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PLANT COMMUNITY WATER USE AND INVASIBILITY OF SEMI-ARID SHRUBLANDS BY WOODY SPECIES IN SOUTHERN CALIFORNIA

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ABSTRACT

Soil moisture is a key limiting resource in arid and semi-arid environments for woody shrub species. We assessed if three arid communities differed in their level of dry season soil moisture content and if the dominant species in these communities differed in their ability to use soil moisture. Water potential of all of the dominant woody plant species occurring in chaparral, coastal sage, and Mojave Desert communities and soil moisture content of these sites were measured seasonally. Species occurring in the Mojave Desert exhibited the most negative water potentials while the coastal sage community displayed the least negative water potentials. Dry season volumetric soil moisture content of the Mojave Desert site was lowest (7%), the chaparral site was intermediate (10%), and the coastal sage scrub site had the moistest dry season soil (20%). These moisture differences developed even though the coastal sage and chaparral communities both received the same annual rainfall and had similar soil characteristics. Of the three communities, the coastal sage community may be particularly susceptible to invasion by woody shrub species because its soil moisture content would allow for germination and persistence of a wider range of potential invaders. Current differences among sites in numbers of non-native woody species are consistent with predicted differences in susceptibility to non-native species based on community water use and dry seasonal soil moisture.

Key Words: Chaparral, coastal sage, invasive species, Mediterranean-type ecosystems, Mojave Desert, R*, soil moisture, water potential.

Much of undeveloped southern California is dominated by arid and semi-arid woody shrublands, including the shrub communities of the chaparral, coastal sage scrub, and Mojave Desert (Fig. 1). Water is a limiting resource in these communities, particularly for the dominant evergreen woody shrub species, which remain active year-round. Indeed, drought-induced mortality of species in these communities at both the seedling and adult stages has been reported (Frazer and Davis 1988; Williams et al. 1997; Davis et al. 2002; Paddock III 2006), suggesting the importance of water availability in shaping these communities.

The use of the same resource by species should lead to the exclusion of species that are competitively inferior at acquiring and using this resource. This principle was described by Gause and is given the name "competitive exclusion" (Hardin 1960). While species persistence depends on many variables, Leibig's law of the minimum states that in any given environment there is one resource that is most limiting to species persistence. Where species compete for a single limiting resource, species resource use can be used to predict the outcome of competitive interactions (R* rule; Tilman 1982). This pattern of resource competition has also been termed exploitation competition (Levine 1976; Vance 1985).

The R* rule predicts the outcome of competitive interactions based on differential dependence of species on a given resource level for positive population growth (Fig. 2A; Tilman 1982). The growth rate of a population will decline as the availability of the limiting resource declines. The level of resource availability at which the population growth rate equals zero is the R*. If two species have different R* then the species with the lower R* will be able to competitively exclude the species with the higher R*. This is because the species with lower R* can draw resource availability down to a level that results in a decline in the population of the species with the higher R* (Fig. 2A). This same model may also be applied to interactions among plant communities (Fig. 2B).

Natural communities are shaped by many factors and models that examine only one or a few factors are undoubtedly simplifications; however, such simplified models have been shown to have utility in predicting outcomes of competitive interactions. The R* rule and similar models have been used to predict the outcome of competition in controlled experiments (Titman 1976; Ciros-Pérez et al. 2001; Fox 2002), patterns of species abundance within communities (Kõiv and Kangro 2005; Harpole and Tilman 2006),

