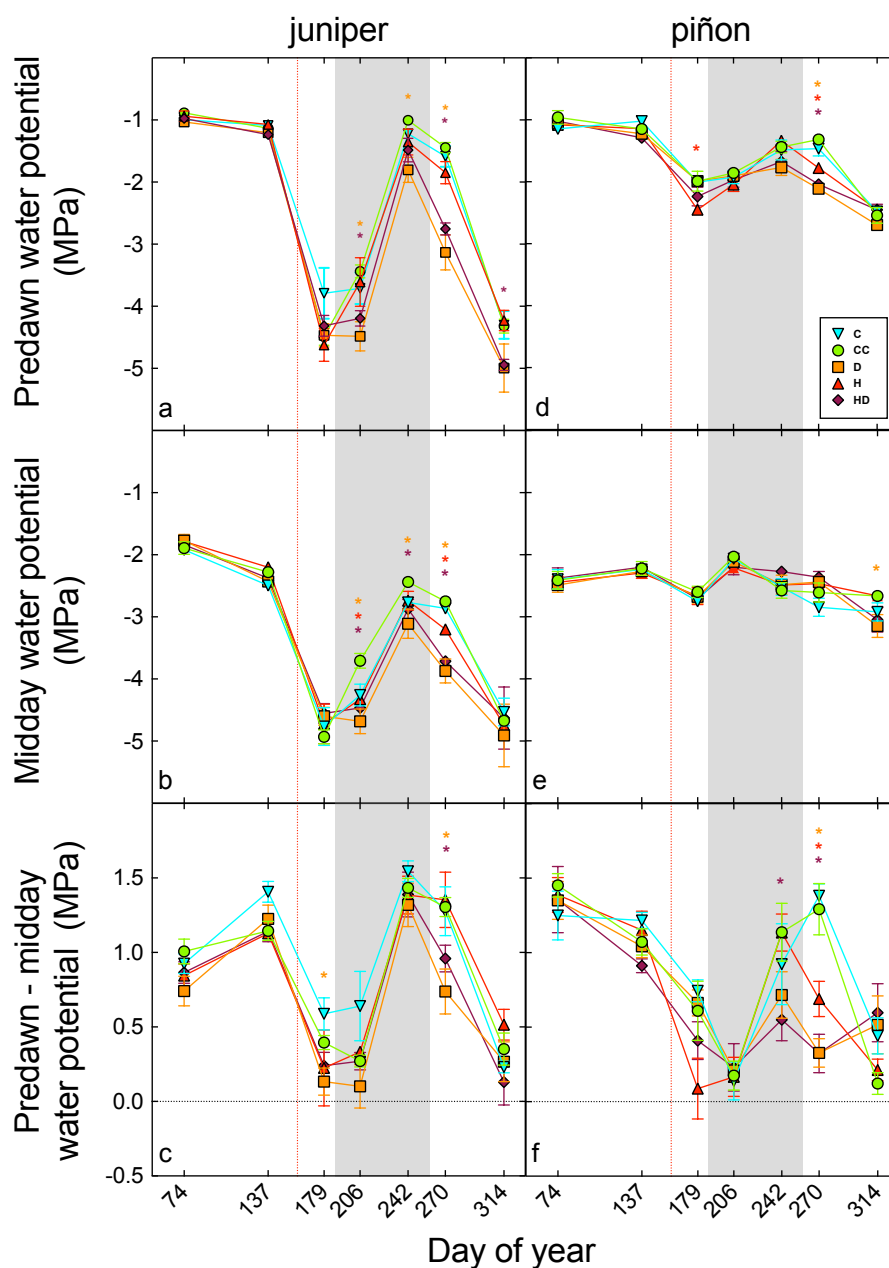


Figure 1-2. Seasonal variation in (a and d) predawn stem water potential (used for Ψ_s), (b and e) midday stem water potential (used for Ψ_l), and (c and f) $\Delta\Psi$ (MPa), in each of the five treatments (C, CC, H, D, HD) for juniper and piñon. Data were collected between April and November 2012. Error bars are standard errors and significant treatment effects on A and g_s for every measurement date are shown above the symbols: * drought vs. control; * heat vs. control; * drought and heat vs. control: $P < 0.05$. Vertical dotted red line indicates when treatments were operational (Day 159). Grey shaded region represents monsoon season.

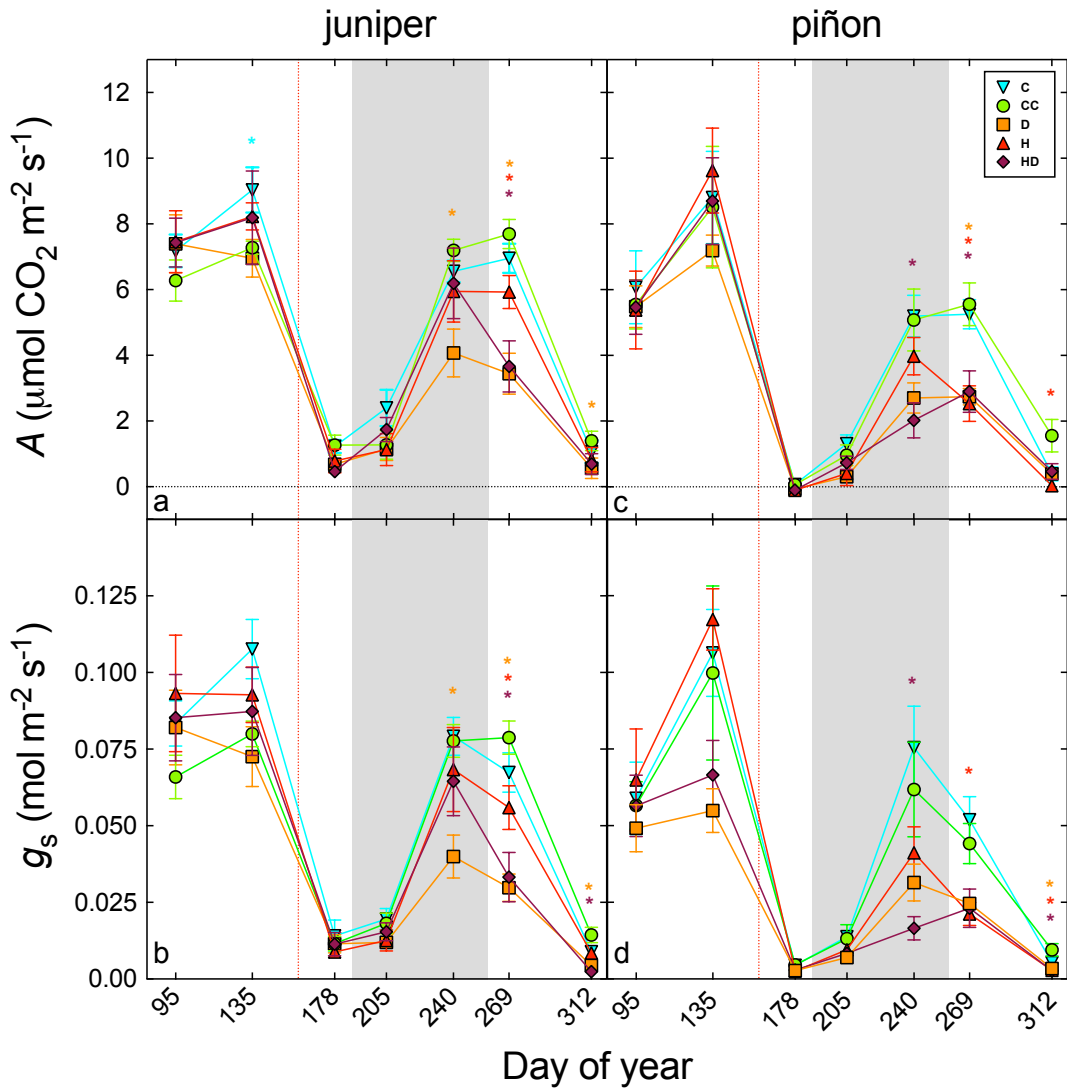


Figure 1-3. Seasonal variations of (a and c) light-saturated photosynthetic capacity (A), and (b and d) stomatal conductance (g_s) in foliage of each of the five treatments (C, CC, H, D, HD) for juniper and piñon. Data were collected between April and November 2012. Error bars are standard errors and significant treatment effects on A and g_s for every measurement date are shown above the symbols: * drought vs. control; * heat vs. control; * drought and heat vs. control: $P < 0.05$. Vertical dotted red line indicates when treatments were operational (Day 159). Grey shaded region represents monsoon season.

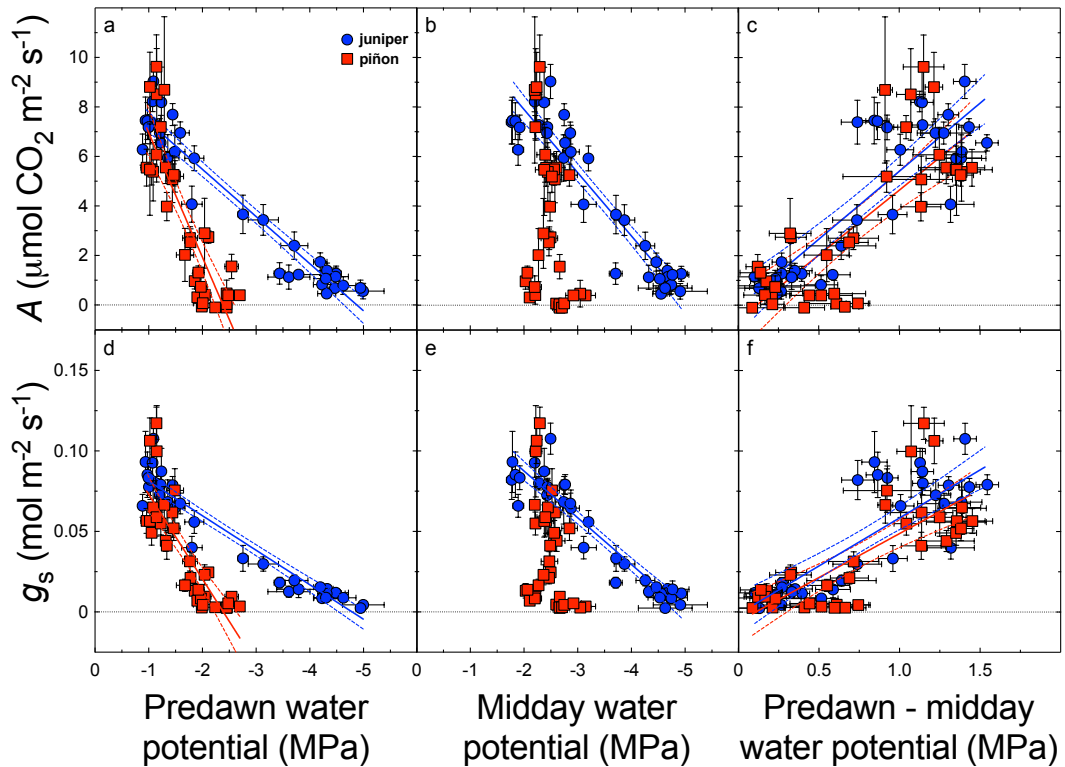


Figure 1-4. Relationship between (a – c) light-saturated photosynthetic capacity (A), (d – f) stomatal conductance (g_s), and Ψ_s , Ψ_l , and $\Delta\Psi$ (MPa), in juniper and piñon (all treatments). Linear regressions and 95% confidence intervals are shown. Data were collected between April and November 2012. Each symbol represents species averages because no significant treatment differences were detected. A summary of A results (separated by treatments) is presented in Table 1-1.

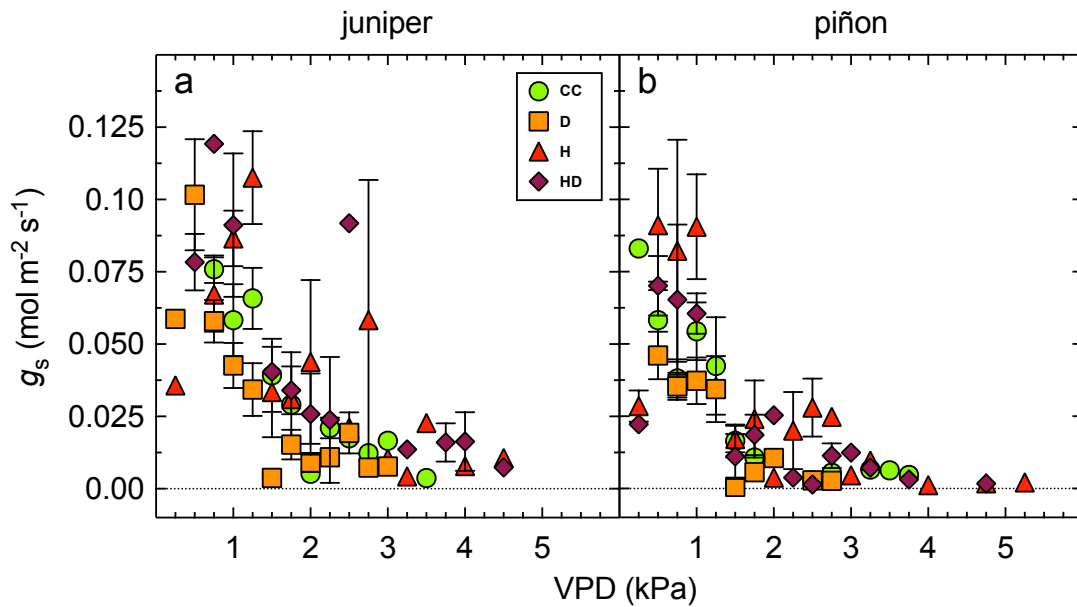


Figure 1-5. Relationship between stomatal conductance (g_s) and vapor pressure deficit (VPD) of piñon and juniper. Data were collected between April and November 2012. Values were binned by 0.25 kPa classes of VPD for presentation. Foliage was the sample unit. Bars are standard errors of g_s for classes of VPD.

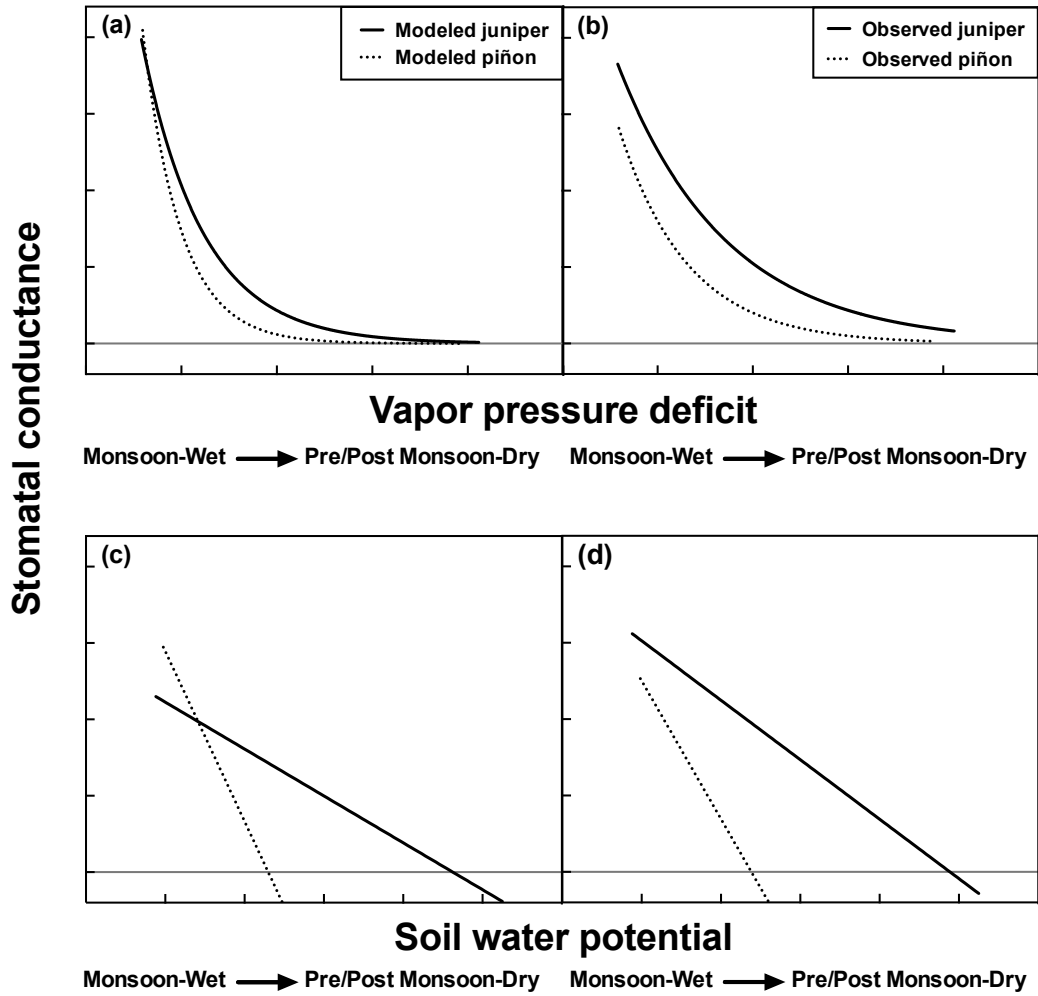


Figure 1-6. Predictions (a and c) and observed (b and d) stomatal conductance (g_s) using Eq. 1-1. (a and b) The response of g_s to increasing VPD. (c and d) The response of g_s to Ψ_s .

