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Shelter provided by wood, facilitation, and density-dependent herbivory influence Great Basin bristlecone pine seedling survival

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ABSTRACT

Microsites created by live plants and non-living structures can be important for plant establishment where abiotic stress is high. The activity of herbivores and resulting pattern of seedling survival also affects plant distributions. We investigated factors thought to influence survival of bristlecone pine (*Pinus longaeva* Bailey) seedlings in the White Mountains, California, USA, with two field experiments in which microsite and exposure to herbivory were manipulated. In the microsite experiment, we planted seedlings underneath wooden shade structures, underneath sagebrush plants, and in exposed locations. In the herbivory experiment, we tested the effects of herbivore exclusion in three different habitat types. We planted seedlings in full wire cages (herbivores excluded), in half cages (herbivores allowed while enabling assessment of possible non-herbivore effects of cages on seedling survival), or with no cage (herbivores allowed), and repeated these treatments in three habitats: below, within, and above a bristlecone woodland. Over three growing seasons, seedlings planted under wooden shade structures had higher survival (28.9%) than seedlings growing under sagebrush (10%) or in exposed areas (3.3%). We found a significant treatment by habitat interaction in the herbivory experiment ($\chi^2 = 12.056$, $P = 0.017$), driven by a clear pattern of high herbivory inside the bristlecone woodland, but not above or below it. Our results suggest that biologically-derived microsites (shelter from dead wood and live shrubs), as well as herbivore-mediated density-dependent mortality, are important determinants of bristlecone pine seedling survival.

1. Introduction

Early life stages of many plants are the most sensitive to abiotic stress and to damage by herbivores, and the seed stage is often the only mobile stage in a plant's life cycle (Nathan and Muller-Landau, 2000). A small proportion of seeds arrive in microsites suitable for germination, a small proportion of germinated seeds survive as seedlings, and herbivores consume many seeds and seedlings. The transitions between these early life stages are regulated by spatial processes that ultimately determine the patterns of adult plant distribution (Bazzaz, 1991; Gomez-Aparicio, 2008; Nathan and Muller-Landau, 2000; Schupp, 1995). In heterogeneous, stressful environments, seed dispersal may have limited influence on the pattern of plant abundance and distribution relative to the availability of suitable microsites for seedling establishment (Gomez-Aparicio, 2008). In this way, survival of seedlings is important to both recruitment of new individuals into a population and to distribution patterns. In long-lived species, which can maintain stable populations even with very sparse recruitment (Eriksson, 2000; Kwit et al., 2004; Wiegand et al., 2004), high seedling mortality coupled with low adult mortality places greater relative importance on the processes mediating seedling survival for determining future distributions.

We examine factors affecting survival in early life stages of an extremely long-lived plant, the Great Basin bristlecone pine (*Pinus longaeva* Bailey). The species is endemic to the arid mountains of Nevada, Utah, and eastern California, USA, between 2750 and 3550 m in elevation (Lanner, 2007). Great Basin bristlecone pine is the longest-lived non-clonal organism known on earth (Currey, 1965; Schulman, 1958). Some individuals in the White Mountains of California are likely over 5000 years (Thomas Harlan, personal communication, August 2008), and individuals over 4000 years are common in some areas (Schulman, 1958). Since Schulman's (1958) and Currey's (1965) discovery of the species' great longev-

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ity, bristlecone pine tree-ring chronologies continue to be elemental in the fields of dendrochronology, dendroclimatology, and archeology (e.g., Ababneh, 2008; Berkelhammer and Stott, 2008; LaMarche and Stockton, 1974; Linick et al., 1986; Salzer et al., 2014). The species has also become an important tourist attraction. For example, in 2013, 92,893 people visited Great Basin National Park in Nevada, USA, a major feature of which are ancient bristlecone pines (National Park Service, Public Use Statistics Office). Recent concern over the threat of white pine blister rust (caused by the introduced fungus *Cronartium ribicola* Fisch.) and mountain pine beetles (*Dendroctonus ponderosae*) has inspired active efforts to monitor and protect bristlecone pine and limber pine (*Pinus flexilis* James) from these threats in Great Basin National Park (Schoettle et al., 2013). However, the basic ecology of Great Basin bristlecone pine populations and communities has received relatively little study (but see Barber, 2013), and factors influencing seedling recruitment and survival constitute a conspicuous knowledge gap.

Subalpine environments present difficult abiotic conditions for seedling establishment. Short growing seasons, strong desiccating winds, cold temperatures, and intense UV radiation negatively affect seedling growth and survival (Arno, 1984; Caldwell, 1968; Körner, 2012). Availability of favorable microsites in which environmental conditions are ameliorated is thus important for survival of subalpine conifer seedlings (Germino et al., 2002; Legras et al., 2010; Maher et al., 2005). Such microsites are created by the presence of and interactions with other plants (facilitation, or 'nurse' plant effects; Bruno et al., 2003) or by non-living structures (e.g., dead wood or rocks; Eckert, 2006; Gray and Spies, 1997; Peters et al., 2008). The stress-gradient hypothesis predicts that the frequency of positive interactions among plants will increase as biotic or abiotic stress increases (Bertness and Callaway, 1994). Field studies have confirmed that positive interactions are important in environments with high abiotic stress (Callaway et al., 2002).