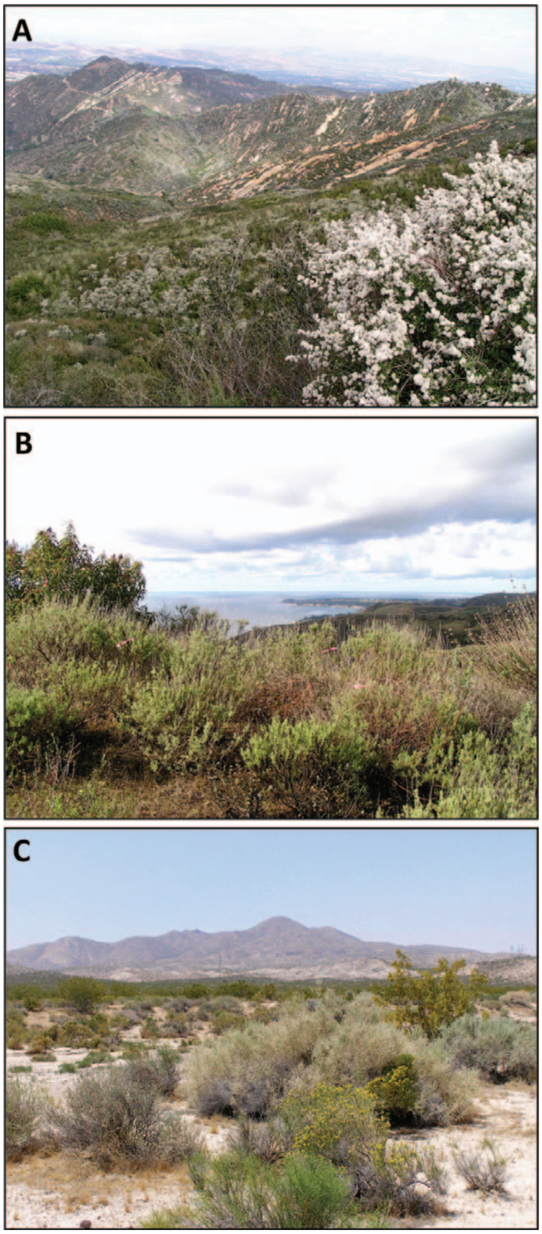

FIG. 1. The semi-arid shrub communities from the winter rainfall region of southern California: chaparral (A), coastal sage scrub (B), and Mojave Desert scrub (C). These photos were taken of the sites that were sampled in the present study in Spring 2006. Photos by A. Jacobsen.

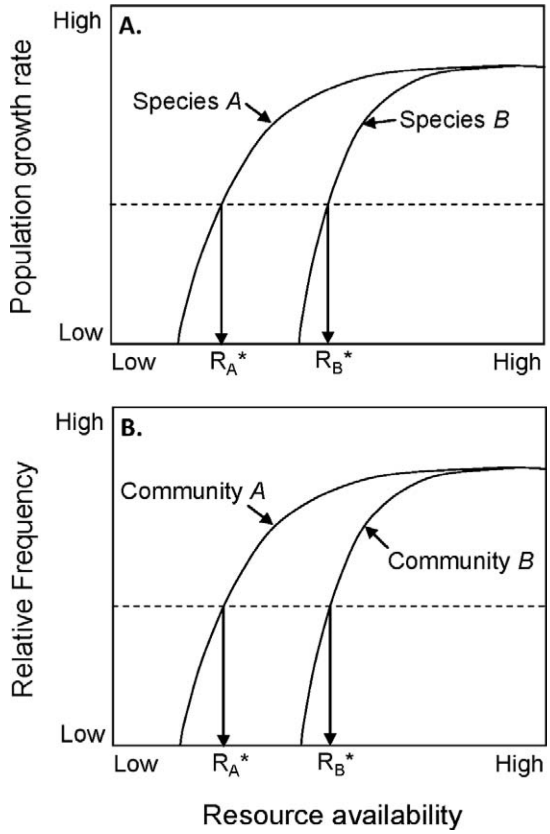

FIG. 2. Solid curves show the dependence of population growth rate on resource availability (A; based on Tilman 1982) and the dependence of species communities on resource availability (B) if a single resource is limiting. In panel A, the dashed line indicates the point at which the mortality rate in a population equals the replacement rate. The R* indicates the amount of resource resulting in zero population growth. Species *B* requires a higher amount of resource than Species *A* for the population to increase (i.e., $R_B^* > R_A^*$); therefore, the long term outcome of competition between Species *A* and Species *B* would be the competitive exclusion of Species *B*. This results because Species *A* is able to reduce resources below the level at which Species *B* can maintain positive population growth. In panel B, the dashed line indicates the point at which individuals are so infrequent in the community that the community cannot be sustained. In this example, Community *A* would be able to competitively exclude Community *B*.

and patterns of species succession (Herron et al. 2001). Recently, these models have also been applied to species invasions and determination of community invasibility and native versus non-native competitive interactions (Herron et al. 2001; Booth et al. 2003; Fargoine et al. 2003; Krueger-Mangold et al. 2006; Funk and Vitousek 2007). While many of these studies have focused on nutrient availability (for plants) or food availability (for animals), moisture availability and plant water use have been shown to predict competitive outcomes in some plant communities, particularly in arid regions (Cleverly et al. 1997; Booth et al. 2003).

We examined differences in plant water potential and soil moisture among three semi-arid plant communities of southern California to assess whether these communities differed in their ability to utilize soil water resources.

TABLE 1. THE DOMINANT WOODY SPECIES PRESENT IN AND SAMPLED IN EACH OF THREE SEMI-ARID PLANT COMMUNITIES.

