Title

Plant functional traits and resource economies describe plant strategies and performance in a semi-arid shrubland

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Plant Functional Traits and Resource Economies Describe Plant Strategies and Performance in a Semi-Arid Shrubland

DISSERTATION

submitted in partial satisfaction of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

in Ecology and Evolutionary Biology

by

Gregory Edward Vose

Dissertation Committee:
Professor Travis E. Huxman, Chair
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2021

DEDICATION

To my parents who sowed in me the seeds of curiosity.

To my friends, family, and community who have offered so much support through the years.

Most of all, this work is for my wife, without whom this would not have been, and to whom I am forever indebted.

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I am the product of the support of so many – friends, family, mentors, and students who have lent their hands and minds in aid of my progress along the trail. I could write a book for each of you, but time is fleeting, and it will have to wait.

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Peer-Reviewed Publications

3. Funk J. L., J.E. Larson, **G.E. Vose**. 2021. Leaf traits and performance vary with plant age and water availability in *Artemisia californica*. Annals of Botany. 127:495-503 https://doi.org/10.1093/aob/mcaa106

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Technical Reports

1. **Vose, G.E.** 2015. Data report: vegetation survey at avian point count stations along Pine Flat Road in northern Sonoma County, California. ACR Tech. Rpt. 2013-3-1 http://egret.org/scientific_contributions

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Abstract of the Dissertation

Plant functional traits and resource economies describe plant strategies and performance in a semi-arid shrubland

By

Gregory E. Vose

Doctor of Philosophy in Ecology and Evolutionary Biology

University of California, Irvine, 2021

Professor Travis E. Huxman, Chair

Functional traits are defined as those having a direct impact of plant fitness, mediating the interaction between species and environments. Thus, they have become an important tool for understanding resource allocation strategies in individuals in the face of a changing climate. Economic models of carbon, nitrogen, and water use have significantly advanced our understanding of the constraints on plant trait strategies, placing plants on a continuum of fast to slow resource use and short to long tissue life span. While economic spectra have been developed for different plant tissue types, less is known about the coordination of resource economies across tissue types and how coordination may impact performance. This is especially true when considering roots for which recent work has described a multidimensional trait framework. Additionally, it is not clear how dynamic these trait strategies may be in response to endogenous (i.e., ontogeny/age) and exogenous (i.e., plasticity to environmental heterogeneity) factors. The coastal sage scrub plant community of Southern California offers a ripe testing ground for questions of resource use as plants from this community have adopted diverse sets of traits and trait responses to manage the region’s pulse-driven water availability. To this end, I investigated 1) aboveground and belowground trait coordination, and 2) shifts in xylem anatomy due to age and differential rainfall. I found aboveground traits ran along an expected fast to slow economic spectrum while roots occupied a two-dimensional trait space. Furthermore, root traits explained variation in the performance metrics of growth and stress tolerance while aboveground traits only explained variation in stress tolerance, suggesting discoordination between tissues. In examining trait responses to differential water availability, we found xylem traits in the shrub *Artemisia californica* were plastic with respect to age and watering treatment. In general, xylem traits became more conductive as plants got older and under higher water availability, with convergence in trait values as plants aged and in water abundant scenarios. These changes in xylem anatomy established strong potential conductivity trajectories and point to the importance of xylem trait plasticity during establishment. These changes will be important to consider under future precipitation regimes as they may impact plant function and ultimately population age structure. Understanding resource use economies in drylands provides evidence for the mechanisms controlling plant establishment and community assembly and structure, information valuable for earth system modeling and land management.

INTRODUCTION

The central questions in ecology include: Where are species located? What are their abundances in these locals? And why is this so? Traditionally, scientists have tackled these questions by looking at species identity, which led to a proliferation of the role of evolutionary history and biological diversification in ecological questions (Swenson et al. 2010, Hawkins et al. 2014). However, in recent years there has been a focus on using functional traits to quantify the differences between species through describing the niche space they occupy (Chase and Leibold 2003, Violle et al. 2007). To this end, functional trait frameworks have been useful in characterizing the organismal physiology and strategy (Sperry 1986, Lachenbruch and McCulloh 2014, Díaz et al. 2015a, Onoda et al. 2017a) that impacts population (Huang et al. 2016) and community dynamics(Lavorel and Garnier 2002, Huang et al. 2016) and ecosystem-level processes (Diaz and Cabido 1997, Chapin et al. 2000, Cadotte et al. 2011).

A well-developed area of functional trait ecology has been to understand how plants respond to the environment including resource allocation strategies and trait coordination (Diaz and Cabido 1997, Wright et al. 2004a, Poorter et al. 2012, Reich 2014a, Díaz et al. 2015a). This literature has traditionally been dominated by “easy-to-measure” leaf and aboveground traits (Westoby 1998, Cornelissen et al. 2003, Wright et al. 2004a) while “hard-to-measure”, integrated life-span or root and stem traits have been less frequently studied (Mommer and Weemstra 2012a, Mccormack et al. 2014). The integrated traits have been long understood to be a challenge for plant biologists (i.e., on what time-scale should we consider the optimizing behavior of stomata? (Cowan 1978)), but this is especially surprising for the latter issue, since organs like roots compose plant’s dominant acquisitive surfaces for water and nutrients. While established trait spectra propose that aboveground strategies mirror whole plant and belowground strategies, few studies have tried to confirm this assumption and ones that have presented conflicting results (Freschet et al. 2010a, Liu et al. 2010a, Bowsher et al. 2016, Kramer-Walter et al. 2016a).

Stem trait strategies have also been understudied, but recent work has recognized the importance of their anatomy and resulting physiology for plant fitness and strategy (Chave et al. 2009, Baraloto et al. 2010, Poorter et al. 2010). Comprising the main plant water transport system, structural and storage tissues, stems are multifunctional and their traits may define a stem economic spectrum driven by wood density and moisture content (i.e. dense wood with low moisture as opposed to low-density wood with high moisture) (Baraloto et al. 2010). An important feature of economic models is that resources are finite and allocation of these resources necessarily establishes trade-offs in plant strategy (i.e. there are costs to a trait strategy)(Bloom 1986). For example, plants that make dense wood cannot also have high moisture content in their wood. A uniquely important trade-off exists concerning stem fluid transport as efficiency comes at the cost of safety (Gleason et al. 2016). While larger xylem vessels, with cheaper construction costs, allow for more efficient water conductivity, and thus supply to photosynthesizing leaves, they are also more likely to cavitate (i.e. fill with air and become non-functional) at relatively less negative xylem tensions encountered during occasional water stress (Markesteijn et al. 2011).

This trade-off in stems becomes more consequential when one considers perennial shrub species of the semi-arid Southern California ecosystem with highly variable inter- and intra-annual precipitation regimes (Yang et al. 2008). With strong variability in water resources, we might expect to see strong interspecific variation in water-use strategies including in stem traits involved in water transport (Pivovaroff et al. 2015). While interspecific variation is important, recent work has found that intraspecific trait variation, through genetic differences and plastic responses, may represent a large portion of community trait variation, especially in species-poor communities (Siefert et al. 2015). In these cases, plasticity may provide a mechanism for perennial species to acclimate to local environmental conditions, thus increasing their fitness (Borges 2009). Indeed, xylem and wood traits can be plastic in response to changes in environment (Noyer et al. 2017), but underlying mechanisms and patterns among species are lacking (Fonti and Jansen 2012). Additionally, since anatomical and physiological traits can impact plant performance by mediating water fluxes that impact productivity (Poorter et al. 2010) and reproduction (Poorter et al. 2008) and through managing vulnerability to cavitation (Markesteijn et al. 2011), this plasticity may be important in altering plants' location on the efficiency-safety spectrum with consequences for individuals and ultimately communities.

Here I present 2 projects that aim to answer the following questions:

1. **How are above- and below-ground traits coordinated in a coastal sage scrub plant community across a range of apparent species strategies for performance in the environment? Are above- and belowground traits aligned with traditional economic trait spectra with plants falling on a**

fast/slow continuum? How do major axes of trait variation explain variation in growth and stress tolerance?

2. **Are stem anatomy traits of *Artemisia californica* plastic in response to variation in rainfall and as a function of age and how does variation in anatomy relate to potential plant performance?**

CHAPTER 1

Belowground traits describe growth and water use strategy and are uncoordinated with aboveground traits in a semi-arid shrub community

ABSTRACT

Functional trait frameworks have been useful in understanding plant traits and their contributions to plant strategies. Recent work has used these traits to establish global spectra of trade-offs between plant growth, resource acquisition, and lifespan. However, questions remain as to how these trait spectra are organized across tissue type and how robust they are water limited systems. Here we looked at how above and below ground tissues are correlated within and among tissue types, and compared trait syndromes to growth and water use strategies.

We examined above and below ground traits in 22 coastal sage scrub forbs, grasses, and shrubs in Southern California. We used correlation analysis to determine trait trade-offs, ANOVA to determine differences in functional type, linear regression for trait spectrum comparison, and principal components analysis to determine the major axes of variation and their relationships to growth and water use efficiency.

Many trade-offs exist and together define fast to slow axes above and below ground. We found expected strong correlations between specific leaf area (SLA), mass-based photosynthetic rate (A_{mass}) and percent leaf nitrogen (N_{leaf}) following LES trends. We observed fast to slow growth trade-offs between functional types with forbs and grasses adopting fast strategies and shrubs demonstrating more conservative ones.

Roots were defined by 2 dominant axes of trait variation across species - the first was defined by the slow to fast trade-off, while the second was defined by differences in resource allocation patterns suggesting differences in coordination between above and below ground traits.

Understanding trade-offs in this water-limited environment may help uncover the mechanisms related to establishment, community assembly and structure, and species distributions. Land managers especially could use these data to understand the species' realized niche space and integrate this into restoration practices.

INTRODUCTION

A primary goal in ecology is to understand species strategies, what traits characterize these strategies and how they trade-off in ways that reveal evolutionary processes (Raunkiaer 1934, Grime 1979, Westoby 1998). Economic spectra have been useful to this end by using traits as proxies for resource allocation strategies and in explaining global patterns in morpho-, physio-, phenological trade-offs while exploring biophysical constraints on plant form and function (Bloom 1986, Reich et al. 1997, 1999, Wright et al. 2004a, Violle et al. 2007, Freschet et al. 2010a, Kimball et al. 2011, Reich 2014a, Kramer-Walter et al. 2016a, Larson and Funk 2016a). These patterns have been described within tissue types, predominantly at a global scale, for leaves, wood, and roots (Wright et al. 2004b, Chave et al. 2009, Reich 2014b, Freschet et al. 2017). However, trait relationships have shown to be complex, with trait-specific scale-dependent variance structure (from metamer to community) (Messier et al. 2017), and influenced by abiotic factors (Wright and Sutton-Grier 2012, Kramer-Walter et al. 2016a) and community composition (Funk and Cornwell 2013a). Furthermore, few studies have linked tissue types to determine if strategies are unified across an organism. Whole plant economic spectra have been proposed (Freschet et al. 2010a), along with some between tissue type coordination (Méndez-Alonzo et al. 2012, Silva et al. 2018), but these relationships remain understudied, especially between above and belowground tissues where trade-offs may be structured differently due to differing environmental pressures. In this paper, we examine trait tradeoffs within and between leaf and root traits for a group of 22 species in a Mediterranean ecosystem along the southern California coast. We test for relationships amongst traits along plant strategy axes of relative growth rate and water use efficiency.

Leaves are the primary organ for capturing light and converting that energy into sugar for use in metabolism, biomass production, and defense. The leaf economic spectrum (LES) (Wright et al. 2004a) identified global patterns in how species allocate those resources that suggest broad leaf trait trade-offs along an acquisitive to conservative resource-use strategy axis. Plants on the acquisitive end of the spectrum construct inexpensive tissues, with short leaf lifespans that maximize carbon gain on a short time scale, while conservative species produce more costly, longer-lived tissues that produce returns on a longer time scale. This continuum describes plant fitness strategies with acquisitive plants having high growth rates making them better competitors and conservative plants having longer lived stress tolerant tissues. (Grime 1974). Carbon, nitrogen, and more recently water (Reich 2014a), have traditionally defined this spectrum and explained broad patterns of variation between species, however, these global trade-offs have been altered, or disappeared entirely, when studies examine climate, scale, and/or community structure. I. J. Wright et al., 2005 found species at drier climates had 3 times greater A_{mass} for a given LMA (log scale) while climates with higher MAT/PET/irradiance had flatter N_{mass} by A_{mass} relationships. Including genetic and ontogenetic drivers of phenotypic variation may further complicate trait relationships, calling into question the “one species, one trait value” assumption (Wright and Sutton-Grier 2012, Messier et al. 2017, Funk et al. 2021a). Lastly, community structure may also change LES trade-offs as deciduous and evergreen species occupy fast and slow ends, respectively, of an economic spectrum defined by leaves and stem hydraulic traits (Méndez-Alonzo et al. 2012). This, coupled with a Funk & Cornwell, 2013 study which found LES trait relationships were determined by leaf life span (LLS) and that they were not as stong when variation in LLS was low, suggests that community type may determine whether LES trait relationships exist, especially when environment is a strong driver of LLS.

Roots are ecologically important on several fronts – water and nutrient acquisition surfaces, anchoring, and symbiotic relationships with soil microbes – yet their trait relationships remain understudied as compared to leaf and, to a lesser extent, stem traits (Mccormack et al. 2014). However, recent work has sought to develop a root economic spectrum (RES) with varied success. Larson & Funk, 2016 found evidence of an RES that explained variation in RGR in a southern Californian shrubland, while another study found grassland and savannah species with different photosynthetic pathways and belowground microbial associations had correlations between respiration and several fine root traits (Tjoelker et al. 2005). Other studies have found correlations between SLA and belowground traits suggesting the presence of an RES (Freschet et al. 2010b, Liu et al. 2010a, Kramer-Walter et al. 2016a, Bergmann 2020) however, describing above and below ground analogues can be problematic (Mommer and Weemstra 2012b, Weemstra et al. 2016b). Several studies have found that root traits may be coordinated along multiple dimensions (Kramer-Walter et al. 2016a, Ma et al. 2018). Kramer-Walter et al., 2016 found root tissue density (RTD) explained variation along the fast slow axis that ran parallel to SLA and LES, while an orthogonal axis was defined by specific root length (SRL) and root diameter (RD) along a soil fertility gradient. Further, higher SRL and thinner roots were found in more resource deficient soils, contrary to what would be expected if SRL were an analogue to SLA, thus describing variation along a fast/slow continuum. In a review and meta-analysis, (Weemstra et al. 2016b) did not find a one dimensional resource economy for tree roots and ultimately advocate for taking a multidimensional approach for several reasons; 1) the soil environment is heterogenous with patchy nutrient/mineral distribution and greater number of resources that roots must uptake; 2) above and below ground trait analogues actually function in very different ways with different pressures; 3) mycorrhizal associations may alter root traits as functionality is shifted to the micro-organism (also Bergmann, 2020).

We assume plant tissue-specific economic spectra are coordinated such that internal resource supply chains are consistent with respect to acquisition, production, and waste. If these links exist, we expect the strength of their relationships to be related in part to their environment, with resource scarce environments having tighter relationships as variation in potential trade-offs is narrowed, along with niche space, leading to canalized trade-off axes (Westoby and Wright 2006, Cornwell and Ackerly

2009, Dwyer and Laughlin 2017a, 2017b). Stem and leaf traits have been linked weakly (Silva et al. 2018) and robustly (Méndez-Alonzo et al. 2012) along economic axes in seasonally dry tropical forests and also coordinated in support of the hydraulic segmentation hypothesis (Pivovaroff et al. 2014). However, many of the root and leaf coordination studies have found differing results. (Freschet et al. 2010a) found evidence of a whole plant economic spectrum linking leaves, stems, and roots, but the study was confined to the tundra. A study across arid and semi-arid northern China found correlations between SRL and SLA suggesting between tissue coordination, but results were mixed with some sites having correlation coefficients with apparent opposite signs if statistically insignificant (Liu et al. 2010a). Aridity can also lead to intraspecific trait dis-coordination, in one case leading to fast above ground traits coupled with slow below ground traits (Welles and Funk 2020). Looking at sites across a resource gradient in New Zealand (Kramer-Walter et al. 2016a) found that while SRL and SLA were not correlated, RTD and SLA were. A multidimensional approach to root traits may lead to more nuanced understanding of root/leaf relationships (Weemstra et al. 2016b). Lastly, leaf /root coordination may be altered by plant functional type – herbaceous species would be expected to occupy the fast end of the spectrum, but deciduous perennials may have dis-coordinated root and leaf traits if leaves are short lived, given leaf trait variability is determined largely by LLS (Funk and Cornwell 2013a).

The Coastal Sage Scrub plant community of Southern California provides a unique study system in which to examine economic models of resource allocation, with a climate shaped by infrequent precipitation pulses and strong seasonality and interannual variability (Cleland et al. 2016). Importantly, CSS communities are diverse, including a wide range of plant types, from herbaceous annuals and perennials to deciduous and evergreen woody species making it a promising venue to explore how environmental variation influences trait strategies (Liu et al. 2010a, Funk and Cornwell 2013a, Messier et al. 2017). Studies in coordination of resource economies have highlighted communities with a seasonal dry period in tropical dry forests (Méndez-Alonzo et al. 2012, Silva et al. 2018), but our system is also comparatively dry during the wet season with a mean of 36.66cm precipitation/per year (Crompton et al. 2005). Plants here have adopted primarily three strategies for coping with an extended hot dry-season including stress-tolerance, stress-avoidance, and escape. Stress-tolerant plants have developed traits that allow them to persist through dry periods such as leaves with high water use efficiency and low vulnerability to cavitation (Jacobsen et al. 2014, Blumenthal et al. 2020, Ocheltree et al. 2020) while root strategies are less understood with some studies surprisingly finding greater root mass and thin roots with high SRL in stress tolerant species from low resource environments while RTD was coordinated with the LES (Mommer and Weemstra 2012b, Kramer-Walter et al. 2016a). Stress-avoidance strategies include species with deep roots that access water and alleviate stress through the dry season and may also include phenological adaptations, such as summer deciduousness, that may relieve plants from the transpirational demand during the hot dry summer(Jacobsen et al. 2008). These species are expected to have shorter LLS (<1yr) than might be expected for evergreen perennial shrubs which may lead to discoordination between above and below ground carbon economies and absence of LES trait relationships (Funk and Cornwell 2013a). Escape strategies are typified by annuals which grow and reproduce when conditions are favorable and lie as dormant seeds during the stressful period. That all these strategies exist in this community suggests species are likely to experience different pressures above and below ground and throughout the year that manifest in diverse traits, however, overlap between strategies may lead to convergent trait suites muddying economic spectrum relationships.

In this study, we measured traits of commonly occurring coastal sage scrub species to address the following questions: 1) Are above and below ground interspecific trait correlations in this plant community organized along a “fast/slow” continuum as described by traditional economic spectra and do these tissue types function separately as coordinated trait suites that describe trade-offs in growth and water use strategy and plant functional type? 2) Do interspecific trait correlations exist between above and below ground traits such that they are organized along a “fast/slow” continuum and do these tissue types function together in coordinated trait suites that describe trade-offs in growth and water use strategy and plant functional type (Wright et al. 2004a, Reich 2014a, Díaz et al. 2015a, Kramer-Walter et al. 2016a)? With a mixture of functional types, and thus supposed variation in LLS, we expect leaf tissues to reflect global trade-off patterns of LES; we expect roots to be multidimensional, reflecting the diverse pressures of the below ground environment, but the main axis of variation will reflect the “fast/slow” continuum (Wright et al. 2004a, Kramer-Walter et al. 2016a). Further, we predict perennial species will occupy the slower end of these spectra, and conversely annuals will be faster, as tissues in perennials are typically longer-lived, and more conservative, than in annuals. However, drought deciduousness in some perennials may shift leaf tissue placement on the continuum representing a faster strategy.

Species may have similar strategies above and below ground to optimize resource acquisition and use, however, differential selection filters above and below ground may lead to discoordination across the plant body, especially in drought deciduous perennials which are expected to have longer lived roots given their relatively short-lived leaves. We expect the fast/slow trade-off to be reflected in species PC score position along fast to slow RGR and WUE.

Understanding how plants in a Mediterranean ecosystem allocate resources above and below ground will shed light on the potentially divergent selective forces operating on different tissue types in plants from a semi-arid plant community.

Materials and Methods

Field Measurements

Our common garden was located in an agricultural field surrounded by native vegetation at the Irvine Ranch Conservancy's native seed farm (33°44'30.20"N, 117°44'5.33"W), west of Loma Ridge, in Irvine, California. The native seed farm is used to generate seed and plant material for local restoration projects. It consists of native species grown from field-collected seeds, with perennial species planted every few years and annual species planted annually. The 12.5 acre farm has a Mediterranean climate with mean annual precipitation of 33.6cm (Crompton et al. 2005), falling mostly from Nov to April, and mean annual temp of 18.4C from 2000 - 2021(data from National Weather Service, Irvine, CA, USA). However, data presented in this paper were collected during a 500-year historic drought in California, when mean annual precipitation and temperature was 16.05 cm and 18.89 °C in 2013, 30.1 cm and 18.9 °C in 2014, 21.41 cm and 20.56 °C in 2015. The drip irrigation system was turned on a few times during each growing season to keep plants alive during the drought. The native seed farm consists of well-tilled, homogenous soil. Plants were grown in 200-ft. long, 4ft. wide beds with 1.5ft. furrows on either side oriented along an approximately north south axis.

In 2013, we measured physiological traits (Table 1.1) on 3-5 replicate individuals of 13 species (Table 1.2). Mass based photosynthetic rate (A_{mass}) and stomatal conductance(g_s) were measured with infra-red gas analyzers (IRGA) (LI-COR 6400, LI-COR Inc.) during peak growing season on March 20, 2013. Measurements were taken on fully expanded sun-exposed leaves. The IRGA chamber environment was set to 400umol mol^{-1} [CO2] at saturating PAR 1800 umol m^{-2} s^{-1} and leaves were allowed to equilibrate for 2 – 5 mins. Relative humidity was kept between 50% - 65% and flow rate between 300 and 500 umol s^{-1}, adjusted as needed to maintain humidity levels. We maintained temperature control using the sensor head block that was set to 25ºC. Leaf area was visually determined or approximated from leaf width and data were area-corrected. Instantaneous water use efficiency was calculated as iWUE = A_{area}/g_s. To compare trait values with the LES A_{area} was transformed using the conversion A_{mass} = A_{area} x SLA.