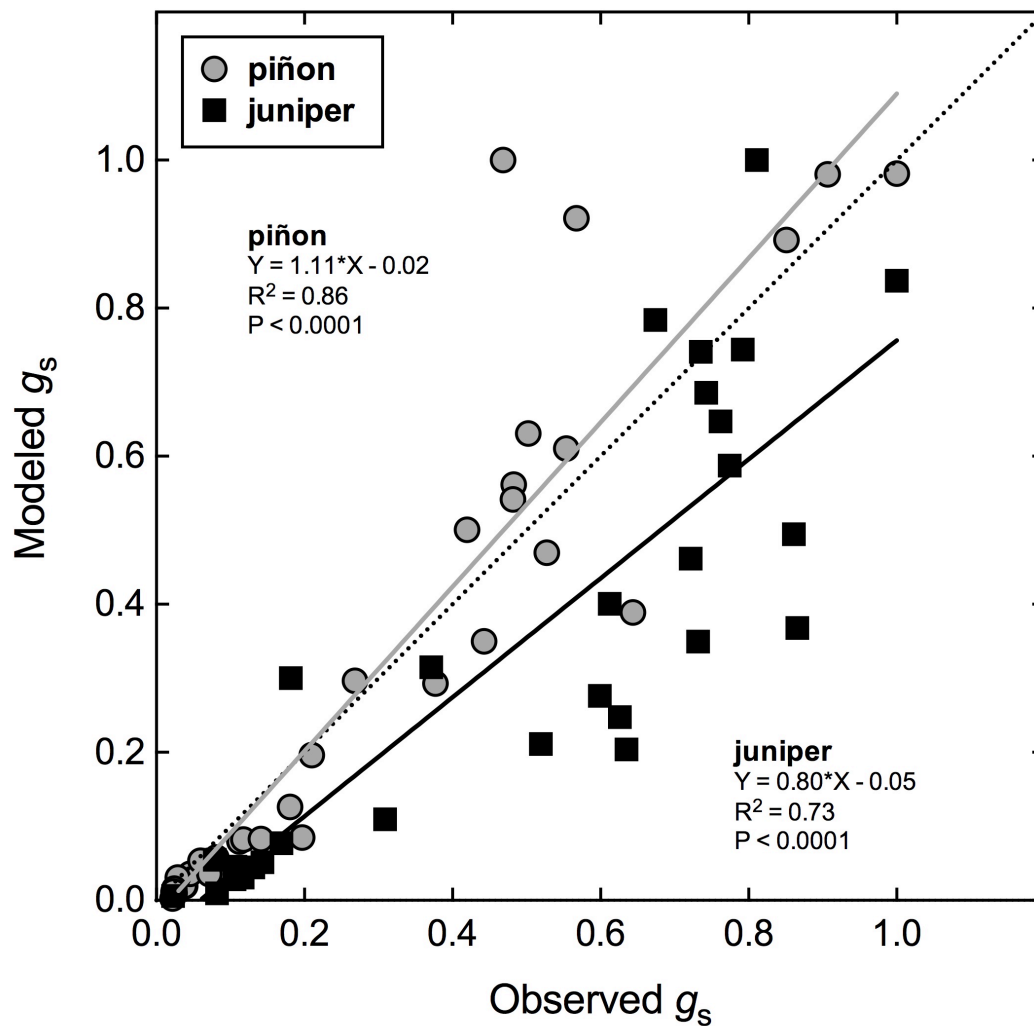


Figure 1-7. Relationship between modeled and observed g_s for piñon and juniper for all treatments. The common linear regression for each species is shown with the line equation, R^2 , and P-value. The dotted line is the 1:1 relationship between modeled and observed g_s .

CHAPTER 2

TEMPERATURE SENSITIVITY OF PHOTOSYNTHETIC CAPACITY IN CO-OCCURRING CONIFER TREES UNDER EXPERIMENTAL HEAT AND DROUGHT

Abstract

Understanding and accurately predicting the long-term effect of increased atmospheric temperature and drought on photosynthetic capacity over a range of leaf temperatures is crucial for modeling carbon uptake and water vapor exchange between vegetation and the atmosphere. We measured leaf photosynthetic capacity (i.e., maximal carboxylation rate, $V_{\text{C}_{\text{MAX}}}$, and maximal photosynthetic electron transport rate, J_{MAX}) for two co-occurring widespread conifer species of the US southwest (*Pinus edulis* and *Juniperus monosperma*) during the second year of increased temperature and reduced precipitation. Photosynthetic capacity was estimated for three trees from each species in all treatments at five leaf temperatures between 10 and 50 °C. We found for both species, $V_{\text{C}_{\text{MAX}}}$ and J_{MAX} were maximal at 30 °C and both piñon and juniper exhibited $V_{\text{C}_{\text{MAX}}}$ at 30 °C in the order control \cong drought > (heat and the combination of heat and drought). We concluded that piñon trees under all treatments are more sensitive to temperature regulation of carbon assimilation than juniper trees, $V_{\text{C}_{\text{MAX}}}$ and J_{MAX} in both species are equally sensitive to temperatures between 10 and 40 °C, and treatments do not seem to change the sensitivity. Moreover, beyond leaf temperatures of 30 °C, biochemical limitations appear to have a more pronounced impact on photosynthesis in piñon than juniper.

This work shows that these species have different sensitivities to temperature, which can help explain the difference in health and mortality rates of these trees under current and future warming scenarios.

Key words: leaf level gas-exchange; water stress; temperature stress; carbon starvation; hydraulic limitation; stomatal conductance; iso- versus anisohydric; needleleaf evergreen trees

Introduction

A warmer and drier future is anticipated for many regions around the globe with longer, warmer, and more frequent droughts (IPCC 2013). This will have profound implications on the function and structure of vegetation at several scales, including individual trees (Waring 1987, McDowell et al. 2008, 2010, Adams et al. 2013, Poyatos et al. 2013), forests (Malhi et al. 2002), and terrestrial biomes (NRC 2007). In addition, biosphere-atmosphere interactions (Foley et al. 1996, NRC 2007), land-surface stability (Thompson et al. 1995, Cox et al. 1999), and ecosystem goods and services (MA 2005, NRC 2007, Running et al. 2000, Anderegg et al. 2013) will be affected by warmer and drier conditions. Despite decades of research on plant drought and temperature tolerance, the current knowledge of physiological mechanisms and photosynthetic responses to stress induced by drought, heat, and their combination are still under debate (Hikosaka et al. 1999, Sala et al. 2010, Sevanto et al. 2014, Woodruff et al. 2015). Recent assessments describe how conifers are particularly vulnerable to the combined stresses of heat and drought, which has

resulted in unprecedented tree and forest mortality of coniferous species around the globe (Adams et al. 2009, Jiang et al. 2013, Williams et al. 2013).

Understanding how different species and plant functional types will physiologically respond to the combination of heat and drought, and describing leaf-level responses to diurnal and seasonal variations in leaf temperature, is critical for modeling and predicting the fate of trees and forests under future climate conditions (Long 1991, Harley and Baldocchi 1995, Sitch et al. 2008, Jump et al. 2009).

Photosynthetic limitations and constraints imposed by water stress have been studied in terms of the relative co-limitation by stomatal and non-stomatal factors (Martin and Ruiz-Torres 1992, Flexas et al. 2002), with the former a result of resistance imposed on the diffusion of CO₂ into intercellular leaf spaces, and the latter resulting from a combination of enzyme and electron transport limitations (Long and Bernacchi 2003). For instance, different plants within the same community may have differing leaf gas-exchange and hydraulic strategies and may occupy a range of positions on the isohydric–anisohydric continuum of stomatal regulation, which is based on their capacity to regulate leaf water potentials (Stocker 1956, Jones 1998, Tardieu and Simonneau 1998; Martinez-Vilalta et al. 2014) and may influence individuals between survival and mortality (McDowell et al. 2008).

In many habitats individual plants can be subject to a wide range of seasonal and diel variation in temperature (Berry et al. 1980). Quantifying the temperature-induced shifts of the biochemical limitations on leaf level gas-exchange at the range

of temperatures vegetation encounters *in situ* is important for understanding forest health, and to improve models of photosynthesis at the canopy level (Harley et al. 1985, Harley and Tenhunen 1991, Harley and Baldocchi 1995, De Pury and Farquhar 1997). It will also help to better compare photosynthetic performance among species within communities (Wullschleger 1993) and enable more accurate modeling of carbon and water exchange between the terrestrial biosphere and the atmosphere.

The model of Farquhar et al. (1980) (FvCB model) has provided a means to quantitatively partition biochemical and stomatal limitations on photosynthesis, from the response of carbon assimilation (A), versus intercellular CO_2 concentration (C_i), (A/C_i) curves (Farquhar and Sharkey 1982, Long and Bernacchi 2003). Two key parameters of the FvCB model are the maximum rate of Rubisco (ribulose-1,5-bisphosphate carboxylase-oxygenase)-catalyzed carboxylation [$V_{\text{C}_{\text{MAX}}}$ ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)], (maximum carboxylation rate) and the regeneration of RuBP controlled by electron transport rate [J_{MAX} ($\mu\text{mol electron m}^{-2} \text{ s}^{-1}$)], (maximum electron transport rate). These photosynthetic parameters are strongly influenced by leaf characteristics including the total amount of nitrogen per unit leaf area and leaf temperature (Dreyer et al. 2001). $V_{\text{C}_{\text{MAX}}}$ and J_{MAX} calculated from A/C_i curves are thought to represent the major biochemical limitations to light-saturated photosynthesis (Armond et al. 1978, Farquhar et al. 1980, Yamasaki et al. 2002, Yamori et al. 2005), which is commonly Rubisco- limited under natural conditions (Harley and Sharkey 1991, Rogers and Humphries 2000) and have been generally accepted as a measure of photosynthetic capacity.

The original FvCB model was parameterized and scaled to a leaf temperature of 25 °C; because variation in $V_{\text{C}_{\text{MAX}}}$ and J_{MAX} is strongly correlated with leaf temperature (Bernacchi et al. 2001, Dreyer et al. 2001, Medlyn et al. 2002, Bernacchi et al. 2003), we expect substantial diel and seasonal variation in these parameters. All published carbon gain models use a temperature response function (Harley and Tenhunen 1991, Leuning 1997, Dreyer et al. 2001); however, few studies have produced data sets for the temperature responses of $V_{\text{C}_{\text{MAX}}}$ and J_{MAX} of field grown co-occurring mature conifer species, particularly for whole trees under experimental heat and drought treatments.

In this study we used temperature response curves (Table 2-1) to determine leaf temperature dependent stomatal and non-stomatal (biochemical; $V_{\text{C}_{\text{MAX}}}$ and J_{MAX}) co-limitations on photosynthesis. We tested hypotheses about the effects on leaf gas-exchange of the second year of induced warming (ambient +~5 °C), drought (~45% precipitation reduction below ambient), and their combination, in a mature piñon pine-juniper (*Pinus edulis-Juniperus monosperma*) woodland. These hypotheses were tested via A/C_i curve analysis and corresponding $V_{\text{C}_{\text{MAX}}}$ and J_{MAX} calculations across a range of temperatures. Specifically, we hypothesized that (H1) there is an optimal range of leaf temperatures, below which photosynthesis will be more biochemically limited and above which photosynthesis will be more constrained by stomatal limitations; (H2) at optimal leaf temperatures, biochemical limitations to photosynthesis will generally match temperature response curve trends with control > drought \cong heat > (drought + heat). In other words, control trees will be more

biochemically limited than trees under drought or heat treatments alone, which will all be more biochemically limited than trees under combined heat and drought treatments; and (H3) as leaf temperatures increase from below to slightly beyond their optimal range, photosynthesis will be more $V_{\text{C}_{\text{MAX}}}$ limited, however, when leaf temperatures are well above the optimal range, (i.e., $> 30^{\circ}\text{C}$), photosynthesis will become more limited by electron transport.

Materials and Methods

Study site and experimental design

The study was conducted in a piñon-juniper woodland located on Frijoles Mesa, 7.9 km south of Los Alamos, New Mexico, USA at Los Alamos National Laboratory Earth and Environmental Science Division's SURvival-MORtality (SUMO) experimental site (35.8180° , -106.3053° , elevation 2180 m). The site is at 2150 m m.s.l. on Hackroy clay-loam soils ranging in depth from 40-80 cm over a layer of meters-thick volcanic-ash-derived tuff. Manipulations of precipitation were designed to mimic historic precipitation conditions during mortality-inducing drought during 2002-2003 in piñon-juniper woodlands ($\sim 50\%$ below the multi-decadal mean) (Breshears et al. 2005). Mean annual temperature from 1987 to 2012 at SUMO was 10.5°C , varying on average from 0.6°C in December to 21.6°C in July, with a mean annual precipitation total for 414 mm (<http://environweb.lanl.gov/weathermachine/>). Manipulations of temperature ($\sim 5^{\circ}\text{C}$ above ambient) were designed to mimic the worst-case emissions scenario (business-as-usual) by 2100 (IPCC 2013). Two

micrometeorological stations located 100m apart collected a data record of ambient temperature, humidity, wind speed, wind direction, and precipitation. For further details of the study site and detailed micrometeorological data, see Adams et al. (2015) and Garcia-Forner et al. (2016).

Open-top-chambers (OTCs) surrounding the canopies (average height of 3.04 m) and precipitation-diversion (drought) troughs and their combination were used to impose heat and drought treatments (Adams et al. 2015, Garcia-Forner et al. 2016). Air temperature in the heat (H), combination of heat and drought (HD) and control chamber (CC) treatments was controlled using custom-built clear polycarbonate-walled and aluminum-framed OTCs surrounding the canopies, and conditioned air provided by air-exchange package heating, ventilation and air-conditioning units (RJPL and RLPL, Ruud Manufacturing, Atlanta GA, USA). Temperature measurement and control was achieved using CR1000 dataloggers and two CS215 temperature and relative humidity probes (Campbell Scientific, Logan UT, USA) per chamber installed at 1.0 m above ground and at 2/3 the height of the chamber. Chamber air temperature was maintained at ambient for CC treatment or set to +5 °C above ambient for H treatment using heating-air conditioning units, and resulting in a +4.8 °C heat treatment over the study period. The below-canopy drought structure used for the drought (D) treatment was constructed using parallel polycarbonate troughs installed at ~1.3 m above the ground and is nearly identical to that described in Pangle et al. (2012). The drought structure was installed on June 1, 2012 and heat treatments became operational on June 11, 2012. For a detailed summary of mean

effect of temperature, vapor pressure deficit, and soil water content difference in treatments from ambient conditions please see Figure S2 in Adams et al. (2015).

