Evaluating the impact of invasive Russian thistle on the endangered Eureka Valley evening-primrose (*Oenothera californica* ssp. *eurekensis*)

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by

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Preface

This report, submitted to the USFWS under permit TE-64547A-0, describes observations and findings made of the endangered Eureka Valley evening-primrose (*Oenothera californica* (S. Watson) S. Watson ssp. *eurekensis* (Munz & J. C. Roos) W. M. Klein) and the invasive alien species, Russian thistle (*Salsola gobicola* Iljin). Both species inhabit the sand dune systems of Eureka Valley in Death Valley National Park. Information included are: (1) the population density estimates of evening-primrose in Eureka Valley sampled from 2010 to 2013 and (2) results of an *ex situ* competition study that determined the effects of competition between evening-primrose and Russian thistle with the top-down effects of herbivory on the competitive interactions.

Section 1
Monitoring of the Eureka Valley evening-primrose population

Introduction

Effective management of endangered species begins with monitoring to obtain quantitative measures of population size, distribution, and spatio-temporal variability. Employing a monitoring strategy that is comprehensive and accurate is important in providing baseline data, analyzing spatial and temporal trends, and determining the stability of a population. Unfortunately, ideal strategies are largely impossible to implement because of constraints such as limited resources, lack of information, and difficulties in counting individuals of a rare species. In consequence we often lack good, consistent monitoring data.

The Eureka Valley evening-primrose (*Oenothera californica* ssp. *eurekensis*) was listed as endangered by the U.S. Fish and Wildlife Service (FWS) in 1978 due to impacts from off-road vehicle (ORV) use on its sand dune habitat. In an attempt to stabilize the population and prevent further habitat degradation, the Bureau of Land Management (BLM) and National Park Service (NPS) implemented the Eureka Valley Dunes Recovery Plan (DeDecker, 1982). Recovery Plan objectives include limiting human access to the dunes, gaining a better understanding of evening-primrose demography, monitoring of the evening-primrose populations, and improving knowledge on the general ecology of the species (e.g. habitat associations, plant-animal interactions). The Recovery Plan has been successful in removing ORV impacts and developing a better understanding of evening-primrose demography and ecophysiology (Pavlik, 1979a, 1979b; Pavlik & Barbour, 1985, 1986). With ORV use banned in the 1970s and prohibition secured by the 1980s, the evening-primrose population appeared to be in recovery. However, managers still lacked consistent and sound data on the population size and distribution.

Monitoring of the evening-primrose population had been limited and sporadic, primarily because of inadequate resources. Early efforts mapped the distribution of the evening-primrose (BLM, 1976; Rowlands, 1982) which provided a coarse estimate of plant abundance but lacked descriptions of methodology, sampling date, and total area surveyed. In 1985, Bagley (1988) established the first permanent plots to estimate evening-primrose abundance, but sampling was repeated only once in 2007. Additionally, this protocol was limited in spatial extent so inferences could not be made for the entire population. Overall, these historic efforts were insufficient to detect trends in abundance or patterns of distribution.

Recent efforts to survey distribution and estimate density of evening-primrose have been much improved. Since 2007, NPS developed and implemented a grid-plot method at a one-ha scale to annually monitor the population (Del Favero, 2009). These data are useful for mapping the known-range of the evening-primrose. However, the one-ha plots are too large to adequately detect plants and thus provide only course estimates of spatial and temporal abundance. Thus, the U.S. Geological Survey and University of California, Davis developed a distance sampling (DS) program to survey the evening-primrose.

Many researchers have tested the efficacy of DS over conventional methods of estimating abundance of individual plants and animals in quadrats (Buckland et al., 2007; Cassey & McArdle, 1999; Focardi et al., 2005; Kissa & Sheil, 2011; Norvell et al., 2003). The main advantage is that it accounts for the observer's probability of sighting an individual plant or animal and thereby allows one to more accurately estimate the number of unobserved individuals. The method is based on the assumption that all individuals at 0 m away from the observer will be detected with a probability of 1 and that detection probability will decrease with

increasing distance. It is also assumed that movements of individuals from the observer are not systematic and that distances are measured accurately. Although immobile, difficulties still arise in detecting plants due to inherent limitations such as small plant size and visual obstructions. Using DS methods would address the limitations of detection and enable us to determine a probability of detection (PD) to provide a more accurate population estimate. Moreover, it is cost-effective and relatively easy to carry out over large sampling areas because it includes just one additional measure of distance between the observer and organism observed. Accordingly, researchers have increasingly been applying DS methods to plant surveys over the last decade (Alexander et al., 2012; Buckland et al., 2007, Correll & Marvanek, 2006; Jensen & Meilby, 2011; Kissa & Sheil, 2011; Prider et al., 2012). We describe our findings from using a DS method to survey the Eureka Valley evening-primrose from 2010 to 2013.

Methods
Field Counts
   Evening-primrose surveys were conducted by observers walking 46 transect lines in 12 blocks that were established in 2010 and 2011 at the three dune systems that evening-primrose inhabit in Eureka Valley. Transect start points were randomly located within blocks and marked by GPS units with the bearing (azimuth) and length selected to be either perpendicular or in parallel to the main axis of dunes. Within each block, one to six parallel transects of the same length separated by ≥ 50 m were established. Initially we aimed to establish 1-km long transects to cover more area since evening-primrose is typically patchily distributed. However, topographic constraints such as steep dunes or non-sand dune habitat limited the distances that could be surveyed, thus some sets of transects were 0.75 and 0.5 km in length (Figure 1). Block areas ranged from approximately 4 to 28 ha.
   We used variable-distance sampling (Buckland et al., 2001) because sighting probability was < 1 due to the irregularity of dune topography and obstructions (e.g. shrubs) of view. Observers recorded azimuth and sighting distance to each plant they saw, the growth stage of the plant (rosette, branched, or senesced), reproductive condition (flowering, fruiting, or neither), and the observer's location along the transect (UTM coordinates marked with a GPS unit). Examples of plant stage and reproductive condition are shown in Figure 2. Surveys were conducted annually from 2010 to 2013. In 2010, Blocks 1, 3, 4 and 5 were surveyed at Eureka Dune. All blocks at all three dunes were surveyed in 2011 to 2013. In 2013, because of the substantial number of plants that germinated in Block 5 and a limited number of workers, only three of the five transects were sampled. Sampling occurred in early June of 2010 and mid- to late May of 2011 to 2013. We conducted surveys in mid- to late May because it was an optimal, phenological time frame in which to minimize detection biases from poor plant visibility and availability (Smolensky & Fitzgerald, 2010). Before May, most evening-primrose plants are still in the rosette stage (of smaller diameter and more appressed to the ground) which decreases plant visibility. After May, plants are more likely to be buried by sand or eaten by herbivores which decreases the availability of individuals for detection.