Table 1.1. List of measured traits, their symbols, and transformations.

Physiological/Morphological Variable	Units	Transformation
A_{mass} = mass based net assimilation rate	umol C m^{-2} s^{-1}	$\log_e$
g_s = stomatal conductance	mol H_2O m^{-2} s^{-1}	none
N% = leaf nitrogen content	g g^{-1}	$\log_e$
SLA = specific leaf area	cm^2 g^{-1}	$\log_e$
WP = midday leaf water potential	MPa	$\log_e$
Height = height of plant	cm	$\log_e$
RD = root diameter	mm	none
RMF = root mass fraction	g g^{-1}	none
R_{mass} = root growth rate	g day^{-1}	none
R_{length} = root elongation rate	cm day^{-1}	$\log_e$
SRL = specific root length	cm g^{-1}	$\log_e$
FRR = fine root ratio	g g^{-1}	none
N_{up} = root nitrogen uptake rate	g day^{-1}	$\log_e$
RTD = root tissue density	g cm^{-3}	$\log_e$
RGR = relative growth rate	g day^{-1}	$\log_e$
WUE = water use efficiency (carbon isotope discrimination	Δ, ‰	none

Table 1.2. Description of which species were contained in each data set along with invasive vs native, and functional type

Species	Native/ Invasive	Functional Type	Leaf Data?	Root Data?	Growth Data?
Acmispon glaber	N	Shrub	X	X	X
Artemisia californica	N	Shrub	X	X	X
Avena barbata	I	Grass		X	
Brassica nigra	I	Forb	X	X	X
Bromus diandrus	I	Grass			X
Bromus madritensis	I	Grass		X	X
Deinandra fasciculata	N	Forb	X	X	X
Encelia californica	N	Shrub	X	X	X
Eriogonum fasciculatum	N	Shrub	X	X	X
Erodium cicutarium	I	Forb			
Escholtzia californica	N	Forb	X	X	
Isocoma menziesii	N	Shrub		X	X
Leymus condesatus	N	Grass	X	X	
Lupinus succulentus	N	Forb			X
Medicago polymorpha	I	Forb		X	
Malacothrix saxitilis	N	Forb	X	X	X
Phacelia cicutaria	N	Forb	X	X	
Plantago erecta	N	Forb			X
Salvia apiana	N	Shrub	X	X	X
Salvia columbariae	N	Forb	X	X	X
Salvia mellifera	N	Shrub		X	X
Stipa pulchra	N	Grass	X	X	X

The height and width of adult plants was measured, as was distance from the ground to the beginning of the canopy. Canopy volume was calculated by subtracting the distance to the canopy from height and then multiplying height by the widths and assuming a cube shape for the plants. Midday water potential was taken using a pressure bomb (PMS; Corvalis, OR) on 3/20/2013 between 10:00 and 13:00. SLA in 2013 was determined using 5-10 leaves from adult plants using a LI-3100 leaf area meter. Leaves were then dried at 65C and weighed to determine biomass. Three dried leaves were ground (ACMGLA leaves were pooled into a single samples due to low biomass harvest) and tissue was analyzed for %N, %C, C:N, along with d13C for integrated water use efficiency estimation.

Root measurements

Due to the difficulty of collecting below-ground trait data from plants growing in the field, we measured seedling root traits for 18 species (Table 1.2) on potted plants at Chapman University (Orange, CA). Seeds were germinated in petri dishes and transplanted to pots between Jan 6 and Feb 5 where they were grown for 28 to 56 days depending on species and then harvested. Details of the methods can be found in (Larson et. al 2016).

Growth Measurements

In Fall 2014, we established four rows of plants in which seeds of 16 species (Table 1.2) were sown in monocultures in 3 replicate 3-m-long blocks. Seeds of all species were collected from multiple (15-20) distinct, intact natural areas across Orange

County, and were mixed together in bulk. The species were seeded by hand on Nov. 20, 2014, just before the first germination-triggering rain event of the growing season on Nov. 29, 2014. Each species was planted in two rows on either side of the bed. Two nails were placed 1 m apart in the middle of each seeded areas to designate the sampling area. The number of days that it took for seeds of each species to germinate was determined by counting seedlings every two to three days, starting on Dec. 5, 2014, 6 days after the rain. Subsequent watering at the site was kept to a minimum to simulate natural conditions, but had to be done twice because it was a dry year. All species sampled each year represent dominant coastal sage scrub shrubs, forbs, and grasses with 2 exotic grasses and 1 exotic forb (Table 1.2).

To determine relative growth rate (RGR), four plants were sampled for each species during the 2014-2015 seasons approximately bimonthly at 5-7 time points. Fewer sampling dates were recorded for plants that senesced earlier. Leaf area was measured as above and plants were separated by tissue type – roots, stems, leaves, and flowers – and dried at 65C to determine biomass for the respective tissues. RGR was determined using the slope of the line obtained from plotting the natural log of the mean total biomass at 4 time points beginning at germination.

Statistics

Data were checked for normality and outliers, identified using boxplots, were removed. We used mean trait values for each species log transforming variables to meet distribution and variance assumptions for parametric statistical methods (Table 1.1). To identify patterns of trait covariation within (Hypothesis 1) and among

(Hypothesis 2) aboveground and belowground tissues, we used Pearson's product moment on all bivariate mean trait trait combinations. To understand how this community's trait structure may be influenced by phylogeny, we used Pagel's λ and Blomberg's K to estimate phylogenetic signal in each trait (Pagel 1999, Blomberg et al. 2003, Revell 2012). Both models use Brownian motion combined with branch lengths to compare against null models of evolution and estimate phylogenetic signal. To account for phylogenetic non-independence between species, we ran phylogenetic independent contrasts (PIC) on all bivariate trait combinations (Hypotheses 1 and 2). We then used linear regression with the intercept fixed to zero to determine slope relationships between trait pairs. In order to examine how traits may be coordinated with one another we used principle components analysis to determine dominant axes of trait variation in aboveground and belowground tissues (Hypothesis 1) and for the whole plant (Hypothesis 2) separately. To avoid traits with large values or high variance from dominating the PCAs, data were centered at zero and scaled to have unit variance. Axes were retained if eigenvalues were > 1. To account for phylogenetic non-independence we also ran phylogenetically PCAs (pPCA) following (Hypotheses 1 and 2) (Revell 2009, 2012). We then used linear regression to plot RGR and WUE, considered here to be emergent traits, respectively against the retained species position along meaningful principal component axis for each of the PCAs and pPCAs (i.e. aboveground and belowground (Hypothesis 1), and whole plant (Hypothesis 2)).

To determine how axes of variation separated functional groups (annual forbs, grasses, or native shrubs) in trait space, we used one-way ANOVAs followed by TukeyHSD tests to determine differences between functional groups along each meaningful PC axis. Not all traits were collected for all species, so a functional group was only included in the ANOVA if 2 or more species from that functional group were represented.

Results

Above-ground trait correlation and coordination

We observed many strong significant correlations within above-ground traits including those predicted by established trait spectra and aligning with the “fast” to “slow” strategy continuum (Fig. 1.1.).

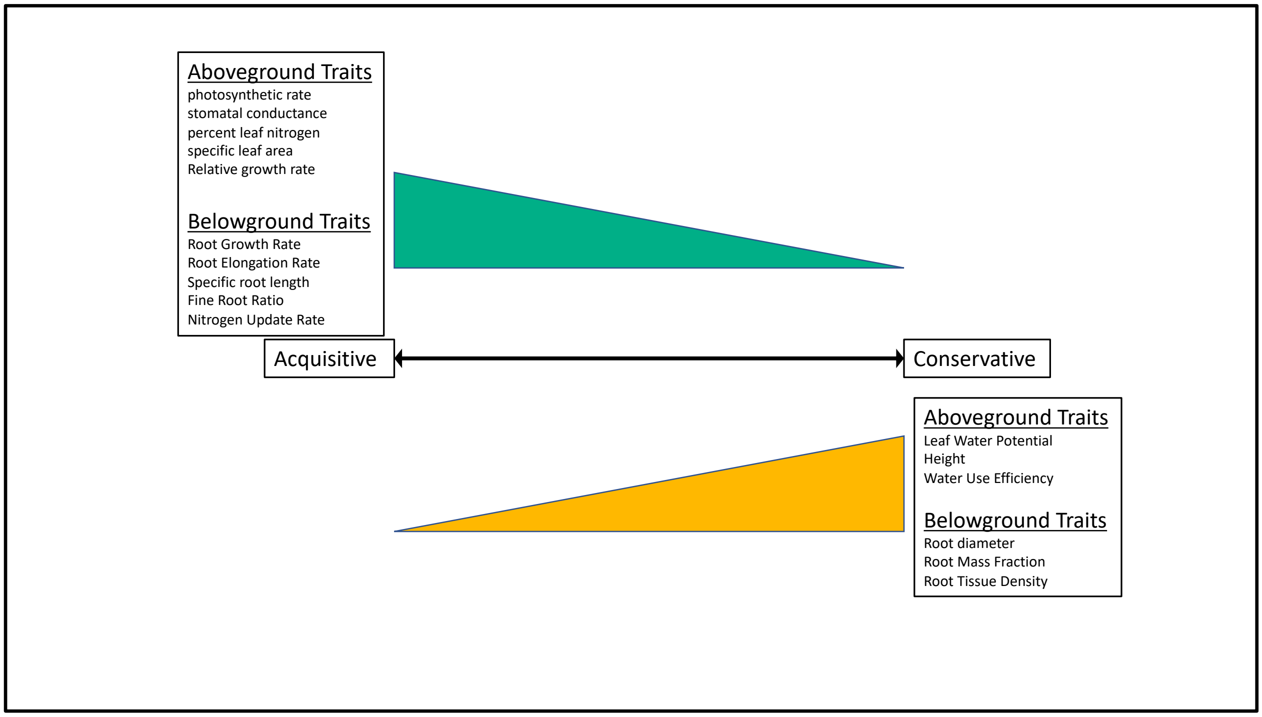
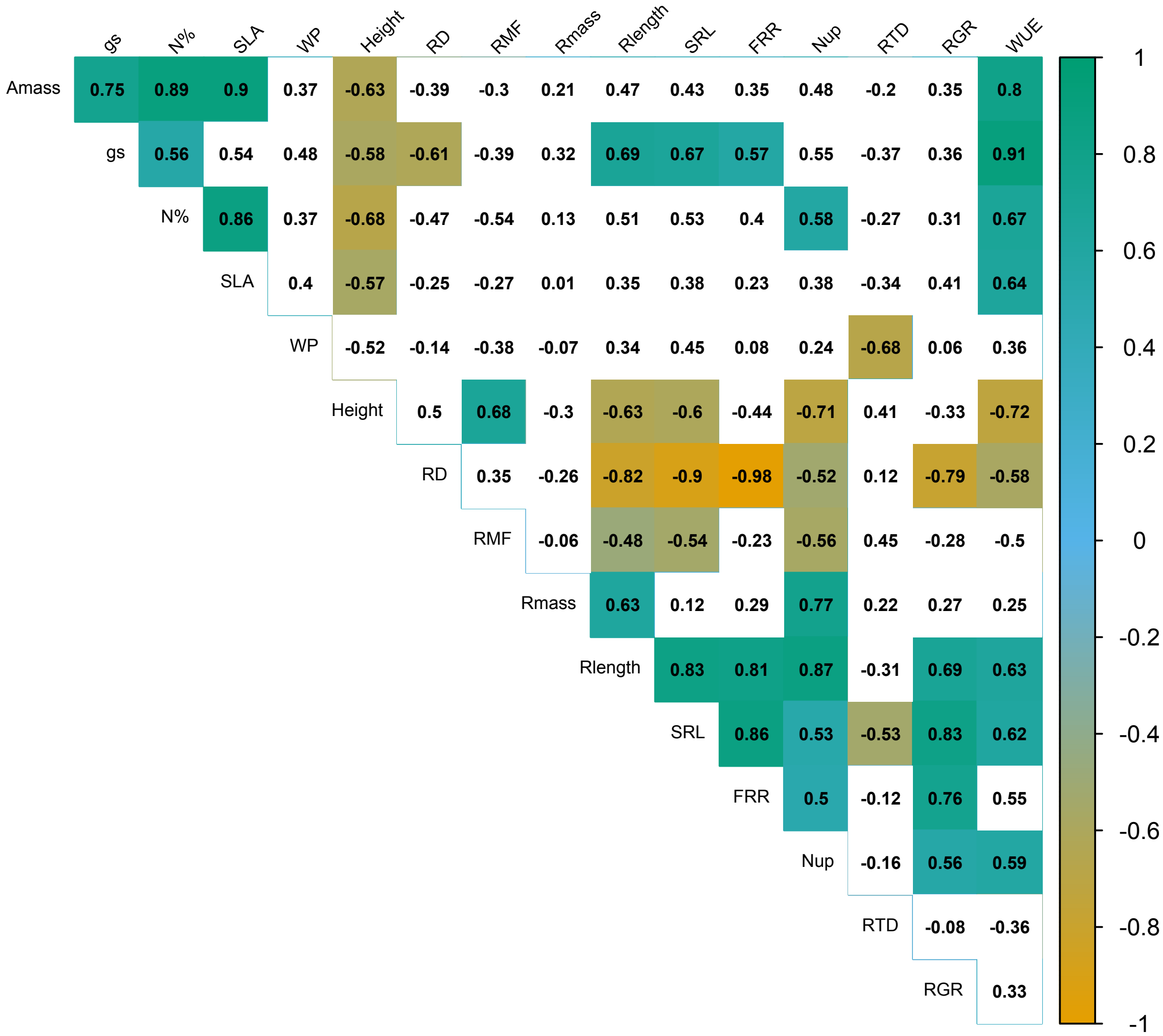


Fig 1.1. Conceptual diagram showing expected above and below ground trait trends if resource economies fall along a single axis from acquisitive to conservative resource

use strategies. Top list represents traits with high values for acquisitive species. Bottom list represents traits with high values for conservative species.

In this plant community we observed significant ($p<0.05$) positive correlations between A_{mass} and g_s ($r = 0.75$), N% ($r = 0.89$), and SLA ($r = 0.90$); between g_s and N% ($r = 0.56$) and between SLA and N% ($r = 0.86$)(Fig 1.2). Height was significantly negatively correlated with A_{mass} ($r = -.63$), g_s($r = -0.58$), N% ($r = -0.68$), and SLA ($r = -0.57$)(Fig 1.2). In trait correlations species clustered by functional type with conservative shrubs typically on one end of the correlation and acquisitive forbs on the other. Surprisingly, Ψ_{leaf}, a proxy for water status and potentially water use strategy, did not show significant correlations with other above-ground traits. Height separated shrubs from forbs with shrubs being taller and “slower” (i.e. low A_{mass}, g_s, N%, and SLA) than shorter and “faster” forbs. Finally, WUE, a multilayered trait, was significantly positively correlated with A_{mass} ($r = 0.80$), g_s ($r = 0.91$), N% ($r = 0.67$), and SLA ($r = 0.64$) and significantly negatively correlated with height ($r = -0.72$), while no traits were significantly corelated with RGR, another aggregate trait (Fig 1.2). None of the aboveground traits showed phylogenetic signal using Pagel’s λ or Blomberg’s K (Appendix 1, Table S1.1). Trends remained similar when accounting for phylogenetic non-independence, with the exception Ψ_{leaf}, for which all relationship became significant (positively, except with height), and a positive relationship between SLA and g_s (Appendix 1, Fig S1.1).



	gs	N%	SLA	WP	Height	RD	RMF	Rmass	Rlength	SRL	FRR	Nup	RTD	RGR	WUE
Amass	0.75	0.89	0.9	0.37	-0.63	-0.39	-0.3	0.21	0.47	0.43	0.35	0.48	-0.2	0.35	0.8
gs		0.56	0.54	0.48	-0.58	-0.61	-0.39	0.32	0.69	0.67	0.57	0.55	-0.37	0.36	0.91
N%			0.86	0.37	-0.68	-0.47	-0.54	0.13	0.51	0.53	0.4	0.58	-0.27	0.31	0.67
SLA				0.4	-0.57	-0.25	-0.27	0.01	0.35	0.38	0.23	0.38	-0.34	0.41	0.64
WP					-0.52	-0.14	-0.38	-0.07	0.34	0.45	0.08	0.24	-0.68	0.06	0.36
Height						0.5	0.68	-0.3	-0.63	-0.6	-0.44	-0.71	0.41	-0.33	-0.72
RD							0.35	-0.26	-0.82	-0.9	-0.98	-0.52	0.12	-0.79	-0.58
RMF								-0.06	-0.48	-0.54	-0.23	-0.56	0.45	-0.28	-0.5
Rmass									0.63	0.12	0.29	0.77	0.22	0.27	0.25
Rlength										0.83	0.81	0.87	-0.31	0.69	0.63
SRL											0.86	0.53	-0.53	0.83	0.62
FRR												0.5	-0.12	0.76	0.55
Nup													-0.16	0.56	0.59
RTD														-0.08	-0.36
RGR															0.33

Fig. 1.2. Correlogram depicting Pearson correlation coefficients between traits. Colored tiles represent significant correlations ($p<0.05$) while color ramp indicates how well the data fit the correlation.

Interspecific variation in above-ground traits was described by a single dimension with an eigenvalue > 1, which explained 68.3% of the variation (Fig. 1.3.; Appendix 1). This axis reflected leaf economic spectrum trait relationships with differences in A_{mass}, SLA, and N_{leaf} describing much of the variation (Appendix 1). Height, and to a smaller extent, stomatal conductance, also contribute to this axis. “Fast” plants had high A_{mass}, SLA, and N_{leaf} and g_s and short stature, while “slow” plants had low A_{mass}, SLA, N_{leaf} and g_s and were taller. A one-way ANOVA followed by a TukeyHSD test found this axis separated species by functional type, with “faster” forbs significantly different than “slower” shrubs ($p < 0.001$, Fig. 1.3) and grasses ($p = 0.02$, Fig. 1.3). Results from the phylogenetic PCA were similar, however, all traits, including Ψ_{leaf}, made similar contributions to the first axis of which the percent variance explained increased to 78.6%.

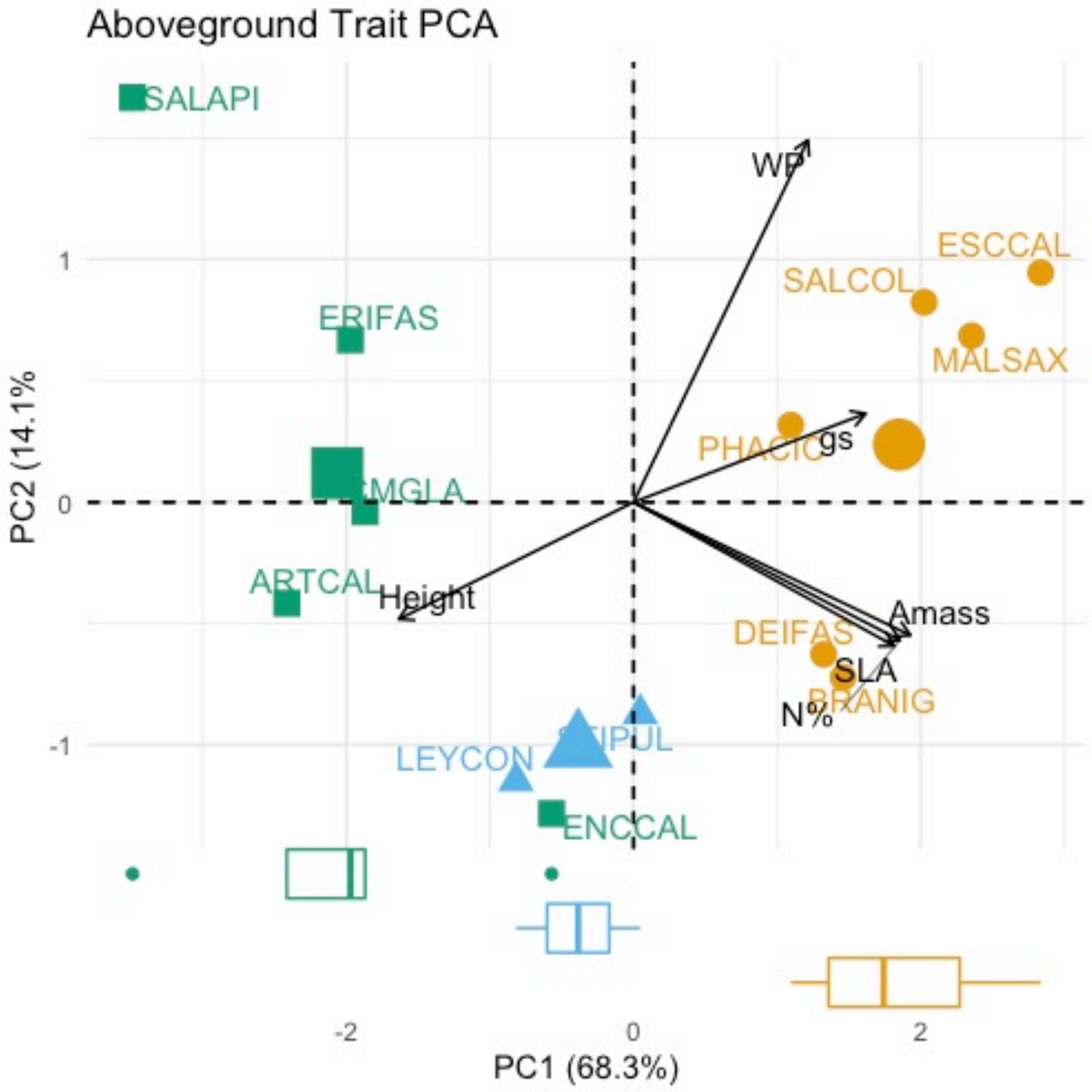


Fig. 1.3. Biplot of first 2 dimensions from PCA of above-ground traits with species mapped to dimension scores. Grn. sqr. = shrub, ylw. circ. = forb, blu. tri. = grass. Larger symbols represent the centroid for functional group. Boxplot depicts differences in functional type position along PC axis 1. One-way ANOVA followed by a TukeyHSD test

found significant differences between shrubs and forbs ($p < .001$) and between grasses and forbs ($p = 0.02$)

Below-ground trait correlation and coordination

Below-ground traits showed strong significant correlations consistent with established trait spectra (Larson and Funk 2016) (Fig. 1.2; Appendix 1). For example, N_{up} was correlated positively with FRR ($r = 0.75$), SRL ($r = 0.74$), R_{length} ($r = 0.95$), R_{mass} ($r = 0.73$) and negatively with RD ($r = -0.52$) and RMF ($r = -0.56$). RD was also negatively correlated with R_{length} ($r = -0.82$), SRL ($r = -0.90$), and FRR ($r= -0.98$). RMF was also negatively correlated with R_{length} ($r = -0.48$), SRL ($r = -0.54$). R_{length} was also positively correlated with R_{mass} ($r = 0.63$), SRL ($r = 0.83$), and FRR ($r = 0.81$). FRR was additionally positively correlated with SRL ($r = 0.86$). RTD was only correlated with SRL ($r = -0.53$), however, when phylogeny was accounted for, correlations between all root traits, except with R_{mass}, and RTD became significant. Phylogenetic signal was detected for RD, FRR, and RTD using Pagel's λ and Blomberg's K, and R_{length}, SRL, and N_{up} with Blomberg's K (Appendix 1). Correlation trends remained similar for all other traits with a few exceptions - RD and RMF were positively correlated while RD and N_{up} were not, RMF and N_{up} were also no longer correlated. Belowground traits were well correlated with the 2 composite traits. RGR was correlated with RD ($r =-0.79$), R_{length} ($r = 0.69$), SRL ($r = 0.83$), FRR ($r = 0.76$), N_{up} ($r = 0.56$). WUE was correlated with RD ($r = -0.58$), R_{length} ($r = 0.63$), SRL ($r = 0.62$), N_{up} ($r = 0.59$). When accounting for phylogenetic non-independence, trends were similar, but neither RGR nor WUE were correlated with N_{up}, and WUE was no longer correlated with RD.