Vegetation type and location	Species	Family
Chaparral—Cold Creek Canyon Preserve, Santa Monica Mountains, CA, USA (34.5N 118.4W)	*Adenostoma fasciculatum* Hook. & Arn.	Rosaceae
	Adenostoma sparsifolium Torrey	Rosaceae
	Arctostaphylos glandulosa Eastw.	Ericaceae
	Ceanothus cuneatus (Hook.) Nutt.	Rhamnaceae
	Ceanothus megacarpus Nutt.	Rhamnaceae
	Ceanothus oliganthus Nutt.	Rhamnaceae
	Ceanothus spinosus Nutt.	Rhamnaceae
	Malosma laurina (Nutt.) Abrams	Anacardiaceae
	Quercus berberidifolia Liebm.	Fagaceae
	Rhus ovata S. Watson	Anacardiaceae
Coastal Sage Scrub—Pepperdine University, Malibu, CA, USA (34.2N 118.4W)	*Artemisia californica* Less.	Asteraceae
	Encelia californica Nutt.	Asteraceae
	Eriogonum cinereum Benth.	Polygonaceae
	Hazardia squarrosa (Hook. & Arn.) Greene	Asteraceae
	Lotus scoparius (Nutt.) Ottley	Fabaceae
	Malacothamnus fasciculatus (Torrey & A. Gray) Greene	Malvaceae
	Malosma laurina (Nutt.) Abrams	Anacardiaceae
	Salvia leucophylla Greene	Lamiaceae
	Salvia mellifera Greene	Lamiaceae
Mojave Desert Scrub—Red Rock Canyon State Park, CA, USA (35.2N 117.6W)	*Ambrosia dumosa* (A. Gray) Payne	Asteraceae
	Atriplex canescens (Pursh) Nutt.	Chenopodiaceae
	Atriplex polycarpa (Torrey) S. Watson	Chenopodiaceae
	Coleogyne ramosissima Torrey	Rosaceae
	Hymenoclea salsola A. Gray	Asteraceae
	Isomeris arborea Nutt.	Capparaceae
	Larrea tridentata (DC.) Coville	Zygophyllaceae
	Lepidospartum squamatum (A. Gray) A. Gray	Asteraceae
	Lycium andersonii A. Gray	Solanaceae

Predawn water potential of woody plant branchlets or leaves estimates availability of soil moisture. More negative values indicate less available soil moisture reserves. Plants that can tolerate more negative water potentials can continue to extract soil water when plants that are less tolerant are no longer able to obtain enough soil moisture. Thus, species and communities that tolerate more negative predawn and midday water potentials and in which water is the most limiting resource will have a lower R*.

Differences in soil moisture and species water potential may also be related to the invasibility of these communities by non-native species. Arid and semi-arid communities with a lower R* would be predicted to be vulnerable to invasion by fewer species (i.e., only the limited number of potential invaders that are most water stress tolerant) (Pratt and Black 2006). Results are discussed as they apply to the invasion potential of communities. However, it should be noted that such results apply only to woody shrub species because predictions of competitive outcomes based on limiting resources appear most useful among similar functional groups (Krueger-Mangold et al. 2006).

MATERIALS AND METHODS

Three diverse semi-arid sites were selected based on their abundance of woody shrub species. These sites represented chaparral, coastal sage, and Mojave Desert plant communities occurring in the winter rain-fall area of southern California (Fig. 2; see Jacobsen et al. 2007, 2008 for site descriptions). The chaparral site was dominated by 10 woody plant species, the coastal sage site was dominated by 9 woody plant species, and the Mojave Desert scrub community was dominated by 10 woody plant species (Table 1). These species accounted for 89, 99, and 73% of the woody plants in each community, respectively. The average annual precipitation for these sites is approximately 440 mm for both the chaparral and coastal sage communities and 180 mm for the Mojave Desert site (average annual precipitation from 1999–2007 based on the July to June rain year).

At each site, woody shrub species were sampled using a modified point-quarter sampling method to determine basic stand structural characteristics (Cox 1985). Fifty-four to 60 points were sampled at each site and plant height, basal diameter, crown diameter, and interplant basal and crown distance were all determined. Differences in traits among communities were tested using ANOVAs (Statview v. 5.0.1, SAS Institute Inc., Cary, NC, USA).

Percentage volumetric soil moisture content (m^3/m^3) was measured monthly from late August 2006 through April 2007 at each of the three sites.

TABLE 2. MEANS AND STANDARD ERRORS OF CANOPY HEIGHT, CROWN DIAMETER, BASAL DIAMETER, AND DISTANCE BETWEEN INDIVIDUAL PLANT BASES AND CROWNS IN THREE PLANT COMMUNITIES: CHAPARRAL, COASTAL SAGE, AND MOJAVE DESERT SCRUB. Different letters in each column indicate significant differences among communities. [1] From outside edge of base to outside edge of base. [2] From edge of crown to edge of crown.