Shrubs function as nurse plants through facilitative interactions with beneficiary plants in extreme environments worldwide (e.g., Valiente-Banuet et al., 2006). Great Basin sagebrush (*Artemisia tridentata* Nutt.) is the most common shrub throughout the range of bristlecone pine. In the only published study, to our knowledge, on Great Basin bristlecone recruitment ecology, Wright and Mooney (1965) found a competitive effect of sagebrush seedlings on bristlecone seedlings in granitic and quartzite soils (though not on dolomite soil) in potted experimental plantings. They concluded that competition with sagebrush is likely a major factor restricting bristlecone establishment on non-dolomitic substrates. In field conditions, however, bristlecone seedlings are less likely to interact with sagebrush seedlings than with large adult sagebrush, which may provide shelter. Great Basin sagebrush is known to have non-neutral interactions with other *Pinus* seedlings. At a site in west-central Nevada where ponderosa pine (*Pinus ponderosa* Douglas) exist almost exclusively on patches of nutrient-poor (and sagebrush-free) hydrothermally-altered andesite, Callaway et al. (1996) found that sagebrush facilitates piñon pine (*Pinus monophylla* Torr. & Frém.) seedlings, but competes with ponderosa pine seedlings on unaltered andesite. The researchers concluded that negative interactions with sagebrush restrict ponderosa pine to nutrient-poor soils, while the absence of sagebrush on those soils prevents piñon pine establishment (Callaway et al., 1996).

Coarse woody debris (CWD) is an important structural element in temperate conifer forests (Harmon et al., 1986), and is known to provide microsites for seedling establishment in forest systems all over the globe via amelioration of abiotic conditions (e.g., shade, protection from wind, or enhanced nutrients or moisture; Gray and Spies, 1997; Heinemann and Kitzberger, 2006; Mori et al., 2004). CWD is abundant in bristlecone stands; bristlecone wood often persists for millennia after a tree's death (Hallman et al., 2006). Because bristlecone pine stands are typically open and park-like, better described as woodlands than forests, CWD may provide sheltered microsites for seedling establishment in this harsh environment (Fig. 1).

Herbivory by small mammals is common in subalpine habitats, and is known to influence pine distributions at lower elevations (Coop and Givnish, 2008; Diemer, 1996; Munier et al., 2010). Coop and Givnish (2008) found that golden-mantled ground squirrels (*Spermophilus lateralis*) caused significant mortality of ponderosa pine seedlings, becoming the major source of mortality at higher elevations, while cold temperatures killed seedlings in lower elevation valleys. Furthermore, herbivory is a major mechanism behind Janzen–Connell effects, where the probability of seed and seedling survival increases with distance from parent trees; a form of density-dependent mortality (Connell, 1971; Janzen, 1970). Originally proposed as an explanation for high tree species diversity in tropical forests, density-dependent mortality at early life stages is now known to be common in productive low-elevation temperate forest ecosystems as well (Hille Ris Lambers et al., 2002; Johnson et al., 2014).

We investigated the influence of microsites and herbivory on bristlecone pine seedling survival in the White Mountains of eastern California, USA, using transplanted seedlings in two field experiments. Two foundational ecological concepts informed our study design—the stress gradient hypothesis (Bertness and Callaway, 1994) and density-dependent mortality (Hille Ris Lambers et al., 2002). The purpose of our study was to identify causes of recruitment limitation in Great Basin bristlecone pine. Our study was guided by three questions:

1. Do bristlecone pine seedlings planted under shade structures, under adult sagebrush plants, or in exposed microsites survive at different rates?
2. Does herbivory by small mammals affect first year bristlecone pine seedling survival?
3. Does the intensity of herbivory differ for seedlings planted within bristlecone woodlands (near parent trees) compared to seedlings planted in adjacent open areas (away from parent trees)?

2. Methods

2.1. Study sites

We installed field experiments at two sites in the White Mountains in eastern California, USA in the summer of 2008. The White Mountains receive an average annual precipitation of 330 mm, about 80% of from snow, the remainder mostly from occasional summer thunderstorms (Hall, 1991). The average daily temperature in July (warmest month) is 10.9 °C. The daily average in January (coldest month) is −6.3 °C. Summer nighttime temperatures are typically above 0 °C, although below-freezing nights do occur infrequently (Hall, 1991). The summer growing season typically lasts June through September (Hall, 1991). The Great Basin ranges are home to many herbivorous mammals, including several rodent species, lagomorphs, and ruminants (Hall, 1991).

Microsite experiment plots were located directly southeast of the White Mountain Research Station (now the White Mountain Research Center) at Crooked Creek, at 3093 m in elevation. The area is a mostly flat basin near a mixed bristlecone/limber pine stand with granitic soils, dominated by sagebrush scrub. Herbivory experiment plots were located on the northwest-facing slope of Campito Mountain. A bristlecone pine woodland occupies this location in a band from about 3338 m to 3414 m in elevation. Bristlecone is the dominant tree species in the woodland, with limber