Below-ground interspecific trait variation was described by 3 dimensions with eigenvalues > 1, which explained 58.4%, 19.8%, and 14.4% of the variation respectively (Fig. 1.4, Appendix 1). The dominant axis was described by root elongation rate (R_{length}), specific root length (SRL), root diameter (RD), fine root ratio (FRR) and nitrogen uptake rate (N_{up}) (Appendix 1). This axis separated species along an acquisitive to conservative strategy with acquisitive species having fast root elongation, high SRL, FRR, and N_{up} and small root diameters and conservative species the opposite. As with the aboveground traits, a one-way ANOVA found this first axis separated plants according to functional type ($p = 0.03$, Fig. 1.4) with shrubs different than forbs and grasses, however, differences were smaller than for aboveground or combined PCAs.

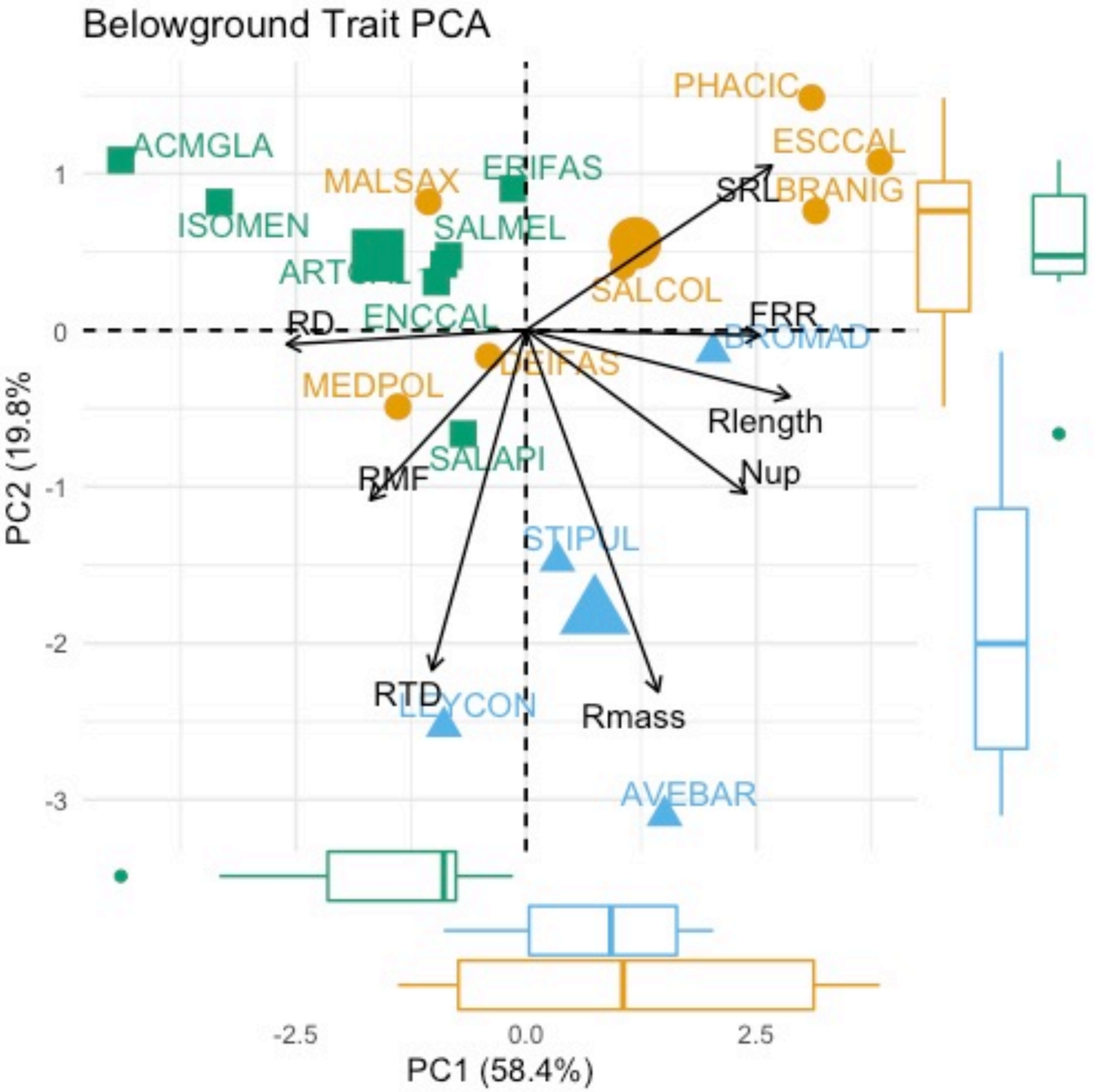


Fig. 1.4. Biplot of first 2 dimensions from PCA of below-ground traits with species mapped to dimension scores. Grn. sqr. = shrub, ylw. circ. = forb, blu. tri. = grass. Larger symbols represent the centroid for functional group. Marginal boxplots depicting mean functional type position along PC1 in below-ground traits. One-way ANOVA followed by a TukeyHSD test found significant differences between shrubs and forbs (p = .029).

Marginal boxplot depicting mean functional type position along PC2 in below-ground traits. One-way ANOVA followed by a TukeyHSD test found significant differences between grasses and shrubs and forbs ($p = 0.001$).

The second axis, incredibly, described variation in root growth rate (R_{mass}) and root tissue density (RTD) separating shrubs and forbs, having low R_{mass} and RTD, from grasses ($p < 0.001$, Fig 1.4, Appendix 1). The third axis explained variation in root mass fraction (RMF), fine root ratio (FRR), RD, and N_{up}. This axis is similar to the first in separating acquisitive and conservative triats, but did not separate functional type ($p = 0.16$). Species grouped by large RD, high N_{up}, low RMF, and FRR; opposing species had small RD and low N_{up}, high RMF and FRR (Appendix 1).

A phylogenetic PCA for belowground traits had notable differences compared with the standard PCA with only two axes describing the variation between species (Appendix 1). All traits, save R_{mass}, contributed to the first axis, including RTD and RMF which switched axes compared with the standard PCA. The second axis was primarily explained by root growth rate and nitrogen uptake rate.

Above/Belowground correlation and coordination

Above- and below-ground traits also showed some, albeit few, correlations between traits. g_s was positively correlated with R_{length} ($r = 0.69$), SRL ($r = 0.67$), and FRR ($r = 0.57$) and negatively correlated with RD ($r = -0.61$). Height was negatively correlated with R_{length} ($r = -0.63$), SRL ($r = -0.6$), and N_{up} ($r = -0.71$) and positively correlated with RMF ($r = 0.68$)(Fig. 1.2). Ψ_{leaf} was negatively correlated with RTD (r = -

0.68) and N_{up} positively with N% (r = 0.58) (Fig. 1.2). Notably there SLA was not correlated with its below-ground analog, SRL. Phylogenetic independent contrasts were similar, however, several relationships were notable(Appendix 1). RTD was positively correlated with all aboveground traits except height, with which it was negatively correlated. FRR and g_s were no longer correlated and the same with N_{up} and N%. RMF and R_{length} were no longer correlated with height, but RMF was correlated positively with RD.

A PCA with all traits combined separated plants by functional type along the first PC axis which appeared to described a primary “fast”-“slow” axis accounting for 54.55% of the variation in traits (Fig. 1.5). Two additional axes with eigenvalues > 1 accounted for 15.7%, and 11.38% of the variation (Fig. 1.5, Appendix 1), respectively. The first axis, describing the “fast/slow” economic spectrum, grouped large values of R_{length}, SRL, FRR, g_s, N_{up}, and N_{leaf} on the fast end of the axis and large values for height and RD on the slow end of the axis (Table 3). The second axis showed some decoupling from the economic spectrum with species grouped by high SLA, Ψ_{leaf}, A_{mass}, and N_{leaf} and low R_{mass} and FRR. Alternatively, plants with high R_{mass}, and FRR had low SLA, Ψ_{leaf}, A_{mass}, and N_{leaf}. The third axis grouped high values for RTD, A_{mass}, RMF, R_{mass}, SLA and N_{leaf} which opposed high values for Ψ_{leaf} and SRL . One-way ANOVAs followed by Tukey HSD tests found PC1 separated species by functional type with forbs and shrubs significantly different than one another (p = 0.001, Fig. 16). There were no differences between functional types for the second axis, but the third axis separated shrubs and forbs from the grasses (Fig 4). A phylogenetic PCA was similar with a few expcetions. R_{mass} was no longer a dominant variable explaining the 2nd PC axis while FRR, Ψ_{leaf} and RD increased their contribution to explaining this axis.

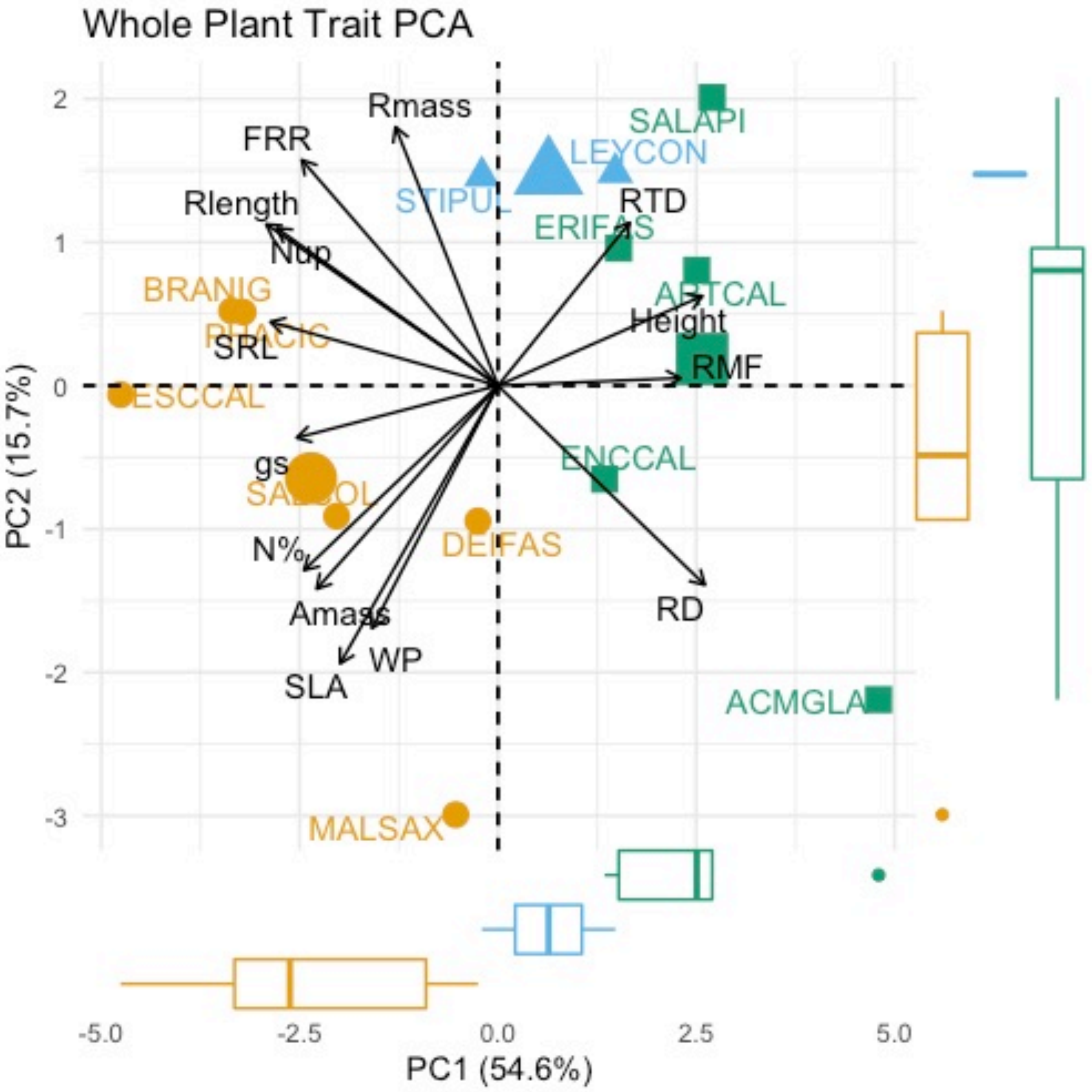


Fig. 1.5. Biplot of first 2 dimensions from PCA of combined above- and below-ground traits with species mapped to dimension scores. Grn. sqr. = shrub, ylw. circ. = forb, blu. tri. = grass. Larger symbols represent the centroid for functional group. Marginal boxplots depict mean functional type position along relevant axis in the PC space. One-way ANOVAs followed by a TukeyHSD test found significant differences between

shrubs and forbs ($p = 0.001$) along PC1, no differences between functional types along PC2, and shrubs and forbs significantly different than grasses along PC3 (not shown).

Plant Strategy and Performance

To examine the relationship between coordinated trait strategy and plant performance, we examined aboveground, belowground, and the traits combined in the context of a well document trade-off between the emergent traits, relative growth rate (RGR) and water use efficiency (WUE) that describes the acquisitive vs. conservative resource capture spectrum. RGR and WUE did not trade-off as expected in this community ($R^2 = 0.11$; $P = 0.35$; Fig. 1.6). RGR was only significantly related to PC1 from the below-ground traits ($R^2 = 0.54$, $P = 0.004$, Fig. 1.7C), however, there was a marginally significant linear relationship between PC1 of the combined traits PCA and RGR ($R^2 = 0.37$, $P = 0.06$, Fig. 1.7E) and no relationship for the above ground traits ($R^2 = 0.15$, $p = 0.27$, Fig. 1.7A). WUE was positively related to PC1 in aboveground, belowground, and combined trait groups ($R^2 = 0.71$, $P < 0.001$, Fig 1.7B; $R^2 = 0.41$, $P = 0.02$, Fig. 1.7D.; $R^2 = 0.65$, $P < 0.001$, Fig. 1.7F, respectively). Plotting PC1 from the phylogenetic PCAs against RGR and WUE presented nearly identical relationships (Appendix 1). The second PC axis did not show a significant relationship with RGR or WUE using standard or phylogenetic PCAs (Appendix 1)

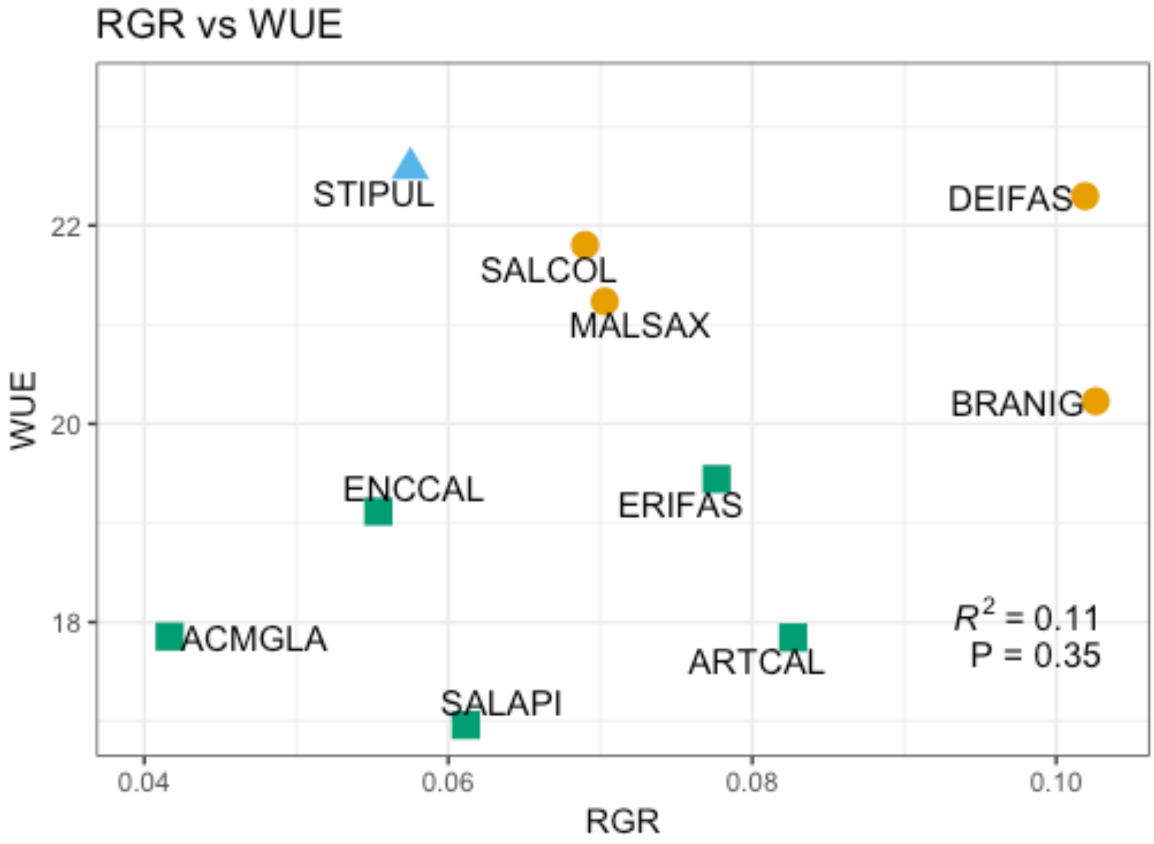


Fig. 1.6. Plot of relative growth rate (RGR) against water use efficiency (WUE), with no significant relationship (R^2 = 0.11; p = 0.35; 95% CI). WUE values are from calculated carbon isotope discrimination with lower numbers indicating more water use efficient. Grn. sqr. = shrub, ylw. circ. = forb, blu. tri. = grass.