Data Analysis
   The sighting distance (D_s, distance between observer and individual plant) and sighting angle (θ, angle between the transect bearing and sighting bearing) were used to derive the perpendicular distance (D_p) of a plant from the transect by the equation $D_p = \sin(\theta) * D_s$

(Buckland et al. 2001). Perpendicular distances > 25 m were discarded to avoid the potential of plants being counted on multiple transects.

The distribution of the perpendicular distances were used to model density (plants per ha) with the program DISTANCE (version 6; Buckland et al., 2001). Two key functions (uniform and half-normal) with cosine and polynomial expansion terms were used to generate different models of density. We produced an initial set of models based on ungrouped perpendicular distances. If the fit of these models was inadequate (based on visual inspection of the observed and estimated distributions), we then grouped the data into intervals to improve model fit. The model with the lowest value for the corrected Akaike Information Criteria (AIC$_c$) was considered the one with the most support. When ΔAIC$_c$ was < 2, model selection was based on the visual fit of the observed to fitted distribution as well as χ^2 values for model fit. The best fit model was used to derive the effective strip width (ESW) and the PD (Figure 3). The ESW is the distance from the observer at which one detects the same number of plants that were missed within that distance as were observed beyond that distance. In effect, the ESW is the area within which the best possible estimate could be obtained if we were able to detect 100% of the organisms. Density was calculated by dividing the total count by the PD at the ESW and then dividing by the total survey area. We pooled the rosette and branched growth stages data for each sampling level (block and dune) to estimate density. We used the coefficient of variation (CV) in the density estimates to evaluate relative levels of variation at the two scales.

To evaluate the spatial variability of evening-primrose over space and time, the positions of plants were mapped from calculations of observer GPS coordinates along transects and the measured distances to plants. We mapped the locations of all observations at all three dunes for the four years of data using ArcMap v.10.1.

Proportions of plants in each growth stage (rosette and branched) and reproductive class (flower, fruit, or neither) were calculated for all dune systems together for each year. Because few senesced individuals were observed they were not included in the proportional data set. Proportions for 2013 data were calculated with and without data from Block 5 in 2013.

Results

The half-normal model with cosine expansion terms best fit our distribution of observed perpendicular distances in all analyses (Figure 3). The PD and ESW were derived for each growth stage and both stages pooled for all observations of the four year data set. The probability of detecting rosettes (0.367) was less than that of branched plants (0.51). The ESW for rosette observations (9.2 m) was less than that of branched plant observations (12.8 m). The PD and ESW of pooled observations were 0.41 and 10.3 m, respectively. Overall, the probability of detecting plants of either stage ranged from about 0.9 within a few meters from the transect to < 0.1 at 25 m (Figure 3). Our furthest observation was made at a perpendicular distance of 50.5 m. Plants closer to this maximal distance were typically in the branched stage. However, as mentioned previously, these observations were excluded from the analysis because we truncated the perpendicular distance to 25 m.

The total numbers of plants observed in each year were 1012, 3006, 547, and 6461 from 2010 to 2013, respectively. In Block 5, we counted 5540 plants along the three transects that were sampled in 2013. Mean annual densities fluctuated between 2.4 and 71.3 plants per ha (Figure 4a). Estimated densities by dune and year ranged from 0 to 110.7 plants per ha (Figure 4b–c). Estimated densities by block and year ranged from 0 to 576 plants per ha. All parameter estimates by year, dune and year, and block and year are in Tables 1 to 3, respectively. Although

no evening-primrose plants were observed along any transects at Eureka Dune in 2012, a handful of individuals were observed outside the blocks. In 2013, density at Block 5 (Eureka Dune; 576 plants per ha) was extremely high compared to all other blocks in all other years; the next highest estimate was 97 plants per ha at Block 0 (Marble Dune). At the dune scale, estimates at Eureka Dune fluctuated by an order of magnitude but with no apparent trend. Estimates from Marble Canyon and Saline Spur dunes had a weak decreasing trend over time (Figure 4). In general, density decreased in the majority of the blocks from 2010 to 2013 (Figure 5). The CVs were highly variable at all scales ranging from: 18%–46% by year, 23%–59% by dune and 21%–100% by block (Tables 1 to 3, respectively). Variation in deriving the detection function had virtually no effect on the CVs (0.6%–1.2%). Rather, the estimated variability in density was almost entirely due to natural spatio-temporal variation in primrose numbers (98.8%–99.4%).

Mapped locations of evening-primrose illustrate how variable the spatial and temporal distribution and abundance of plants was over the four years of monitoring (Figures 6 to 8). At Eureka Dune for example, evening-primrose occurred in one large patch of about a 2.5 ha area out of the total 27.6 ha area of Block 2 (Figure 6). Within this patch, 457 plants were recorded in 2011, none in 2012, and six plants in 2013. In Blocks 3 and 4, patches of evening-primrose of various abundances appeared in different parts of both blocks and in different years (Figure 6). Block 5 had the most extreme spatio-temporal pattern; an exceptionally high number of plants were observed in 2013 when, in previous years, we consistently recorded much lower counts (Figure 6). Overall, observations of plants varied along transects, among transects within blocks, among blocks, and among the dune systems.

The growth and reproductive stage data indicated that the majority of evening-primrose plants occur in the rosette stage. Respectively, in 2010 through 2013, 59.5%, 50.2%, 95.6% and 70.1% of plants were rosettes and 40.5%, 49.8%, 4.4%, and 29.9% were branched. When Block 5 data were removed, rosettes and branched plants made up 72.3% and 27.7% of the sample population. Few senesced individuals were observed (three in 2010 and one in 2011). Across all years, 0.4%–14.8% of all plants produced flowers, 0.5%–16.8% produced fruits, and 68.3%–99.1% produced neither flowers nor fruits (Table 4). The greatest percentage of reproductive plants was observed in 2011 (31.7%) and the least in 2012 (0.9%). In spite of the substantial number of plants observed in Block 5, the proportion of reproductive plants in 2013 amounted to a less than a third of that observed in 2011. Overall, the number of reproductive rosettes was consistently below 4% over the four years and more branched plants were in reproduction than rosette plants (Figure 9, Table 4).

Discussion

Despite the fact that plants are stationary, difficulties can still arise in detection due to plant size, distance from observer, and visual obstructions in the landscape. By using a DS technique to survey evening-primrose, we were able to derive PDs and ESWs which allowed us to evaluate by how much and how far our sightings were limited. We found that, on average, we were able to detect less than half of the plants at up to approximately 10 m in perpendicular distance from the transect. Our data also showed that the size of the plant affects detectability; smaller rosettes were less detectable than larger, branching plants. Survey methods that account for the PD are more likely to accurately estimate abundance over large sampling areas. Moreover, the ESW can be used as a guide when determining appropriate plot sizes for future studies on the evening-primrose.