Naturally-occurring mature juniper and piñon trees (> 10 cm diameter at breast-height) were selected and assigned to the following treatment groups: chamber control (CC, trees in ambient-temperature OTCs to account for chamber effects), drought (D, trees in the drought plot), heat (H, trees in OTCs maintained at +4.8 °C) and heat and drought combined (HD, trees in heated OTCs and in the drought plot). The sample sizes for this study were N = 3 for both species all treatments.

Photosynthetic measurements

Fully expanded sunlit needles from mature piñon and juniper trees during the second year of experimental warming, drought, and their combination were measured for *in situ* temperature response curves at a range of temperatures (10-30 °C) described below during May 2013 (pre-monsoon) and for *in vivo* A/C_i curve analysis at a range of temperatures (10-50 °C) described below during late July and early August 2013 (monsoon). The order of individuals measured for each response curve was random. Leaf level gas-exchange measurements were conducted using multiple portable open-mode photosynthesis systems (model LI-6400, Li-Cor, Lincoln, NE, USA) with a 2 × 3 cm light source chamber (6400-02B LED, Li-Cor Inc.) and an external CO₂ source for the temperature response and A/C_i curves. Field measurements were limited to morning hours (7:00-9:00 h local time) on south-facing twigs supporting green, turgid foliage. The Li-Cor 6400 systems were inter-calibrated

each day and re-zeroed with fresh Drierite and new soda lime. Measurements were made with leaf temperature controlled to within ± 1 °C of the target temperature. An airflow rate of 300 mmol s^{-1} was used to maintain a significant differential of CO_2 and H_2O concentration between the reference and sample infrared gas analyzers. The light source was set to a saturating photosynthetic photon flux density (PPFD) of $1500 \mu\text{mol m}^{-2} \text{ s}^{-2}$ for measurements of A and to $0 \mu\text{mol m}^{-2} \text{ s}^{-2}$ for measurements of dark leaf respiration (R_D). For each measurement, the tip of the twig was clamped into the chamber and the chamber gaskets were coated with G35 Qubitac Sealant (Qubit Systems Inc., Kingston, ON, Canada) to minimize CO_2 leakage. During all measurements, vapor pressure deficit (VPD) was allowed to vary with conditions inside the cuvette. Measurements were recorded after stability criteria were met for at least 3–5 min. At the end of each measurement day, the projected area and mass of needles enclosed in the chamber were determined.

% Stomatal vs. biochemical limitations on photosynthesis

Farquhar and Sharkey (1982) provided a graphical method to give a relative measure of stomatal limitation (Long and Bernacchi 2003). When a leaf is considered with a certain photosynthetic rate and stomatal conductance at the ambient atmospheric CO_2 concentration, a prediction can be made of the hypothetical A that would be obtained if the mesophyll had free access to the CO_2 in the ambient air, in which $C_i=C_a$. Therefore, to determine % stomatal limitation vs. non-stomatal limitation, the assimilation rate that actually occurs, A , is subtracted from the rate

which would occur if resistance to CO₂ diffusion were zero (A_0), divided by A_0 . These calculations were conducted using *in vivo* derived A/C_i curve data discussed below.

Temperature response curves

In 2013, *in situ* temperature response curves were measured during pre-monsoon season between May 7 (28 day since last precipitation) and 19. Temperature responses were obtained by applying temperature control to leaves that were maintained inside the cuvette for the duration of the gas-exchange measurements. The temperature response of light-saturated photosynthesis was measured on the same set of needles for three trees per species for all treatments. Five measurements were made per needle set at five leaf temperatures: 10, 15, 20, 25, and 30 °C. Measurements were recorded after leaf temperatures had been maintained constant for 20 min. Predawn branch (Ψ_{PD}) and midday branch (Ψ_{MD}) water potentials (MPa) collected on May 22, 2013 are provided in supporting information Table 2-3.

Determination of $V_{C_{MAX}}$ and J_{MAX}

Measurements of the photosynthetic response to varying substomatal CO₂ concentration at a range of temperatures were conducted between July 29 (3 days since last precipitation) and August 9 2013 during monsoon season. Predawn branch (Ψ_{PD}) and midday branch (Ψ_{MD}) water potentials (MPa) collected on July 23, 2013 are provided in supporting information Table 2-3. Five measurements were made per needle set at each of five temperatures, after leaf temperature had been maintained for 20 min: 10-15, 20, 30, 40 and 50 °C. Branches with a southerly orientation were cut

under water just after sunrise and remained underwater during transport to the laboratory to be re-cut under water (< 45 min) and kept underwater throughout the measurement day. Branches were kept under saturating light during transport and between measurements by keeping the branches in full sun during transport and in a greenhouse between measurements. Sample needle sets used for gas exchange measurements had rates equal or higher to fluxes measured *in situ*, suggesting that the photosynthetic capacity of these needles was unaffected by this short-term detachment (<6 hours). This suggests the A/C_i responses reflected the potential photosynthesis on the day of measurement, and were not affected by transient decreases that may have resulted during the day due to photo-inhibition and/or water stress. Each curve consisted of thirteen steps, starting with a concentration of 400 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ and then decreasing to 300, 200, 100 and 50 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ before increasing to 400, 400, 600, 800, 1200, 1400, 2000, and then returning to 400 $\mu\text{mol CO}_2 \text{ mol}^{-1}$. Leaves were allowed to equilibrate for at least 4 min at each step before logging data. After the completion of the A/C_i curve, the light was switched off, and leaf dark respiration $\text{mmol m}^{-2} \text{ s}^{-1}$ (R_D) at ambient CO_2 concentration was measured after being stable for at least 5 min.

The apparent $V_{\text{C}_{\text{MAX}}}$ were estimated from A/C_i curves according to the FvCB model of leaf photosynthesis (Farquhar et al. 1980). The kinetic properties of Rubisco that depend on temperature are Rubisco specific factor, τ (Jordan and Ogren 1984), and K_c and K_o , which are the Michaelis-Menten constants for CO_2 and O_2 ,

respectively. Their temperature functions were based on Bernacchi et al. (2001), as described below for Rubisco at 25°C.

$$K_u(T_1) = 27840e^{[(36380/RT_0)(1-T_0/T_1)]}$$

$$K_c(T_1) = 40.49e^{[(79430/RT_0)(1-T_0/T_1)]}$$

$$\tau(T_1) = 2407.834e^{[(37930/RT_0)(1-T_0/T_1)]}$$

In the above equations, R is the universal gas constant ($8.314 \text{ J mol}^{-1} \text{ K}^{-1}$), T_1 is the leaf temperature (K) (Tenhunen et al. 1976, Harley and Tenhunen 1991) and the reference temperature, $T_0 = 298.15\text{K}$. A similar equation was used to describe the temperature dependence of J_{MAX} .

Leaf area, leaf mass area, C and N content

After gas exchange measurements were completed, leaves were collected for analysis of area, leaf mass per area g m^{-2} (LMA), carbon (C), and nitrogen (N) content. Needle area was determined with an optical area meter (Li-Cor Li-3100). Then needles were oven dried at $70 \text{ }^\circ\text{C}$ for at least 48 h to assess dry mass. Leaf samples were ground and analyzed for %N, %C, C:N, and $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ by the University of California, Santa Cruz Stable Isotope Laboratory using a CE Instruments NC2500 elemental analyzer coupled to a ThermoFinnigan Delta Plus XP isotope ratio mass spectrometer. For accurate N isotope ratio analysis, residual CO_2

gas was removed *via* automated inline trapping. All sample measurements were normalized to in-house standard reference materials that are calibrated against international standards. Precision of all isotope ratio measurements is better than 0.2 per mil AIR and VPDB for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively.

Data analysis

Statistical analyses were performed using the R Programming Language (R Core Team (2015)) and GraphPad Prism version 6.0d for Mac OS X (GraphPad Software, San Diego California USA). Differences for A , V_{CMAX} , and J_{MAX} between the two types of conifer trees in the study, at each temperature within treatment were analysed using independent sample t -tests (two-sided). We also used t -tests for differences in A rates, V_{CMAX} and J_{MAX} within species at each temperature between control and treatments (Table 2-1 and Figure 2-3). t -tests were used to determine how % biochemical limitations within species and within treatments were different at 10, 20, and 40 °C vs. an optimum temperature of 30 °C (Figure 2-2). This was also used to determine how J/V within species and within treatments were different at 10, 20, and 40 °C vs. an optimum temperature of 30 °C. ANCOVA was performed to explore differences for A rates among treatments and temperatures within species. For differences in LMA, %C, %N, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, C:N, $J_{\text{MAX}}/V_{\text{CMAX}}$ ratio, or % biochemical limitation within species between treatments we used ANOVA while t -tests were used for differences between species within treatments.

Results

Temperature response curves

A was generally highest at 15 °C for both species, which we defined as the optimal leaf temperatures during pre-monsoon temperature response curves. Significantly different A rates were generally found at lower temperatures in treatments within and between species (Table 2-1). For a particular temperature, juniper trees had higher photosynthetic rates than piñon trees irrespective of treatment conditions (Table 2-1; Figure 2-1). In particular, differences between piñon and juniper were found to be statistically significant at 10°C ($P < 0.05$), and 15°C ($P < 0.01$) under D conditions, while A for heated trees was significant only at 15°C ($P < 0.05$). Assimilation was highest for needles in the CC treatments both species and at all temperatures. Increasing temperatures substantially reduced photosynthesis of piñon trees under control conditions. However, photosynthesis of piñon trees under D, H, and HD treatments did not change much in response to elevated temperatures. Control juniper trees had higher A rates than trees in the D, H, and HD treatments. Initially, elevated temperatures increased photosynthesis for juniper trees in all treatments until an optimum value was achieved, and then photosynthesis gradually declined. Junipers in CC, D, and H treatments had highest photosynthetic rates around 15 °C, whereas for needles in the HD treatment, the optimum occurred around 25 °C.

Biochemical vs. stomatal limitations

Photosynthesis was limited more by stomata at higher leaf temperatures for both species in all treatments (Figure 2-2). No significant differences were found within species or across treatments, or between species within treatments, at each leaf cuvette measurement temperature. Linear regression showed how stomatal vs. non-stomatal limitations varied within species and treatments across temperatures (Table 2-2, Figure 2-2). The slope of linear regression lines were significantly non-zero for piñon CC ($R^2 = 0.95$; $F = 35.74$; $P = 0.027$) and D ($R^2 = .94$; $F = 33.59$; $P = 0.029$) and juniper CC ($R^2 = 0.95$; $F = 41.67$; $P = 0.023$) and HD ($R^2 = 0.91$; $F = 19.54$; $P = 0.048$) (Table 2-2). Biochemical limitations in droughted piñon at 10°C ($P = 0.046$) and 20 °C ($P = 0.027$) and for heated juniper at 40 °C ($P = 0.029$) were significantly different than the optimum temperature of 30 °C.

$V_{C_{MAX}}$ and J_{MAX}

We determined $V_{C_{MAX}}$ and J_{MAX} (Figure 3-3) estimated from A/C_i curves (Figure 2-S1). Maximum $V_{C_{MAX}}$ and J_{MAX} values were found at 30 °C, which was identified as the optimal temperature during monsoon, in all treatments both species and dropped substantially at 40 °C, with one exception, juniper HD. At 30 °C, $V_{C_{MAX}}$ in piñon was significantly different in CC trees compared to H and HD trees, and J_{MAX} was significantly different in all treatments compared to control trees. There were no significant differences between treatments in juniper at 30 °C for $V_{C_{MAX}}$, and J_{MAX} was significantly different in control trees compared to HD.

We found significant differences between species in V_{CMAX} and J_{MAX} in CC at all leaf temperatures, with one exception for each parameter, 30 °C for V_{CMAX} (Figure 2-3 a and b) and 10 °C for J_{MAX} (Figure 2-3 c and d). Significant differences between species for V_{CMAX} in D and H (Figure 2-3 a and b) and J_{MAX} in D, H, and HD (Figure 2-3 c and d) treatments were found at lower than leaf temperatures.

The $J_{\text{MAX}}/V_{\text{CMAX}}$ ratio (J/V) was generally lowest at 30 °C for both species in all treatments (Figure 2-4). No significant differences were found within species across treatments (ANOVA) or between species within treatments. Likewise, there were no significant differences in J/V for either species at the optimum temperature of 30 °C compared to 10, 20, or 40 °C. The slope of linear regression line was significantly non-zero for needles from juniper under heat ($R^2 = 0.99$; $F = 270.4$; $P = 0.039$; Table 2-2).

Foliar carbon and nitrogen

We found no significant differences in LMA, %C, %N, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, or C:N content of leaves used in gas-exchange measurements on piñon or juniper trees within species across treatments (data not shown). There were significant differences between species across treatments for LMA ($F = 72.83$, $P < 0.0001$). Comparing between species within treatments we found significant differences for %C ($P = 0.015$) and $\delta^{13}\text{C}$ ($P = 0.04$) of needles from trees in the drought treatment.

Discussion

Our temperature response curves show that piñon trees under all treatments are more sensitive to temperature regulation of carbon assimilation than juniper trees (Figure 2-1). As temperature was increased stomata play more of a role regulating assimilation for control and drought vs. heat and the combination of heat and drought in piñon trees, and stomata regulate carbon assimilation less in juniper trees (Figure 2-2). For both species, $V_{C_{MAX}}$ and J_{MAX} were maximal at 30 °C with (control \cong drought) > (heat and the combination of heat and drought) (Figure 2-3). Beyond leaf temperatures of 30 °C, biochemical limitations appear to have a more pronounced impact on photosynthesis in piñon than juniper. $V_{C_{MAX}}$ and J_{MAX} in both species are equally sensitive to temperatures between 10 and 40 °C, and treatments do not seem to change the sensitivity (Figure 2-3 and 2-4).

These temperature dependent patterns of stomatal and biochemical limitations across a range of temperatures that these species regularly encounter diurnally and seasonally (-15 to 35 °C) (Garcia-Fornier et al. 2016) demonstrate the sensitivity of photosynthetic capacity for these two tree species. Piñon and juniper are often compared in terms of their isohydric or anisohydric responses of leaf water potential to changes in soil water availability and atmospheric moisture demand (Linton et al. 1998, Willson et al. 2008, Plaut et al. 2012, 2013, Limousin et al. 2013, Woodruff et al. 2015, Garcia-Fornier et al. 2016). Although embolism resistance should be considered (Garcia-Fornier et al. 2016), our findings for water potential in this study are consistent with iso- versus anisohydric behaviour in piñon and juniper,

respectively. Woodruff et al. (2015) found leaf hydraulic vulnerability was significantly lower in the relatively anisohydric juniper than in the more isohydric piñon. Additionally, *P. edulis* has been shown more vulnerable to drought-induced xylem embolism than *J. monosperma* (Linton et al. 1998; Willson et al. 2008). Here we show how these iso- and anisohydric tree species respond to warming and drought in regards to leaf temperature and photosynthetic capacity; which is, they differ in the amount of control, biochemical versus stomatal, and the way $V_{\text{C}_{\text{MAX}}}$ and J_{MAX} vary with leaf temperature.

The observed rates and patterns of the temperature dependencies of $V_{\text{C}_{\text{MAX}}}$ and J_{MAX} for these two species are generally consistent with numerous studies across many species and plant functional types (Falge et al. 1996, Wang et al. 1996, Walcroft et al. 1997, Hikosaka et al. 1999, Wilson et al. 2000, Bunce 2000, Dreyer et al. 2001, Bernacchi and Long 2003, Werten et al. 2011, Lin et al. 2013). However, the findings of this study improve our mechanistic understanding of how these trees and other needleleaf evergreen trees will respond to future climate conditions and add important components to the well studied and documented gas-exchange mechanisms in these species.