Vegetation type	Height (m)	Crown diameter (m)	Basal diameter (m)	Distance between bases[1] (m)	Distance between crowns[2] (m)
Chaparral	2.57 ± 0.07 a	1.87 ± 0.08 a	0.17 ± 0.01 a	0.64 ± 0.05 a	−1.15 ± 0.06 a
Coastal Sage Scrub	0.83 ± 0.03 b	0.99 ± 0.05 b	0.10 ± 0.01 b	0.61 ± 0.03 a	−0.47 ± 0.04 b
Mojave Desert Scrub	0.75 ± 0.03 c	1.03 ± 0.04 b	0.18 ± 0.00 a	1.67 ± 0.08 b	0.70 ± 0.08 c

Volumetric soil moisture content of the upper soil layers (upper 30 cm) was measured at the base of the same individuals at each sampling time (n = 14–26) using a TDR probe (CS615, Campbell Scientific, Inc., Logan, UT, USA) attached to a datalogger (CR23X Micrologger, Campbell Scientific, Inc., Logan, UT, USA). Within each site, values for sample locations were compared using repeated measures ANOVAs. Minimum seasonal soil moisture of each site was determined as a community wide mean from the month with the lowest soil moisture values. Minimum volumetric soil moisture across communities was compared using ANOVA followed by a Bonferroni/Dunn post-hoc analysis (Statview v. 5.0.1, SAS Institute Inc., Cary, NC, USA).

Monthly water potential was measured at midday on all dominant woody shrub species at each site from February 2006 and continuing through April 2007 (see Jacobsen et al. 2008 for Methods) using a pressure chamber (Model 2000 Pressure Chamber Instrument, PMS Instruments, Corvalis, OR, USA). Predawn water potentials were sampled during the dry season in August and September 2006. Water potential was measured on leaves or small branchlets (for species with very small leaves) from six individuals per species at each sampling period. Mean water potentials were calculated for each species at each sampling time. These values were pooled across species and the frequency of water potentials were calculated for each community in order to determine the community wide range in soil moisture resource use.

The invasibility of communities was compared to current non-native and invasive species presence in communities by determining the number of woody species occurring in each community, including the percentage of these woody species that are native to the region, not native, and which are both non-native and also invasive. Species were included as woody species if they were reported by Hickman (1996) to be trees, shrubs, subshrubs, or woody perennials. Species presence in communities was determined based on species geographic ranges and ecology reported in Hickman (1996), The Jepson Manual Online (University of California and Jepson Herbaria 2001) and regional floras (McAuley 1996; Dale 2000; Faull 2005).

RESULTS

Plants within these three communities differed in height, crown diameter, and basal diameter (Table 2). Overall, chaparral species were taller and had greater crown diameters relative to the other two communities (Table 2). The distance between plants was not different among the chaparral and coastal sage communities although crown overlap was greater in the chaparral due to their significantly wider crown diameters. Individuals occurring at the Mojave Desert site were further apart than in the other two communities and this, combined with their smaller canopy sizes, resulted in an open canopy (Table 2).

Dry season volumetric soil moisture of the shallow soil layers significantly differed among the sites and with season (Figs. 3 and 4C). These sites do not differ in soil texture at the measured soil depth (Jacobsen et al. 2007) so these differences should equate to differences in soil water potential of the shallow soil layers of these sites; however, we did not measure soil water potential versus volumetric soil moisture for these sites.

Dry season soil moisture values for the fall of 2006 followed an average rain year and thus should be representative for soil moisture conditions in average years during the dry season. The three communities significantly differed in their dry season volumetric soil moisture content (Fig. 4C, $P < 0.001$). Minimum volumetric soil moisture content of the Mojave Desert site was the driest (7.1 ± 0.1%, $P \leq 0.001$ compared to the chaparral and coastal sage scrub), the chaparral site was intermediate (10.3 ± 0.6%, $P < 0.001$ compared to the coastal sage scrub), and the coastal sage scrub site had the most moist dry season soil (20.3 ± 1.0%). All of the sites exhibited significantly higher soil moisture values during the wet season from December to March (Fig. 2); however, rainfall during the winter 2006–2007 wet season was much less than average (approximately 100–130 mm across all sites), so wet season soil moisture values may deviate from the typical pattern in an average rainfall year.

Midday water potentials were strongly correlated with predawn water potentials in August and September ($P < 0.001$, $r^2 = 0.771$; Jacobsen