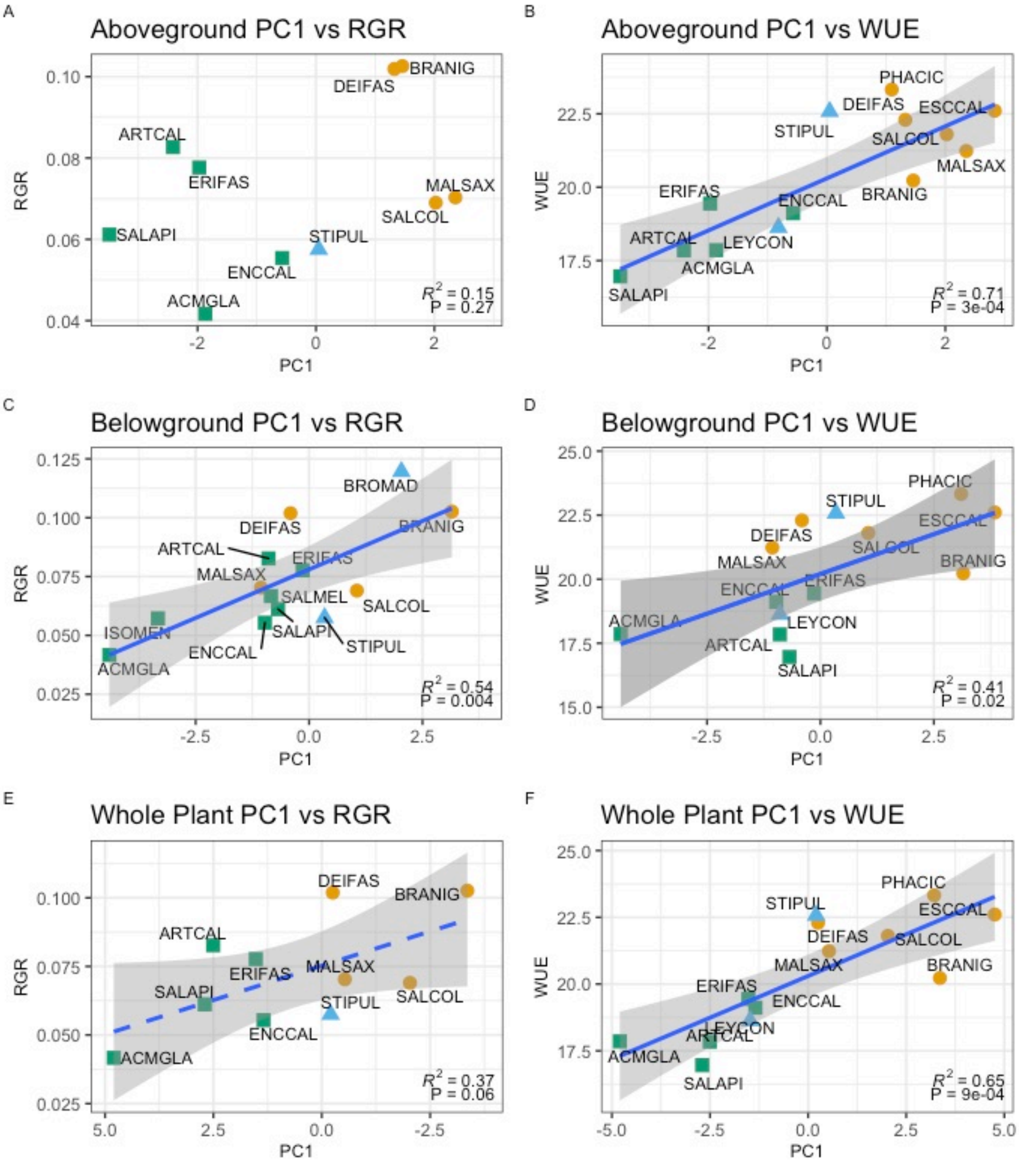


Fig. 1.7 A. Plot of above-ground PC1 against relative growth rate (RGR), with no significant relationship (R^2 = 0.15; p = 0.27). Grn. sqr. = shrub, ylw. circ. = forb, blu. tri. = grass. **B.** Plot of above-ground PC1 against water use efficiency (WUE), with strong

significant relationship ($R^2 = 0.71$; $p < 0.001$; 95% CI). WUE values are from calculated carbon isotope discrimination with lower numbers indicating more water use efficient. Grn. sqr. = shrub, ylw. circ. = forb, blu. tri. = grass. **C.** Plot of below-ground PC1 against relative growth rate (RGR), with significant relationship ($R^2 = 0.54$; $p = 0.004$). Grn. sqr. = shrub, ylw. circ. = forb, blu. tri. = grass. **D.** Plot of below-ground PC1 against water use efficiency (WUE), with significant relationship ($R^2 = 0.41$; $p = 0.02$; 95% CI). WUE values are from calculated carbon isotope discrimination with lower numbers indicating more water use efficient. Grn. sqr. = shrub, ylw. circ. = forb, blu. tri. = grass. **E.** Plot of combined traits PC1 against relative growth rate (RGR), with marginally significant relationship indicated by dotted line ($R^2 = 0.37$; $p = 0.06$). Grn. sqr. = shrub, ylw. circ. = forb, blu. tri. = grass. **F**. Plot of combined traits PC1 against water use efficiency (WUE), with significant relationship ($R^2 = 0.65$; $p < 0.001$; 95% CI). WUE values are from calculated carbon isotope discrimination with lower numbers indicating more water use efficient. Grn. sqr. = shrub, ylw. circ. = forb, blu. tri. = grass.

Discussion

Understanding how aboveground and belowground traits are structured within a semi-arid, Mediterranean type ecosystem can shed light on the resource economies operating in a water limited community and provide insight on plant strategy and performance, valuable information for land manages and ecosystem modelers. In a group of 20 species from a coastal sage scrub community, we found many tight correlations between traits within aboveground and belowground tissues, but correlations between above and belowground traits were scarce suggesting discoordination between above and belowground traits. Phylogenetic signal was only present in belowground traits and phylogenetic independent contrasts left many trait relationships unchanged, but evidence is present for conserved strategies for coping with belowground pressures. Variation among traits above, below, and for traits combined, described dominant axes that separated plants by functional group and were similar to established acquisitive vs. conservative trait spectra, however, aboveground this axis was decoupled from RGR suggesting LES traits may not well describe a fast-slow growth continuum in this community, and belowground trait variation described a multidimensional root economics space, perhaps reflecting a broader set of pressures roots encounter (Weemstra et al. 2016b, Weigelt et al. 2021). Accounting for phylogenetic non-independence led to similar results, with some notable exceptions. Lastly, variation in WUE was well correlated with each of the primary axes in our PCAs, highlighting the importance of leaf water use strategy in structuring above and below ground traits suites in this water limited system, while RGR and the carbon economy was only correlated with our belowground trait syndrome and marginally in the whole plant PCAs.

Aboveground Trait Correlation and Coordination

Strong aboveground trait correlations confirmed LES trait relationships supporting the generalizability of the fast-slow spectrum at the community level in a semi-arid climate; however, water use traits, g_s and Ψ_{leaf}, only being correlated after conducting phylogenetic independent contrasts highlight the importance of accounting for shared evolutionary history in aboveground traits. The universality of leaf construction points to biophysical constraints that may impose structural and physiological limitations on the way leaves are built and the mechanisms by which carbon is assimilated. (Onoda et al. 2017b) although the slopes of these relationships may be influenced by environment(Wright et al. 2005). Paradoxically, none of the aboveground traits showed phylogenetic signal, which may indicate abiotic pressures driving convergence in trait strategies (Ackerly and Reich 1999, Kerkhoff et al. 2006). Further, leaf strategies may be more related to plant functional type than evolutionary history, a pattern we see in our data with forbs and grasses occupying the fast end of the correlations and woody species occupying the slower end (Kerkhoff et al. 2006, Flores et al. 2014). However our study may also suffer from low replication as phylogenetic signal analyses using Pagel's λ becomes less reliable with fewer than 20 species (Freckleton et al. 2002).

When evaluated together, these traits describe a coordinated aboveground, fast-slow, continuum that separated functional types as in the correlations. However, this axis did not describe variation in relative growth rate, a surprising result given the LES continuum was originally based on carbon and nitrogen acquisition and allocation strategy. This may result from discoordination in allocation between leaf and other tissues in the plant and/or may reflect age dependent scaling in trait-growth relationships (Gibert et al. 2016, Funk et al. 2021b), especially given leaves in this study were taken from mature plants while RGR measurements were taken in the first year. Water use efficiency was a different story with the primary aboveground axis describing much of its variation along with separating functional types pointing to water use strategy as an important feature of plant syndrome in this community. Indeed, recent work has highlighted water as an important resource to consider in terms of plant economics (Reich 2014b) especially in water limited environments where the water-use strategy may converge along a trade-off axis (Flo et al. 2021). Alternatively, we may see aboveground relationships with WUE and not RGR because the former is a trait measured at the leaf scale and closely related to the traits in the PCA while the latter is a whole plant trait use strategy as an important dimension of the variation in WUE also separated species by functional type highlighting the importance of growth form diversification in this strongly seasonal environment.

Belowground trait correlation and coordination

Root tissues, like aboveground tissues, were tightly correlated with one another following trait trade-offs found elsewhere for this community (Larson and Funk 2016a) highlighting differences between acquisitive species that employ traits which maximize exploration of the soil matrix with a minimum biomass investment per tissue unit (i.e. high values of root elongation rate, specific root length, and nitrogen uptake rate) and conservative species which typify opposite strategies - these differences typically separated slow shrubs and faster grasses and forbs. Phylogenetic non-independence in root traits, confirmed elsewhere, was common, lending support to the hypothesis of root trait phylogenetic conservatism which suggests that soil microbial associations along with diversification patterns driven by a drying climate since the cretaceous, have influenced root phenotypes and point to the need to account for these in analyses (Comas et al. 2012, 2014, Valverde-Barrantes et al. 2017). After phylogenetic correction, root tissue density was strongly correlated with all belowground traits except root growth rate supporting the importance of this trait in structuring belowground strategies (Kramer-Walter et al. 2016b). RTD has been thought to structure root trait relationships along resource gradients with high RTD found in infertile soils and also differs by phylogenetic grouping, a point made by the lack of RTD correlations without phylogenetic correction (Kramer-Walter et al. 2016a). RTD was positively correlated with RMF and negatively correlated with SRL. Furthermore, a strong negative correlation between SRL and RD and a positive correlation between RD and RTD points to an interactive effect of RTD and RD on SRL in which thicker roots are also denser with these relationships separating species by functional type with forbs more acquisitive and shrubs more conservative, with some overlap. However, the relationships involving RD and RTD may be ontogenetic as plants were grown for different lengths of time and these traits may increase due to secondary growth in older plant roots(Vetterlein and Doussan 2016, Funk et al. 2021b). Ignoring these caveats, our findings suggest that roots are constrained with respect to their construction. In our study plants with large root mass fractions also had denser, and thicker roots which contribute to a low SRL and vice versa. This speaks to strategies in which conservative plants invest more greatly in long lived below ground tissues as a way to access scarce water resources and survive during the dry season while forbs (typically annuals in this system) invest little in below ground structures, growing only during the wet season and instead focusing on aboveground tissue construction (Vetterlein and Doussan 2016). The RTD/SRL decoupling that Kramer-Walter (2016) found was in a much wetter environment, thus, our dry system may present constraints to root construction(Kramer-Walter et al. 2016a). This may be the result of fewer biotic stresses, often associated with more mesic sites, and a unifying strategy of mitigating water loss. Correlation of RTD and SRL oppositely with RMF may indicate a combined strategy for reducing water loss by producing a large proportion of dense roots; increasing total resource exchange surface, while minimizing water loss through root density. However, an interesting question remains whether these relationships are the result of convergent evolution to some trade-off optima or biophysical constraints on how tissues can be constructed. In the case of root traits, convergence seems to be driving these patterns in this environment as others have seen multidimensional root trait construction (Kramer-Walter et al. 2016a). Few traits were correlated with root growth rate, a surprising finding given numerous correlations and a documented root economic spectrum (Larson and Funk 2016b). This suggests root biomass can be allocated in a variety of ways and that a single fast-slow tradeoff axis may not describe trait trends. This may also be explained by rooting strategies that change as plants mature - plants may be selected to have fast growth during establishment, to ensure water and nutrient acquisition potential, that shifts to a more conservative strategy as the plant ages (Hamberg et al. 2018, Funk et al. 2021b). This may also be the result of our choice to combine datasets such that root traits and RGR were measured on different plants and that their environments (pots versus field) and growing times were different which has been shown to change the nature of the root growth to whole plant growth relationship (Freschet et al. 2017). Specific root length, thought to be a belowground analogue for SLA, was negatively correlated with RTD a surprising result because other studies have suggested that SRL and RTD define axes of variation orthogonal to one another (Kramer-Walter et al. 2016b), but SRL was correlated with RGR while RTD was not, suggesting SRL defines an acquisition/conservation trade-off potentially better than RTD. However, R_{mass} not being correlated with SRL again highlights the complexity of how root biomass is allocated and its potential multidimensional nature.

An important recent debate among root ecologists has been whether root trait variation is structured, as leaves with the leaf economic spectrum, along a root economic spectrum - a single trade-off axis describing an acquisitive to conservative resource use continuum. A PCA including all root traits revealed 2 axes of variation when adjusted for phylogeny, supporting the hypothesis that root traits are multidimensional. However, these axes differed from recently described multidimensional root frameworks. The first dimension described a fast-slow axis with slow plants having a relatively large mass of dense, thick roots with low SRL, low fine root ratio and low root elongation rate with fast plants having high SRL, FRR, R_{length}, and low RTD, RMF and RD. This supported findings from other studies that described an RES in this community and others (Kramer-Walter et al. 2016b, Larson and Funk 2016a, Roumet et al. 2016). High RD and RTD reflects species making roots with long lifespans, built for efficient transport, a function more associated with a tolerance strategy (Gu et al. 2011). Similar to the above ground PCA, this first axis appears to separate species based on functional type (significantly between forbs and shrubs and apparently for shrubs and grasses), however, there is far more overlap between the groups creating a more continuous spectrum of trait suite values which suggests that below ground trait suites are less constrained by growth form diversification patterns in how they are constructed and how they meet the nutritive and transpirative demands of the above ground tissues(Kerkhoff et al. 2006, Flores et al. 2014). This makes sense in light of other studies which have found that root traits are multidimensional and speaks to the heterogenous soil environment, biotic interactions (Bergmann 2020), multiple functions roots play, ((Kramer-Walter et al. 2016a, Weemstra et al. 2016b, Weigelt et al. 2021). We must, however, keep in mind that these are seedling roots, structures adaptive for the relatively resource rich wet season in this environment. While we are potentially looking at relatively more mature roots for fast developing annual species, the perennial grasses and shrubs may have rooting strategies that change with ontogeny (Mcconnaughay and Coleman 1999, Ristova and Busch 2014)Thus, we may see greater distinction between functional types if we were to examine root traits of each functional type at maturity.

Additionally, we found 21.7% of the variation in root traits explained by a 2nd orthogonal PC axis which was largely defined by root growth rate and to some extent nitrogen uptake rate. While our study also included RTD and took phylogenetic non-independence into account, contrasting with other studies in this system (Larson and Funk 2016b), this is still a surprising result since one would expect root growth rate to load on the first axis if indeed that axis described a trade-off between resource acquisition and conservation. However, in a pulse driven system this axis may explain variation in establishment strategy coupled with maternal effects of seed size, with some species putting down larger root mass as a way to ensure access to water as pulse effects/inputs wane by allocating more resources to seed biomass which leads to a seedling with a larger root and overall mass increasing its chance for survival. (Jurado and Westoby 1992, Leishman and Westoby 1994). We also see that grasses occupy the high root growth end of this axis, while most shrubs occupy the lower root growth end, which may result from grasses requiring fewer resources for stem construction which can instead be used for root construction, along with having fibrous root architecture, while tap-rooted shrubs have a slower growth habit. We may see our results partially reflected in a recently developed framework that describes a dominant collaboration axis (roots with high dependence on mycorrhizal associations to acquire resources - RD opposed to SRL) that contrasts with a conservation axis (the classical fast-slow trade-off describe in the LES,) of root trait variation (Bergmann 2020, Weigelt et al. 2021). RD and SRL loaded on the first axis, opposed to one another, which is consistent with a collaborative axis, and root growth rate and N_{up} loaded in the same direction on the second axis which points to the conservation axis. Bolstering this interpretation, legumes, with well documented root collaborations with rhizobium and AMFs loaded on the outsourcing side of the collaborative axis. We also see this axis separating functional groups which might reflect differences in the time scale of plant maturation. Because shrubs persist for multiple seasons, they have more time to form and develop microbial associations which might make these more important for this functional type. This contrasts with forbs which persist for only a season and might be better served employing the "do-it-yourself' model of resource acquisition. Our data however, contrasts with this recent framework in that RTD loads on the collaborative first axis, instead of the conservation axis. While puzzling, this may reflect differences in functional type as persistent shrubs are likely to have longer lived, root tissues with higher density that protect against herbivory and resource loss while lower RTD might signal the importance of water acquisition strategy in this water limited system (Freschet et al. 2021).

While supporting a multidimensional framework for root systems, the coordinated root trait axes in our data didn't align with plant strategies as expected when compared with RGR and WUE. That the first axis explained variation in RGR and WUE (the aboveground axis only explained variation in WUE) is puzzling since this is supposed to represent the collaboration axis, however, it may indicate that the collaboration vs. conservation axis space is not quite as broad in our system, a point reinforced by RTDs loading on the first axis, and that both axes can explain growth. This narrowing of the root economic space could be the result of differences in growth form as this is tied tightly to resource use strategy (Herms and Mattson 1992) as well as collaborative status (Koziol and Bever 2015), with "do-it-yourself" plants representing the early successional, fast growth strategy, while late successional species grow slower and outsource their resource acquisition to mycorrhizae. Variation in WUE explained by the dominant root trait suite supports the idea that resource use strategies would be unified especially in a water limited environment (Reich 2014b) but this again likely also reflects differences in life history strategy.

Correlation and coordination between aboveground and belowground tissues

Examining the correlations between above and belowground traits led to some surprising results. Finding few correlations between paired traits provides evidence against the idea of aboveground and belowground trait analogues (Weemstra et al. 2016a, Bergmann et al. 2017), however, relationships with stomatal conductance and height point to the importance of water use strategy and functional type as drivers of variation in this system. Stomatal conductance, indicative of a plant's water use strategy, was correlated with root diameter (-), root elongation rate (+), and specific root length (+), traits that represent differences in plant's structural investment in, and metabolic capacity to create, extractive surface area and speaks to the resource, especially transpirative, demand of the plant. These trade-offs point to the importance of water use strategy in structuring this community and demonstrates the unity between aboveground and belowground traits hypothesized (Reich 2014b) and supported (Freschet et al. 2010b, 2015, Liu et al. 2010b), but may also represent differences in mycorrhizal associations and differences between the “do-it-yourself” and the “outsourcing” plants. This is likely a reflection of differences in life history and reflect a safety-efficiency trade-off with respect to stomatal conductance (Henry et al. 2019), with annuals adopting a riskier, high conductance water use strategy so as to increase gas exchange and potential carbon assimilation during the favorable growing season, while shrubs adopt a more conservative low conductance strategy that maximizes water use efficiency and embolism reduction - a point supported by our data (Fig. 1.2 and 1.3). Supporting the idea that trade-offs in this community are to some extent structured by life form, height, a proxy for life form here, was correlated with SRL (-), N_{up} (-), and RTD (+), while root tissue density was correlated with all above ground traits, pointing to differences in biomass allocation that prioritizes resource conservatism and defense (low SRL, and high RTD) instead of growth and metabolism (high SRL and high N_{up}) (Herms and Mattson 1992). Root tissue density has been found to mirror the acquisitive vs. conservative axis in several studies making it an important trait for exploring above and belowground linkages (Kramer-Walter et al. 2016b, Bergmann 2020). Here we find it separates species by functional type again point to seasonally dependent strategy in this system. Plant size, for which height is a proxy, has also been shown to be an important trait in describing global plant diversity, separating woody and herbaceous species, a dichotomy we see here between the shrubs and grasses and forbs (Díaz et al. 2015b). Height was also positively correlated with seed mass in this study which could account for the high root growth of some shrubs if larger seeds meant a greater initial root growth rate (Díaz et al. 2015b).

The idea of analogous functional traits above and belowground has been challenged in recent years (Mommer and Weemstra 2012c, Weemstra et al. 2016a, Bergmann et al. 2017) and our study supported a lack of analogous function. Specifically, SRL which has been thought of as a belowground SLA analog, was not well correlated with aboveground traits other than g_s and height. This likely reflects the multidimensional root economic space that describes the numerous functions of roots. However, as mentioned above, correlation with g_s may speak to the paramount importance of water use strategy. Furthermore, the SLA vs. SRL relationship, may have been impacted by shrubs such as ENCCAL, ARTCAL, and ACMGLA that are facultatively deciduous and have leaves with relatively high SLA given their perennial, shrub habit (note values relative to SALAPI and ERIFAS which are also facultatively deciduous, but which retain leaves for longer in the year and are from hot/arid locals (Westman 1981a, Kimball et al. 2017). High SLA has been associated with short leaf life span and in these deciduous shrubs represent a low-cost investment for short-lived leaves. Furthermore, some CSS shrubs, including ARTCAL, have dimorphic leaves that are deployed at different times of the year, lower SLA leaves typically in the dry season, which may represent an adaptation that favors leaf construction appropriate for the season (Westman 1981b). Our study took adult leaf samples from spring leaves which may be getting the higher SLA end this plastic response. Indeed, studies suggest leaf trait variation in communities dominated by herbaceous and deciduous species should be interpreted with caution (Funk and Cornwell 2013b). We also found a surprising result in N_{up} being uncorrelated with leaf N% suggesting a mismatch in how nitrogen is allocated in different tissues. Other studies have found no or weak correlations between root nitrogen and leaf nitrogen which may be related to what we found however, we did not measure root N specifically, only the uptake rate (Weemstra et al. 2016b, Ma et al. 2018). It seems entirely possible that roots may provide an apparatus to uptake large amounts of nitrogen, but without a great need, export it to the leaves leading to different relationships between leaf and root N. We did, however, have 2 species that behaved contrary to what we would have expected; nitrogen fixing ACMGLA had both low N_{up} and N%. This may arise for a couple reasons. Low N_{up} may be explained by the fact that this data is from seedlings and these plants may not have had time to form the associations with nitrogen fixing rhizobium; or the rhizobium was not present in the microbial slurry or growing medium to begin with. Furthermore, the relationship with rhizobium may not be as beneficial to the plants. Studies have found variation in quality of plants mutualistic partners and selection will favor a rhizobium that gets as much from its symbiontic host as it can (Simms et al. 2006). SALAPI also had very low N% in adult leaves, but relatively high seedling N_{up}. A plant known for think leathery leaves with very low SLA in adult plants, this may represent alternative strategies for this plant at different stages of life. As a germinating seedling, high N% will allow the plant to acquire carbon and establish quickly when resources are plentiful, while low N% in adult leaves is indicative of a conservative strategy that prioritizes leaf structural components that typically lead to long leaf lifespan. This may also be the result of seedlings having insufficient amount of time to build the low SLA leaves typical in adult plants, coupled with lower SLA having a higher %C and potentially lower N%.

