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Analyzing root traits to characterize juniper expansion into rangelands

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A B S T R A C T

Juniper expansion into sagebrush-dominated communities is a phenomenon occurring across large regions of the western U.S. in the past century. We investigated the competitive abilities for belowground resources of *Juniperus osteosperma* (Utah juniper) and *Artemisia tridentata* (big sagebrush) based on fine root traits and spatial patterns of water uptake inferred from stem and soil stable oxygen isotopes ($\delta^{18}O$). Data were collected from neighboring *J. osteosperma* and *A. tridentata* plants in northern Colorado and included measurements of different size classes of *J. osteosperma*: short (< 30 cm), intermediate (30 cm–3 m), and tall (> 3 m). Short *J. osteosperma* switched from utilizing shallow to primarily deep water sources across the growing season. *Artemisia tridentata* had root traits associated with faster root proliferation and resource acquisition (significantly greater specific root length and smaller root diameter, $p < .01$), but greater *J. osteosperma* fine root biomass ($p < .01$) resulted in similar root length densities between the two species at most soil depths ($p > .1$). Additionally, we found that short *J. osteosperma* individuals can quickly develop deep root systems, but there is little difference in below-ground foraging between individuals of *J. osteosperma* and *A. tridentata* based on the depth of water uptake and root length density.

1. Introduction

Piñon-juniper woodlands cover approximately 40 million hectares in the western United States (Romme et al., 2009), with significant infill and expansion occurring in the last century. Since the mid 1800s the land area occupied by juniper has increased by 140%–600% across the region (Miller et al., 2008), resulting in major changes to ecosystem function. Juniper encroachment typically occurs across ecotones, with juniper establishing into areas primarily dominated by sagebrush resulting in decreased forage availability (Miller et al., 2008), development of hydrophobic layers that decrease water infiltration into the soil (Robinson et al., 2010), increased erosion promoting loss of soil nutrients (Law et al., 2012), changes in microbial populations (Haskins and Gehring, 2004), and increased carbon sequestration (Fernandez et al., 2013). Fire suppression and increased grazing activity since the late 1800s are commonly considered as the primary drivers of expansion but they do not explain all instances of the phenomenon (Romme et al., 2009). Changes in water availability or responses to changing CO_2 concentrations may alter the competitive outcomes between the species involved, but neither hypothesis has been fully evaluated, in part, because we lack an understanding of the water-use strategies of these species during the initial phase of encroachment. Given the arid and semi-arid regions in which *Juniperus osteosperma* (Torr.) Little (Utah juniper) and *Artemisia tridentata* Nutt. (big sagebrush) occur, competition for limiting resources, particularly water, may play an important role in driving changes in species composition.

A primary role of roots is the foraging of water and nutrients from the soil and therefore it is vital for understanding the growth and survival of plants in resource-limited environments. Generally, species with long Specific Root Length (SRL, m root length/g root mass), low Root Tissue Density (RTD), and small diameter fine roots typically exhibit greater competitive ability in foraging for belowground resources (Bardgett et al., 2014; Comas et al., 2013) through greater resource exploitation relative to carbon investment into the root system (Pregitzer et al., 2002). Additionally, species with small diameter, fine roots may have greater hydraulic conductivity than larger diameter fine roots due to differences in the path length of water transport from the root surface to the vascular system (Comas et al., 2013). Gymnosperms, like *J. osteosperma*, generally have lower SRL than angiosperms (Comas and Eissenstat, 2009), like *A. tridentata*, which would suggest that in this system *A. tridentata* would have roots indicative of greater competitive ability. However, differences in the allocation of carbon to roots could offset lower SRL, but measurements of root traits and root biomass for collocated individuals of *J. osteosperma* and *A. tridentata* are not available, preventing a better understanding of the competitive abilities of these species for belowground resources.

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In addition to fine root traits, the presence of deep roots provide access to water and nutrients deep in the soil profile, which can be particularly important in ecosystems that commonly undergo periods of drought. Woody species, including *A. tridentata* (Foxx et al., 1984) and *J. osteosperma* (Gottfried et al., 1995), are known for developing roots that extend several meters below the soil surface (Mandel and Alberts, 2005). Roberts and Jones (2000) suggested that *Juniperus* species, in general, develop root systems deeper than *A. tridentata*, accessing resources that *A. tridentata* cannot. Isotopic analyses of stem and soil water samples have been used to confirm that *A. tridentata* and *J. osteosperma* are both capable of extracting water from deep in the soil profile in the Great Basin (Leffler et al., 2002; Ryel et al., 2008). However, *A. tridentata* uses shallower water in the presence of mature individuals of *J. osteosperma* (Leffler and Caldwell, 2005), suggesting that *A. tridentata* shifts its rooting depth in response to juniper expansion. This conclusion was based on a comparison of two different sites without pre-encroachment data and so it is unclear if the shallower water-extraction was in response to the presence of juniper or other unmeasured variables. Furthermore, it is still unclear how early in their development *J. osteosperma* individuals can access deep water, preventing a clear understanding of competition between these species as juniper encroachment occurs.