Previous analysis of leaf level gas-exchange in piñon and juniper has demonstrated that juniper can conduct photosynthesis at much lower Ψ than piñon, and demonstrates far more hydraulic acclimation to experimental reduction in precipitation (Limousin et al. 2013, McDowell et al. 2008, Williams and Ehleringer

2000, Lajtha and Barnes 1991), less vulnerability to drought-induced xylem cavitation and embolism (Linton et al. 1998, Willson et al. 2008, Delzon et al. 2010, Plaut et al. 2012, Garcia-Forner et al. 2016), enhanced drought stress recovery through potential refilling of embolized root xylem (Plaut et al. 2013), lower levels of non-structural carbohydrates in isohydric pinyon that push it towards exhaustion of energy reserves for much of the growing season (Woodruff et al. 2015), both species having delayed phenological development and reduced growth with higher temperatures and drought (Adams et al. 2015). Notably, our experiment is the first manipulation of both drought and temperature on mature trees growing in the field to examine the physiological responses of two co-occurring species with contrasting hydraulic strategies. Furthermore, the addition of increased temperature and corresponding impacts on physiological processes are novel, and advance the knowledge of these model global species representing iso- and anisohydric water strategies.

Many current models utilizing the FvCB model of photosynthesis for forest CO₂ exchange assume the temperature response of photosynthesis is constant (e.g. Thornley and Cannell 1996, Williams et al. 1996, Kellomäki et al. 1997, Baldocchi and Meyers 1998, Grant and Nalder 2000, Medlyn et al. 2000). However, $V_{C_{MAX}}$ and J_{MAX} are temperature dependent, and the dependence varies significantly between and within species (Leuning 2002). Our analysis of the temperature response of A (Table 2-1; Figure 2-1), stomatal vs. non-stomatal limitations (Table 2-2; Figure 2-2), and the temperature dependence of the biochemical parameters of photosynthesis, across

treatments highlights how seasonal as well as diurnal temperature variations could affect the photosynthetic response in these trees.

Our leaf N results suggest that variation in photosynthetic capacity between species, among treatments, and across temperatures was due to factors other than leaf N, although previous studies have suggested this variation may be ascribed to differences in leaf nitrogen concentration (Field 1983, Field and Mooney 1986, Leuning et al. 1991, Harley et al. 1992, Kellomäki and Wang 1997, Medlyn et al. 2002b). It is most likely the case that trees of both species in all treatments were limited in their photosynthetic capacity due to *in situ* nitrogen limitations to some extent (Lajtha and Barnes 1991).

Consistent with our first hypothesis, our results show that when leaf temperatures are below their optimal range photosynthesis was more biochemically limited, and above the optimal range photosynthesis became more constrained by stomatal limitations (Figure 2-2). Although not specifically documented in this study, if the relative humidity of the air remains the same, but the air temperature increases, VPD (vapor pressure deficit (kPa); atmospheric moisture demand) will also increase. If the water availability of vegetation remains unchanged, then increased VPD will place a larger tension on a plants' xylem, and depending on the hydraulic regulation (i.e. iso- versus anisohydric behaviour) and embolism resistance (i.e. strength of xylem to avoid cavitation), this will generally lead to increased stomatal limitations as identified in these trees on a diurnal time scale by Woodruff et al. (2015) and

seasonally by Garcia-Forner et al. (2016). Plants that regulate their water content more towards the isohydric end of the hydraulic behaviour spectrum, such as piñon, respond quickly to declining water availability and rising atmospheric moisture demand (increased VPD) by limiting excessively low leaf water potentials by controlling water losses through stomatal closure to avoid cavitation and potential hydraulic failure (Garcia-Forner et al. 2016).

We hypothesized (H2) that within a certain range of leaf temperatures near the optimum, which was defined as 15 °C for pre-monsoon (Figure 2-1) and 30 °C during monsoon, biochemical limitations to photosynthesis would generally match temperature response curve trends with control > (drought \cong heat) > the combination of heat and drought. However, our findings do not support this hypothesis. In piñon, as leaf temperatures increased beyond their optimum range stomata became the more dominant photosynthetic limitation in control and drought trees and in all heated treatments biochemical limitations remained dominant. These trends were further supported in Figure 2-3, which shows maximum $V_{C_{MAX}}$ at 30 °C for piñon in control and droughted trees. Which supports the predictions, and adds to the mechanistic understanding, of evaluated regional models by McDowell et al. (2015) that increased temperature will cause many needleleaf evergreen trees to fall below their predawn water potential mortality thresholds beyond which photosynthesis, hydraulic and stomatal conductance, and carbohydrate availability approach zero. We observed similar trends for juniper in control and the combined treatment of heat and drought, which according to IPCC (2013) projections is the most realistic scenario.

The differences in the patterns between the temperature response curve trends and photosynthetic capacity (Figure 2-1 and 2-3) could have been influenced by the time of year the measurements were conducted i.e. pre-monsoon (28 days since last precipitation, -2.49, -2.45 and -4.61, -4.92 (MPa) for piñon and juniper pre-dawn and midday water potentials, respectively (Table 2-3)) for the temperature response curve trends and monsoon (3 days since last precipitation, -1.72, -2.08 and -3.08, -3.65 (MPa) for piñon and juniper pre-dawn and midday water potentials, respectively (Table 2-3)) for photosynthetic capacity.

Our third hypothesis (H3) was as leaf temperatures increased from below to slightly beyond their optimal range, photosynthesis would be more $V_{\text{C}_{\text{MAX}}}$ limited, and when leaf temperatures are well outside the optimal range photosynthesis would become more J_{MAX} limited. Photosynthetic capacity at 30 °C was most limited by electron transport for RuBP generation, J_{MAX} , in both species and all treatments (Figure 2-4). Outside the optimal temperatures, $V_{\text{C}_{\text{MAX}}}$ was the more limiting biochemical parameter (Figure 2-4), which does not support H3. Our estimates of $V_{\text{C}_{\text{MAX}}}$ are consistent with rates observed in other studies on the same species (Limousin et al. 2013) and J_{MAX} values are consistent with rates observed in other conifer species (Manter and Kerrigan 2004, Wullschleger 1993). Temperature variations in $V_{\text{C}_{\text{MAX}}}$ were identified in a study of *Pinus densiflora* (Han et al. 2004) that are similar to our findings with maximum $V_{\text{C}_{\text{MAX}}}$ rates roughly between 50 and 60 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at temperatures between 25 and 30 °C. However, J_{MAX} values identified in their study were roughly half the values in our trees, and their site received over

three times the precipitation (1597 mm compared to 414mm at the SUMO site) and very similar mean annual temperature (10.3 °C compared to 10.5 °C at the SUMO site). Mean values of $V_{C_{MAX}}$ and J_{MAX} at a reference temperature of 25 °C were 77.3 and 139 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively, and a decrease in the J/V ratio with increasing temperature was observed for seedlings of seven temperate tree species (Dreyer et al. 2001). These results suggest that the temperature sensitivity of $V_{C_{MAX}}$ and J_{MAX} may be somewhat similar across species.

Conclusion

In recent years, drought, insect, and wildfires have ravaged the forests of Southwestern North America at unprecedented scales. In 2009, the state of New Mexico entered a severe record setting drought, which by some measures was the worst the state has seen in more than a century. This followed an intense drought in the early 2000s that caused a massive die-off of piñon trees with mortality rates for mature trees exceeding 90 percent in some locations (Breshears et al. 2005). An estimated 350 million piñons died across the west (Meddens et al. 2012). The difference between the early 2000s and 2009 to 2015 droughts, and that of previous droughts is the more recent droughts are also associated with hotter temperatures (Adams et al. 2009). The period from 2011 to 2013 was the hottest and driest on record since recordkeeping began in 1895 (Cart 2013). The effects of warmer temperatures accompanied with longer droughts in this region on tree mortality could result in a forest ecotone shift. Furthermore, the U.S. Forest Service projects piñons

will most likely disappear from their current range by 2030 (Rehfeldt et al. 2012).

This work shows that these species have different sensitivities to temperature, which can help explain the difference in mortality rates and health of these tree types under current and future warming conditions.

Table 2-1. Carbon assimilation rate (A) of needles at leaf chamber temperatures of 10, 15, 20, 25 and 30 °C for piñon and juniper in control chamber (CC), drought (D), heated (H), and combined heated + droughted (HD) treatments. In all cases asterisks indicate significance from controls (CC) and treatment within species (ANCOVA).

Plus symbols indicate significance between species treatment based on a t -test. Sample size ($n = 3$) for all treatments for both species. Visual representation of these data is provided in Figure 2-1.

Species	Temp °C	CC		D		H		HD	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE
(μmol m ⁻² s ⁻¹)									
Piñon	10	2.60	0.70	0.15 ^{***}	0.15	0.26*	0.22	0.18*	0.29
	15	2.23	0.54	0.32 ^{****}	0.28	0.41 ^{***}	0.07	0.45*	0.35
	20	1.60	0.63	0.31	0.27	0.19	0.12	0.40	0.27
	25	0.34	0.18	-0.02	0.04	0.14	0.04	0.10 ⁺	0.07
	30	0.08	0.07	0.05	0.05	0.00	0.02	0.10	0.13
Juniper	10	3.28	0.05	1.44 ^{****}	0.16	1.29*	0.52	0.41 ^{**}	0.36
	15	3.53	0.15	2.36 ^{*****}	0.27	1.80 ^{****}	0.32	0.90 ^{***}	0.24
	20	3.35	0.78	1.87	0.67	1.70	0.57	1.09*	0.21
	25	2.33	1.01	1.45	0.53	1.14	0.59	1.58 ⁺	0.42
	30	1.53	0.82	0.65	0.35	0.29	0.52	1.19	0.47

* $P < 0.1$

** $P < 0.05$

*** $P < 0.01$

+ $P < 0.1$

++ $P < 0.05$

+++ $P < 0.01$

Table 2-2. Linear regression parameters ($y = ax + b$) for the data shown in Figures 2 and 4, which describe the relationships between % biochemical limitations on photosynthesis and temperature (from Figure 2) and J/V ratio and temperature (from Figure 4). The statistical significance of the non-zero slopes are indicated as: * = $P < 0.1$, ** = $P < 0.05$.

Species	Treatment	% Biochemical Limitation			J/V		
		a	b	r^2	a	b	r^2
Piñon	CC	-1.17**	89.00	0.95	-0.06	4.50	0.24
	D	-1.04**	89.50	0.94	-0.04	3.21	0.47
	H	-0.76*	81.50	0.88	-0.04	4.23	0.66
	HD	-0.30*	77.50	0.83	-0.05	3.85	0.55
Juniper	CC	-0.75**	82.50	0.95	-0.11*	5.62	0.99
	D	-0.39	68.50	0.74	-0.17*	7.69	0.88
	H	-0.80	88.00	0.66	-0.09**	5.19	0.99
	HD	-1.03**	88.50	0.91	-0.09	5.16	0.70

Table 2-3. Predawn branch (Ψ_{PD}) and midday branch (Ψ_{MD}) water potentials.

Species	Treatment	May 22, 2013		July 23, 2013	
		Ψ_{PD}	Ψ_{MD}	Ψ_{PD}	Ψ_{MD}
(MPa)					
Piñon	CC	-2.37	-2.25	-1.36	-2.20
	D	-2.59	-2.54	-1.72	-2.15
	H	-2.56	-2.35	-1.97	-1.94
	HD	-2.44	-2.67	-1.83	-2.05
Juniper	CC	-4.19	-4.76	-1.81	-3.10
	D	-4.67	-5.05	-3.28	-3.83
	H	-4.23	-4.64	-3.43	-3.41
	HD	-5.37	-5.23	-3.81	-4.26

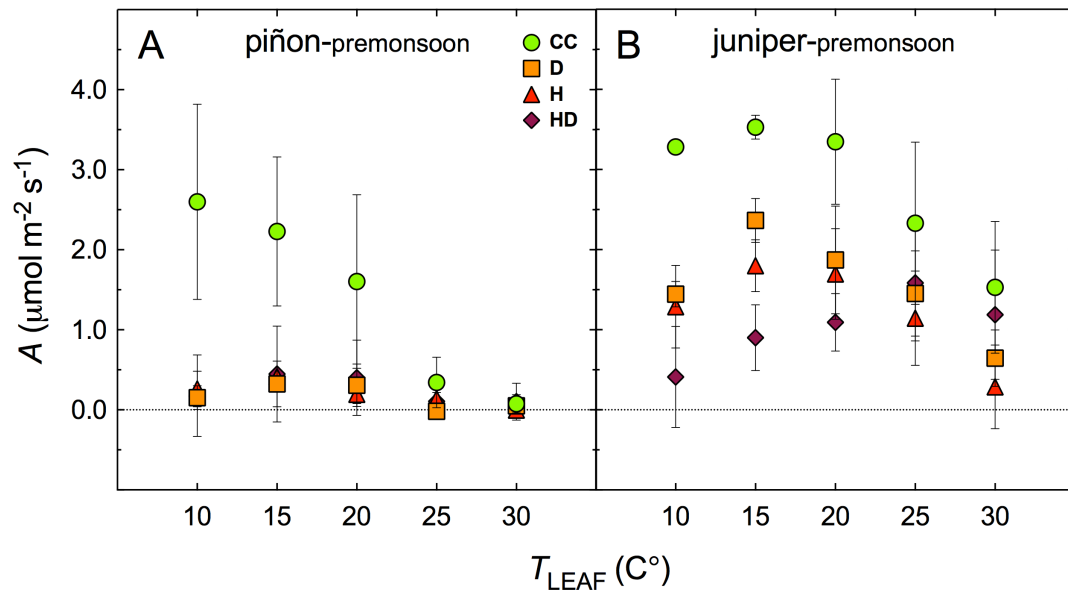


Figure 2-1. The leaf temperature (T_{LEAF}) dependence of assimilation rate (A) in piñon (A) and juniper (B) in control chamber (CC), drought (D), heated (H) and heated + drought (HD) treatments. Error bars show standard errors. Sample size ($n = 3$) for all treatments both species. Statistical results are provided in Table 2-1.

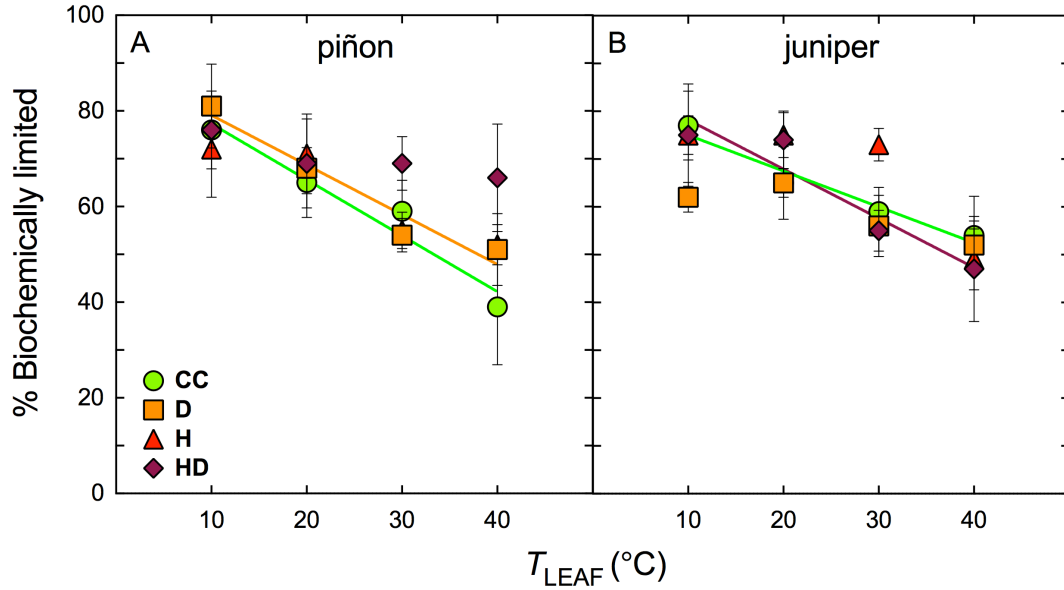


Figure 2-2. Percentage of biochemical limitations on photosynthesis for piñon (A) and juniper (B) in control chamber (CC), drought (D), heated (H) and heated + drought (HD) treatments at leaf temperatures (T_{LEAF}) of 10, 20, 30 and 40 °C. Data are means \pm 1 s. e. for $n = 3$ for all treatments both species. Regression lines are shown for treatments where the slope of the regression line is significantly non-zero at $P < 0.05$. Regression parameters for all treatments and statistical results are provided in Table 2-2.