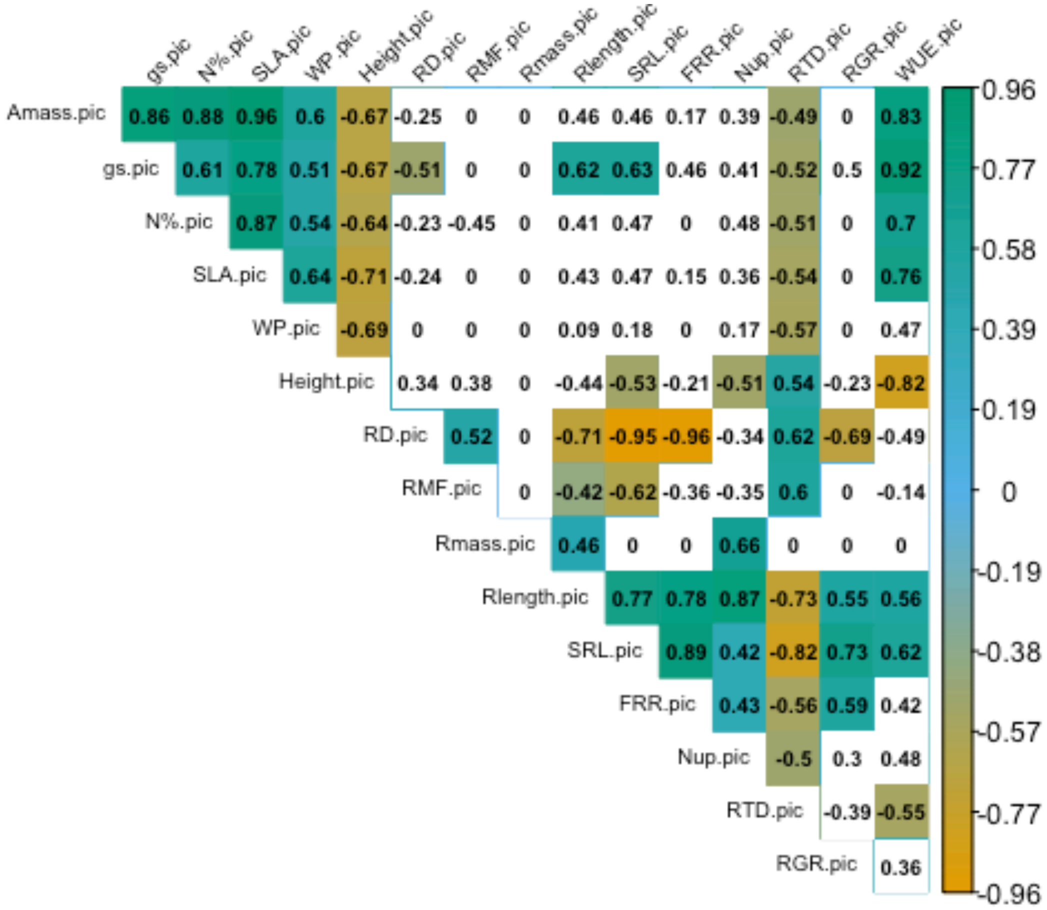
In recent years a whole plant economic spectrum (PES) that hypothesizes a unified fast or slow strategy across plant tissues has been supported, (Freschet et al., 2010b, 2015; Reich, 2014b; Riva et al., 2016; Wahl & Ryser, 2000) however, discoordination along with multidimensionality has also been found (Craine and Lee 2003, Craine et al. 2005, Kramer-Walter et al. 2016b, Bergmann 2020, Weigelt et al. 2021). Our data illustrate complex trait suites at the whole plant scale. To examine coordination between above and belowground traits that may define we examined a PCA that combined all traits to see how their variation may represent combined above and below ground trait suites. While we noticed few above/below ground correlations, PCA identified a fast to slow syndrome that explained first axis of variation when all traits were combined. The first PC axis represented the fast slow economic spectrum, but again we see clear differences between functional type, shrubs at the extremes and grasses in the middle. Most traits had relatively large eigenvector contributions to this axis suggesting a coordinated strategies between above and below ground trait suites. However, traits appear clustered in orthogonal axes comprised of the above ground traits (including RTD) and the root traits suggesting multidimensionality in how roots and leaves may be coordinated!!! That RTD is aligned with the traditional LES traits is supported by other studies (Kramer-Walter et al. 2016b, Bergmann 2020) that point to its importance in differentiating a resource conservation vs acquisition strategy. That the remainder of the roots traits, especially SRL, R_{length}, and FRR opposed to RD, were clustered orthogonally to the “traditional” fast-slow axis is also supported by previous studies that describe the “do-it-yourself” vs. “outsourcing” strategy of root fungal collaboration. Species are clustered by growth form with a few notable exceptions with shrubs and grasses on the “slow” end of the first axis and mostly on the “outsourcing” end of the collaboration axis and forbs on the fast side of the conservation axis and toward the “do-it-yourself" end of the collaboration axis. This follows what we have mentioned elsewhere in that early successional forb species are more likely to employ a fast, but also “do-it-yourself,” strategy as they complete their life cycle quickly and don’t have time to foster fungal mutualisms. Shrubs, conversely, adopt a slower, stress tolerant and collaborative strategy as they foster fungal collaboration. We also notice that there are no species that occupy the “slow” and “do-it-yourself” group and few that occupy the “fast,” “collaborative” quadrant. A notable exception for the latter is *Malacothrix saxatilis*, a perennial herb, which has roots that are “collaborative” (large RD, low SRL), but with fast aboveground traits as we’d expected given the need to regrow from roots each year. That certain strategy combinations are uncommon harkens to the empty corners idea inherent in trade-offs and negative correlations that supposes you can’t have a species that occupies high values for two traits that trade-off (Kimball et al. 2013). Two studies that have posited the “collaboration” vs. “conservative” economic space have demonstrated that species occupy all quadrants of this trait space, however, the first compared only trees along a fertility gradient (Kramer-Walter et al. 2016b), and the second, when species were separated by biome, arid system species were poorly represented(Bergmann 2020). Future studies should further examine the “collaborative” vs “conservative” trait space in arid systems to determine if certain trait suite combinations represent non-viable strategies.

While we observed a two-dimensional framework that structured aboveground traits in one direction and root traits in the orthogonal direction, the first PC axis still explained variation in RGR and WUE well with contributions from both above and below ground traits. That both contributed to explaining RGR and WUE strategy speaks to our earlier point that variation among species may be constrained by certain above-below trait combinations (i.e., fast plants with “do-it-yourself” roots and slow plants with “outsourcing” roots) with notable exceptions highlighted earlier (see MALSAX). In contrast to many studies which document a trade-off between growth rate and survival, this plant community is largely organized around water use efficiency, a proxy for stress tolerance. In fact, RGR and WUE were independent of one another (Fig. 1.6), potentially the result of 2 mechanisms 1) plant adaptation to pulse driven resource availability in which fast growth response to infrequent precipitation events is advantageous for all functional types and 2) summer dormancy of above ground tissues in perennials which favors production of leaves more similary to annuals with a drought escape strategy. Some segregation of species by RGR was noticed, however, functional types were clearly segregated by WUE indicating contrasting strategies of escape (low WUE) and tolerance (high WUE). That WUE was well correlated with the 1st PC axis for above, below, and for all traits combined reinforces the idea of water use strategy as an important trait for describing variation in this system. RGR on the other hand was only correlated with the belowground syndrome which suggests rooting strategy is of prime importance for whole plant resource acquisition.

Ecologically, organized variation in WUE instead of RGR in this environment makes sense in how species partition niche space. Water use efficiency and RGR represent strategies for plants dealing with abiotic (WUE) and biotic (RGR) stress (Grime 1977). We'd expect RGR to be a stronger trait for sorting variation in a more productive environment with greater competition. In this water limited environment plants emphasize stress tolerance, instead of competition (with the exception of belowground). A shrubland, this community also lacks the strong aboveground competitive interactions for light resources which might cause plants to sort by competitive ability and reinforces the independence of RGR.

Appendix 1

Supplementary Figures



	gs.pic	N%.pic	SLA.pic	WP.pic	Height.pic	RD.pic	RMF.pic	Rmass.pic	Rlength.pic	SRL.pic	FRR.pic	Nup.pic	RTD.pic	RGR.pic	WUE.pic
Amass.pic	0.86	0.88	0.96	0.6	-0.67	-0.25	0	0	0.46	0.46	0.17	0.39	-0.49	0	0.83
gs.pic		0.61	0.78	0.51	-0.67	-0.51	0	0	0.62	0.63	0.46	0.41	-0.52	0.5	0.92
N%.pic			0.87	0.54	-0.64	-0.23	-0.45	0	0.41	0.47	0	0.48	-0.51	0	0.7
SLA.pic				0.64	-0.71	-0.24	0	0	0.43	0.47	0.15	0.36	-0.54	0	0.76
WP.pic					-0.69	0	0	0	0.09	0.18	0	0.17	-0.57	0	0.47
Height.pic						0.34	0.38	0	-0.44	-0.53	-0.21	-0.51	0.54	-0.23	-0.82
RD.pic							0.52	0	-0.71	-0.95	-0.96	-0.34	0.62	-0.69	-0.49
RMF.pic								0	-0.42	-0.62	-0.36	-0.35	0.6	0	-0.14
Rmass.pic									0.46	0	0	0.66	0	0	0
Rlength.pic										0.77	0.78	0.87	-0.73	0.55	0.56
SRL.pic											0.89	0.42	-0.82	0.73	0.62
FRR.pic												0.43	-0.56	0.59	0.42
Nup.pic													-0.5	0.3	0.48
RTD.pic														-0.39	-0.55
RGR.pic															0.36

Fig. S1.1. Correlogram depicting regression coefficients between phylogenetic independent contrasts. Colored tiles represent significant correlation while color ramp indicates pearson correlation coefficient.

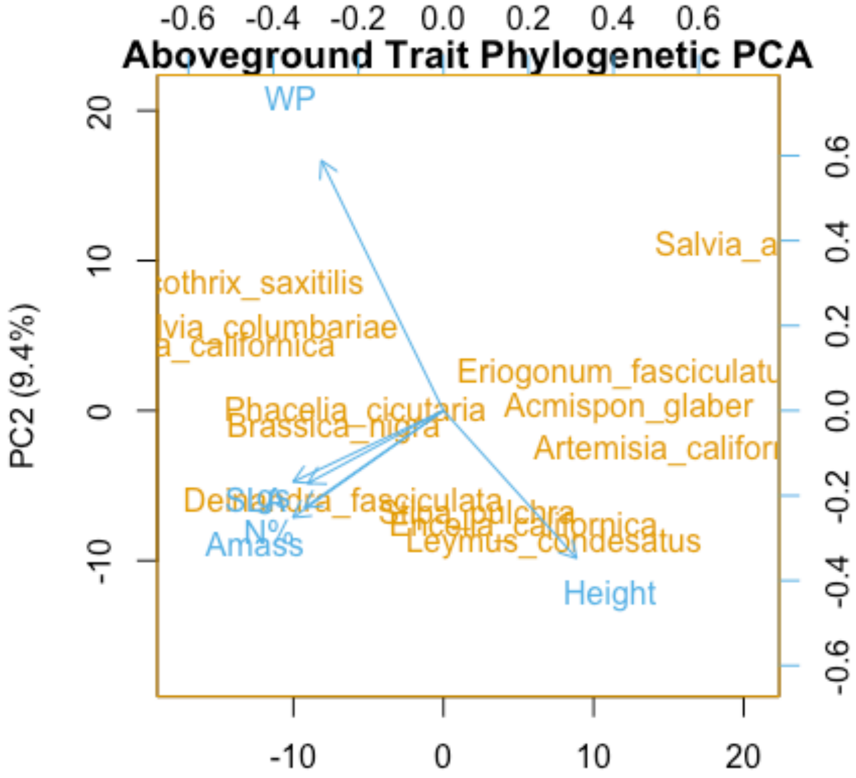


Fig. S1.2. Phylogenetic PCA for Aboveground traits

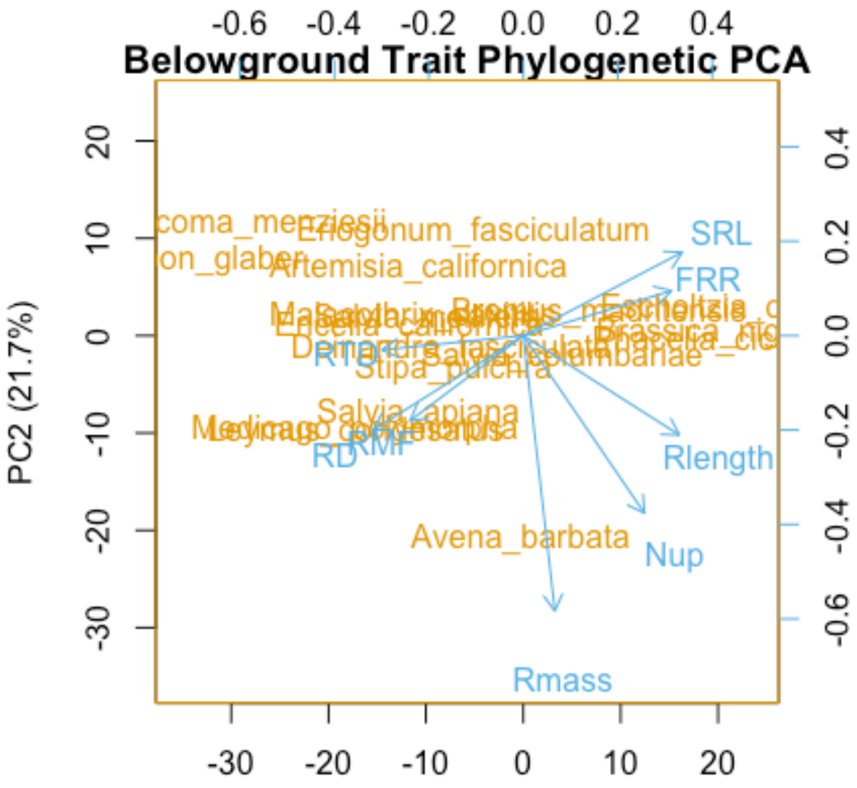


Fig. S1.3. Phylogenetic PCA for belowground traits

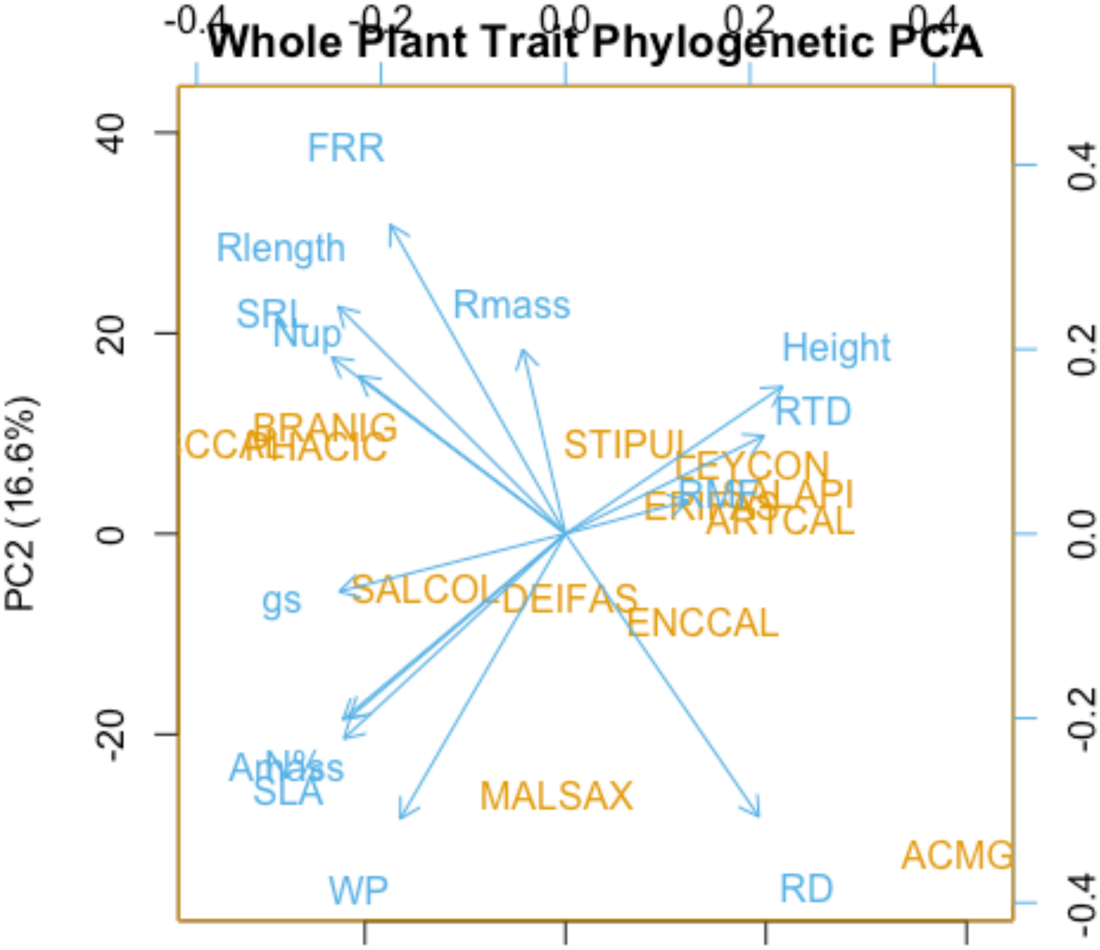


Fig. S1.4. Phylogenetic PCA for all trait combined.

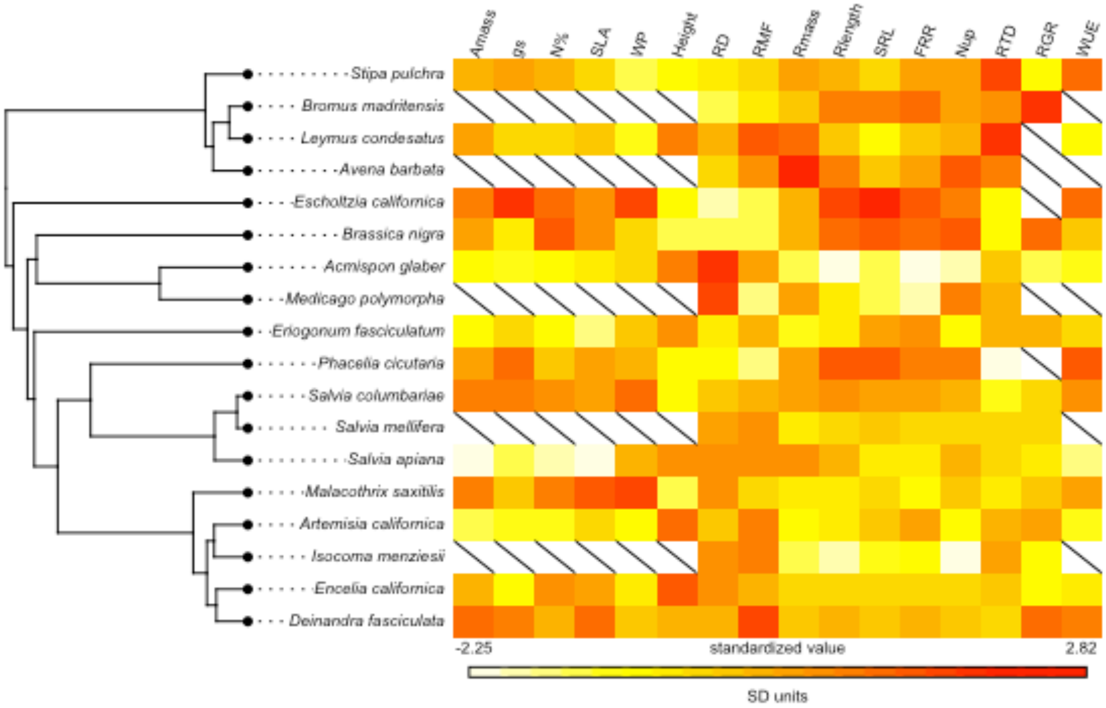


Fig. S1.5. Hierarchical clustering heatmap by phylogeny for 18 coastal sage scrub species in study.

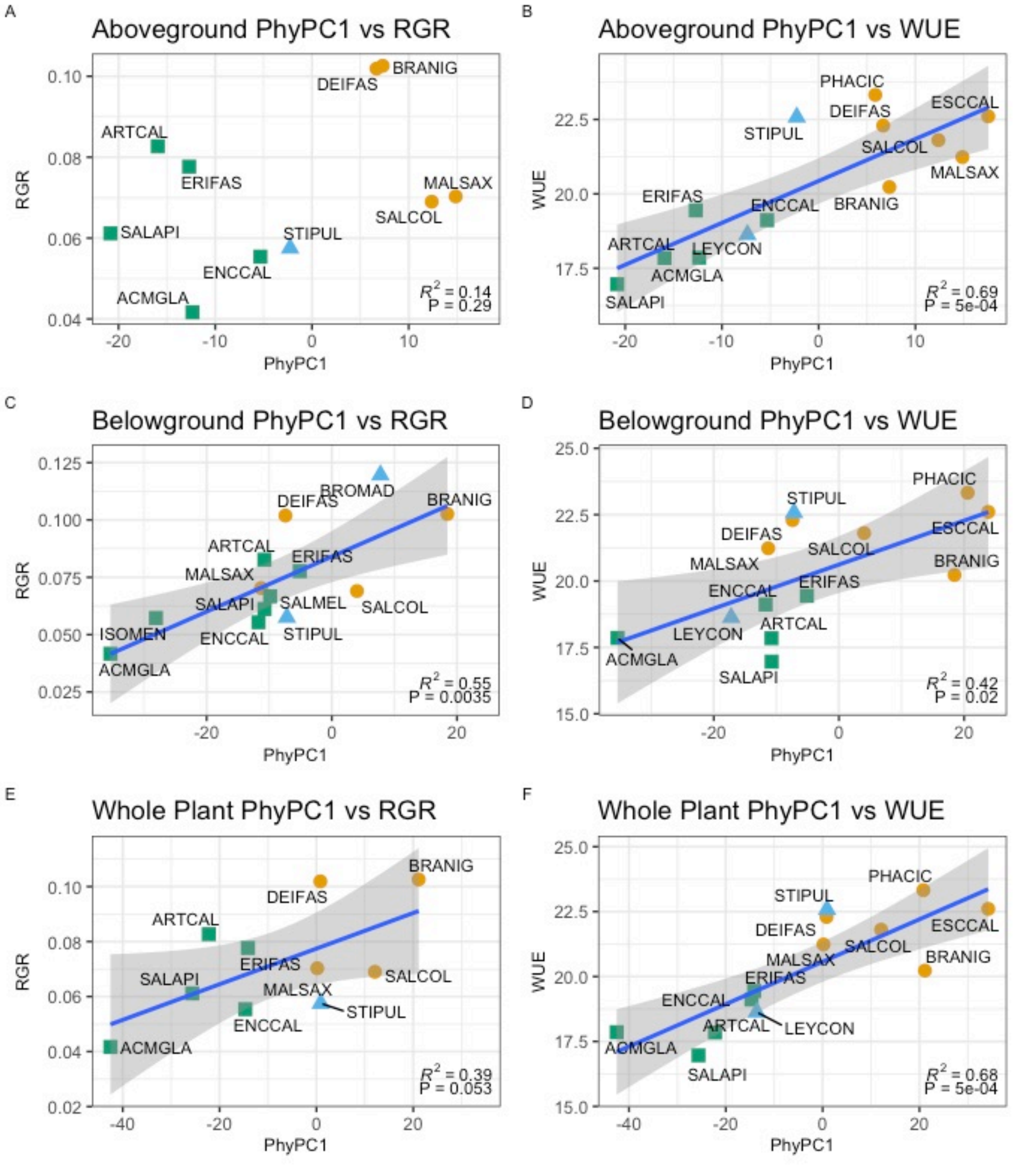


Figure S1.6. A. Plot of above-ground pPC1 against relative growth rate (RGR), with no significant relationship (R^2 = 0.14; P = 0.29). Grn. sqr. = shrub, ylw. circ. = forb, blu. tri. = grass. **B.** Plot of above-ground pPC1 against water use efficiency (WUE), with strong significant relationship ($R^2 = 0.69$; $P = 0.0005$; 95% CI). WUE values are from calculated carbon isotope discrimination with lower numbers indicating more water use efficient. Grn. sqr. = shrub, ylw. circ. = forb, blu. tri. = grass. **C.** Plot of below-ground pPC1 against relative growth rate (RGR), with significant relationship ($R^2 = 0.55$; $P = 0.004$). Grn. sqr. = shrub, ylw. circ. = forb, blu. tri. = grass. **D.** Plot of below-ground pPC1 against water use efficiency (WUE), with significant relationship ($R^2 = 0.42$; $P = 0.02$; 95% CI). WUE values are from calculated carbon isotope discrimination with lower numbers indicating more water use efficient. Grn. sqr. = shrub, ylw. circ. = forb, blu. tri. = grass. **E.** Plot of combined traits pPC1 against relative growth rate (RGR), with marginally significant relationship indicated by dotted line ($R^2 = 0.39$; $P = 0.053$). Grn. sqr. = shrub, ylw. circ. = forb, blu. tri. = grass. **F**. Plot of combined traits pPC1 against water use efficiency (WUE), with significant relationship ($R^2 = 0.68$; $P < 0.001$; 95% CI). WUE values are from calculated carbon isotope discrimination with lower numbers indicating more water use efficient. Grn. sqr. = shrub, ylw. circ. = forb, blu. tri. = grass.