The four-year data set offers preliminary indications of population stability and trends. First, the patterns depended on sampling scale and location. At the largest scale, which includes all three dune systems, the annual pattern appeared to decrease until 2013 when the estimate at Block 5 of Eureka Dune inflated the data by an order of magnitude greater than the previous year. At the dune scale, density estimates at Eureka Dune were similar to the annual estimates and drove the observed annual patterns. At the block scale of Eureka Dune the patterns were highly variable. In contrast, there were slight decreasing trends in density from 2011 to 2013 at Marble Canyon and Saline Spur dunes at both dune and block sampling scales. We suspect the patterns observed at the Marble Canyon and Saline Spur dunes were due to our surveys occurring in the decline phase of normal population flux following two successive years of low precipitation. Because our surveys only spanned three to four years, it would be premature to conclude that these patterns indicate a declining population. However, it is worth noting that most of the trends did not indicate population growth, with the exception of the extremely high number of plants observed at Block 5.

Evening-primrose abundance and distribution were too variable across space (multiple spatial scales) and time to make any definitive statements about trends in the population as a whole. However, we were able to accurately map locations of every observation and these effectively showed the aggregated distribution, variable changes in abundance, and unpredictable appearance and disappearance of plants from one year to the next. For example, patches of plants of varying densities commonly blinked on and off within and among blocks from one year to the next. Variability at the block scale was greater than the larger scales, suggesting that fine scale variability has a greater influence on patterns of evening-primrose abundance than large scale variability. Nevertheless, the fluctuations of plant presence/absence could clearly occur at the larger dune scale. We observed the absence of evening-primrose along all transects at Eureka Dune in 2012 and similarly, Pavlik (1979b) observed the absence of evening-primrose at Marble Canyon Dune in 1979.

The most unexpected example of variability in abundance was the singular mass germination event that occurred at Block 5 in 2013. Although the simultaneous germination was unexpected, especially because it was a year of low rainfall, it may not be that anomalous of an event. The first density record of evening-primrose collected in the 1970s suggested a high concentration of plants on the east side of the Eureka Dune where Block 5 is located (BLM, 1976; Rowlands, 1982). Furthermore, Pavlik (1979a) was able to determine the controlling factors that could cause such an event based on findings from his laboratory germination study of evening-primrose seeds. He concluded that simultaneous (rather than the typical continuous) germination of seeds can be triggered by the concurrence of three independent factors of sand burial, soil moisture, and range of climatic temperature with one dependent factor of sand thermoperiodicity.

Simultaneous germination events may be localized to the eastern side of the Eureka Dune due to its environmental features. Compared to the north and western side of this dune, the eastern side may be most uniform in soil characteristics across the landscape. It is horizontally level and appears to have the least change in amount of sand burial/depletion by wind. Thus, sand burial of the seed bank is at a more consistent depth and, accordingly, moisture levels and soil temperatures may be more uniform. With the occurrence of Pavlik's environmental factors, seeds would likely be triggered to germinate simultaneously across the homogeneous landscape. At the other blocks, the greater topographic heterogeneity and greater sand movement create more variable environmental conditions; therefore, the concurrence of Pavlik's factors is less

likely to occur. Thus, the relative heterogeneity of environmental conditions at a local scale may be most influential on population abundance and distribution.

Additional speculation of the cause of the mass germination event is the existence of a clay lake bed below the sand layer on the east side of Eureka Dune (BLM, 1976; Rowlands, 1982). The clay bed likely increases soil moisture availability to seeds in the sandy layer above. However, we lack information on the clay bed depth and area of coverage below the sand layer. Block 4 is on the same side of the dune as Block 5 and is potentially within the boundary of the clay bed but we did not observe the same simultaneous germination of seeds there.

The occurrence of the simultaneous germination event after a previous year of estimated evening-primrose absence shows that a perennial herb can be similar to annual herbs by having "boom and bust" years (Odum & Barrett, 2005), but on a local scale. It is questionable though whether a boom year is beneficial to the perennial population. Several seed germination studies have concluded that some perennial species evolved mechanisms to avoid simultaneous germination. Instead, it may be more advantageous to spread the risk of seedling mortality throughout the growing season via continuous germination. The latter mode of germination ensures long-term survival of the population in a highly variable environment (Pemadasa & Lovell, 1975; Kigel, 1995). Moreover, large simultaneous germination events could deplete the seed bank for relatively long periods. Thus, local population booms could ultimately be a bust for the evening-primrose population in the long run because, as Pavlik & Barbour (1986) have stated, the seed bank most likely ensures its survival.

Proportionally, plants were more commonly observed in the rosette than branched stage and more reproductive plants were observed in the branched than rosette stage. Sand dunes are low resource environments that may limit the number of plants that can transition to later stages of growth and reproduction. Those that branched may have either germinated earlier in the growing season or been produced vegetatively from a true perennial individual. A perennial individual may have energetic reserves from the previous year to use in the current year and mature faster. Evening-primrose rosettes, nevertheless, have been observed to successfully produce fruits each year. Thus, most individuals may have a chance of producing flowers. Seed production could then be dependent upon fertilization by moth pollinators (Moody-Weis & Heywood, 2001).

The Block 5 germination event did not result in high reproduction even with the large number of individuals observed. This boom in germination may imply stability of the Eureka Dune population; however, the proportion of reproductive individuals at Block 5 was lower than the total proportion of reproductive individuals sampled in 2010 and 2011. Therefore, simultaneous germination events may not be a reliable indicator of population recruitment. We speculate that a cause of decreased reproduction was due to an increase in competitive interactions. Evening-primrose individuals at Block 5 may have depleted the soil moisture more quickly due to the greater abundance of plants, which also increased the effects of both intra- and interspecific competition. Other native plant species, such as the perennial *Sphaeralcea ambigua* (apricot mallow), also appeared to experience a germination boom at the same time as the evening-primrose and could have exerted strong competitive effects.