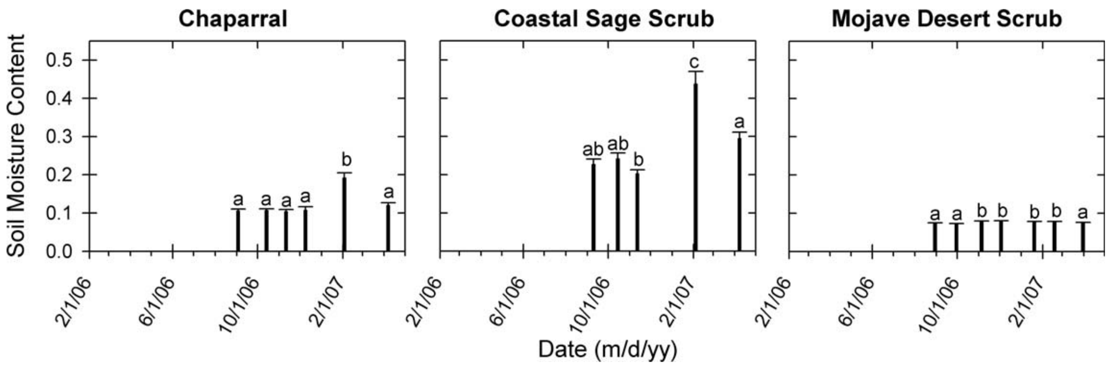

FIG. 3. Volumetric soil moisture content of the upper soil layers (upper 30 cm) measured from late August 2006 through April 2007 at each of the three arid shrub communities (chaparral, coastal sage, Mojave Desert). Within each panel, different letters indicate soil moisture values that are significantly different.

et al. 2007; Pratt et al. 2008). Midday water potentials were approximately one MPa lower than predawn water potentials measured on the same plant (range of 0.88 to 1.17 MPa difference between predawn and midday).

The three communities examined in the present study differed in the minimum midday water potentials that could be tolerated by species within each community (Fig. 4A and B). Species within the Mojave Desert community reached the lowest water potentials (−9.2 MPa), species within the chaparral were intermediate (−8.7 MPa), and woody species from the coastal sage scrub community experienced the least negative water potentials (−5.4 MPa). All of the communities had some species that maintained relatively high water potentials even in the dry season (Fig. 4A and B). These minimum water potential values are consistent with site differences in dry seasonal soil moisture content (Fig. 4C).

At present, the coastal sage contains more non-native and invasive woody species than the chaparral and Mojave Desert communities (Table 3). In the coastal sage, 39% of the woody species are non-native, compared to only 21.1% for the chaparral, and 7.1% for Desert Scrub. Of woody species that are categorized as invasive or noxious, the coastal sage contains 4.4% invasive/noxious species compared to only 2.5% for the chaparral and 0% for the Mojave Desert scrub.

DISCUSSION

Species of woody shrubs in the chaparral, coastal sage, and Mojave Desert communities are able to tolerate relatively low water potentials (less than −7 MPa in all communities compared to a limit of −2 MPa for most crop plants; Tyree and Zimmerman 2002). Among these three communities, the Mojave Desert community contains the species that experience the lowest water potentials seasonally and therefore are able

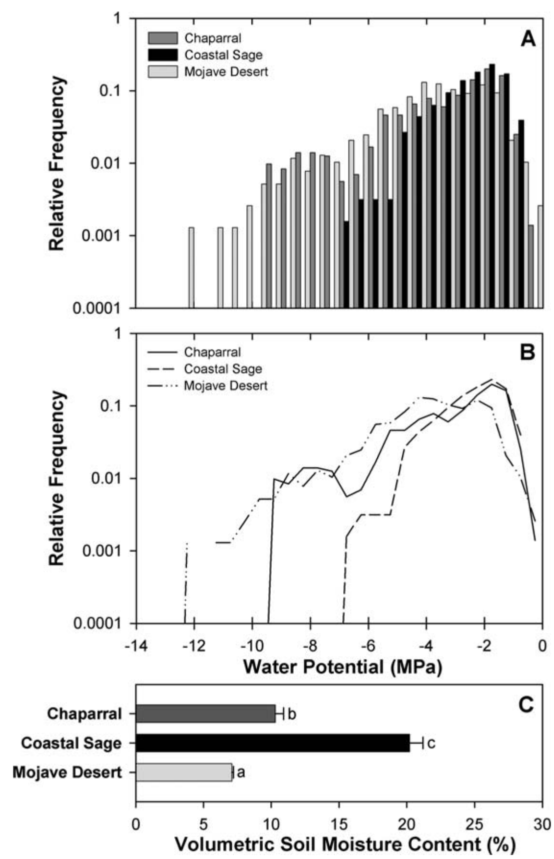

FIG. 4. The frequency of water potential occurrence in three arid plant communities, the chaparral (medium gray fill, solid line), coastal sage scrub (black fill and dashed line) and Mojave Desert scrub (light grey fill, dashed-dotted line) (A and B) and the minimum seasonal volumetric soil water content for these same three communities (C). Different letters after bars in panel C indicated soil moisture values that are significantly different.

TABLE 3. THE NUMBER OF WOODY SPECIES OCCURRING IN THREE PLANT COMMUNITIES OF SOUTHERN CALIFORNIA, INCLUDING THE PERCENTAGE THAT ARE NATIVE TO THE REGION, NOT NATIVE, AND ARE BOTH NON-NATIVE AND INVASIVE. [1] Includes only chaparral and coastal sage species that are distributed in the western Transverse Ranges of southern California. This includes species that have distributions that are more extensive than this region but which include it, such as species that have ranges of the south west of California or the California Floristic Province.