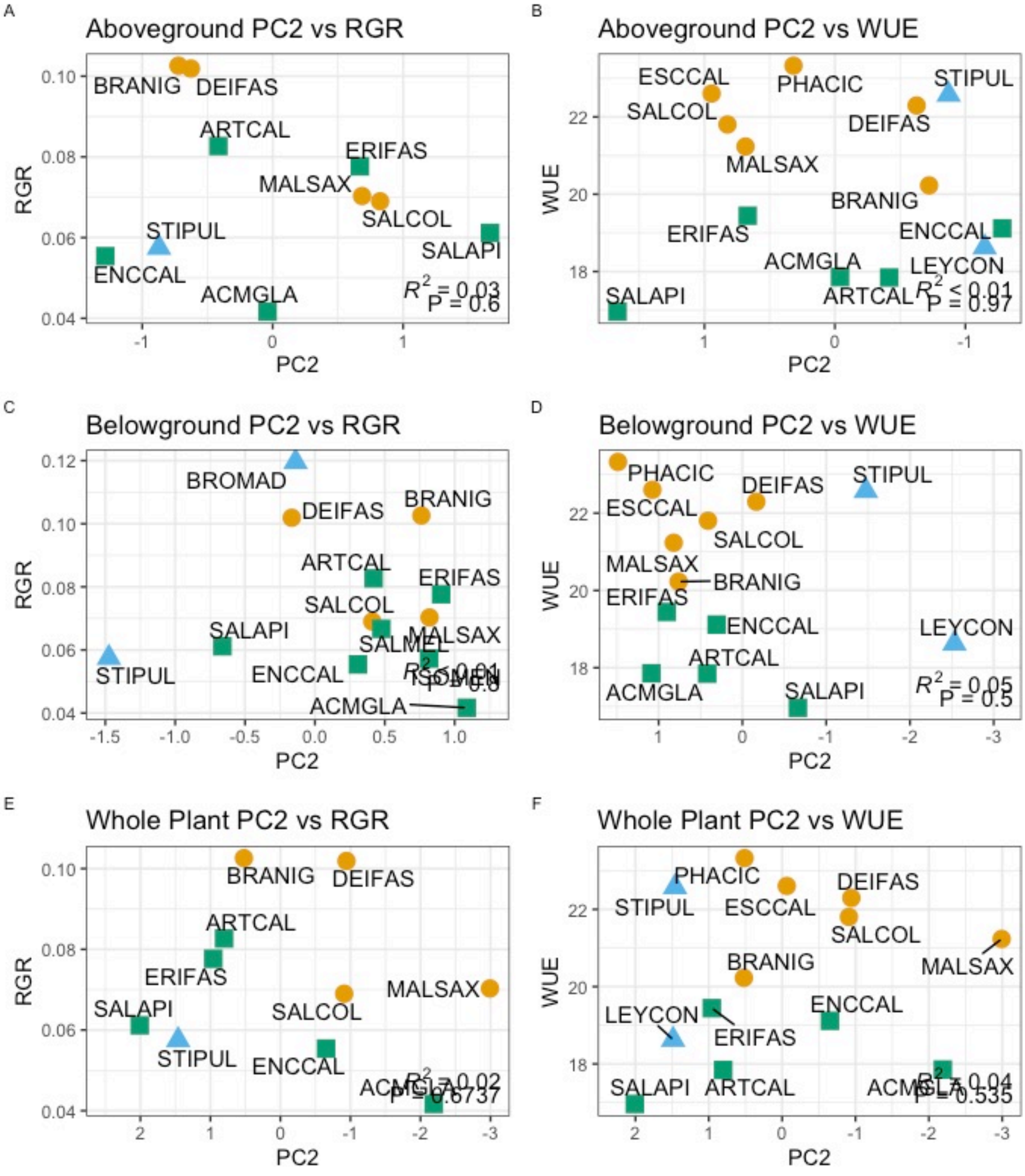


Fig. S1.7A. Plot of above-ground PC2 against relative growth rate (RGR), with No significant relationship (R^2 = 0.03; p = 0.6). Grn. sqr. = shrub, ylw. circ. = forb, blu. tri. =

grass. **B.** Plot of above-ground PC2 against water use efficiency (WUE), with strong significant relationship (R^2 <0.01; p = 0.97). WUE values are from calculated carbon isotope discrimination with lower numbers indicating more water use efficient. Grn. sqr. = shrub, ylw. circ. = forb, blu. tri. = grass. **C.** Plot of below-ground PC2 against relative growth rate (RGR), with significant relationship (R^2 <0.01; p = 0.8). Grn. sqr. = shrub, ylw. circ. = forb, blu. tri. = grass. **D.** Plot of below-ground PC2 against water use efficiency (WUE), with significant relationship (R^2 = 0.05; p = 0.5). WUE values are from calculated carbon isotope discrimination with lower numbers indicating more water use efficient. Grn. sqr. = shrub, ylw. circ. = forb, blu. tri. = grass. **E.** Plot of combined traits PC2 against relative growth rate (RGR), with marginally significant relationship indicated by dotted line (R^2 = 0.02; p = 0.67). Grn. sqr. = shrub, ylw. circ. = forb, blu. tri. = grass. **F**. Plot of combined traits PC2 against water use efficiency (WUE), with significant relationship (R^2 = 0.04; p = 0.54). WUE values are from calculated carbon isotope discrimination with lower numbers indicating more water use efficient. Grn. sqr. = shrub, ylw. circ. = forb, blu. tri. = grass.

Supplementary Tables

Table S1.1. Blomberg's K and Pagel's lambda values for species in the study. Values in bold represent significant phylogenetic signal and asterisk indicate marginally significant phylogenetic signal.

	K	*P*	lambda	*P*
Amass	0.238	*0.952*	0	*1*
gs	0.31	*0.747*	0	*1*
N%	0.307	*0.772*	0	*1*
SLA	0.331	*0.674*	0	*1*
WP	0.515	*0.238*	0.143	*0.855*
Height	0.342	*0.633*	0	*1*
RD	**0.579**	***0.008***	**0.813**	***0.034***
RMF	0.396	*0.084*	0.285	*0.676*
Rmass	0.344	*0.242*	0.328	*0.166*
Rlength	**0.506**	***0.022***	0.752	*0.112*
SRL	**0.455**	***0.049***	0.716	*0.219*
FRR	**0.577**	***0.012***	**0.837**	***0.033***
Nup	**0.467**	***0.043***	0.243	*0.483*
RTD	**0.67**	***0.002***	**0.809**	***0.003***
RGR	0.285	*0.391*	0	*1*
WUE	0.266	*0.913*	0	*1*

Table S1.2a. Above-ground trait loadings for each principal component

	PC1	PC2	PC3	PC4	PC5	PC6
gs	0.389	0.193	-0.835	0.050	0.025	0.332
N%	0.447	-0.301	0.271	-0.052	0.744	0.283
Height	-0.394	-0.255	-0.169	0.832	0.237	0.043
WP	0.292	0.790	0.306	0.419	0.102	-0.105
SLA	0.438	-0.314	0.284	0.324	-0.616	0.381
A_{mass}	0.465	-0.290	-0.164	0.145	-0.020	-0.807

Table S1.2b. Eigenvalues and percent variance explained by dimension in above-ground trait PCA

	Eigenvalue	Variance %	Cum. Variance %
Dim1	4.10	68.26	68.26
Dim2	0.85	14.13	82.39
Dim3	0.49	8.18	90.58
Dim4	0.42	6.92	97.50
Dim5	0.12	1.93	99.42
Dim6	0.03	0.58	100.00

Table S1.3a. Below-ground trait loadings for each principal component

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
RD	-0.410	-0.025	0.412	-0.176	0.092	-0.048	0.273	0.738
RMF	-0.267	-0.294	-0.499	-0.684	0.276	0.189	-0.112	-0.023
R_{mass}	0.226	-0.626	0.271	-0.266	-0.590	-0.156	-0.198	0.027
R_{length}	0.452	-0.115	0.057	-0.176	0.040	0.361	0.779	-0.097
SRL	0.421	0.285	-0.169	-0.052	-0.186	0.520	-0.368	0.519
FRR	0.400	-0.009	-0.457	-0.005	0.100	-0.683	0.155	0.361
N_{up}	0.377	-0.282	0.396	0.028	0.721	0.001	-0.318	0.014
RTD	-0.161	-0.589	-0.332	0.629	0.041	0.265	0.074	0.211

Table S1.3b. Eigenvalues and percent variance explained by dimension in below-ground trait PCA

	Eigenvalue	Variance %	Cum. Variance %
Dim1	4.67	58.37	58.37
Dim2	1.58	19.76	78.13
Dim3	1.15	14.43	92.55
Dim4	0.51	6.36	98.92
Dim5	0.06	0.69	99.61
Dim6	0.02	0.30	99.91
Dim7	0.01	0.08	99.99
Dim8	0.00	0.01	100.00

Table 1.4a. Above- and below-ground trait loadings for each principal component.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11	PC12	PC13
g_s	-0.287	-0.077	-0.108	-0.020	0.532	-0.355	-0.546	-0.019	0.068	0.065	0.397	0.104	0.119
N%	-0.277	-0.272	-0.273	0.167	-0.285	0.106	0.105	0.408	-0.450	0.064	0.235	0.441	0.125
Height	0.292	0.132	0.018	0.223	0.348	0.474	-0.154	0.652	0.120	-0.082	0.062	-0.166	0.018
WP	-0.180	-0.357	0.316	-0.354	0.296	-0.282	0.519	0.381	0.099	-0.118	-0.023	-0.087	0.004
RD	0.295	-0.293	-0.039	-0.361	-0.095	0.132	-0.177	-0.031	-0.027	-0.058	0.144	0.159	-0.171
RMF	0.261	0.011	-0.325	-0.079	0.555	0.198	0.410	-0.310	-0.310	0.312	0.041	0.096	0.052
R_{mass}	-0.146	0.381	-0.316	-0.613	0.011	0.119	-0.095	0.131	0.072	-0.236	-0.312	0.233	0.315
R_{length}	-0.331	0.238	0.042	-0.133	0.088	0.181	0.012	0.063	0.085	0.189	0.011	0.241	-0.814
SRL	-0.325	0.094	0.273	0.206	0.090	0.095	-0.009	0.036	0.079	0.519	-0.414	0.154	0.302
FRR	-0.280	0.332	0.012	0.336	0.172	0.020	0.270	-0.165	-0.110	-0.619	0.130	0.071	0.002
N_{up}	-0.316	0.232	-0.082	-0.245	-0.202	0.191	0.125	0.017	-0.048	0.266	0.475	-0.591	0.131
RTD	0.188	0.240	-0.518	0.179	-0.106	-0.517	0.226	0.267	0.327	0.194	-0.005	0.005	-0.105
SLA	-0.225	-0.409	-0.302	0.116	-0.009	0.377	0.135	-0.207	0.670	-0.074	0.062	0.067	0.086
A_{mass}	-0.259	-0.299	-0.404	0.073	0.110	-0.016	-0.176	0.040	-0.287	-0.113	-0.495	-0.480	-0.220

Table S1.4b. Eigenvalues and percent variance explained by dimension in combined above- and below-ground trait PCA.

	Eigenvalue	Variance %	Cum.Variance %
Dim1	7.64	54.55	54.55
Dim2	2.20	15.70	70.25
Dim3	1.59	11.38	81.63
Dim4	0.92	6.55	88.18
Dim5	0.71	5.10	93.28
Dim6	0.39	2.81	96.09
Dim7	0.28	1.99	98.08
Dim8	0.19	1.38	99.47
Dim9	0.04	0.28	99.75
Dim10	0.02	0.12	99.87
Dim11	0.01	0.09	99.95
Dim12	0.01	0.05	100.00
Dim13	0.00	0.00	100.00

CHAPTER 2

Wood trait plasticity in *Artemisia californica* across water treatments and age

Introduction

Dryland environments are known for highly variable precipitation regimes that lead to systems driven by pulse dynamics with strong inter- and intra-annual variability (Yang et al. 2008). Furthermore, climate models predict that this precipitation variability will only become more extreme, dramatically altering soil water availability for plants in these systems (IPCC 2013). These changes have dramatic implications for plant water relations, the regulation of photosynthesis, growth, and reproduction. However, phenotypic plasticity, the capacity for a plant, within genetic constraints, to adopt a range of phenotypes given exposure to particular environmental conditions, in functional traits related to resource-use, may provide long-lived species, such as shrubs, a mechanism to mitigate environmental stress (Borges 2009). This flexibility may allow plants to produce tissues more suitable to an altered precipitation regime delaying or preventing shifts in abundance and distribution and allowing a path to adaptation. At the same time, such shifts in morphology may canalize plant developmental trajectories to influence other plant processes (Coleman et al. 2017). There remain knowledge gaps in how traits structuring resource-use will respond to altered precipitation and how this will impact performance for many key species important for ecosystem function.

A critical component to hydraulic function in vascular plants can be found in stem tissue anatomy. Xylem vessels, representing the plumbing of a plant, are arranged one after another in a stem and connected via perforated plates forming a continuous path transporting water from the roots, where plants uptake soil water, to the leaves where it is transpired. This water transport happens as a result of the combination of cohesion, adhesion, and tension with water following an increasingly negative pressure potential gradient (Henry and Joly 1895, Tyree 1997, Floto 1999, Steudle 2001). Vessels with larger diameters can transport water more efficiently while narrow-vessel plants are more resistant to cavitation (Gleason et al. 2016) establishing a trade-off between hydraulic efficiency and safety (Sperry 1995). In addition to hydraulic transport, stems also provide structural support through sclerenchymatous stem fibers, and water storage through parenchyma cells. Selection on the multiple functions and trade-offs involved in stems has led to a diversity of xylem vessel sizes and densities, wood densities, and tissue type proportions within plants (Chave et al. 2009, Lachenbruch and McCulloh 2014).

Stem and xylem anatomical traits have been shown to impact physiology determining plant strategies. Recent efforts to describe trait trade-offs using economic models that place plants on a productivity to persistence spectrum have found that stem traits reflect these broad fast/slow strategies well established for other plant tissues (Chave et al. 2009, Reich 2014a). Increasing wood density has been correlated negatively with stem hydraulic conductivity, positively with increased P_{50}, an important drought tolerance indicator that describes the stem water potential that results in a 50% loss of conductivity, negatively with photosynthetic capacity, and negatively with minimum daily leaf water potential (Santiago et al. 2004, Markesteijn et al. 2011). (Pratt et al. 2007)) found that greater xylem density was associated with water stress tolerance traits like lower P_{min}, greater modulus of rupture (MOR), and greater $(t/b)^2_h$ in South African chaparral species. However, in growth analyses, wood density, an integrated measure that combines features like vessel wall thickness, vessel number, and tissue type proportions, was less predictive than mean vessel diameter, a proxy for hydraulic conductivity, in explaining the performance of 40 Amazonian trees (Fan et al. 2012). Furthermore, wood density and vessel traits were found to be independent in shrub species (Martínez-Cabrera et al. 2011) suggesting that strategies in stem traits need further investigation.

During sapwood tissue construction, the structures built are immutable, forming the foundation on which future tissues will be built, and thus it is difficult to view these traits as plastic. However, xylem and wood traits are plastic in response to the environment with this flexibility manifesting at the time the tissues are constructed. (Martínez-Vilalta et al. 2009, Fonti and Jansen 2012, Von Arx et al. 2012). Recent studies have found that xylem plasticity was related to drought and deciduousness with deciduous species having greater vessel plasticity and plants in dryer sites having smaller vessels (Scholz et al. 2014). In another study researchers found water transport traits to vary positively with increased water availability in a perennial herb (Von Arx et al. 2012). However, this plasticity is fraught because plants cannot shed these tissues, which may lead to anatomical features poorly suited to future environmental states. This asymmetry may be especially important for xylem vessels because flow rates are approximated using the Hagen-Poiseuille equation for fluid movement through an ideal capillary, which states hydraulic conductance is proportional to the 4 power of the xylem vessel diameter leading to large changes in flow rates for small changes in vessel diameter. For example, a doubling of a vessel radius makes for a 16-fold increase in flow, which may also increase vulnerability to cavitation. Recent work has demonstrated that anatomical traits impact performance and demographic rates (Poorter et al. 2008, 2010) and reflect plant strategy (Adler et al. 2014), however, little work has been done to understand how plasticity may alter these relationships (Fonti and Jansen 2012).

Trait plasticity may play an important role in variation within communities. When deconstructing the components of species trait variation, a large portion (~25% in a global meta-analysis, but even higher numbers in context-specific studies (30% (Albert et al. 2010) and 83% (Hulshof and Swenson 2010)) has been determined to be intraspecific (Siefert et al. 2015)). This intraspecific variability is shown to be an important component of variation in relatively species-poor environments (Siefert et al. 2015). This variation may be caused by underlying genetic variation or through phenotypic plasticity in response to the environment. Phenotypic plasticity is hypothesized to allow for species coexistence by providing plants a mechanism for partitioning resources (Bolnick et al. 2003, 2011, Fridley and Grime 2010). However, recent research has suggested that nonlinearity of plant traits effect’s on vital rates may mean that plasticity can hamper coexistence (Hart et al. 2016). Either way, phenotypic plasticity may have important consequences for plant fitness and indirectly for populations and communities. Plasticity may have an especially important role in xylem and stem traits with changes to anatomical traits potentially impacting the inherent trade-off between efficiency and safety. Specifically, if under wet conditions plants produce xylem vessels with larger diameters, gains in water conductivity may come at the cost of a heightened risk of hydraulic failure. Alternatively, plants grown under dry conditions may develop smaller vessels reducing their conductive potential, but protecting them from drought-induced mortality. The question becomes, how will plants respond to differential resource availability, and will shifts in trait values have impacts on fitness?

We investigate how wood traits in *Artemisia californica* vary over a precipitation gradient as a function of age and how this variation impacts the fitness components of growth and reproduction. We think:

1. Wood anatomical traits will differ with age, becoming more conductive (i.e., larger vessel size, greater vessel frequency, etc.) as plants get older.
2. Wood anatomical traits will differ depending on water treatment, with plants grown in higher water being more conductive (i.e., larger vessels, greater specific conductivity, etc.). However, we may also see that plasticity is limited given the vital role of hydraulic architecture and which may represent a conservative strategy.
3. Plants will experience interactive effects of water and age on wood traits, such that older plants in high water treatments will have wood traits that are more than additively conductive

Methods

Study System

Artemisia californica is a perennial, facultatively drought-deciduous shrub native to the west coast of North America, whose range extends from mesic sites north of San Francisco Bay, to arid Baja California. It is a dominant and foundational member of coastal sage scrub plant communities which exist in Mediterranean-type ecosystems and which has seen a drastic reduction in its range, threatened largely by development (Cleland et al. 2016). This diffuse-porous species with distinct growth ring boundaries has extensive branching from the base and is typical of semi-arid shrubs from this region in having relatively narrow xylem vessels. We believe this to be a ripe system for studying wood trait plasticity with respect to age and precipitation as *A. californica* as plasticity in other tissues has been documented. Furthermore, *A. californica* reaches maturity quickly, forming flowers as early as the first year, and can live between 10 and 40 years (citation?), a span during which legacy wood traits may be important. Additionally, this ecosystem has strong interannual and seasonal abiotic variability which have shaped the evolution of this species, and which are only predicted to intensify under future climate scenarios. Plants used for this experiment were grown by The Tree of Life Nursery (San Juan Capistrano, CA, USA), from locally sourced seeds and transplanted at 5 months.

Site and Experimental Design

To test the effects of altered precipitation, we established nine rain-out structures (7.3m long x 2.6 m wide x 2.6 m high) in a former agricultural field at the University of California South Coast Research and Extension Center (Irvine, CA, USA, (33°41′N, 117°43′W; 125 m elevation, 330 mm mean annual precipitation (MAP)). Eight 1 m^2 plots were established in each structure in a centrally located 2 x 4 plot arrangement with 1 plant per plot (N = 72). Structures had raisable clear plastic coverings that were deployed for rain events greater than 6 mm to exclude rainfall which was then diverted away from plots via channels. Precipitation was monitored at the field site using ECRN-50 rain gauge (1 mm resolution; Decagon Devices, Inc. Pullman, WA, USA) and data were checked against regional weather stations. Precipitation treatments were established using spray irrigation with 1.5 m tall sprinklers (6 per structure), 14 mm hr^{-1} flow rate, and >75% distribution uniformity. We placed soil moisture probes (EC-5 sensor; decagon Devices, Inc., Pullman WA, USA) 15 cm deep at one corner of each structure, 1.8 m from the end and 0.15 m from the side. Watering treatments were applied from January to April to mimic the wet season in semi-weekly watering events which were calculated to establish three separate watering treatments (3 structures each at 50% MAP - 110 mm, 100% MAP (ambient) - 220 mm, and 150% MAP - 330 mm). All structures were enclosed in a chicken wire fence to reduce herbivory and weeded bi-weekly to remove non-focal species.