Conclusions

Results of this four-year study indicate highly variable distribution and abundance of the Eureka Valley evening-primrose over multiple spatial scales and time. We cautiously suggest that the population is stable and the high spatio-temporal variability may be normal in the population dynamics of this species. The sampling design proved to be efficient in terms of

sample size, spatial coverage and generating a precise probability of detection function. However, the high natural variability will pose challenges in detecting trends, especially over time periods less than ten years. Given this natural spatio-temporal variability, we stress that more years of survey data and the addition of environmental data (such as precipitation and sand burial) would help to not only determine population trends and stability, but also potentially reveal underlying mechanisms affecting the species population dynamics. The DS method in combination with the NPS grid system would likely provide a comprehensive and robust survey design to monitor population changes of the evening-primrose. The grid system, used to collect presence/absence data in more recent years (Cipra & Fuhrman, 2012) would provide data on changes in the population range and the DS data would provide estimates on changes in population distribution and abundance. Additionally, using the presence-absence data of the grid system, managers could potentially locate new areas to establish additional blocks of transects to sample by the DS method.

The strength of the DS method depends on species characteristics, survey environment characteristics, sampling design and observer experience. We do not recommend using DS to monitor common species because it could be inefficient and overly time-consuming. Using DS would be effective at monitoring rare or uncommon species (Kissa & Sheil, 2011). Moreover, a well-planned sampling design would allow adjustments to avoid inefficiencies and time-constraints, as we did by reducing the number of transects at Block 5 to save time and effort yet retain sufficient statistical replicates. We encourage the use of the DS method in combination with the grid-plot method as a comprehensive monitoring strategy for managing the rare and endangered Eureka Valley evening-primrose.

References

Alexander H.M., Reed, A.W., Kettle, W.D., Slade, N.A., Bodbyl Roels S.A., Collins, C.D., & Salisbury, V. (2012). Detection and plant monitoring programs: Lessons from an intensive survey of *Asclepias meadii* with five observers. *PLOS ONE*, 7: e52762.

Bagley, M. (1988). A sensitive plant-monitoring study of the Eureka Dunes, Inyo County, California. *Plant Biology of Eastern California*, 2, 223–243.

Bureau of Land Management. (1976). *Eureka Dunes Environmental Analysis*. U.S. Dept. Bureau of Land Management, Bakersfield , CA, Desert District Office.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., & Thomas, L. (2001). *Introduction to distance sampling*. London, England: Oxford University Press.

Buckland, S.T., Borchers, D.L., Johnston, A., Henrys, P.A. and Marques, T.A. (2007). Line transect methods for plant surveys. *Biometrics*, 63, 989–998.

Cassey, P. & McArdle, B. H. (1999). An assessment of distance sampling techniques for estimating animal abundance. *Environmetrics*, 10, 261–278

Cipra, J. & Fuhrmann, K. (2012). Understanding endangered plant species population changes at Eureka Dunes, Death Valley National Park. *Park Science*, 29(1), 62–68.

Correll, R. & Marvanek, S. (2006). Sampling for detection of branched broomrape. In *Fifteenth Australian Weeds Conference*, Adelaide (pp. 618–621).

DeDecker, M. (1982). *Eureka Valley Dunes recovery plan*. Portland, OR. U.S. Fish and Wildlife Service.

Del Favero, S. (2009). *Monitoring, management efforts, and overview of threats for three rare plant species at the Eureka Valley sand dunes*. Death Valley National Park, CA.

Focardi, S., Montanaro, P., Isotti, R., Ronchi, F., Scacco, M., & Calmanti, R. (2005). Distance sampling effectively monitored a declining population of Italian roe deer *Capreolus capreolus italicus*. *Oryx*, 39(4), 1–8.

Jensen, A., & Meilby, H. (2012). Assessing the population status of a tree species using distance sampling: Aquilaria crassna (Thymelaeaceae) in Northern Laos. *International Journal of Forestry Research*, 2012.

Kigel, J. (1995). Seed germination in arid and semiarid regions. In J. Kigel and G. Galili (Eds.), *Seed development and germination* (pp. 645-7 00). New York, NY: Marcel Dekker, Inc.

Kissa, D.O. & Sheil, D. (2011) Visual detection based distance sampling offers efficient density estimation for distinctive low abundance tropical forest tree species in complex terrain. *Forest Ecology and Management*, 263,114–121.

Moody-Weis, J. M. & Heywood J.S. (2001). Pollination limitation to reproductive success in the Missouri evening primrose, *Oenothera macrocarpa* (Onagraceae). *American Journal of Botany* 88(9), 1615–1622.

Norvell, R. E., Howe, F. P., & Parrish, J. R. (2003). A seven-year comparison of relative-abundance and distance-sampling methods. *The Auk*, 120(4), 1013–1028.

Odum, E. P., Barrett, G. W., & Brewer, R. (2005). *Fundamentals of Ecology* (5th Ed.). Belmont CA; Thomson Brooks/Cole.

Pavlik, B. M. (1979a). *A synthetic approach to the plant ecology of desert sand dunes, Eureka Valley, California* (unpublished M.S. thesis), University of California at Davis.

Pavlik, B. M. (1979). *The biology of endemic psammophytes, Eureka Valley, California, and its relation to off-road vehicle impact*. Bureau of Land Management, Desert Plan Staff.

Pavlik, B. M. & Barbour, M. G. (1985). *Demography of endemic psammophytes, Eureka Valley, California, I. Seed production, dispersal and herbivory*. California Department of Fish and Game, Rare Plant Project, Sacramento, CA.

Pavlik, B. M. & Barbour, M. G. (1986). *Demography of Endemic Psammophytes, Eureka Valley, California, II. Survivorship, Seed Bank Dynamics and Frequency of Establishment*. State of California, Department of Fish and Game, Rare Plant Project, Sacramento, CA.

Pemadasa, M. A. & Lovell, P. H. (1975). Factors controlling germination of some dune annuals. *Journal of Ecology*, 63, 41–59.

Prider, J., Correll, R., & Warren, P. (2012). A model for risk-based assessment of *Phelipanche mutelii* (branched broomrape) eradication in fields. *Weed Research*, 52(6), 526–534.

Rowlands, P. G. (1982). *Physical and biotic attributes of the Eureka Dunes region, Eureka Valley, California*. Riverside, CA: Bureau of Land Management, California Desert District.

Smolensky, N. L., & Fitzgerald, L. A. (2010). Distance sampling underestimates population densities of dune-dwelling lizards. *Journal of Herpetology*, 44(3), 372–381.

Section 2
Competition and herbivory of the Eureka Valley evening-primrose and Russian thistle

Introduction

Park managers and conservationists believe the endangered Eureka Valley evening-primrose (*Oenothera californica ssp.eurekensis*) is under direct threat from the invasion of Russian thistle (*Salsola gobicola*) in Eureka Valley (Dedecker, 1988). The most recent field data collected on both the density and distribution of the evening-primrose and Russian thistle suggested a negative correlation of spatial distribution and abundance of the two species (unpublished data). Density of evening-primrose decreased where density of Russian thistle increased. This indirectly implies a competitive effect between the two species, but the data do not indicate if one species is directly outcompeting the other.