Community	Number of woody species	Native (%)	Non-native (%)	Invasive/noxious (%)
Chaparral	203	78.8	21.2	2.5
Coastal Sage Scrub	182	61.0	39.0	4.4
Mojave Desert Scrub	154	92.9	7.1	0.0

to utilize more limited shallow soil moisture reserves than species in the other two communities. This suggests that among these communities, the Mojave Desert community has the lowest R* value compared to the other communities, assuming that soil moisture availability is the most limiting resource. Differences in soil moisture availability between the Mojave Desert community and the chaparral and coastal sage communities are likely related to differences in precipitation as well as differential water use by the species present in these communities (Jacobsen et al. 2008).

Among sites that receive the same amount of precipitation, differences in woody plant water use significantly affect soil moisture availability. In the present study, the chaparral and coastal sage sites experienced similar annual rainfall (approximately 440 mm) and had similar soil texture (Jacobsen et al. 2007), yet they have different dry season soil moisture levels. This is presumably because of differences in water use by species in these communities (Jacobsen et al. 2008). Species in the chaparral community are able to attain and survive lower water potentials than species within the coastal sage community allowing them to draw shallow soil moisture down to lower levels. Such biotically mediated differences in water resource availability are predicted to occur (Huxman et al. 2005) and have been reported in other communities (reviewed in Levine et al. 2003). Among the chaparral and coastal sage communities, this difference in water use may be related to the drought evading strategy of coastal sage species, many of which have seasonally dimorphic leaves or reduce their canopies during the dry season, compared to the evergreen chaparral species which maintain a full canopy and utilize a drought resisting strategy (Mooney 1989).

Community water use of deeper soil layers may be very different than the patterns found in the present study, which examined only shallow soil layers (<30 cm soil depth). Indeed, different species within these communities tap different soil layers (Hellmers et al. 1955) and shift between shallow and deeper soil layers seasonally. Additionally, plants in different communities display differential water use patterns (Jacobsen et al. 2008). However, differences in the soil moisture of shallow soil layers may be particularly important in the establishment of woody plant seedlings and in determination of the invasibility of these communities.

Dry season soil moisture has been found to be linked to seedling survival for five woody species from the Mediterranean Basin (Spain) (Padilla and Pugnaire 2007). Since most of the invasive or naturalized species already present in these California communities are native to other Mediterranean-type climate regions (Knops 1995; Salo 2004; Keeley 2006), the results of this recent study may be particularly applicable to these southern Californian communities. At dry season soil moistures over 18% nearly all of the studied Mediterranean seedlings survived, whereas there was very little survival at <12% soil moisture, and no survival predicted for soil that had <8% soil moisture (Padilla and Pugnaire 2007). The amount of available water for a given soil moisture content varies depending on soil texture, which differed between the study by Padilla and Pugnaire (2007) and the sites in the present study. Therefore, at the same percentage soil moisture there would be slightly more water available to plants in the southern California communities (with sandy and loamy sand soils; Jacobsen et al. 2007) compared to the site in Spain where plants were grown in silt soil. Yet, the results suggest that while the chaparral and Mojave Desert communities (with 10% and 7% dry season soil moisture content, respectively) would be able to resist invasion (in an average year), nearly all seedlings of these Mediterranean species would be able to persist in the coastal sage community through the dry season (20% dry season soil moisture content).

While dry season data in the present study were collected during an average rainfall year, it should be noted that the invasion process is likely dependent on stochastic abiotic events including disturbances such as land use changes or fire, and altered weather patterns that result in greater than average levels of precipitation (Davis et al. 2000; Mazia et al. 2001; Lloret et al. 2005). These factors also suggest that, at present, the coastal sage community may be the most susceptible to invasion relative to the chaparral and Mojave

Desert communities. When sites experiencing similar rainfall are examined, coastal sage shrub species are less able to lower the level of available soil water resources relative to chaparral species. Additionally, the coastal sage community is at least partially disturbance dependent and likely experiences more disturbance than the other two communities at present.

The predicted differences in susceptibility to non-native and invasive species among these communities (predicted by water resource limitation of these communities and R*) are consistent with current numbers of non-native woody species in these communities (Table 3). The coastal sage contains more non-native and invasive species than the chaparral and Mojave Desert communities. In both the coastal sage and chaparral communities woody invaders are predominantly native to other Mediterranean-type climate regions and include, *Acacia* spp., *Nicotiana glauca*, *Cytisus* spp. and *Spartium* spp. (Knops et al. 1995; Keeley 2006).