In December 2013 we transplanted one *A. californica* seedling, into each 1 m^2 plot within each structure. Each plot also contained one individual of each of seven other CSS species located randomly within each plot with 30 cm between plants. Plants were allowed to establish for one month, during which all plants received approximately 20 mm of precipitation and any dead individuals were replanted. Watering treatments began in January 2014 and continued through the 2016 wet season. There was some mortality across the three-year experiment with 2 and 3 plants lost in the 100 and 150% respectively in year 1 and 5 additional plants lost in the 100% treatment in year 3.

During the 3-year experiment, soil moisture readings in each structure reflected their given treatments. Mean growing season soil moisture for each treatment by year was: 50% (Y1, 18.3 %; Y2, 17.4 %; Y3, 19.5 %); 100 % (Y1, 19.8 %; Y2, 20.1 %; Y3, 20.9) and 150 % (Y1, 25.7 %; Y2, 22.7 %; Y3, 23.7 %). Structure covers were not raised during the dry season (May - December) with any precipitation that did fall added to the target precipitation totals for the coming year. Dry season rain events were rare and minor save a September 2015 storm which added 53 mm of precipitation.

Wood traits

Sample processing

To examine wood trait plasticity over time, we sampled mature branches in mid-October of 2016, the final year of the study, at the end of the dry season. We randomly selected 1 representative branch from 6 plants in each treatment (6 plants/treatment x 3 treatments = 18 plants; 2 from each structure except for the 100% treatment in which 3 plants were sampled from 1 structure and only 1 from another). We cut 10-20 cm segments approximately 10cm from the ground of vertically oriented, unbranched stems containing growth rings for all three growing seasons. To avoid desiccation, stem segments were immediately placed in humid zip-lock bags, placed in a cooler, and transported to UC Irvine where they were stored in a -20°C freezer until processing.

To prepare our samples for data collection, we made slides of transverse sections of each of the 18 individuals. We removed a 1cm piece of the proximal end of the stem segments to avoid sampling potentially desiccated wood and then cut a 2-5 cm section of the field harvested sample. These were sectioned using a sledge microtome

(Base Sledge Microtome Model 1300, Ernst Leitz, Germany), to a thickness of 20 - 50 µm and mounted in glycerol.

Data Collection

Data collection involved using a photo microscope (Eclipse 90i, Nikon Instruments Inc., Minato City Tokyo, Japan) to image samples at 2 different magnifications and subsequent image processing (Fiji, 2.3.0/1.53n; Schindelin et al., 2012). We measured growth ring area and xylem vessel density from 2 perpendicular transects through the center of the stem taken at 40x magnification. We averaged 4 radii taken at the boundary of each ring and used the following formula to estimate ring area:

$$\mathrm{Area}_{\mathrm{ring}} = \pi\,(r_2^2 - r_1^2) \qquad \text{Eq. 1}$$

where r_2 (mm) is the average outer radius and r_1 (mm) the average inner radius of each ring. To avoid including non-woody tissue in our analyses, the inner most radius, which accounted for the pith and primary xylem, was measured to the approximate transition between primary and secondary xylem.

To measure vessel frequency (VF; vessels mm^{-2}) for each ring, we counted all vessels ($N > 150$, in all but 2 samples from) in a wedge-shaped radial area between ring transitions for each ring. Vessels less than 10 µm in diameter contribute negligibly to potential flow and were not counted in density measurements.

Vessel areas (µm) were measured at 400x magnification and used, in conjunction with $\text{Area}_{\text{ring}}$ and VF, to calculate several important parameters. We measured at least 70 vessels per ring along radial transects using 2 perpendicular dimeters, crossing the widest part of the vessel, and assuming an ellipsoid area. Vessel areas were calculated as:

$$\text{VA} = \pi\, ab \qquad \text{Eq. 2}$$

where *a* and *b* are the radii of each measured vessel taken at perpendicular angles.

We calculated the Hagen-Poiseuille diameter (D_{HP}) for each ring on each sample, which is the diameter, if multiplied by the vessel density, that renders the same potential specific conductivity as would the actual distribution of vessel diameters. We calculated the D_{HP} assuming ellipsoid vessel areas (Steppe and Lemeur 2007) using the following:

$$D_{HP} = \sqrt[4]{\frac{1}{n}\sum_{i=1}^{n}\frac{2a_i^3b_i^3}{a_i^2+b_i^2}} \qquad \text{Eq. 3}$$

where n is the number of vessels, a and b are the perpendicular vessel diameters (µm).

We calculated three potential conductivity measures, K_s, K_{ring}, K_{stem}. Potential specific hydraulic conductivity, assuming Hagen-Poiseuille fluid flow dynamics, was calculated as K_s (kg m^{-1} s^{-1} MPa^{-1}):

$$K_s = \left(\frac{\pi\rho}{128\eta}\right) \times {D_{HP}}^4 \times VF \qquad \text{Eq. 4}$$

where ρ is the density of water 998.21 (kg m^3), η is the viscosity of water $1.002x10^{-9}$ (MPa s^{-1}), D_{HP} is the Hagen-Poiseuille diameter (m), and VF is the vessel frequency (vessels m^{-2}). Potential hydraulic conductivity for a given ring, K_{ring} (kg m s^{-1} MPa^{-1}), was calculated as:

$$K_{ring} = K_s \text{ x } Area_{ring} \qquad \text{Eq. 5}$$

Where K_s is the potential specific hydraulic conductivity and $Area_{ring}$ is the corresponding ring area. Potential stem hydraulic conductivity, K_{stem} (kg m s^{-1} MPa^{-1}), was calculated as follows:

$$K_{stem(1)} = K_{ring(1)}$$

$$K_{stem(2)} = K_{ring(1)} + K_{ring(2)} \qquad \text{Eq. 6}$$

$$K_{stem(3)} = K_{ring(1)} + K_{ring(2)} + K_{ring(3)}$$

Where $K_{ring(1)}$ is the potential hydraulic conductivity for the first year's ring, etc.

Data Analysis

To test for differences between watering treatment and age we constructed linear mixed models for each variable with watering treatment, ring, and their interaction as continuous fixed effects along with a random effect of individual. Due to the controversy surrounding how to estimate degrees of freedom in mixed effects models and the resulting difficulty in declaring a p-value, we have instead opted for a K_{ring}, $Area_{stem}$, and

$\text{Area}_{\text{ring}}$ were log transformed to meet model assumptions of normality. To examine allometric relationships between $\text{Area}_{\text{ring}}$ and VA, we constructed a linear mixed effects model with treatment, ring and their interaction, and $\text{Area}_{\text{ring}}$ as continuous fixed effects and individual as a random effect.

Results

Xylem vessel traits

Mean vessel area increased with age (χ^2 = 31.70, P < 0.001, Fig. 2.1) and watering treatment (χ^2 = 12.54, P < 0.001, Fig. 2.1). We also detected a marginally signifcant interaction between age and watering treatment (χ^2 = 3.50, P = 0.062, Fig. 2.1) with differences between watering treatments in year one and two with positive slopes converging to be indistinguishable in year three.

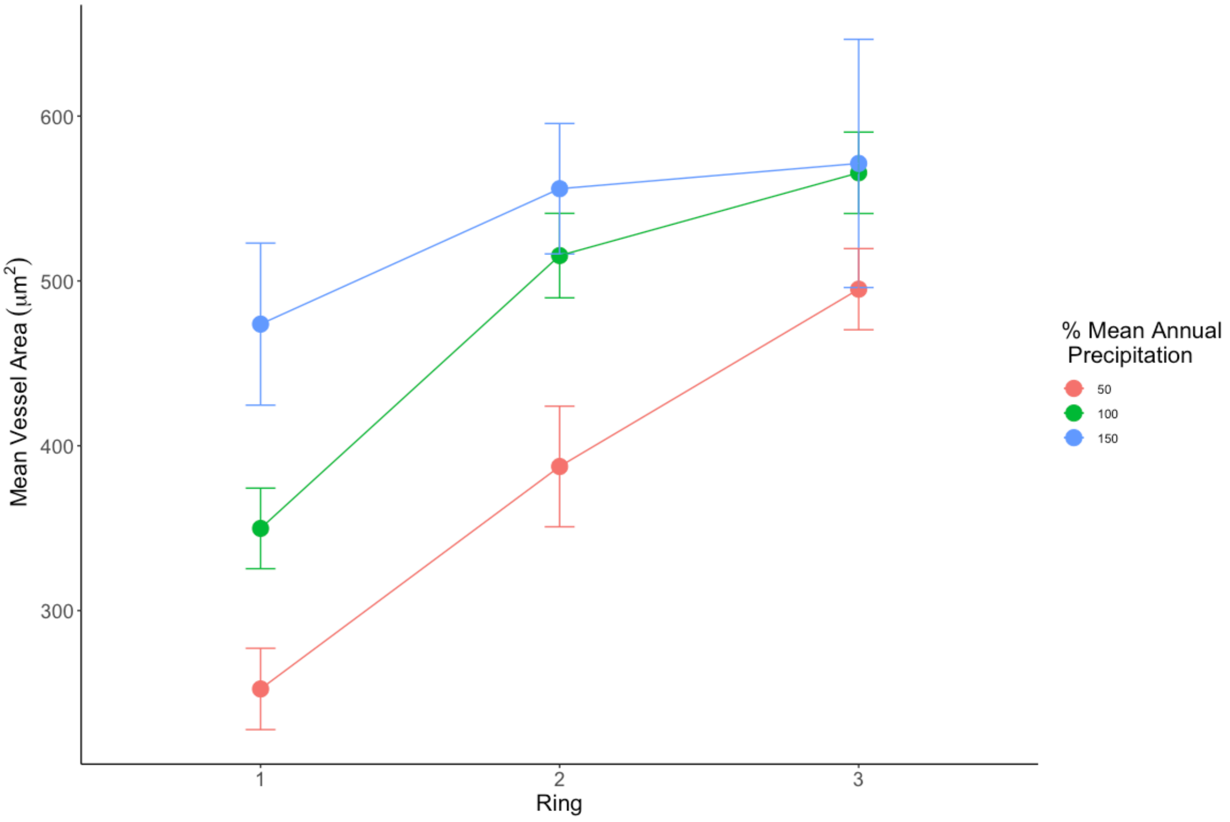


Figure 2.1. Mean vessel area (μm^2) (± SE) across cambial age, indicated by ring, and watering treatments 50% (red), 100% (green), and 150% (blue) of mean annual precipitation.

Vessel density was not impacted by treatment ($\chi^2 = 0.04$, $P = 0.852$, Fig. 2.2). There was a maginally significant response to age with plants having lower vessel densities as they became older ($\chi^2 = 2.77$, $P = 0.096$, Fig. 2.2), however, this pattern was largely driven by high vessel densities in year one with values becoming mostly constant in years two and three. A notable exception to the impact of treatment can be seen in year one when the 100% watering treatment had lower vessel densities than the 50% and 150% treatments which were similar to one another (Fig. 2.2).

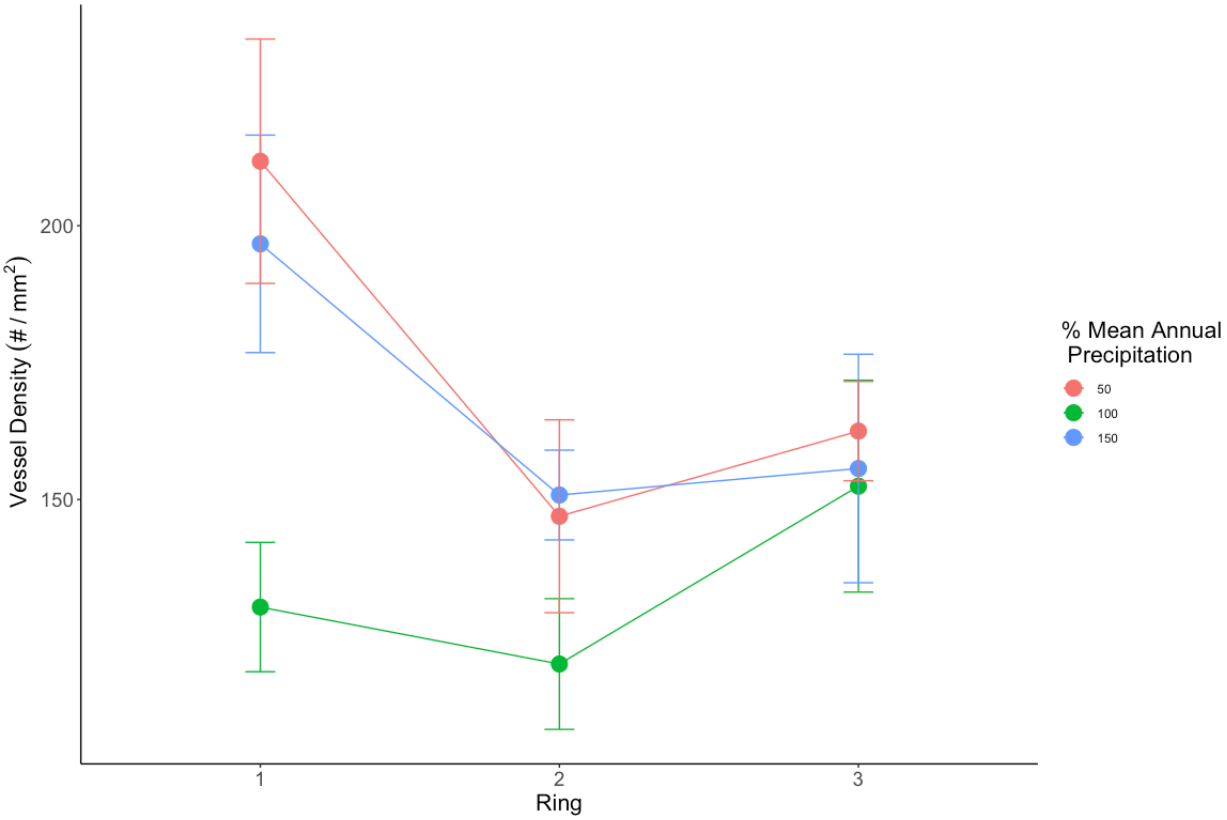


Figure 2.2. Vessel density (vessels/mm^2) (± SE) across cambial age, indicated by ring, and watering treatments; 50% (red), 100% (green), and 150% (blue) of mean annual precipitation.

Ring area

The logarithm of Area$_{\text{ring}}$ increased significantly with main effects of age (χ^2 = 539.51, $P < 0.001$, Fig. 2.3) and watering treatment (χ^2 = 13.66, $P < 0.001$, Fig. 2.3) with the 50% MAP watering treatment having a lower interept than the 100% and 150% treatments, which were statistically indistinguishable from one another. However, the pith area and 1st year's wood growth of the 100% treatment was slightly higher than the 150% treatment, a pattern which reversed itself for wood from year two and three. We did not detect an interaction between age and water treatment, however, the logarithmic transformation masks the large apparent differences between treatments — differences that grow larger with age (Fig. 2.3).

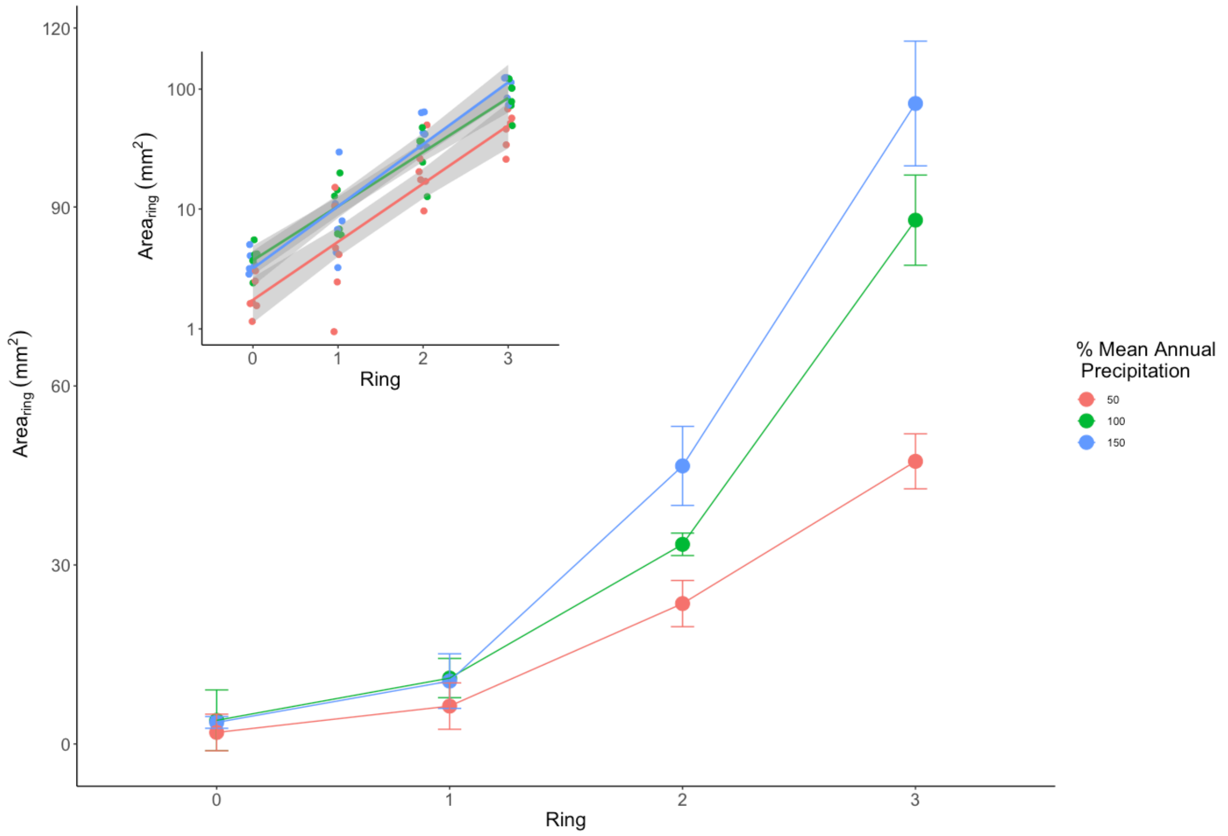


Figure 2.3. Ring area ($\text{Area}_{\text{ring}}$) ($\text{mm}^2$) (± SE) across cambial age indicated by ring and watering treatments; 50% (red), 100% (green), and 150% (blue) of mean annual precipitation. Ring = 0 represents non woody tissue including pith and primary xylem at the center of the stem. Inset shows log transformed y-axis with least squares regression lines and shaded region representing 95% C.I. Points are jittered around each ring stage only to improve.

Allometric relationships between ring area and vessel diameter

We found VA increased with the logarithm of Area$_{\text{ring}}$ (χ^2 = 12.35, P < 0.001, Fig. 2.4) such that VA was larger in rings with larger area. Treatment alone (χ^2 = 5.85, P = 0.016, Fig. 2.4) and its interaction with ring (χ^2 = 5.85, P = 0.016, Fig. 2.4); χ^2 = 3.93, P = 0.047, Fig. 2.4, respectively) were also significant such that larger vessles were found in higher water treatements and VA was more greatly affected by treatment in year one, with greater VA with increasing water than in year there, where there was little difference.

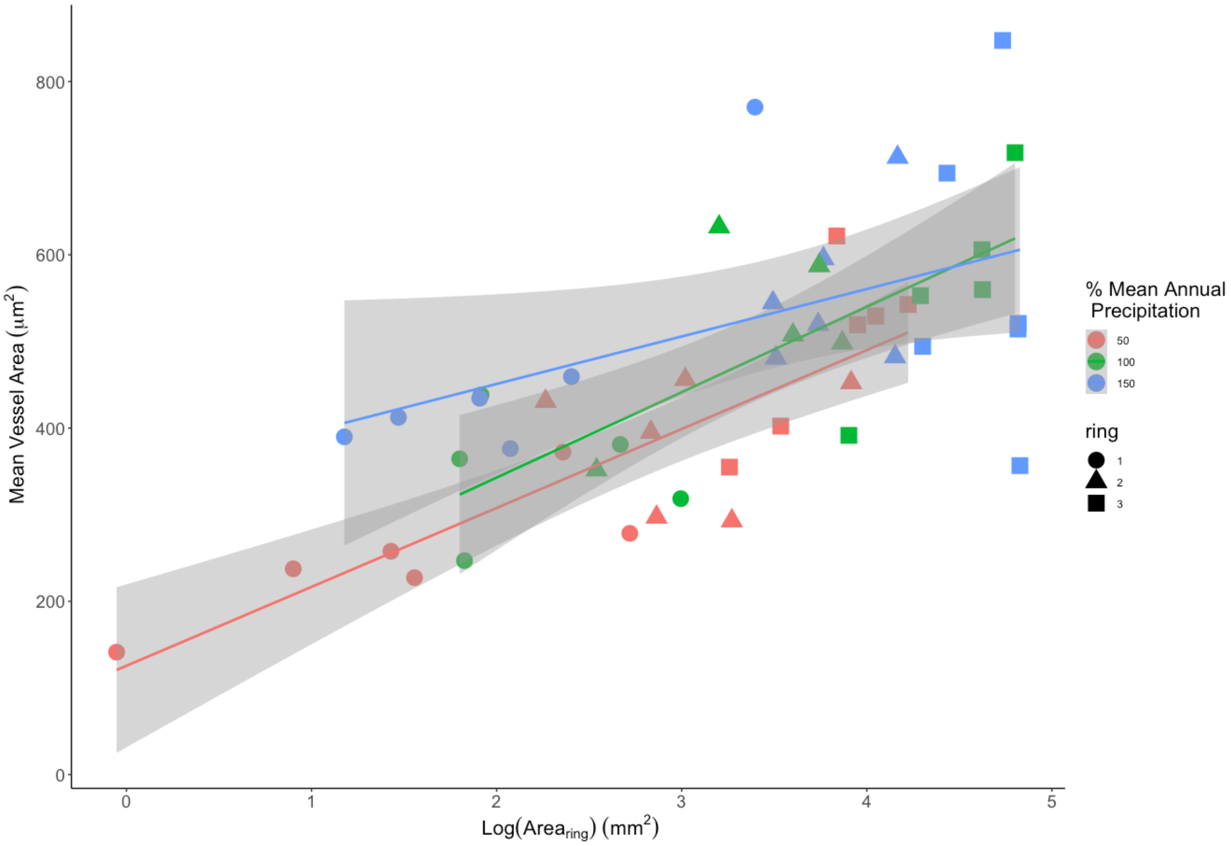


Figure 2.4. Relationship between logarithim of ring area ($Area_{ring}$; mm^2) and mean vessel area. Cambial age is indicated by ring (ring 1 = circle, ring 2 = triangle, ring 3 = square); watering treatments: 50% (red), 100% (green), and 150% (blue) of mean annual precipitation.