Because the evening-primrose is endemic to one location in the world and its population was notably in decline due to off-road vehicle usage in previous decades (which resulted in its endangered status), our perception of the species is inclined towards seeing the evening-primrose as a frail species in need of protection from all biological threats (e.g. the Russian thistle invasion, herbivory). In contrast, but on a parallel level, the local abundance and wide-scale distribution of the non-native Russian thistle bolsters a viewpoint that it is a strong competitor that actively excludes other species in the communities it invades. However, the inherent biology of the two species must not be overlooked. The perennial evening-primrose has persisted over thousands of years and is adapted to the harsh sand dune environment of Eureka Valley (Klein, 1970) while the annual Russian thistle may be opportunistically dominating within this plant community where environmental factors happen to promote its growth. Moreover, perennial species often have biological advantages over annual species such as clonal reproduction (Crawley and May, 1987). Thus, it is important to have as unbiased as possible of information to aid our understanding of biological interactions to provide a rational basis of making management decisions on both endangered and invasive species.

Extrinsic factors such as herbivory are also important to address when examining plant-plant interactions. Though one species may have a competitive advantage over another species, the interaction can potentially be modified by top-down effects of herbivory (Notzöld et al., 1998; Hunt-Joshi et al., 2004). Native black-tailed jackrabbits (*Lepus californicus*) and desert cottontail rabbits (*Syvilagus audubonii*) are known to feed on the evening-primrose in Eureka Valley (Pavlik and Barbour, 1985). Unfortunately no data exist on the influences that frequency and degree of herbivory may have on the evening-primrose population or of the mediating effect herbivory may have on the competitive ability of an evening-primrose individual.

We hypothesize that a rare endemic may be the superior competitor and the abundantly dominant and widespread invader may be incorrectly assumed to be a strong competitor because it opportunistically invaded the native species' habitat due to negative impacts of native herbivores on the native species. We also hypothesize that in the absence of herbivory and because the endemic is a perennial species, it would hold a competitive advantage over the invasive annual species. To test these hypotheses, our study (1) evaluated the magnitude and direction of competition between evening-primrose and Russian thistle, (2) evaluated the magnitude of intraspecific competition in each species and (3) determined the impact of rabbit herbivory and simulated herbivory by leaf-clipping on the competitive ability of evening-primrose. The latter hypothesis regarding the competitive superiority of a perennial species will continue to be tested in 2014.

Methods

Experimental Design

A target-neighborhood approach with a factorial design (Mckee 2012) was used to evaluate interspecific competition between evening-primrose and Russian thistle and intraspecific competition within each species. Target individuals of each species were planted with three levels of density of neighboring plants of the same or other species which were categorized as a variable called neighbor group. There were eight replicates of each combination of a target plant grown with plants of one of the five neighbor groups (Figure 10): zero neighbors (None), three evening primrose (P3), six evening-primrose (P6), three Russian thistle (S3), and six Russian thistle neighbors (S6).

To evaluate effects of herbivory on plant competition, two types of herbivory treatments were established: (1) simulated-herbivory by clipping shoots with scissors and (2) natural herbivory by allowing native rabbits and hares full access to plants. To test specific degrees of herbivory, target plants were clipped at amounts of 0% (Clip-0), 25% (Clip-25), and 50% (Clip-50) of the shoot. Clipping occurred at two time points during the experiment. Eighty pots of the same target species and neighbor group combinations mentioned above were established for each of the four herbivory treatment groups. Controls for all combinations of each target species with neighbor group and herbivory treatment were the pots of target plants without neighbors in the 0% clipping treatment. There were a grand total of 320 pots where 240 pots (Control, Clip-25, and Clip-50 sets) were enclosed in mesh fencing to exclude all mammals and 80 pots were outside of the exclosure for rabbits to fully access all evening-primrose plants (targets and neighbors). The rabbit herbivory group of pots was enclosed by a chicken wire fence during the first month to allow seedling establishment; afterwards, the enclosure was opened to allow full access of these pots to rabbits.

Plants were potted in 2-gal containers of silica (quartz) sand mixed with approximately 10% calcined clay to simulate soil texture in the field. Pots were watered daily until all seedlings were fully established (about eight weeks) and then watering was gradually reduced to twice a week. Evening-primrose seeds were intentionally germinated 3-4 weeks prior to germination of Russian thistle seeds because evening-primrose germinates earlier in the year (January-February) than Russian thistle (March-April) in the desert (Pavlik, 1979; Young and Evans, 1979; and personal observations). Plants were grown outdoors at the White Mountain Research Center's, Owens Valley Station. Shoots from target and neighbor plants were harvested, oven dried (48 hrs at 80 °C) and weighed separately at the end of an 18-week growing period (July-November, 2013).

Unexpectedly, herbivory of many Russian thistle plants occurred within a week before opening the exclosures to the rabbit herbivory set of pots, thus negating the main competitive factor in the experiment. Subsequently, we continued with plans of allowing rabbit herbivory of evening-primrose but instead of collecting biomass at the end of the experiment, we collected weekly observational data on rabbit browsing of each individual. We kept track of the level of rabbit browse of each target and neighbor plant. We noted whether plants were never browsed, partially browsed, and completely browsed (disappearance of the entire shoot). We noted whether individuals were browsed multiple times after new shoots emerged after the initial browsing. We recorded whether plants clonally reproduced, naturally senesced or senesced immediately after browsing. Plants were considered senesced if aboveground shoot color turned

brown and new rosettes were not produced in place of the senesced rosette within the duration of this portion of the experiment (approximately 6 months).

Rabbits were never directly observed to graze on evening-primrose plants. Photos captured with motion-sensing cameras of pilot study plants confirm that black-tailed jackrabbits and cottontail rabbits will eat the evening-primrose in pots. For this study, indications that rabbits (instead of other animals) fed on evening-primrose after shoot loss was observed included: rabbit tracks, fecal pellets, and urine on the sandy ground around the pots and pellets in the pots (Figure 11). Rabbits will hop on top of pots to gain better access to the plants. Other tracks observed on the sandy ground also included kangaroo rats, deer mice, lizards and raccoons of which none seemed interested in evening-primrose. Small animals such as insects, birds, and small reptiles were discounted as potential herbivores during this experiment because not a single evening-primrose in the exclosure lost any shoot material when they all had full access to these pots.