Arid and semi-arid sites that exhibit low productivity appear to be less broadly susceptible to invasion than more moist and productive sites (Stohlgren et al. 2002; Otto et al. 2006); however, semi-arid and arid plant communities in southern California have still experienced significant invasion by non-native species. Most of these invasive species are annual herbs and grasses (Knops et al. 1995; Sax 2002; Salo 2004; Keeley 2006; Lambrinos 2006). While invasion of these communities by annuals appears to be at least partially dependent on increased nitrogen availability (Brooks 2003; however see Padgett and Allen 1999), the timing and availability of soil moisture is also important (Salo 2004). Indeed, the shallow moisture available in the coastal sage site examined in the present study would be readily utilized by shallow rooted annuals and herbaceous species and we observed a greater density of non-native annuals and herbaceous species at this site compared to the chaparral and Mojave Desert sites.

The R* rule and similar models have been useful for predicting invasibility of some communities. Using this model to predict susceptibility to invasion by woody shrub species in these three woody shrub communities of southern California suggests that the coastal sage community may be most susceptible to woody species invasion if soil moisture is a limiting resource. This suggests that monitoring and control of woody naturalized shrubs may be most efficient if efforts are focused on this southern Californian plant community, as the chaparral and Mojave Desert communities appear to be more impervious to shrub invasion.

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Literature Cited

Booth, M. S., M. M. Caldwell, and J. M. Stark. 2003. Overlapping resource use in three Great Basin species: implications for community invisibility and vegetation dynamics. Journal of Ecology 91:36–48.

Brooks, M. L. 2003. Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. Journal of Applied Ecology 40:344–353.

Ciros-Pérez, J., M. J. Carmona, and M. Serra. 2001. Resource competition between sympatric sibling rotifer species. Limnology and Oceanography 46:1511–1523.

Cleverly, J. R., S. D. Smith, A. Sala, and D. A. Devitt. 1997. Invasive capacity of *Tamarix ramosissima* in a Mojave Desert floodplain: the role of drought. Oecologia 111:12–18.

Cox, G. W. 1985. Laboratory manual of general ecology, 5th ed. WCB/McGraw-Hill, New York, NY.

Dale, N. 2000. Flowering plants: the Santa Monica Mountains, coastal and chaparral regions of southern California. California Native Plant Society, Sacramento, CA.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88:528–534.

Davis, S. D., F. W. Ewers, J. S. Sperry, K. A. Portwood, M. C. Crocker, and G. C. Adams. 2002. Shoot dieback during prolonged drought in *Ceanothus* chaparral of California: a possible case of hydraulic failure. American Journal of Botany 89:820–838.

Fargoine, J., C. S. Brown, and D. Tilman. 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. Proceedings of the National Academy of Sciences USA 100:8916–8920.

Faull, M. 2005. Toward a flora of Red Rock Canyon State Park: a preliminary checklist. California Native Plant Society, Kern County, CA. Website http://www.kerncnps.org/PlantLists/redrockcyn/rrcflora.pdf [accessed 27 January 2010].

Fox, J. W. 2002. Testing a simple rule for dominance in resource competition. The American Naturalist 159:305–319.

Frazer, J. M. and S. D. Davis. 1988. Differential survival of chaparral seedlings during the first summer drought after wildfire. Oecologia 76:215–221.

Funk, J. L. and P. M. Vitousek. 2007. Resource-use efficiency and plant invasion in low-resource systems. Nature 446:1079–1081.

Hardin, G. 1960. The competitive exclusion principle. Science 131:1292–1297.

Harpole, W. S. and D. Tilman. 2006. Non-neutral patterns of species abundance in grassland communities. Ecology Letters 9:15–23.

HELLMERS, H., J. S. HORTON, G. JUHREN, AND J. O'KEEFE. 1955. Root systems of some chaparral plants in southern California. Ecology 36:667–678.

HERRON, G. J., R. L. SHELEY, B. D. MAXWELL, AND J. S. JACOBSON. 2001. Influence of nutrient availability on the interaction between spotted knapweed and bluebunch wheatgrass. Restoration Ecology 9:326–331.

HICKMAN, J. C. (ed.). 1993. The Jepson manual. University of California Press, Berkeley, CA.

HUXMAN, T. E., B. P. WILCOX, D. D. BRESHEARS, R. L. SCOTT, K. A. SNYDER, E. E. SMALL, K. HULTINE, W. T. POCKMAN, AND R. B. JACKSON. 2005. Ecohydrological implications of woody plant encroachment. Ecology 86:308–319.

JACOBSEN, A. L., R. B. PRATT, S. D. DAVIS, AND F. W. EWERS. 2007. Cavitation resistance and seasonal hydraulics differ among three arid Californian plant communities. Plant, Cell and Environment 30:1599–1609.

———, ———, ———, AND ———. 2008. Comparative community physiology: non-convergence in water relations among three semi-arid shrub communities. New Phytologist 180:100–113.

KEELEY, J. E. 2006. Fire management impacts on invasive plants in the western United States. Conservation Biology 20:375–384.