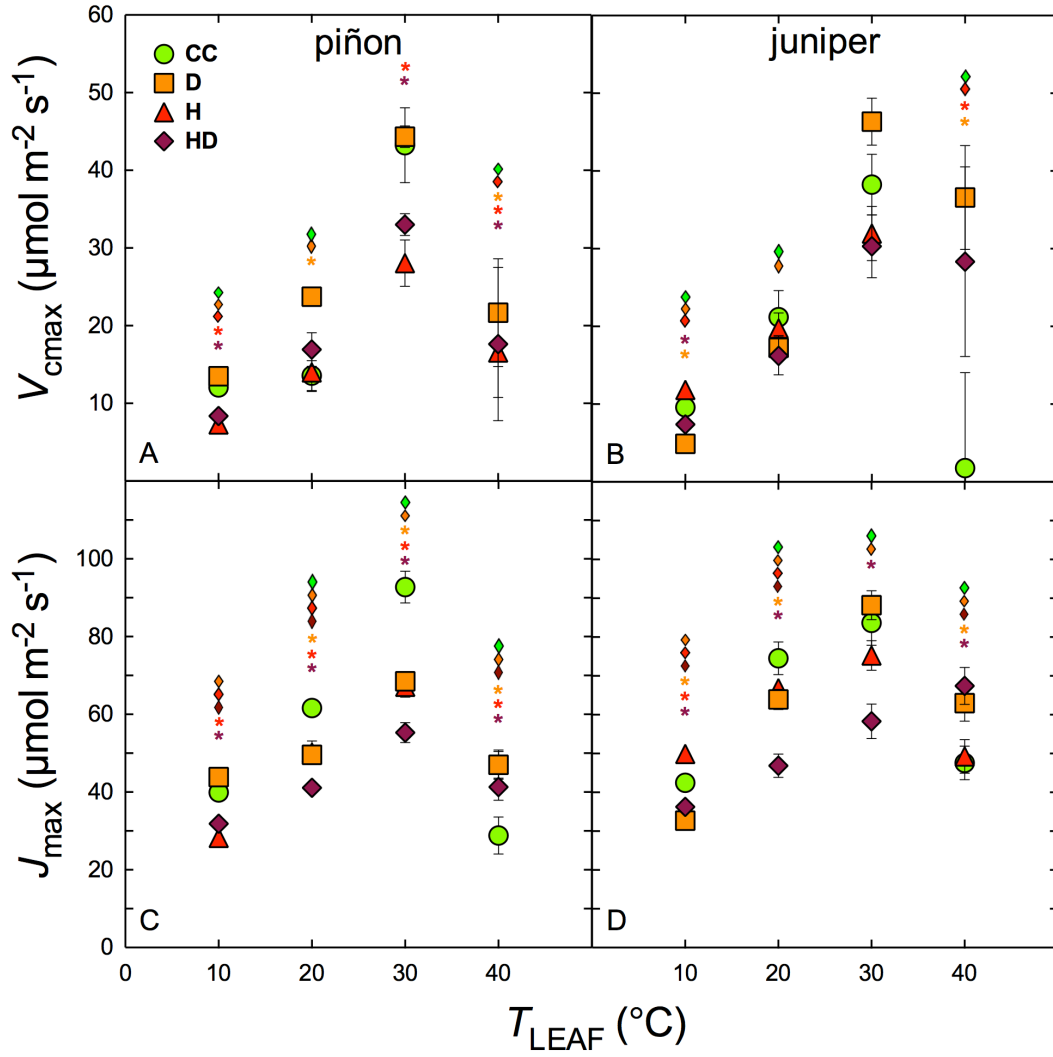


Figure 2-3. The leaf temperature (T_{LEAF}) responses of V_{cMAX} for piñon (A) and juniper (B) and J_{MAX} for piñon (C) and juniper (D) in control chamber (CC), drought (D), heated (H) and heated + drought (HD) treatments 10, 20, 30 and 40 $^{\circ}C$. Asterisks indicate significance between controls and treatment within species ($P < 0.05$, t -test). Diamond symbols indicate significance between species treatment ($P < 0.05$, t -test). Data are means ± 1 s. e. for $n = 3$ for all treatments and for both species.

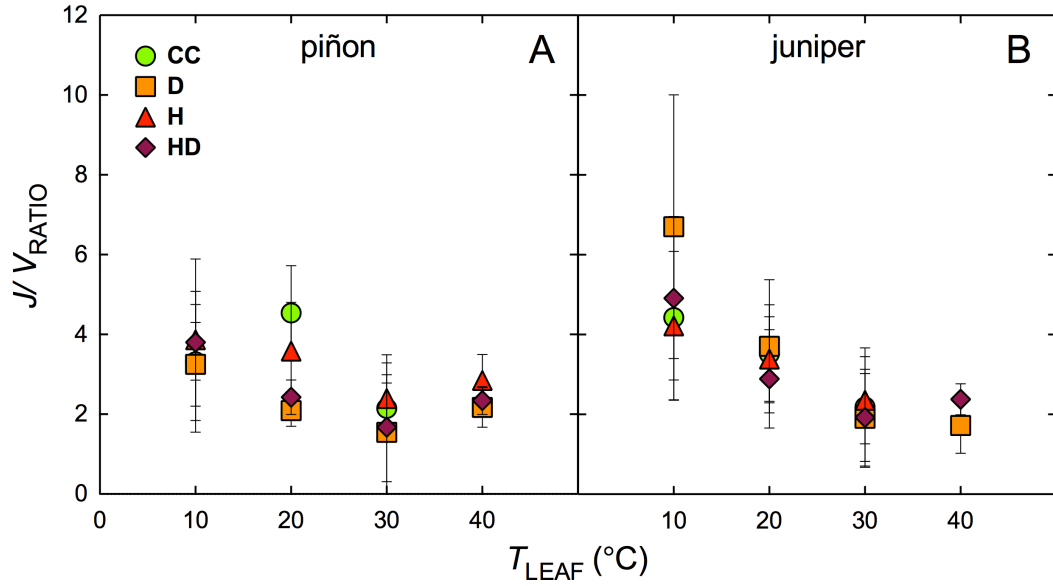


Figure 2-4. The leaf temperature (T_{LEAF}) responses of J_{MAX} to $V_{C_{MAX}}$ (J/V) ratio for piñon (A) and juniper (B) in control chamber (CC), drought (D), heated (H) and heated + drought (HD) treatments at 10, 20, 30 and 40 °C. Data are means \pm 1 s. e. for $n = 3$ for all treatments both species. Regression lines are shown for treatments where the slope of the regression line is significantly non-zero at $P < 0.05$. Regression parameters for all treatments and statistical results are provided in Table 2-2.

Supporting Information

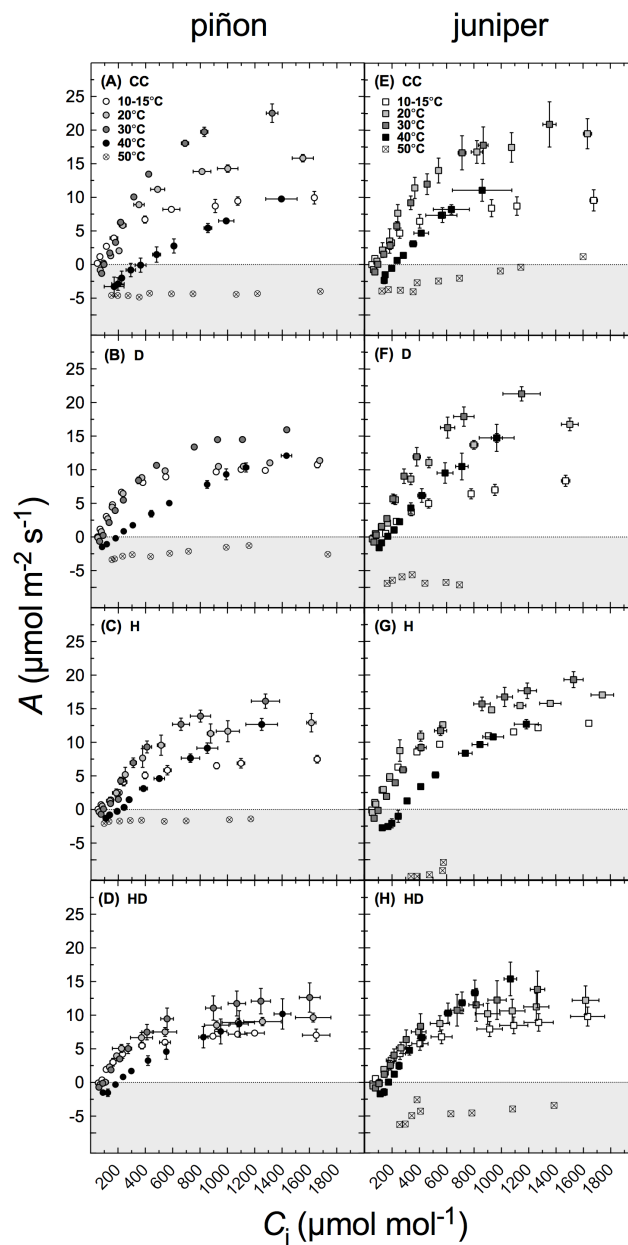


Figure 2-S1. Carbon dioxide assimilation rate (A) as a function of substomatal [CO_2] (C_i) at various temperatures (10, 20, 30, 40, and 50 °C) for piñon (A, B, C, D) and juniper (E, F, G, H) in control chamber (CC), (A & E), drought (D), (B, F), heat (H), (C, G) and the combination of drought and heat (HD), (D, H) treatments.

CHAPTER 3

MANAGED MIGRATION OF COAST REDWOODS INTO OREGON: SUBJECTIVITY OF STAKEHOLDERS IN OREGON'S LAND USE PLANNING COMMUNITY

Abstract

The Earth's climate is changing at a faster pace than the slow natural adjustment rates of most species to their rapidly shifting habitat conditions, especially for long-lived tree species, such as the iconic coast redwood *Sequoia sempervirens*. This may leave some species stranded in less than optimal environments, resulting in population extinctions and/or the need for human-assisted migration. However, the implementation of assisted migration does not come without economic, legal, political, ecological, and ethical issues. One of the most important and complex social questions regarding assisted migration is that of land use planning community in the area being considered. This article explores the subjective beliefs among stakeholder perspectives of the land use planning regarding managed migration of coast redwood trees into suitable habitats in Oregon. Q-methodology was used in this study to structure the complexity of participants' subjective beliefs into a few manageable themes, to reveal broader socio-economic and environmental perspectives and shared ways of perceiving and valuing the relationship between social, economic, and environmental concerns. Due to the unstructured (since there are not yet assisted migration policies to investigate) nature of this study the perspectives evaluated were used to suggest how the stakeholders may or may not support future assisted migration policies. The findings of this study suggest two main factors with each

factor having 2 sides (disagreement and agreement): Factor 1) strong disagreement with conservatism, ecological ignorance and a mechanistic, reductionist worldview seeing land primarily in terms of capability to yield desired goods, and identifying factors that limit production, and the major objective of management is to remove or reduce those limitations, and relationships among different resources treated and thought of as constraints on the dominant use, and strong agreement for values that align on new perspectives of ecological utilitarian values that encompass the complexity of society's concerns including biological diversity, ecological function and balance, product yields, social values, and the beauty and integrity of natural environments with a goal of sustaining the health, diversity, and productivity of land to serve the needs of this and future generations, and Factor 2) strong disagreement with the general multiple use management paradigm and notions of management strategies, scientific knowledge, and technology aimed at producing the traditional multiple uses that can only partially satisfy people's interest in land use and the environment, and strong agreement for values that align from a land based communitarian perspective such as, land is an essential part of our community and we are social animals, part of human and natural communities, linked to past and future generations, and dependent for our well-being on the health of the whole. As an artifact of the unstructured nature of this Q-study, the distribution of respondent perspectives shows a single general grouping of all respondents on the positive side of both defined axes. This convergence suggests ecological awareness and environmental enlightenment as opposed to the view of favoring man's dominion

over nature and this converged axis represents the difference between the dominant social paradigm on the strong disagreement side of the axis, which prioritizes hard-power industrial development over nature preservation and health risks. On the strong agreement side, is that of the New Ecological Paradigm, which stresses risk avoidance, generalized compassion for nature and future generations, limits to growth, and a simple participatory, post-materialistic lifestyle that requires planning and regulation of development. I conclude that the findings of this study suggest the potential for a future successful land use policy promoting managed migration of coast redwoods into suitable habitats in Oregon.

Introduction

The changing coast redwood forest environment: Implications for present and future status and health

Many ecosystems are rapidly being transformed into non-historical configurations that differ in composition and/or function from present and past systems, which is increasingly being recognized as an almost inevitable consequence of environmental alteration and changing species distributions through climate and land use change (Root and Schneider 2006, Harris et al., 2006). Climate change scenarios and species distribution models (SDMs) predict modest to major geographic shifts in the distribution of species over the next century; however, the magnitude of the changes vary depending on assumed emission scenarios and circulation models used, species altitudinal and latitudinal distribution, and on the ability of species to migrate (Douhovnikoff 2011). The response of species to past (Overpeck et al. 2002,

Benton and Twitchett 2003) and recent (Pounds 1999, Parmesan and Yohe 2003, Root 2003) climate change and the fact that the Earth is set to become warmer than any period in the last 1-40 million years (Houghton et al. 2001) raises the concern that anthropogenic climate change could act as a major cause of mass extinctions in the near future (Thomas et al. 2004).

Climate change over the last ~30 years has resulted in numerous shifts in the abundances and distributions of species (Parmesan and Yohe 2003, Root 2003). The Earth's climate is changing at a faster pace than the slow natural adjustment rates of most species to their rapidly shifting habitat conditions (Peters 1985, Davis and Shaw 2001, Hulme 2005), especially for long-lived tree species. Where the bioclimatic envelope changes but there is no immediate biotic response and the abiotic infrastructure remains intact, systems can initially remain as relicts of the historic system (Hobbs et al. 2009). However, low rates of vagility may leave some tree species stranded in less than optimal environments, resulting in population extinctions or the need for human-assisted migration (Jump and Penuelas 2005). Global patterns of forest mortality along the geographic or elevational margins of a tree species or forest type are commonly reported, where trees are assumed to be near the thresholds of climatic suitability (Jump et al. 2009).

Broad-scale changes in forest composition and structure are occurring in many parts of North America owing to changes in temperature (Adams et al. 2009, Allen et al. 2010), hydrological regime (Boyer 1982, Nemani et al. 2003), and increased

occurrences of insect pests and pathogens (Crowl et al. 2008). A recent study of the endemic flora of California by Loarie et al. (2008) suggests species diversity will shift towards coastal areas, particularly in north-west California and under extreme and moderate scenarios the majority of coastal species are predicted to undergo northward range shifts.

California's Mediterranean-type climate is characterized by long summer droughts and it is during these periods water deficits in coastal vegetation is potentially large. Low water availability is considered the dominant environmental factor/stress limiting plant growth, health, and yield (Boyer 1982, Nemani et al. 2003), and drought is the primary factor limiting plant water availability and further reduces growth, survival, and distribution of trees around the globe (Boyer 1982, Allen and Breshears 1998, Engelbrecht et al. 2007). A report from Rehfeldt et al. (2006) suggests that 88% of the western United States will see a turnover in the kinds of tree communities it hosts by the end of the century. Models projecting vegetation cover change over the next 100 years suggest that in western North America needle-leaf evergreen trees will be reduced by approximately 15% and in southwestern North America most needleleaf evergreen trees will be lost (Jiang et al. 2013).

In 2011, California entered a multiyear record setting drought event that set the lowest 12-month and lowest calendar-year precipitation measurements, the most extreme drought indicator values, and the highest annual temperature on record (Diffenbaugh et al. 2015). The drought caused rapid drawdown of groundwater

reserves (Famiglietti 2014, Harter and Dahlke 2014), water use restrictions, fallowed agricultural fields (Howitt et al. 2014), and ecological disturbances, such as large wildfires and widespread tree mortality (Moore and Heath 2015, Worland 2015).