Data Analysis

To evaluate the direction and level of interspecific and intraspecific competition of evening-primrose and Russian thistle, we compared target plant biomass by a one-way analysis of variance (ANOVA). First we standardized biomass before comparing the two species because they may have differential growth rates. We relativized the biomass of each target plant by taking the natural log of the ratio of each treatment sample biomass to the randomly-assigned control sample biomass of the respective target species. Then a one-way analysis of variance (ANOVA) was applied to determine the main effects of neighbor group and target species and their interaction effects on the biomass ratio.

We evaluated the effects of simulated herbivory on target biomass of evening-primrose in competition with each neighbor group by a two-way ANOVA of the main effects of neighbor group and leaf-clipping and their interaction effects. Multiple comparisons between each treatment combination were assessed using Tukey's HSD test with the Bonferroni's correction to avoid false positives among the 118 comparisons. When we found little significance of difference in effect between species of neighbors in the relativized biomass analysis, we used an analysis of covariance (ANCOVA) to determine the relationship of target and neighbor biomass of both species of neighbors pooled for each level of leaf-clipping.

Russian thistle target data from all leaf-clipping treatments were pooled because they were not clipped and were thus considered more replicates of each neighbor group. A one-way ANOVA was conducted to analyze the effect of neighbor group on target biomass. A potential outlying record of a Russian thistle target measured at 0.897 g within an average of 0.226 g was observed in the control set of pots; however, Cook's Distance showed that it still fell within an acceptable range and was thus kept in all analyses.

We were unable to analyze the effect of natural herbivory on the competitive interactions between evening-primrose and Russian thistle but we summarized the data on the natural herbivory of evening-primrose and Russian thistle plants.

Results

Relative Target Response of Evening-primrose and Russian thistle

By relativizing target biomass we were better able to compare the target responses between the two species. The overall growth of evening-primrose targets was significantly greater than growth of Russian thistle targets (Table 5). The estimate of relativized biomass ratio of evening-primrose (-0.81±0.316 SE) was 44% greater than that of Russian thistle (-1.436±0.316 SE).

Comparing relativized biomass ratios also showed that the identity of neighbors (evening-primrose vs. Russian thistle) and density of neighbors (three vs. six) had no differences in effect on either target species (Figure 12).

Target Response of Evening-primrose

Main effects of neighbor group and leaf-clipping treatments were significant in reducing target biomass of evening-primrose while no significant interaction effect was detected in the two-way ANOVA (Table 6). Within each neighbor group (None, P3, P6, S3, and S6), mean biomass of un-clipped targets was greatest and mean biomass of targets with 50% of leaves clipped was lowest. Within each clipping treatment (Clip-0, Clip-25, and Clip-50), mean target biomass in the absence of neighbors was greater than that in the presence of three or six neighbors, regardless of neighbor species identity. Presence of neighbors reduced target biomass from that of the control group (Clip-0/None) by a range of 28%-50% in the Clip-0 level, 17%-66% in the Clip-25 level, and 56%-83% in the Clip-50 level. The majority of clipping/neighbor group combinations had significant reductions of plant target biomass compared to the control targets where all significant differences had a p-value < 0.0004 with Bonferroni's correction (Figure 13). Exceptions were the Clip-25/None, Clip-0/P6, Clip-0/S3, and Clip-0/S6 combinations (Figure 13). The greatest difference observed from the control biomass was in the Clip-50/P6 treatment combination by an 83% reduction. Fewer significant reductions were observed when making comparisons among all other treatment combinations. Significant differences between target plants grown without neighbors and target plants grown with evening-primrose neighbors were observed in the Clip-25 treatment while no significant differences were observed between any neighbor groups in the Clip-50 treatment (Figure 13). Across clipping treatments with presence of neighbors, only the Clip-50/P3 and Clip-50/P6 treatment combinations were significantly lower in biomass than three of the four Clip-0 plus neighbors treatment combinations (P6, S3 and S6).

In the ANCOVA with total biomass of neighbor plants as a covariate, effects of neighbor mass and clipping treatment were significant; the interaction effect was not (Table 7). Target biomass was negatively related to neighbor biomass with similar slopes across the three levels of clipping (Figure 14). The proportional difference in biomass estimates between non-clipped and clipped plants corresponded well with the 25% and 50% levels of leaf-clipping (Clip-0 = 0.383±0.016 SE, Clip-25 = 0.291±0.016 SE, and Clip-50 = 0.224±0.018 SE). Linear contrasts to test for differences of intercepts among the clipping levels significantly differed from one another with Clip-0 targets having the greatest biomass and Clip-50 targets having the lowest biomass (Table 8).

Russian thistle Target Response

Biomass of Russian thistle targets were greatest when grown without neighbors and significantly decreased when grown with neighbors of primrose or Russian thistle of both densities (Table 9). Similar to observations made of primrose targets, no differences in effect between neighbor species and between three and six neighbors were observed by ANOVA on target biomass (Figure 15).

Reproduction

Russian thistle produced more flowers and fruits than evening-primrose. The singular, largest Russian thistle target plant produced 109 fruits. All other Russian thistle targets produced

between 1 and approximately 45 fruits. All 120 Russian thistle targets in the non-rabbit herbivory treatments reached fruit production before harvesting. The 40 Russian thistle targets in the rabbit herbivory treatment were eaten while in an early stage of growth before flower and fruit production began.

Of all 320 primrose targets across the four herbivory treatments (no clipping, 25% clipping, 50% clipping, and natural rabbit herbivory), one plant produced one flower that matured into a fertilized fruit. Another single target plant within the control set of pots vegetatively produced two new shoots. None of the evening-primrose targets in the clipping treatments produced new shoots. Of the rabbit herbivory treatment, none of the plants produced flowers; however, many of them produced new shoots.

Rabbit Herbivory

Rabbits began browsing evening-primrose plants within two days of opening the exclosure. Emergence of new rosettes in place of browsed rosettes occurred as quickly as two weeks of initial browsing. Some individuals continued to produce new rosettes after repetitive occurrences of complete removal of all aboveground shoots. A few individuals, we presume, naturally senesced because the rosette was never browsed and died early on in the experiment where no new rosettes emerged from the soil in the space of the dead rosette.

At the end of six months of herbivory observations, approximately 2% of 184 Russian thistle target and neighbor plants survived (Table 10). Of the 184 evening-primrose target and neighbor plants, 7.1% were never browsed, 54.9% were only partially browsed, 38% were completely browsed at least once, and about 27.2% produced new rosettes at least once (Table 10). Of the non-browsed plants, 15.4% clonally reproduced. Of the partially browsed plants, 15.8% clonally reproduced. Of the completely browsed plants, 45.7% clonally reproduced. About 47% of plants that were completely browsed never produced new rosettes and were presumed dead (Table 10). Some individuals (15.8%) were revisited by rabbits and partially or completely browsed again after each time new shoots were produced.