KNOPS, J. M. H., J. R. GRIFFIN, AND A. C. ROYALTY. 1995. Introduced and native plants of the Hastings reservation, central coastal California: a comparison. Biological Conservation 71:115–123.

KÕIV, T. AND K. KANGRO. 2005. Resource ratios and phytoplankton species composition in a strongly stratified lake. Hydrobiologia 547:123–135.

KRUEGER-MANGOLD, J., R. SHELEY, AND R. ENGEL. 2006. Can R*s predict invasion in semi-arid grasslands? Biological Invasions 8:1343–1354.

LAMBRINOS, J. G. 2006. Spatially variable propagule pressure and herbivory influence invasion of chaparral shrubland by an exotic grass. Oecologia 147:327–334.

LEVINE, L. M., M. VILÀ, C. M. D'ANTONIO, J. S. DUKES, K. GRIGULIS, AND S. LAVOREL. 2003. Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal Society of London B 270:775–781.

LEVINE, S. H. 1976. Competitive interactions in ecosystems. The American Naturalist 110:903–910.

LLORET, F., F. MÉDAIL, G. BRUNDU, I. CAMARDA, E. MORAGUES, J. RITA, P. LAMBDON, AND P. E. HULME. 2005. Species attributes and invasion success by alien plants on Mediterranean islands Journal of Ecology 93:512–520.

MAZIA, C. N., E. J. CHANETON, C. M. GHERSA, AND R. J. C. LEÓN. 2001. Limits to tree species invasion in pampean grassland and forest plant communities. Oecologia 128:594–602.

MCAULEY, M. 1996. Wildflowers of the Santa Monica Mountains. Canyon Publishing Company, Canoga Park, CA.

MOONEY, H. A. 1989. Chaparral physiological ecology–paradigms revisited. Pp. 85–90 *in* S. C. Keeley (ed.), The California chaparral: paradigms reexamined. The Natural History Museum of Los Angeles County, Science Series No. 34.

OTTO, R., B. O. KRÜSI, C. A. BURGA, AND J. M. FERNÁNDEZ-PALACIOS. 2006. Old-field succession along a precipitation gradient in the semi-arid coastal region of Tenerife. Journal of Arid Environments 65:156–178.

PADDOCK, III, W. A. 2006. Adult mortality of chaparral shrubs following severe drought. M.Sc. Thesis, Michigan State University, East Lansing, MI.

PADGETT, P. E. AND E. B. ALLEN. 1999. Differential responses to nitrogen fertilization in native shrubs and exotic annuals common to Mediterranean coastal sage scrub of California. Plant Ecology 144:93–101.

PADILLA, F. M. AND F. I. PUGNAIRE. 2007. Rooting depth and soil moisture control of Mediterranean woody seedling survival during drought. Functional Ecology 21:489–495.

PRATT, R. B. AND R. A. BLACK. 2006. Do invasive trees have a hydraulic advantage over native trees? Biological Invasions 8:1331–1341.

———, A. L. JACOBSEN, R. MOHLA, F. W. EWERS, AND S. D. DAVIS. 2008. Linkage between water stress tolerance and life history in seedlings of nine chaparral species (Rhamnaceae). Journal of Ecology 96:1252–1265.

SALO, L. F. 2004. Population dynamics of red brome (*Bromus madritensis* subsp. *rubens*): times for concern, opportunities for management. Journal of Arid Environments 57:291–296.

SAX, D. F. 2002. Native and naturalized plant diversity are positively correlated in scrub communities of California and Chile. Diversity and Distributions 8:193–210.

STOHLGREN, T. J., G. W. CHONG, L. D. SCHELL, K. A. RIMAR, Y. OTSUKI, M. LEE, M. A. KALKHAN, AND C. A. VILLA. 2002. Assessing vulnerability to invasion by nonnative plant species at multiple spatial scales. Environmental Management 29:566–577.

TILMAN, D. 1982. Resource competition and community structure. Monographs in Population Biology 17. Princeton University Press, Princeton, NJ.

TITMAN, D. 1976. Ecological competition between algae: experimental confirmation of resource-based competition theory. Science 192:463–465.

TYREE, M. T. AND M. H. ZIMMERMANN. 2002. Xylem Structure and the Ascent of Sap. Springer-Verlag, Berlin, Germany.

UNIVERSITY OF CALIFORNIA AND JEPSON HERBARIA. 2001. Online interchange for California floristics. The Regents of the University of California, Berkeley, CA. Website http://ucjeps.berkeley.edu/interchange.html [accessed 01 January 2010].

VANCE, R. R. 1985. The stable coexistence of two competitors for one resource. The American Naturalist 126:72–86.

WILLIAMS, J. E., S. D. DAVIS, AND K. PORTWOOD. 1997. Xylem embolism in seedlings and resprouts of *Adenostoma fasciculatum* after fire. Australian Journal of Botany 45:291–300.