In the conifer forest of the Pacific Northwest, one of the most characteristic and famous components is that of the iconic coast redwood (*Sequoia sempervirens* D. Don (Endl.)), whose current natural distribution is restricted to a narrow (~50 km) belt 900km long from ~42°N to 36°N along the NE Pacific rim (Johnstone and Dawson 2010). Coast redwood is a California Floristic Province endemic, which is the tallest living tree species, attaining heights of 115 m (Sawyer et al. 2000b) and notably long-lived, with some individuals exceeding 2,000 yr in age (Noss 1999). The redwood ecoregion has been identified by the World Wildlife Fund as being in the highest conservation priority class among ecoregions in the U.S. based on biological uniqueness, conservation status, and impending threats (Ricketts et al. 1999, Noss 2000). Redwood National Park is one of 12 natural World Heritage Sites in the U.S. and is also an International Biosphere Reserve.

The redwood region generally has mild cool rainy winters and dry summers with mean daily minimum temperatures in January ranging from 0.4-7 °C and mean daily maximums in July range from 14-30 °C (Lorimer et al. 2009). Temperatures seldom rise above 38 °C or drop below -9 °C. Mean annual precipitation varies along the latitudinal range from 72 cm in some parts of the southern region and more than 200 cm in the northern most part of the range (Sawyer et al. 2000a), but is generally

more than 100 cm (Sawyer 2000a). The northern rainforests that coast redwoods occupy have been considered the southern extent of coniferous forests in the Pacific Northwest (Waring 1979) and identified as ecologically similar to coastal rainforests in Washington and Oregon (Sawyer 2000a).

Coast redwoods and their many associated species are impacted by a variety of stressors, including climate change and a variety of land use practices, which threatens their continued persistence on the landscape. The greatest overall stressor to the ecosystems of coast redwoods is climate change, which exacerbates pre-existing stressors that severely limit ecological function and resilience (Koopman et al. 2014). Increasing emerging threats to tree mortality and frequency of large-scale forest-die backs, which are all linked to climate change, include but are not limited to increased warming and water stress (van Mantgem et al. 2009, Allen et al. 2010), insect invasion and infectious diseases, such as Sudden Oak Death (Metz et al. 2013), more severe storms and heavy downpours potentially causing greater runoff and erosion (Melillo et al. 2011), increased outbreaks of wildfires (Westerling et al. 2011), decreased incidence of fog (Johnstone and Dawson 2010), and enhanced encroachment of invasive species (Sawyer 2000a).

These environmental pressures on the productivity of coast redwoods in combination with physiological mechanisms make this species extremely vulnerable to climate change induced stressors. Despite high levels of genetic diversity (Douhovnikoff and Dodd 2011) and growth performance (Anekonda 1992) this

species appears to not have adapted to environmental gradients at the limits of its range. This has been suggested to be in part due to its predominate asexual mode of reproduction; although large quantities of seeds are generated, their viability is extremely low (Olsen et al. 1990), of short duration (Fritz and Rydellius 1966), and seedlings are extremely susceptible to damping off (Hepting 1971). This results in a lack of recombination that would otherwise allow new adaptive gene combinations to be expressed (Douhovnikoff and Dodd 2011). Coast redwood is a shallow-rooted species, which suggests that it does not benefit from access to stable groundwater reserves and is inefficient at preventing transpirational water loss (Burgess and Dawson 2004). The growth and reproductive physiology are likely to mean that it will be unable to adapt to present and future environmental conditions or migrate into the displaced habitat. Assisted migration therefore may be the only means for coast redwood to allow populations to match new climates.

Bioclimatic models using geographic information system (GIS) can be used to identify current and projected suitable habitats and range distributions (e.g., Rehfeldt and Jaquish 2010, McLane and Aitken 2012, Notaro et al. 2012). Items such as accuracy of future climate predictions, specific species physiological responses, and parameters outside of the data used to develop range distribution maps cause some uncertainty in modeled projections. They do however provide an indication of how climatic conditions will change for a particular site. The state of Oregon is likely to have areas on its coast that will encompass the conditions of the small climatic

envelope required by coast redwoods and are projected to maintain suitable range conditions well into the future (Figure 3-1).

Human assisted migration

Forests cover approximately 30% of Earth's terrestrial surface (42 million km²) (Bonan 2008) and provide numerous social, economic, aesthetic, and ecological benefits across a range of spatial and temporal scales (Bonan 2008, MEA 2005). The goods and services provided by ecosystems to society, or ecosystem services, have been previously examined and divided into four broad categories: cultural services (e.g. recreation, aesthetics); regulating (e.g. water quality, climate control); provisioning (e.g. timber, food); and supporting (e.g. soil formation, nutrient cycling) (MEA 2005), which can all be dramatically altered due to widespread tree and forest death. Assisted migration can potentially minimize economic loss, prevent loss of biodiversity and species extinction, and sustain ecosystem services (Aubin et al. 2011, Ste-Marie et al. 2011, Winder et al. 2011, Schwartz et al. 2012). However, the implementation of assisted migration does not come without economic, legal, political, ecological, and ethical issues (Schwartz et al. 2012).

The level of understanding and willingness to put in place effective policies regarding the preservation of climate change threatened species is far from adequate, which poses a major challenge for management, conservation, and preservation strategies and policies. The location of particular species in particular geographic locations is a key consideration of what to conserve or restore and where, and has

been the prime focus of most conservation practices (Hobbs et al. 2009). Traditional practices of conserving and restoring biodiversity by direct appeal to historical conditions are increasingly being reconsidered in the light of rapid environmental change (Harris 2006, Seastadt 2008, Choi 2008, McClanahan 2008).

For a species to survive the projected climate change in their current ranges they must either tolerate or adapt to the new conditions, or successfully colonize and occupy new areas with suitable conditions. Plant species have a very limited set of options to survive climate-induced potential extinction, which include plastic responses, such as changing their phenology or physiological responses, adapting to the new and changing climatic conditions via selection, or migration (Davis and Shaw 2001). However, the projected rates of climate change will make it difficult or impossible for some species to survive or to move rapidly enough, especially given extensive habitat fragmentation and other concurrent pressures (e.g., Schloss et al. 2012, Zhu et al. 2012).

Therefore the current traditional conservation/preservation methods, such as providing migration corridors and increasing suitable habitat at range margins will need to be supplemented with a more direct, innovative, and adaptive approach (Hunter et al. 2010, Krosby et al. 2010). One such approach is that of managed migration (also called assisted migration/relocation and assisted colonization), which is the intentional translocation of species outside their current habitat in order to reduce anticipated loss of biodiversity (Vitt et al. 2010). Many scientists have stressed

that ignoring or rejecting assisted migration will ‘greatly increase the threat of climate-driven extinction’ (McLachlan et al. 2007). Such decisions will depend significantly on cultural values toward nativeness and exoticism (Higgs 2003), and will involve multiple stakeholders who will not always necessarily agree on the best course of action and will involve cultivating and maintaining a delicate balance between ecological integrity and cultural values, and between ecosystem services and natural processes.

In a recent opinion paper by Hobbs et al. (2009) regarding conservation and restoration of ecosystems the authors suggest:

Decisions about how much conservation and restoration investment is appropriate will depend on shifting cultural values about historic fidelity and ecological integrity, sentimentality about ecosystems of the past, local species diversity, priorities for livelihood and sustainability (i.e. historically faithful restorations versus ecosystem services-oriented projects), and designs for resilience. In many parts of the world, primary motivations for ecosystem management relate more to human survival rather than to considerations of historic fidelity.

Retention or restoration of many historic ecosystems, and/or conserving certain species in their current range is no longer feasible or possible; however, there are species, sites and scenarios where options do exist and are appropriate (Hunter 2007, Hoegh-Guldberg et al. 2008).

Coast redwood is an exemplary candidate species for human assisted migration as defined by Hunter (2007), which can be characterized by three features: their probability of extinction due to climate change, their vagility, and their

ecological roles. However, these biological considerations are just a part of the decision-making process, debate, and social acceptance of assisted migration. Much of the ecological debate can be traced back to fundamental perspectives on nature, and more particularly to the ethical question of whether to deliberately manage natural systems or to allow them to adapt or not on their own (Aubin 2011).

Technical and biological issues are central to managed relocation; however, ethical, legal, and social components pose equally challenging questions about the appropriate use and social feasibility of managed migration (Schwartz 2012). Furthermore, a necessary first step towards the development and widespread success of assisted migration practices is the inclusion of biological considerations in tandem with both social and economic concerns, for which different stakeholders have their own multi-dimensional and extremely complex objectives, metrics and definitions. Consequently, a natural science approach is limited in its capacity and/or unable to answer these questions (Sarewitz 2004). We must therefore turn towards a social science investigation to shed a better light on these types of questions.

Oregon's Land Use Planning Community

One of the most important and complex social questions regarding assisted migration is that of land use policies and regulations in the area being considered. The United States, and in particular the state of Oregon, have historically had an intimate relationship with property rights, environmental discourse and environmental policy (Knapp and Nelson 1992). Both country and state have been sites of dynamic fluxes

in a range of discourses and swings in environmental policy and property rights (Walker and Hurley 2011). The politics of land use planning in Oregon is a subject that holds an intense and passion-filled set of emotions and feelings from a wide group of players. Oregon along with Hawaii, Vermont, Florida, and California are recognized as first-generation planning states, and led what became known as the “quiet revolution,” where the power to control and regulate land use returned partially or nearly entirely to state governments (Knapp and Nelson 1992).

In 1973, Oregon passed the country’s first statewide program for land use planning SB 100 with the initial intention to limit sprawl and protect Oregon’s farmlands, open spaces, and beautiful landscapes (Walker and Hurley, 2011). The bill created the Department of Land Conservation and Development (DLCD) and the Land Conservation and Development Commission (LCDC). The program was designed and intended to “[a]fford all Oregonians predictability and sustainability to the development process by allocating land for industrial, commercial and housing development, as well as transportation and agriculture” (https://www.oregon.gov/LCD/Pages/about_us.aspx). The DLCD administers the program and the LCDC guides the DLCD.

The guiding principles of the DLCD are to: provide a healthy environment; sustain a prosperous economy; ensure a desirable quality of life; and provide fairness and equity to all Oregonians. The DLCD’s mission statement reads:

To help communities and citizens plan for, protect and improve the built and natural systems that provide a high quality of life. In partnership with citizens and local governments, we foster sustainable and vibrant communities and protect our natural resources legacy.

Oregon's seven-member LCDC, adopts state land-use goals and implements rules, assures local plan compliance with the goals, coordinates state and local planning, and manages the coastal zone program.

The LCDC's first major task was to adopt Statewide Planning Goals (Table 3-1), which expressed the State's policies on land use and related topics to govern the development of local comprehensive land use plans. The LCDC accomplished this first task on December 27, 1974. The first goal in the Statewide Planning Goals is that of citizen involvement (Table 3-1). State law requires each city and county to adopt a comprehensive plan that must be consistent with the Statewide Planning Goals, as well as ordinances regarding zoning and land-division to put the plan into effect (Knapp and Nelson 1992). Plans are then reviewed for consistency by the LCDC and if approved become the controlling document for land use in the area covered by the plan.

An unintended consequence of the approved land use regulations was a substantial reduction of private landowner rights. In the first decade after SB100 passed, three different statewide ballot measures (1976, 1978 and 1982) directly challenged the legal power of state regulation in SB100, with all attempts failing. However, twice in the early 2000s the Oregon planning system had near-death

experiences influenced by economic and political shifts in voting populations, which forced land use regulations proponents to concede important legal and conceptual ground to opponents with the passing of measure 37 and 49 (Walker and Hurley 2011). In Walker and Hurley (2011) the authors express concern that:

[M]any in Oregon's planning community continue to attribute the rocky first decade of the 2000s mainly to clever political tactics by opponents (and some tactical errors of their own), while failing to consider possible deeper, underlying sources of political vulnerability.... Oregon's statewide planning system earned the praise it received for limiting the effects of growth (and nearly eliminating "sprawl"), we also find that the SB100 model failed to provide ways to address two inexorable facts of history and society: change and social inequality.... The Oregon planning system did not, however, create mechanisms to adjust to demographic, economic, and ideological change.

Measures 37 and 49 fundamentally altered land use and private landowner rights in Oregon and allowed either compensation from the state for reductions in land value and/or altering the regulation of the land to allow landowners to do what they want with their land. With respect to the politics behind land use policy, two primary levels are available for analysis: the popular level, which helps explain why particular land use policies are adopted at particular locations at particular points in time, and at the interest-group level, which helps explain why land use policies take particular forms and result in particular outcomes. Knapp and Nelson (1992) state:

[The] focus of planning changed from resource conservation and urban growth management to economic development and affordable housing, largely in response to changes in the Oregon economy and to changes in the relative influence of interest groups. This suggests that the general thrust of state planning is determined by the general population

but that specific policy issues are resolved by competition among interest groups.

Hales (1991) suggests the winners in state land use planning were those able to influence state legislatures, agencies, commissions, and courts, which explains the success in protecting environmentally sensitive areas by environmentalists, protecting farmland and forest land by conservationists, and encouraging economic development by industrialists. Groups that did not fare well in their agendas included county governments who wanted to maintain local control, farmers who wanted to develop their farmland, and exclusionists who wanted to zone out lower economic groups (Hales 1991, Knapp and Nelson 1992).

Land use regulation and policies, assisted migration debates and decisions, as well as many other management issues can generally be characterized by limited technical knowledge and disagreement about the goals to achieve. The first step towards finding the appropriate solution is to elicit and identify the subjective beliefs (the way a person experiences things in his or her own mind, based on feelings or opinions rather than facts) behind stakeholder perspectives in order for stakeholders to reach an agreement on goals, or at least on the measures to be taken (Raadgever et al. 2008). The importance of the identification of stakeholder perspectives is further emphasized by Raadgever et al. (2008):

A stakeholder perspective is the cognitive representation that a stakeholder makes of the external reality and his or her position in this reality. It includes the stakeholder's preferences concerning management options, as well as the values, specific interests, and

knowledge that underlie these preferences.... Developing an overview of the different stakeholder perspectives can increase awareness of other perspectives, facilitate discussion and support critical reflection on the rationality behind stated positions. This may result in better mutual understanding and consensus between stakeholders.

This study is focused on the subjective beliefs among stakeholder perspectives involved with land use regulation in Oregon and in particular regarding managed migration of coast redwood trees into the Oregon Coastal Zone (Figure 3-1). A major goal of this research is to provide a first step towards successful managed migration policies and strategy by developing an understanding of the current beliefs, thoughts, and subjectivity of stakeholders in the land use planning community; and particularly by exploring the idea of using managed migration to save the world-renowned coast redwood tree from climate change induced habitat loss, by transitioning it via managed migration into Oregon, which will be identified using Q-methodology (Stephenson 1935).

Methodology

There has been a vast amount of literature regarding the state of Oregon's land use regulation. However, much of the literature was focused on conditions in the early 1970's as well as early 2000's. To fill in this lack of more recent knowledge, the following Q-method-based research procedure was followed. The Q-method is primarily an exploratory technique. It is not a technique to test, support, or prove hypotheses (Watts and Stenner 2005). However, it can bring coherence to research questions that may have multiple, potentially complex and socially contested answers

(Stainton Rogers 1995) and is specifically designed for the direct measurement of an individual's subjective point of view (Brown 1980).

William Stephenson first introduced Q-methodology in his letter to *Nature* in 1935 as an inversion of conventional factor analysis (a process in which the values of observed data are expressed as functions of a number of possible causes in order to find which are the most important). Q correlates persons instead of tests; “[w]hereas previously a large number of people were given a small number of tests, [in Q] we give a small number of people a large number of test-items” (van Exel and de Graaf 2005). The Q-method is capable of exploring the nature of discourses and also has the potential to uncover unanticipated attitudes and patterns of subjective views and attitudes held by a group of people.

Q-methodology systematically identifies groups of individuals with a common attitude structure by seeking patterns of responses across individuals. It is designed to elicit coherent subject positions for controlled comparison (Brown 1980, McKeown and Thomas 1988, Robbins and Kreuger 2000). Respondents' ‘idealized accounts’ or ‘personal discourses’ arise from inductive self-sorting of a range of statements. It also has the capacity to reveal unrecognized or underlying social ‘discourses’ that can represent other agendas associated with an issue. With the goal of ensuring what Armatas et al. (2014) refer to as ‘comprehensiveness and diversity, rather than representativeness or quantity’ the Q-method is ‘intended to identify subjectivities

that exist, not to determine how those subjectivities are distributed across a population?.