Discussion

Inter- and Intraspecific Competition

Competition from neighboring plants undeniably reduced plant biomass of target individuals however; analyses of relative and absolute biomass produced partially incongruent results regarding levels of inter- and intraspecific competitive effects on evening-primrose and Russian thistle. Comparisons of relative biomass indicated that both neighboring species of both levels of density have similar effects on both target species, differing only in a greater overall reduction of biomass of Russian thistle than evening-primrose. When comparing absolute biomass, evening-primrose targets were more variably affected by neighbor groups than Russian thistle targets. No matter the number or species of neighbor present, Russian thistle target plants were equally negatively affected across the neighbor groups with neighbors present. In contrast, evening-primrose targets were better able to tolerate interspecific competition and the increasing number of neighbors than Russian thistle targets. Unexpected were the results of intraspecific competitive effects where three neighbors reduced target biomass more so than six evening-primrose neighbors. With more competitors in a pot, each plant would more likely experience competition from a neighbor plant as well as the target plant. Thus neighbor plants may have reduced other neighboring plants' competitive strengths against the target plant (Figure 16).

These results differed from those of a pilot study conducted in the preceding year (Chow and Klinger, 2013). We previously determined that evening-primrose was a stronger competitor than Russian thistle in both inter- and intraspecific competition. The difference in results may be related to the size that plants reached by the end of each study. Target biomass of control plants in this study was less than that of the pilot study for both species: for evening-primrose by about 70% and for Russian thistle by almost 90%. Changes in environment such as decreasing daylight hours and temperatures towards the end of this study may have slowed plant growth because the study was conducted later in the year than the pilot study; in July-November rather than in May-September due to logistical constraints. Additionally, earlier germination time in the growing season can increase the likelihood of growth to greater sizes and reproductive success (Ross and Harper, 1972; Fowler, 1984). The earlier germination time of the pilot study may also explain the larger size of those plants compared to the plants in this study. In its natural setting, the earlier germination time of evening-primrose than Russian thistle is likely an additional advantage for the evening-primrose beside it being a perennial plant.

Intensity of competition has been shown to increase as plant size increases (Schwinning and Weiner, 1998). The competitive effect of an individual may depend on the size of the plant where competitive intensity is relative to its size; the larger the plant, the greater the competitive effect on a competitor and vice versa (Turner and Rabinowitz, 1983; Weiner, 1990; Connolly and Wayne 1996). Size-symmetric or -asymmetric competition (Weiner1990) is likely why we observed stronger competitive effects among evening-primrose targets and neighbors in the pilot study than in this study. Plants in this study may not have reached a large enough size to experience as intense levels of competition, therefore competitive levels were more similar among neighbor groups. Overall, evening-primrose produced larger plants than Russian thistle in both studies which may explain its stronger competitive ability over Russian thistle. Also, inter- and intraspecific competition of evening-primrose may only be more evident towards the latter half of the growing season when competing individuals take up more space above- and belowground due to larger shoots and more extensive roots.

In arid environments, belowground competition is more likely to occur than aboveground competition because desert plants are typically sparsely distributed and root systems can often grow far beyond the cover area of the shoot (Fowler, 1984; Richards, 1986; Casper and Jackson, 1997). Furthermore, belowground competition has often been reported as size-symmetric (Weiner, 1990; Weiner et al, 1997; Cahill Jr. and Casper, 2000) but can be size-asymmetric in soils with heterogeneous distributed resources (Rajamieni, 2003). Roots were informally harvested, dried and weighed from the pilot study plants. We observed a greater production of roots in evening-primrose than in Russian thistle plants which may explain the stronger intraspecific interactions of evening-primrose than interspecific interactions with Russian thistle in the pilot study (unreported data). Root strands of evening-primrose were longer and thicker than Russian thistle. Additionally, location of root production differed between the two species. Evening-primrose accumulated the majority of its finer roots at the bottom of the pot whereas Russian thistle roots did not produce as much root material to accumulate en masse at the bottom, although it was much more difficult to separate strands of Russian thistle roots from that of evening-primrose because they were so fine. However, the main and lateral roots of Russian thistle were more easily extracted and typically found in the mid-section depths of the pots. Therefore, belowground intraspecific competition of evening-primrose was compounded at the bottom of pots whereas below-ground interspecific competition may have had more spatial separation. Without the limitation of a pot, it is possible that evening-primrose roots are more

likely to reach deeper depths than Russian thistle roots in the field. However, maximum rooting depths of both species is unknown in the sand dunes of Eureka Valley.

Simulated Herbivory Effects on Evening-primrose

Because interaction effects of leaf-clipping and neighbor groups were insignificant, our hypothesis that herbivory diminishes the competitive ability of evening-primrose against competitors was only partially supported. The main effect of leaf-clipping significantly reduced target biomass because it was simply a physical removal of above-ground biomass. If leaf-clipping diminished the competitive ability of evening-primrose against Russian thistle, then we would have observed a significant reduction in target biomass of leaf-clipped plants grown with Russian thistle neighbors from target biomass of leaf-clipped plants of the same clipping levels grown without neighbors. We did however observe significant reductions in biomass from plants clipped at the 25% level and grown with primrose neighbors compared to biomass of plants from the same clipping level grown with zero neighbors. Clipping at the 50% level in combination with the presence of conspecific neighbors did not alter biomass significantly from the Clip-50 control. However, the addition of 50% clipping with six conspecific neighbors was significantly different from the lone effect of six conspecific neighbors and three or six heterospecific neighbors. Therefore the effect of simulated herbivory at 25% is not stronger than the effect of neighbors but at a 50% level, leaf-clipping may have a stronger effect on biomass reduction than the effect of neighbors. Furthermore, these results indicate that intraspecific competition is stronger than interspecific competition with the effects of leaf removal by clipping.

Because the effect of species of neighbors was not influential like the effect of presence of neighbors on target biomass, we analyzed the effect of leaf-clipping with neighbor mass as a covariate, regardless of species identity. Negative slopes in the relationship between target and neighbor biomass indicate competition between target and neighbor plants (Goldberg and Werner 1983) and were observed in our data. However the similarity of slopes lends further support to our previous finding that clipping had no interactive effect on the competitive ability of targets against neighbors.

Although this study was specifically designed to evaluate the effects of neighbors on targets, we found that the data do have potential implications of the effects of targets on neighbors. Leaf-clipping decreased target biomass as expected but increasing levels of clipping may have allowed an increase in the maximum amount of total neighbor biomass. At the Clip-0 level, not a single measurement of neighbor mass was recorded beyond 0.373g, at Clip-25 neighbor biomass reached a maximum of 0.505 g, and at Clip-50% neighbor plants reached the highest value of 0.583 g. This indicates that leaf-clipping of target plants can potentially extend the maximum total biomass gained by its neighbors.