Potential Conductivity

The potential specific hydraulic conductivity K_s (kg m^{-1} s^{-1} MPa^{-1}) increased significantly with both age (χ^2 = 27.65, $P < 0.001$, Fig. 2.5) and watering treatment (χ^2 = 7.12, $P = 0.008$, Fig. 2.5). The interaction between age and watering treatment was marginally significant (χ^2 = 3.45, $P = 0.063$, Fig. 2.5) with slopes converging as plants aged with the strongest differences appearing in year one. Similarly, the logarithm of potential ring hydraulic conductivity increased significantly with age (χ^2 = 175.91, P = 0.001, Fig. 2.6). There also was a significant effect of watering treatment (χ^2 = 16.96, $P < 0.001$, Fig. 2.6) but this separated the 50% treatment from the 100% and 150% treatment which were indistinguishable from one another. The interaction of these two variables was also significant (χ^2 = 5.12, $P < 0.024$, Fig. 2.6) with a steeper positive slope in the 50% watering treatment, however, slopes had not converged by the third year. Additionally, the logarithmic scale masks large differences in real K_{ring} which by the 3 year have establsihed apparent trajectories with the 50% watering treatment having lower K_{ring} that the 100% and 150% treatments which were the same.

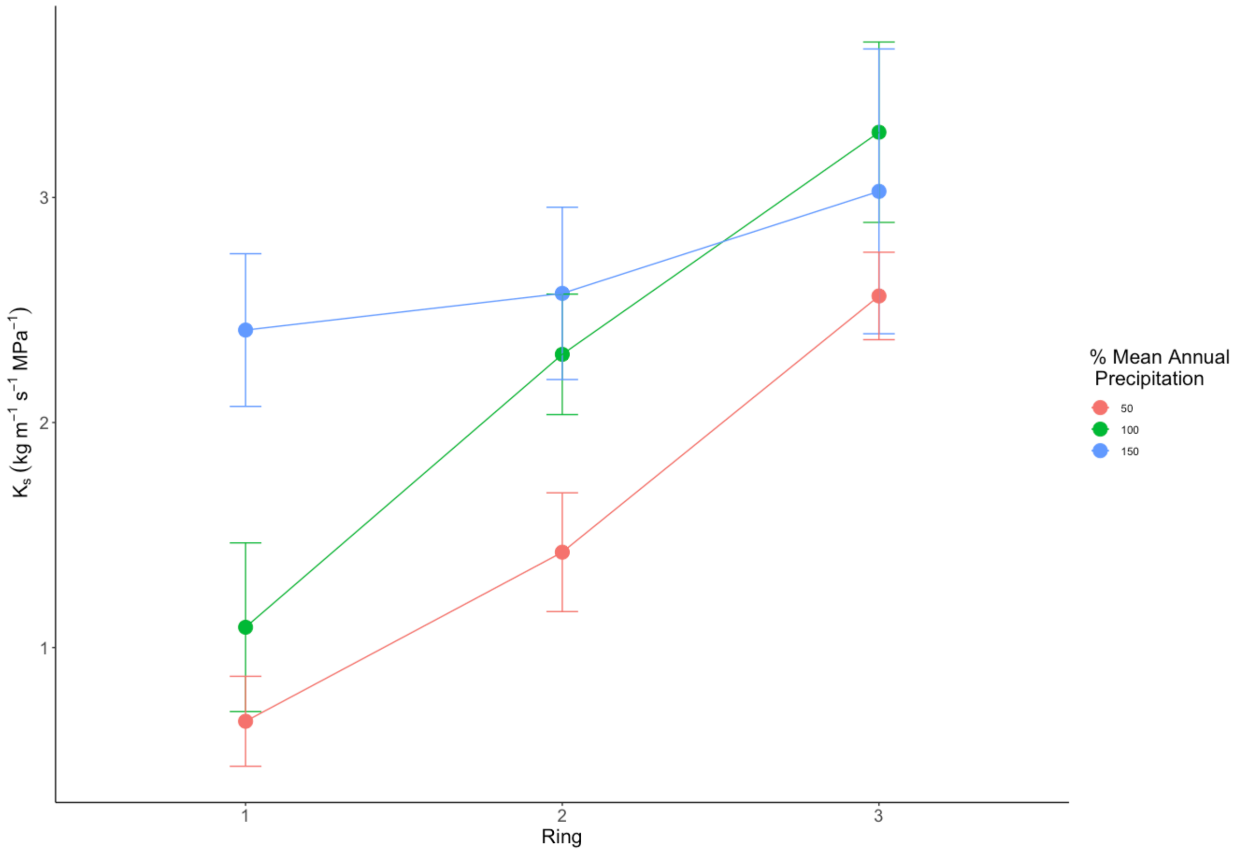


Figure 2.5. Mean potential specific hydraulic conductivity K_s (kg m^{-1} s^{-1} MPa^{-1}) (± SE) across cambial age, indicated by ring, and watering treatments; 50% (red), 100% (green), and 150% (blue) of mean annual precipitation.

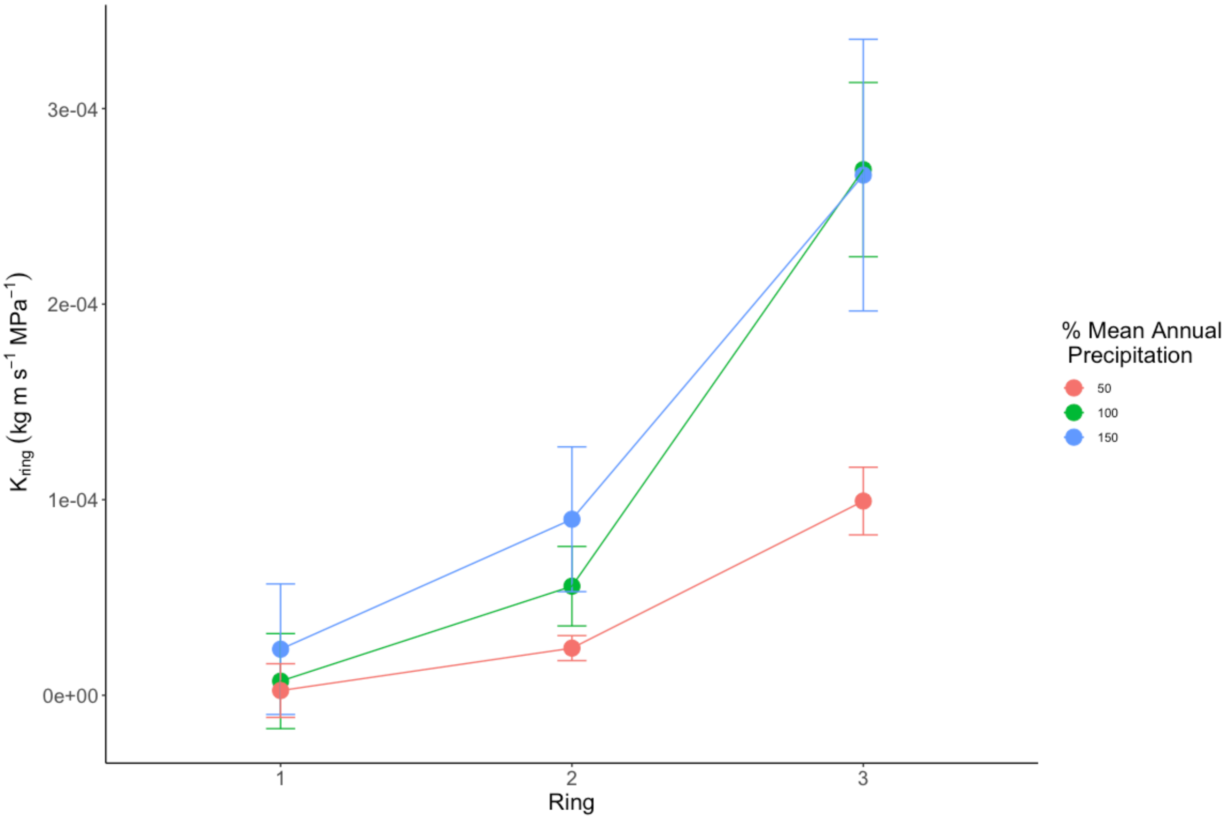


Figure 2.6. Mean potential ring hydraulic conductivity K_{ring} (kg m s^{-1} MPa^{-1}) (± SE) across cambial age, indicated by ring, and watering treatments; 50% (red), 100% (green), and 150% (blue) of mean annual precipitation.

Discussion

Our study examined the impact of varied precipition and age on wood traits of the semi arid shrub *Artemisia californica*, xylem vessel area and density, ring area, and potential hydraulic conductivity, specific and for the whole ring. In general plants developed traits that would make them potentially more conductive as they aged and with increased water availability. Specifically, VA, $Area_{ring}$, K_s, and K_{ring} all increased with age and water but differences between watering treatments was most prominent in the first year. Vessel density showed slight variation in year 1, but was generally constant. Our results suggest older plants grown in high water environments have greater conductive potential and thus may transport water more efficiently, but they may incur a cost in becoming more vulnerable to cavitation. Further, differences in water availability had the biggest effects in year one making hinting at the importance these changes at the establishment time scale.

Wood traits with age

Our findings were consistent with studies showing increasing vessel areas and increased potential hydraulic conductivity with increasing age (Rodriguez-Zaccaro et al. 2019). One explanation for xylem vessel area increasing with age may lie in the tapering of conduits and packing patterns observed along the hydraulic path from stem to leaves (Anfodillo et al. 2006, McCulloh et al. 2010). Because sap ascent is driven by a negative pressure gradient, there is a risk of embolism which requires sufficient redundany in the xylem network to avoid runaway hydraulic failure (Ewers et al. 2007). Thus, narrower vessels in terminal branches of trees may be required if enough vessels are to fit in the smaller sapwood of the branches and achieve this redundancy (i.e. not enough big vessels will fit)(McCulloh et al. 2010). If we consider our study a space for time substitution, we can view the first year wood as functionally similar to wood in terminal branches of a mature individual and that older wood hosts the basal, widest part of tapering conduits. This is further supported in our study by 1) smaller ring areas in younger rings, such that greater packing is required to achieve redundancy, and 2) relatively constant vessel densities across age as vessel areas scale with wood area. We noticed an exception with slightly higher vessel densities in year one for the 50% and 150% MAP treatments. However, the 50% treatment may require a greater number of the comparatively smaller vessels (Fig. 2.1) to meet the canopy's transpirative demand while the 150% treatment may be taking advantage of a reource rich environment.

Increasing potential hydraulic conductivity (K_s, and K_{ring}) with age is expected when considering the increase in vessel area with age (Jacobsen and Pratt 2018). The Hagen-Poiseuille equation estimates large increases in potential conductivity for small changes in vessel diameter, thus the increase in vessel area with age along with ring area and relatively constant vessel frequencies, ensure multiplicative increases in K_s and K_{ring}. Increases in conductivity are required for increasing a plant's canopy and plants may benefit from the fast growth efficient water transport allows. However, increased efficiency in conductivity may increase vulnerability to cavitation through the safety vs. efficiency trade-off (Hacke et al. 2006, Gleason et al. 2016), but this trade-off may not be operating in all systems (Rodriguez-Zaccaro et al. 2019). Furthermore, we must exercise caution when interpreting potential/theoretical conductivity calculated from anatomical features as they may substatnitally over estimate actual conductivity (Tyree and Ewers 1991). Future work to determine how these potential hydraulic parameters relate to function across time will be important for undertanding hydraulic responses in age structured populations.

Water availability and its interaction with age

Similar to age, higher water availability generally increased potential hydraulic conductivity and the traits underpinning it. However, water was unique in that its effect often interacted with age – an interaction which generally converged in later years. Mean vessel area is a perfect example with differences largest in year one after which they decreased and almost converged. This points to the importance of the establishment phase in determing vessel structure and may hint at a strategy for the species to recruit in dry years. Because plants cannot migrate away from stressful abiotic conditions such as drought, smaller vessels areas may provide a safe water transport system to tolerate the dry year while incuring a cost to water transport efficiency. This is generally supported by the assumption that young plants should be more plastic, especially in variable environement (Niinemets 2004). The convergence in later years may have also resulted from older plants being buffered against environmental stressors with more extensive root networks and potentially more developed storage tissues. Likewise, this may point to our 50% water treatment not being extreme enough to induce differential trait responses. We also considered whether the vessel size was an allometric relationship with ring area, however, the interactive effects seen between vessel area, ring area, and age support our interpretation.

Ring area was a notable trait in that it was greatly impacted by watering treatment and also established ring growth tragectories. Our plot of the logarithm of ring area i fsunctionally a wood radial relative growth rate plot and demonstrates similar slopes for each of the treatments, but a lower intercept for the 50% treatment. Thus, secondary wood growth is largely determined by the size of the stem. Further the plot suggests that pith area at least partially establishes the growth trajectory with a larger pith area leading to larger ring areas. Drought affects pith growth with supressed growth hormone activity (Paul et al. 2018), but pith area has also been linked to seedling height such that shorter seedlings have smaller piths(Vander Mijnsbrugge et al. 2020). We also might expect that cell expansion during acid growth may be hinded in low water environments if plants have low turgor pressure.One reason this may result is that individuals exposed to greater water availability may have a greater. This again points to the importance of abiotic conditions during establishment in shaping trajectories.

Specific hydraulic conductivity showed an interactive effect of water availability and age with K_s having large differences in year one and converging by year three. This is largely driven by the convergence in mean vessel area since vessel densities, the other parameter used to calculate K_s, remained unchanged in year two and three. This is consistent with other studies that found more constant specific hydraulic conductivity in older plants than younger ones (Noyer et al. 2017). This again bolsters the idea that younger plants will be more plastic in their response to environmental factors, while older plants reach some species optima. While K_s converges, the exponential growth of ring area causes K_{ring} to have pronounced differences by year 3 with the 100% and 150% watering treatments conducting much more water. One important area of study is to detemine how much of the xylem from past years in functional. If prior rings were hydraulicly functional, this would serve to make the distinctions more stark. With greater K_{ring} as a result of increased water availability we expect these plants to be more efficient in their water transport and be able to support a larger canopy.

Supplementary Material

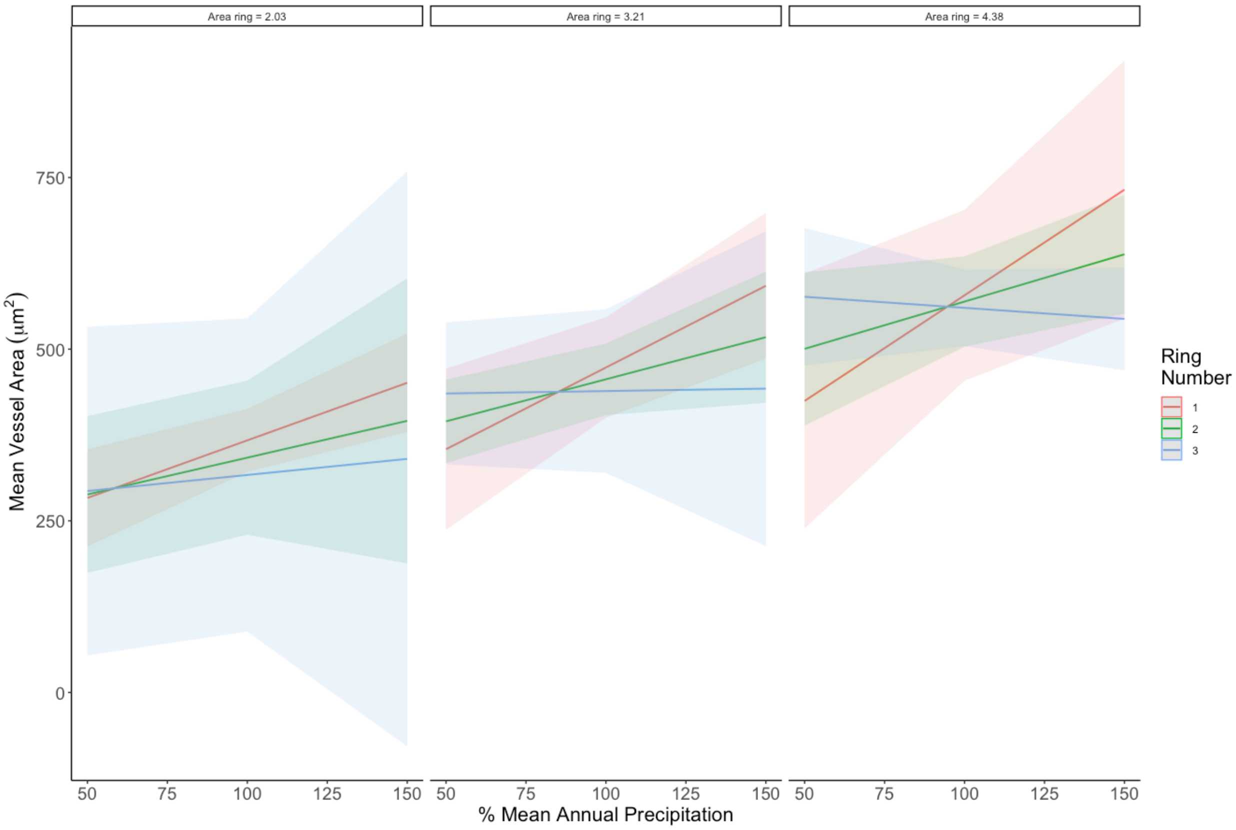


Figure S2.1. Interaction plot of affect of $\text{Area}_{\text{ring}}$ on VA accounting for watering treatment and age. Linear relationships are predicted values based on marginal means (accounting for watering treatment, age, and individual). Colors correspond to ring year (red = 1, green = 2, and blue = 3) with shaded regions representing ±SE. Plots are faceted by representative values of $\text{Area}_{\text{ring}}$

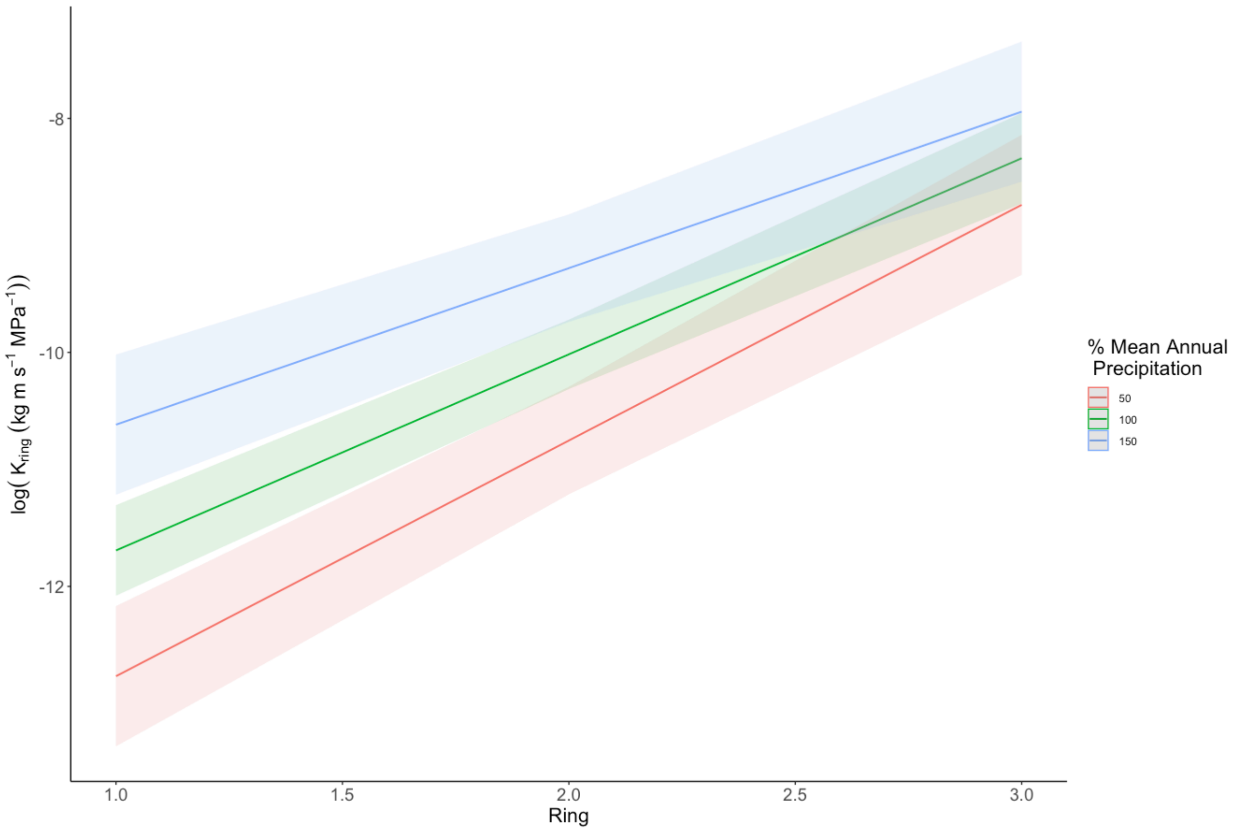


Figure S2.2 Interaction plot of affect of watering treatment and age on the logarithm of K_{ring}. Linear relationships are predicted values based on marginal means (accounting for watering treatment, age and individual). Colors correspond to % mean annual precipitation (red = 50%, green = 100%, and blue = 150%) with shaded regions representing ± SE.

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