Environmental discourses and policy have underlining competing theories and philosophies in regards to the need to be more participatory, just, and inclusive while at the same time dealing with the scope and aim of national, international and global environmental problems and solutions. By and large, the scholarship of land use in the state of Oregon has stressed the differing attitudes of groups of citizens as well as agencies and changes through time of items such as the economy, political ideology, and demography. This study investigates the subjective beliefs among stakeholder perspectives involved with land use regulation in Oregon and in particular regarding managed migration of coast redwood trees into the Oregon Coastal Zone.

Q-Method in Practice

In its most frequent form, the Q-methodological approach follows the general summary provided by van Exel and de Graaf (2005):

[I]n a Q methodological study people are presented with a sample of statements about some topic, called the Q-set. Respondents, called the P-set, are asked to rank-order the statements from their individual point of view, according to some preference, judgment or feeling about them, mostly using a quasi-normal distribution. By Q sorting people give their subjective meaning to the statements, and by doing so reveal their subjective viewpoint. These individual rankings (or viewpoints) are then subject to factor analysis.

Q-sets can be constructed following one of two general paths, structured or unstructured. The selection of Q-statements chosen from the flow of communication,

which is usually developed using a number of sources such as interviews, participant observations, scientific literature, books, newspapers, etc. (called a *concourse*), to be used in the Q-set may or may not be theoretically driven. In structured Q-studies statements are chosen to reflect relevant theoretical themes and an even distribution of these themes that most inclusively summarized the issues identified in the concourse, in unstructured exploratory studies such as this study the Q-set do not rely on strict theoretical perspectives. Hogan (2008) in an unpublished doctoral thesis regarding Q-studies summarized this distinction as:

Guided by Fischer's (1960) experimental design principles, structured Q samples are more systematically composed than unstructured samples. Firstly, the parent concourse is organised into overarching categories of response. The Q sample items are conceptualised theoretically and organised into a factorial framework. Once the main theoretical issues have been identified, a set of statements that cover each of the issues are selected to make it representative of the parent concourse. Such an experimental design procedure provides a reasonable way of selecting the Q sample theoretically. However, not all Q samples can be theoretically conceived a priori to the commencement of the study. Some studies are necessarily explorative in nature and so categories of response cannot be deduced in advance. In these circumstances, unstructured Q samples are utilised.

Unstructured Q-studies include items presumed to be relevant to the issue being investigated and may or may not fit well into predefined thematic groupings. The Q-set includes items that are more broadly representative of the issues in the parent concourse. With unstructured Q-studies, it is possible that some aspects of the investigation might be over- or under- represented, therefore skewing could unintentionally be incorporated into the final Q-set (McKeown and Thomas, 1988).

The methodological process in this study was completed through a series of five steps, which are the general steps of a typical Q-method study and match the summary mentioned above:

- 1) Defining the concourse and creating the Q-set;
- 2) Recruitment of Q-sort participants (P-set);
- 3) Completion of the Q-sort;
- 4) Data analysis; and
- 5) Factor interpretation.

Defining the Concourse and creating the Q-set

A flow of communication referred to here as the concourse was developed using a number of sources: interviews, participant observations, scientific literature, books, newspapers, and audio recordings of recent public meetings. Preliminary interviews were also conducted during a research trip to a two-day public meeting with the DLCD on September 24 and 25th in Astoria, Oregon, and information gathered was used to develop the concourse. One way this study departed from the general Q-method approach was the fact that assisted migration of redwoods into Oregon is not a current issue and does not have policies or potential future policies to construct statements around and is not an issue being discussed or debated. Therefore, the Q-set was specifically chosen and tailored to understand the subjectivity of stakeholder perspectives regarding socioeconomic and environmental issues that would be relevant if assisted migration were a proposed project and had specific

policies to investigate. A list of about 150 statements, which covered a range of values associated with environmental and socio-economic viewpoints of which a subset of these statements were chosen as the final sample of 32 statements to be used as the Q-set (see Figure 3-2).

P-set

The P-set (Q-sorting participants) focused upon recruiting participants from the two leading and most influential land use agencies in the land use planning community in Oregon the DLCD and the LCDC, as well as non-agency citizen interested stakeholders, which were identified as Goal 1 in Oregon's Statewide Planning Goals (Table 3-1).

Completion of the Q-sort

The Q-sort (titled: Oregon Land Use Survey, Figure 3-3) was sent out via email to a set of agency representatives from Oregon's DLCD and LCDC as well as non-agency citizen stakeholders. Each participant was asked to rank order the statements from the Q-set within a predefined distribution of 32 boxes from "least agree" (-3) to "most agree" (+3) in order to ensure that participants utilize the full range of rating positions, respondents compare the statements relative to each other, which decreases the risk of arbitrary or biased sorting, and increases the repeatability of the sort as illustrated in Figure 3-2 (Raadgever et al. 2008).

Further research and the seeking out of any additional subjects to take part in the Q-sorting/survey was conducted during a second research trip to another two-day public meeting with the DLCD on December 3 and 4th in Salem, Oregon. During this second trip an on the spot Q-sorting/survey was developed to entice participants to take part in the survey and avoid the potential lack of email responses (Figure 3-3). Each participant was asked to rank order the statements from the Q-set and then place each individual numbered statement/card onto the Q-board (Figure 3-3). The Q-board required participants to again distribute the cards in a predefined distribution of 32 boxes from “least agree” (-3) to “most agree” (+3).

Data analysis

Both the Q-sort results (email responses and in person card and board sorts P=22 in total) were then entered into the computer program PQMethod2.35 software (available at <http://www.qmethod.org>) (Schmolck 2002). Principle Component Analysis (PCA) algorithm was used to complete a factor analysis of the 22 participant sorts, which was accomplished by entering the participants’ unique distributions into PQMethod2.35 software and rotating factors to identify the best solution using Varimax algorithm (Schmolck 2014). This part of Q-methodology data analysis was summarized well by Raadgever et al. 2008, which states:

This software uses factor analysis to explain as much of the variance among the individual Q sorts as possible in terms of a few scoring patterns called factors. “Factor” is thus the more technical term for “shared perspective” and both terms are used interchangeably. PQMethod maximize[s] the total variance between the factors using

Varimax rotation, and calculate[s] Pearson's correlation coefficients (for forced distribution data) between individual Qsorts and the resulting factors: the factor loadings.

Results are represented by factor arrays, which represent the general viewpoint of all the participants that load onto a particular factor. People with similar views on the topic will tend to share the same factor. The number of factors in the final set of results depends on the variability in the Q-sorts (Ghoochani et al. 2015).

Factor interpretation

The analysis of Q-sorts is conducted using the statistical technique of factor analysis, which simplifies complicated data into overarching patterns by reducing a large number of variables into a smaller set of 'factors', uncovering the latent structure of the dataset. In Q factor analysis is used to identify correlations between persons (as opposed to variables in R Methodological studies) and determines whether a set of people cluster together (rather than a set of variables).

Results

Q-sorting revealed a common base of agreement, as well as two shared perspectives or factors (factor statistics are summarized in Table 3-2). To interpret these factors, factor scores were used, such that the three statements with the highest weighted composites were assigned +3 and the next highest were assigned +2 and so on to -3. Their distinguishing statement sets are shown in Tables 3-3 and 3-4. The converted factor scores were then used to interpret how the statements were ranked

both within and between factors. In each case, the factor is given a label that succinctly summarizes its broader meaning (see discussion section).

Each factor shows a degree of association between land and people and the management of natural resources and the underpinning perspectives of the groups and individuals included in this study, which will be discussed in terms of how these values and subjective beliefs may influence policies regarding assisted migration of coast redwoods into Oregon. The distinguishing statements for both factors are the most significant shared opinions of stakeholders in the land use planning community in Oregon based on the Q-sorts, and are therefore the defining viewpoints. The two-factor solution provided four perspectives for interpretation due to the fact that a factor is defined by both positive and negative loading Q-sorts or viewpoints. The factor scores of respondents are summarized in Figure 3-4. Summarizing the factor scores that load highest and lowest on that factor and then reinterpreting these distinguishing statements through qualitative analysis revealed links between Q-sorters' underlying values an array of distinct socio-economic and environmental perspectives that will guide the discussion.

Discussion

It is argued that the view of nature and the relationship between human beings and nature that each of us holds impacts our decisions, actions, and notions of environmental responsibility and consciousness. With the advent of ecology, all its subfields, and the many scales of investigation utilized, we know far more about the

land than ever before (Pimm 1991, Shrader-Frechette and McCoy 1993). Although we have held tightly to inherited ideas about land and what we expect from it, our understanding of the natural world has matured considerably. Freyfogle (1996) emphasize these points stating:

We realize better how we have eroded its soils, disturbed its biology, polluted its air and water, and degraded its riparian corridors and coastlines. We also know more about ecosystems and cumulative impacts. The message from all this is painfully clear: we are pushing the land too hard. We are expecting too much of it. The health of the land is declining and something needs to change.... The goal—and we are progressing toward it—is to combine ethics and ecology, to develop scientifically justified indicators of land integrity that we can use in determining whether or not a given land use promotes the long-term well-being of the surrounding natural community.

Land-use policies and decisions tend to be multidimensional and complex with complexity here referring to the number and variety of elements and interactions in the environment of a decision making process. When environmental problems confront human decision systems, they are confronted with two orders of complexity and the more complex a situation, the larger number of plausible perspectives upon it—because the harder it is to prove any one of them wrong in simple terms (Dryzek 1997). When you add future scenarios and policies that are less certain, less understood, more debated and/or not yet discussed or considered, as is the case of assisted migration of coast redwoods into Oregon, to this complexity, the level of complexity becomes indefinable. Q-methodology was used in this study to structure the complexity of participants' subjective beliefs regarding environmental responsibility and consciousness to a few manageable themes, to reveal broader

socio-economic and environmental perspectives, i.e. shared ways of perceiving and valuing the relationship between social, economic, and environmental concerns. Due to the unstructured (since there are not yet assisted migration policies to investigate) nature of this study the perspectives evaluated were used to suggest how the stakeholders may or may not support future assisted migration policies.

The findings of this exploratory unstructured Q-study study suggest the stakeholders researched in this study share a level of proenvironmental behavior. For example, in response to statement #2 (Living human beings do have obligations towards future generations) and #32 (Climate change is not caused by humans), a respondent with 40+ years involved as a non-agency representative citizen states:

*[statement] #2 is how I live my life and hope others do also.
[statement #32] Climate change is real and we must address the causes as well as work on mitigation where necessary.*

Another non-land use agency representative states:

My agency is responsible for managing about 17,000 acres of parks and (mostly) natural areas in the Portland Metro region. We have given assisted migration serious consideration, but do not intend to practice it as of yet. Our climate change strategies at present are focused on 1. enhancing resilience at sites; 2 enhancing regional connectivity to facilitate species migration over time; 3. Broadening our genetic source material for plants to include populations further south.

Factor 1 reflects common themes representing strong disagreement with conservatism (i.e. traditional values and ecological ignorance) and positively ranked values that align on new perspectives of ecological utilitarian values (Figure 3-4).

This factor shows a high support for ideas that encompass the complexity of society's concerns including biological diversity, ecological function and balance, product yields, social values, and the beauty and integrity of natural environments. This new perspective of utilitarian values includes a reemergence of earlier philosophical themes of maintenance of nature's balance, resource development without waste, and protection and restoration of the beauty of natural environments (Glacken 1956) with a goal of sustaining the health, diversity, and productivity of land to serve the needs of this and future generations (Kessler et al. 1992), which were identified in high ranking statements in Table 3-3.

This factor also shows strong disagreement with the notions of ecological ignorance and a mechanistic, reductionist worldview, which represent the traditional values of conservatism. These values can be generalized as seeing land primarily in terms of their capability to yield desired goods, and identifying factors that limit production, and the major objective of management is to remove or reduce those limitations, and relationships among different resources were treated and thought of as constraints on the dominant use (Kessler et al. 1992), which were identified in low ranking statements in Table 3-3.

Factor 2 reflects common themes representing strong disagreement with the general multiple use management paradigm and positively ranked values that align on a land based communitarian perspective. This factor shows a high support for ideas that support a land based communitarian perspective such as, land is an essential part

of our community and we are social animals, part of human and natural communities, linked to past and future generations, and dependent for our well-being on the health of the whole (Freyfogle 1996), which were identified in high ranking statements in Table 3-4.

This factor also shows strong disagreement with the notions of management strategies, scientific knowledge, and technology aimed at producing the traditional multiple uses that can only partially satisfy people's interest in land use and the environment. The traditional multiple-use philosophy encompasses two views of land and intertwines both. One view emphasizes the production of valuable commodities, such as fiber, food, water, and minerals, for human use and the other sees public lands as special setting for aesthetic, spiritual, recreational, and educational experiences (Kessler et al. 1992), which were identified in low ranking statements in Table 3-4.

As an artifact of the unstructured nature of this Q-study the distribution of respondent perspectives from the QM survey (Figure 3-4) shows a single general grouping of all respondents on the positive side of both defined axes. This convergence suggests ecological awareness and environmental enlightenment as opposed to the view of favoring man's dominion over nature. Thomas (1992) in a summary of changing attitudes of Americans regarding land and the environment summarizes this transition as:

The definition of resources, products, and services are changing. Societal demands derived from personal nonconsumptive values now rival traditional uses of the public's forest land. These changing values

are altering the multiple-use concept, and interpretations of that concept are expanding. It is clear now that forests are more than trees and that trees are more than timber. It is clear now that wildlife is more than animals to be hunted and that days spent in the woods are more than recreation. It is clear now that public concern over the forest transcends economic analysis and that costs and benefits of forest management decisions involve more, much more, than dollars and cents.

This recognition that human activities are altering the ecosystems on which our existence—and that of all living species—is dependent is transforming our relationship and understanding of the physical environment (Milbrath 1984), and the growing acknowledgement and acceptance of developing and achieving more sustainable forms of development, land use practices, and relationships with nature has been previously defined as the New Environmental/Ecological Paradigm (NEP) (Dunlap and Van Liere 1978). The bold black line intersecting the two defined axes in Figure 3-4 shows the difference between the dominant social paradigm (DSP), which prioritizes hard-power industrial development over nature preservation and health risks and that of the NEP which stresses risk avoidance, generalized compassion for nature and future generations, limits to growth, and a simple participatory, post-materialistic lifestyle that requires planning and regulation of development held by the respondents of the Oregon Land Use Planning Community.

So what does all this mean to the possible future of developing and implementing a successful policy of assisted/managed migration of coast redwoods into Oregon? The diversity of thought required to see, understand, and possibly implement land use policies that will be needed in order to save a species such as

coast redwoods from human caused climate change induced extinction is vast and confusing. It does and will continue to encompass varied ways of recognizing moral worth in other species, ecological communities, and future generations of humans; as well as deep individually held and often inconsistent or changing factors involved in making moral judgments, including background, education, politics, economics, and religion. There is also the need for our long held commitment to individuality and land/property rights to transition to a mode of thought that joins land and people together into a larger community and making it clear that land is an essential part of that community, land and community is far more than their market equivalents, and a proper land use is not just whether or not it makes money for the owner (Freyfogle 1996).

Conclusion

What this study has shown is the values needed are in place in the three dominant groups involved in the land use planning community in Oregon. That is not to say that there are not important groups outside of those included in this study, or that it will be an easy task to accomplish. One important component that this trend towards the new environmental/ecological paradigm that Oregon's land use planning community has shown must always entail is not to diminish the importance of products and services, but instead to treat them within a broader ecological and social context (Kessler et al. 1992), which the land use planning community does. Moreover, land use planning needs to put the human bond with the nature and land in

the foreground, rather than treating it as interesting but unworthy of taking out of the background of planning, which again the groups researched in this study have shown. The take away message from this study is simple: in the land use planning community in Oregon, and in the traditions they carry on, there lies promise and hope for the future of a successful policy to save threatened species from human caused extinction.