Encroachment relies, in part, upon the successful establishment and survival of seedlings, but encroachment is typically discussed in terms of infill and expansion of larger trees (Romme et al., 2009). Little research has been conducted on smaller, shorter *J. osteosperma* plants (Schupp et al., 1998) and their ability to compete for belowground resources with *A. tridentata*. Measurement of root traits at earlier developmental stages of *J. osteosperma* will provide valuable information related to their survival that could be useful to those managing encroachment. Hypotheses have been made suggesting competitive interactions between short, developing *Juniperus* plants and *A. tridentata* for nutrients (Roberts and Jones, 2000), however, facilitative interactions in which *A. tridentata* serves as a nurse plant for short juniper plants has also been suggested (Gottfried et al., 1995; Van Auken et al., 2004), particularly given the discovery that *A. tridentata* can redistribute water from deep to shallow soil layers (Ryel et al., 2002; Prieto et al., 2014). This apparent discrepancy can be resolved, at least partially, by understanding if small, short *Juniperus* can develop deep roots and identifying if they utilize water from the same or different sources than *A. tridentata* individuals.

To improve our understanding of the role of belowground foraging behavior in the expansion of *Juniperus* we measured fine root traits and root biomass of *J. osteosperma* and *A. tridentata* down to 180 cm soil depth in an area of active encroachment in northwestern Colorado to compare a suite of root traits between *A. tridentata* plants and *J. osteosperma* individuals spanning a large size gradient (short, intermediate, and tall). We address three primary research questions, including: (1) Does *J. osteosperma* have fine root traits (longer SRL, lower RTD, and smaller fine root diameter) that would suggest it is a better competitor than *A. tridentata* and contribute towards its encroachment success? (2) Do *A. tridentata* and *J. osteosperma* compete for the same water source or do they utilize different sources? (3) Are root traits and depth of water extraction by *J. osteosperma* consistent across *J. osteosperma* size classes?

2. Materials and methods

2.1. Site description

The study site was located in Moffat County in the northwest region of Colorado, approximately 97 km (60 miles) west of Craig, CO (12T 707673 E, 4502118 N). The site was established in an area managed by the Bureau of Land Management Little Snake Field Office and considered to be under active encroachment by juniper (D. Beckerman, personal communication, May 2015). The site had not been grazed for approximately 20 years and experienced minimal to no fire activity for at least the last three decades (D. Beckerman, personal communication, May 2015). Elevation ranged from 1500 to 2100 m and soils at the field site were predominately composed of the Carmody Rock River Crestman complex (NRCS, 2014). This region is considered semi-arid, experiencing harsh, cold winters and long, dry summers characterized by relatively small precipitation events (Fig. 1). Average annual precipitation of the area is 400 mm (Linton et al., 1998; PRISM Climate Group, 2004), with the majority of precipitation received as winter snowpack. *Juniperus osteosperma* and *A. tridentata* were the dominant vegetation on the field site, but the perennial C_3 bunch grass *Hesperostipa comata* (Trin. & Rupr.) Barkworth was also abundant on the field site.

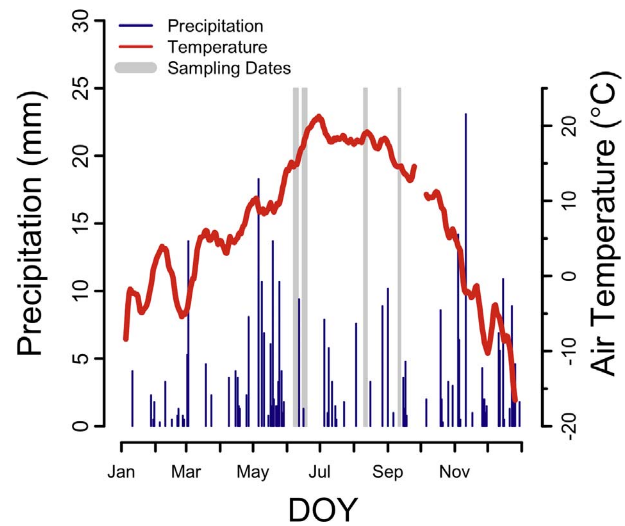

Fig. 1. Cumulative precipitation (mm) and average temperature (°C) in 2015 at Maybell, CO, approximately 50 km from the field site. Grey bars represent sampling periods when water was extracted from soil and plant tissue for isotopic analysis.

2.2. Establishing plant pairs

In order to investigate interactions between *J. osteosperma* and *A. tridentata* we established pairs of these species growing within ~1 m. Plant pairs were established within a 300 m^2 area on the field site, bounded by stands of monospecific *A. tridentata* on the eastern edge and near monospecific stands of *J. osteosperma* on the western edge. Plants were identified along five transects by first identifying the nearest *J. osteosperma* to a randomly selected point along the transect and then the nearest neighboring *A. tridentata* plant was selected to complete the pair. Each transect had three plant pairs, with each pair having a juniper from a different height class. *Juniperus osteosperma* plants were categorized into three height classes that have been correlated with age (Miller and Rose, 1999): short (< 30 cm, juvenile), intermediate (30 cm–3 m, sapling), and tall (> 3 m, mature). *Artemisia tridentata* plants were not categorized into height classes as part of our study design. At the end of the study all *J. osteosperma* individuals were aged from cross sections.

In addition to the pairs, *J. osteosperma* and *A. tridentata* plants growing in monospecific stands at either end of transects were also randomly selected for sampling. These samples are referred to as 'monospecific *A. tridentata*' and 'monospecific *J. osteosperma*' and were taken to allow for intraspecific comparisons of roots traits between *A. tridentata* or *J. osteosperma* plants growing in monospecific stands to *A. tridentata* or *J. osteosperma* plants in the established pairs.

2.3. Soil coring

Three soil cores were taken associated with each plant pair: (1)