Table 3-1. Oregon’s 19 Statewide Planning Goals, which set requirements for the content of land use plans. Goals 1-14 apply to the entire state, while Goals 15-19 focus of specific geographic areas.

Statewide Planning Goals
1. Citizen Involvement
2. Land Use Planning
3. Agricultural Lands
4. Forest Lands
5. Natural Resources
6. Air, Water and Land Quality
7. Natural Hazards
8. Recreational Needs
9. Economic Development
10. Housing
11. Public Facilities
12. Transportation
13. Energy Conservation
14. Urbanization
15. Willamette Greenway
16. Estuarine Resources
17. Coastal Shore Lands
18. Beaches and Dunes
19. Ocean Resources

Table 3-2. Factor characteristics

	F1	F2
No. of defining variables	11	8
Average relative coefficient	0.800	0.800
Composite reliability	0.978	0.970
SE of factor scores	0.149	0.174

Table 3-3. Distinguishing statements for Factor 1–Conservatism (traditional values) versus New Perspectives of Utilitarian Values.

Statement	Rank	z-score
Land is part of a community to which we belong	3	1.68
We have a history of land mismanagement in the United States, which has left us with degraded forests, grasslands, and cities; that legacy requires profound reform	2	1.52
Global sustainable land use serves the needs (for food, energy, housing, recreation etc.) of all human beings living on Earth today and in the future	2	1.48
Research and development, economic growth, and profit are more important than environmental management, pollution prevention, standards of living, education, and equal opportunities	-2	-1.34
Climate change is not caused by humans	-3	-2.04
Land use regulation is preventing economic growth	-3	-2.06

Table 3-4. Distinguishing statements for Factor 2–Multiple Use Management Paradigm vs Land Based Communitarian Perspective.

Statement	Rank	z-score
Living human beings <u>do</u> have obligations towards future generations	3	2.43
Natural resources should be used in a manner that will meet present day needs for resources without jeopardizing the supply of resources for future generations	3	1.64
Land use regulation should safeguard timber resources to secure future supply	2	1.29
Goal 4 of the Oregon Statewide Planning Goals addresses issues related to “maintain[ing] the forest land base and [protecting] the state’s forest economy”. I see preserving and dedicating land to managed migration of coastal redwood trees as being in direct opposition to Goal 4	-2	-1.45
It would require the adoption of a new statewide planning goal regarding preserving land for managed migration in order for any agency in the land use planning community to really have an influence	-2	-1.28
Lands and their natural resources should not be consumed by humans and should instead be maintained in as close to “pristine” form possible	-3	-1.97

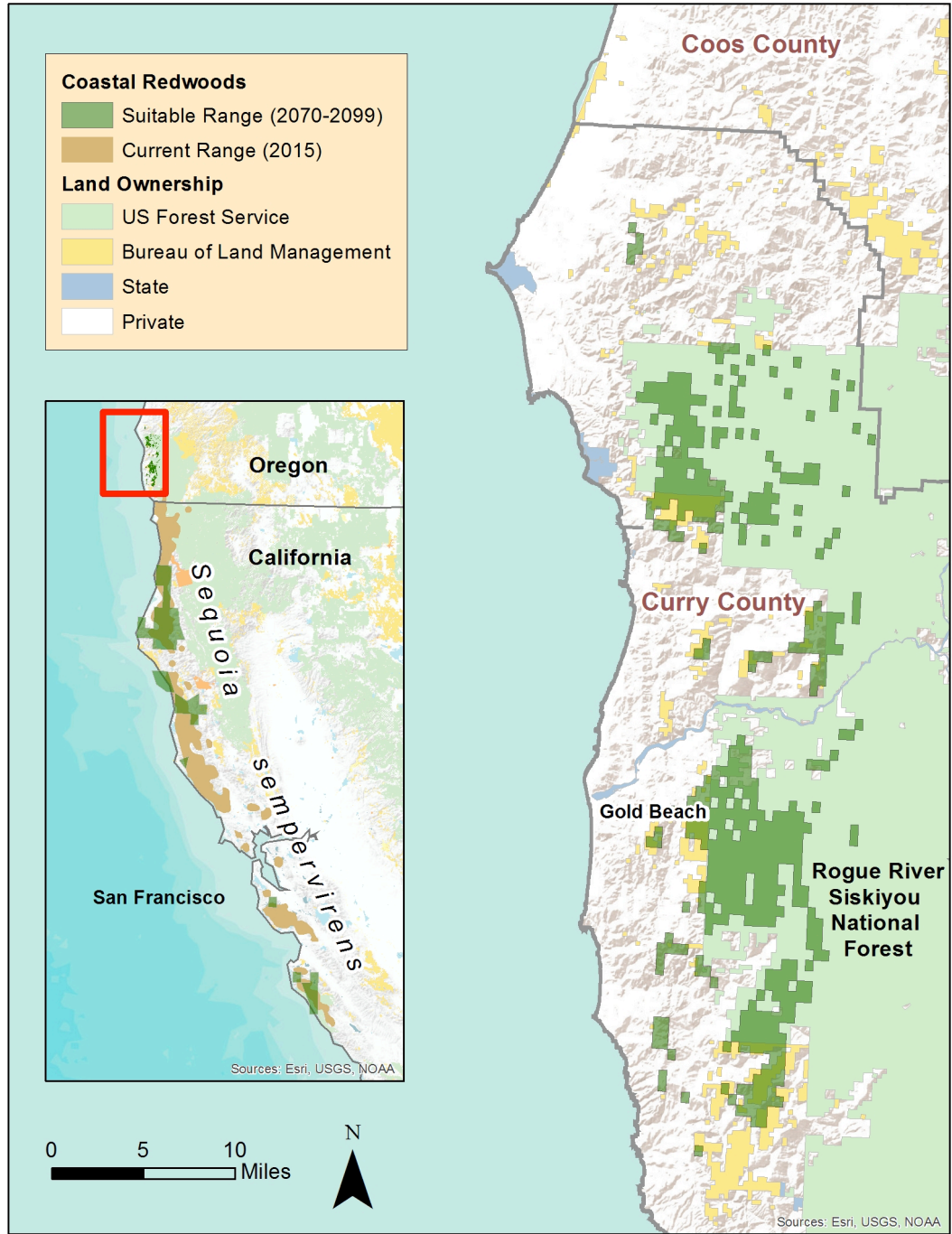


Figure 3-1. *Sequoia sempervirens* (coast redwood) future habitat suitability. GIS data sources: ESRI base map. Current range from Save the Redwoods League.

Oregon Land Use Survey:

Managed Migration of Coastal Redwood Trees into the Oregon Coastal Zone to Save the Species from Climate Change Induced Habitat Loss and potential extinction

This study is being conducted as a component of a doctoral dissertation and has been given approval by the Office of Research Compliance Administration at the University of California, Santa Cruz which guarantees the protection and identity of survey participants through Federalwide Assurance #FWA00002797. Please allow approximately 30 minutes to complete.

Steps:

- 1) Please read through *all* 32 statements below to gain familiarity and confidence with the content. You will recognize that many of the statements do not pertain specifically to redwood trees or managed migration. However the statements are specifically tailored to gain an understanding of respondents' feelings and perspectives regarding social theories that are related to land use ethic and managed migration.
- 2) As you are reading, it is recommended you take notes regarding which statements you "most agree" with, are "neutral about", and "least agree" with. This will help you in completing Table 1. When you are ready, proceed to the table and type in the number (#) of the statement that best fits on the spectrum of "least agree" to "most agree". You may only provide one response per statement.
- 3) Please fill out the Demographic Information as it provides context for the sort.

-----Step 1. Please read through the statements-----

#1. We have a history of land mismanagement in the United States, which has left us with degraded forests, grasslands, and cities; that legacy requires profound reform.

#2. Living human beings do have obligations towards future generations.

#3. Dedicating areas of land in the Oregon Coastal Zone for the preservation of coastal redwood trees via managed migration and restricting logging or other deleterious land uses in the future will create many great life long jobs for Oregon residents.

#4. Land use regulation is preventing economic growth.

#5. It would require the adoption of a new statewide planning goal regarding preserving land for managed migration in order for any agency in the land use planning community to really have an influence.

#6. The current level of forest protection is inadequate.

#7. Global sustainable land use serves the needs (for food, energy, housing, recreation etc.) of all human beings living on Earth today and in the future.

#8. Land is part of a community to which we belong.

#9. Standard of living, community, and equal opportunities are more important than profit, economic growth, protection of natural resources, and pollution

prevention.

#10. Land use regulation should ensure that negative environmental impacts of logging are controlled to acceptable levels of risk.

#11. Public lands are "special settings" for recreational, spiritual, aesthetic, and educational experience. Preserving and protecting land areas and saving threatened species through managed migration will enhance the great social rewards of these "special settings".

#12. Land use regulation should safeguard timber resources to secure future supply.

#13. Lands and their natural resources should not be consumed by humans and should instead be maintained in as close to "pristine" form possible.

#14. Local governments should have the authority to adopt laws to protect natural resources, which by-pass the need for State regulatory approval. An example could include a law which facilitates the managed migration of plant species northward due to threats to their current habitat resulting from climate change.

#15. Land is a commodity that belongs to us.

#16. Protection of natural resources, pollution prevention, and environmental management are more important than economic growth, profit, standards of living, and equal opportunities.

#17. To preserve and maintain agricultural land through farm zoning should not include preservation land to save trees from potential extinction from a changing climate.

#18. Saving threatened species from the next great extinction event should not be restricted through state land use regulations.

#19. Human activity has produced the global warming we are witnessing and the consequent pressure on many species, necessitating that we intervene in ways that may help save species from extinction.

#20. I love nature and wilderness but a successful and thriving economy is more important and will actually protect nature and wilderness more than restrictions and regulations.

#21. The value of the environment is in the goods and services it can provide to people.

#22. Natural resources should be used in a manner that will meet present day needs for resources without jeopardizing the supply of resources for future generations.

#23. Citizens should have the opportunity to engage in managed migration of coastal redwood trees on the land they own.

#24. In 2015, Oregon's Land Conservation and Development Community's Strategic Plan stated its goal to "Develop a "non-resource lands" policy that is integrated with resource lands protection strategies, including consideration of carrying capacity, environmental and habitat protection, infrastructure requirements and availability and other factors. There are currently no standards to guide counties in identifying and zoning non-resource lands". I believe dedicating protected land for managed migration to save coastal redwood trees from extinction should be included in such a "non-resource lands" policy.

#25. Forest land should be maintained to provide long-term economic opportunities for timber and logging activities.

#26. The American Planning Association's 2002 Growing Smart Legislative Guidebook explains, "States and communities across the country are slowly, but increasingly, realizing that simply responding to natural disasters, without addressing ways to minimize their potential effect, is no longer an adequate role for government." Land use regulation should include means to prevent loss of species such as the coastal redwood *Sequoia sempervirens*, which is arguably the tallest living organism that has ever existed on Earth and one of the most massive, because biodiversity loss and species extinction are natural disasters.

#27. Research and development, economic growth, and profit are more important than environmental management, pollution prevention, standards of living, education, and equal opportunities.

#28. Policies should be in place that promotes sound pre- and post-logging site evaluation to ensure best management practices for a healthy future ecosystem.

#29. Goal 4 of the Oregon Statewide Planning Goals addresses issues related to "maintain[ing] the forest land base and [protecting] the state's forest economy". I see preserving and dedicating land to managed migration of coastal redwood trees as being in direct opposition to Goal 4.

#30. The focus should not only be on saving a species or on the land itself, but equal thought should be given to those who use the land and live on it.

#31. It will not be possible to save all species threatened by climate change, but efforts should be made to save the coastal redwood *Sequoia sempervirens*.

#32. Climate change is not caused by humans.

-----Step 2. Main sort of statements-----

			#				
			#				
		#	#	#			
		#	#	#	#		
	#	#	#	#	#	#	
	#	#	#	#	#	#	
#	#	#	#	#	#	#	#
#	#	#	#	#	#	#	#
	-3	-2	-1	0	+1	+2	+3
	Least Agree			Neutral			Most Agree

*****Step 3. Demographic information*****

Please explain your choice of placement for one or two statements that you thought were particular noteworthy by providing the number (#) of the statement and a short explanation:

Please state your profession / livelihood / land use agency you are most involved with:

How long have you been residing in Oregon? _____

What county do you live in? _____

Do you live in an Urban Growth Boundary, farm/agricultural land, other? _____

Please state your gender and age: _____

Please state your political affiliation: _____

Thank you for participating in this survey! Please send this completed and saved document back via email to:

Michael W. Jenkins, mwjenkin@ucsc.edu

Figure 3-2. Q-survey.



Figure 3-3. (clockwise from upper left): Public meeting with the DLCD on September 24 and 25th in Astoria, Oregon; public meeting with the DLCD on December 3 and 4th in Salem, Oregon; Q-sorting/survey board.

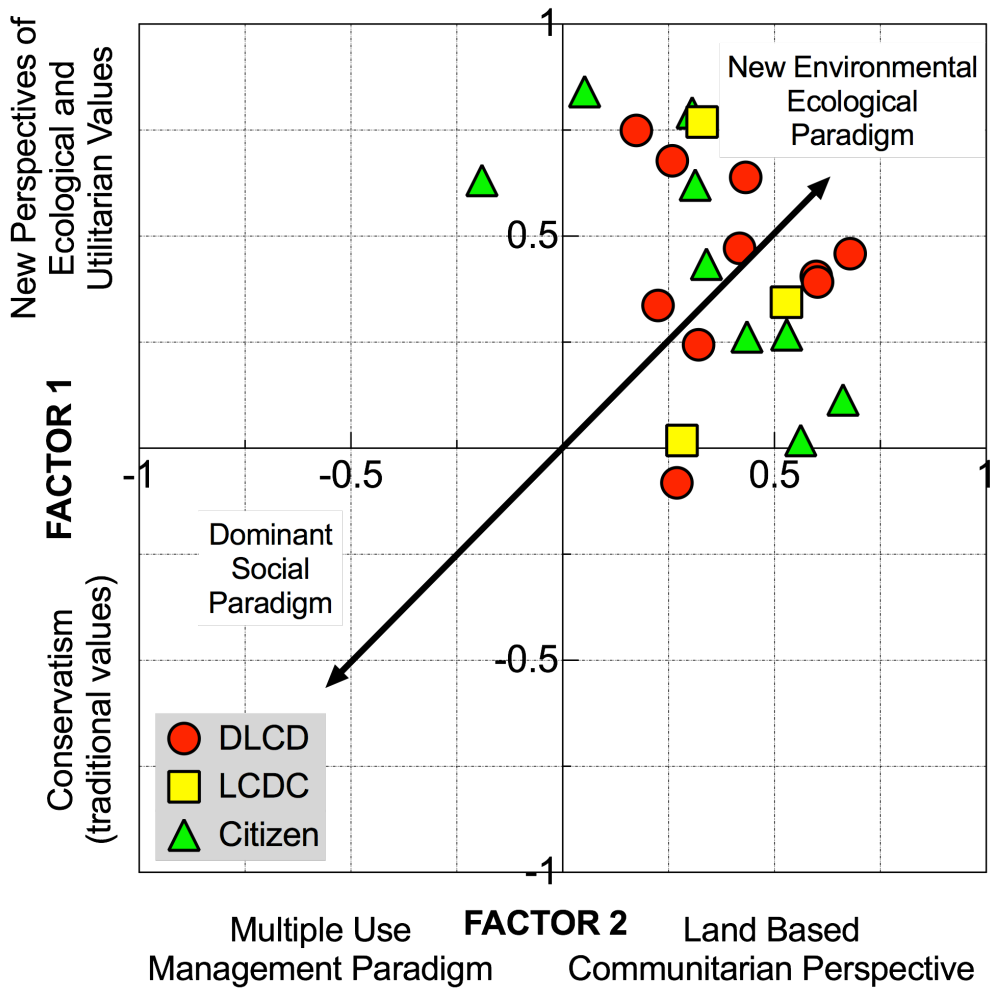


Figure 3-4. Axes of environmental enlightenment and socio-economic perspectives of Dominant Social Paradigm (DSP) and New Environmental Paradigm (NEP).

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