Natural Herbivory of Target Plants

Herbivory of evening-primrose may have negative and positive effects on the evening-primrose. Rabbit herbivory affected over 90% of individuals in our experimental population from varying degrees of leaf removal to the complete loss of the whole rosette. Partial-browse of individuals may have caused the death of a few individuals because they senesced soon after the initial browse. The consumption of whole rosettes may have caused at least 17.9% mortality of all individuals. Because this perennial species can clonally propagate more rosettes, 17.4% of individuals survived complete herbivory of initial rosettes. Completely-browsed plants were more often observed to produce new rosettes than partially-browsed and non-browsed rosettes

combined. Of the individuals that were wholly eaten, about half of them produced new rosettes and about half of them did not recover. Thus herbivory can promote vegetative reproduction as observed in other plant species (McNaughton, 1983; Tolvanen and Laine1997; Loeser et al. 2004) but less than 50% of the time, new rosettes will replace the lost rosette.

The percentage of individuals that lost all aboveground material to herbivory in our experiment (38%) was much lower than what we have cursorily observed in the field. In 2010, during an overnight observation of 51 individuals, we observed about a 90% loss of whole rosettes in the field but are uncertain if those individuals recovered or not (personal observations). The disparity of shoot losses may be due to differential foraging behavior of rabbits at the station and rabbits in the field. The natural vegetation surrounding our experimental site is dominated by shrubs with some herbs and grasses, but no species closely related to the Eureka valley evening-primrose has been personally observed here. Thus it is a new plant and an odd growth medium (sand in a pot) for the local rabbits to learn to feed upon whereas, in the sand fields of Eureka Valley, evening-primrose has been a common staple for many generations of rabbits. Often, field-rabbit feeding behavior of evening-primrose (and other perennial herbs such as *Tiquilia plicata*) is shown by the many depressions in the sand where roots were exposed, eaten, and the shoot left to dry on the sand (Figure 17). Only one individual plant in our experiment was dug out during the last month of observations (Figure 17). We may have observed less herbivory of whole rosettes because it took months before one station-rabbit learned to dig into the sand and eat the fleshy root instead of just the shoots aboveground.

In the natural environment, rabbit herbivory may influence the population dynamics of the evening-primrose depending on the timing and frequency of browsing and amount and type of plant tissues consumed. Additionally, the effects of herbivory may shift from positive to negative or vice versa. A positive effect for instance is if whole rosettes are consumed, vegetative growth may be stimulated to produce more photosynthetic tissues. However, if the plant is frequently browsed after a new clone emerges to replace the lost clone, browsing would likely hinder or delay floral reproduction. If a plant spends the majority of the growing season on constantly producing new rosettes, fewer resources would be available for sexual reproduction. Consequently, herbivory may decrease the amount of flowers and fruits produced by the end of the season. Currently, we do not have information on all the types of tissues consumed. Leaf, rosette, and root crown herbivory have been observed but floral and fruit losses have not been observed with the same certainty. Additionally, other species of herbivores of evening-primrose that have been observed but not studied are the larvae of *Hyles lineata* (white-lined sphinx moth) and a dune beetle *Eusattus muricatus* (Figure 18). The potential consequence of reduced fecundity of individuals due to herbivory is decreased abundance of the whole population.

Rabbits have been observed to eat the full-grown Russian thistle plants found on the research station grounds. Thus, there is a possibility that rabbits ate some of the Russian thistle plants after the exclosure was opened. However, we mainly suspect rodents, such as deer mice, consumed many of the juvenile plants because pots were still enclosed by chicken wire fencing when plants began to disappear. The animals left only the thin hypocotyls still standing in the pots as well as droppings in some pots. Rodent traps had been placed around herbivory pots but raccoons quickly disabled them before any mice were caught. We did successfully trap deer mice that found their way into the exclosure of the control and leaf-clipping treatment plants where rabbits and raccoons were excluded.

Reproduction

Evening-primrose produced more vegetative material than Russian thistle while Russian thistle produced more reproductive material than evening-primrose. The greater reproductive success of Russian thistle compared to evening-primrose is likely due to the different phenologies of an annual compared to a perennial plant relative to the timeframe of this study. Annual plants complete their life cycle from seed to mature, reproductive individual in only one growing season. On the other hand, perennials have more complexities than annuals in development and reproduction (Bernier 1988, Albani and Coupland 2010). Perennials like evening-primrose can grow from seed to any combination of sexual and/or asexually reproductive individual for multiple growing seasons depending on the exogenous and endogenous signals an individual receives. Endogenous signals such as critical leaf area (Vilela et al. 2008) and exogenous signals such as day length (Bernier 1988) can trigger asexual or sexual reproduction. In the field, evening-primrose typically grows from late winter to summer and Russian thistle from spring to summer; however, our experimental time frame shortened the growing season to summer and fall. The temporal shift and shortened growing time may have shifted exogenous and endogenous signals from normal patterns of the field. The annual Russian thistle may have less restrictive and complex signals for inducing reproduction in plants, therefore all Russian thistle individuals in our study were able to reach reproductive maturity. The more complex signals needed for evening-primrose reproduction must have been very weak because only one evening-primrose plant produced a flower and fruit and one other plant produced a new rosette of the non-rabbit herbivory treatments. As previously mentioned, rabbit herbivory may promote asexual reproduction and delay sexual reproduction. Overall, both species produced less vegetative and reproductive material than what has typically been observed in the field.

Conclusions

Our competition studies resulted in a range of potential conclusions on the competitive relationship between evening-primrose and Russian thistle: (1) the magnitude of inter and intraspecific competition may be equivalent in evening-primrose and Russian thistle, (2) intraspecific competition of evening-primrose may be stronger than interspecific competition with Russian thistle, or (3) evening-primrose may be a stronger competitor than Russian thistle in both inter- and intraspecific competition. Although variable, the summation of results from the pilot study and the additional effects of leaf clipping and rabbit herbivory in this study showed that Russian thistle competitors never outdid evening-primrose competitors. This lends further support to our hypothesis that this invasive annual species is unlikely to outcompete the native perennial species. Management may be relieved of concerns that the Russian thistle invasion is threatening the evening-primrose population.

Should the threat of Russian thistle become stronger than the population of evening-primrose or any other species can withstand, population control of Russian thistle would be necessary in Eureka Valley. A good option may be some form of biological control or manual method that removes Russian thistle seedlings. Deer mice quickly reduced almost our entire experimental population of Russian thistle before they were able to mature to produce seed. This is an ideal timing of Russian thistle removal because (1) it reduces the amount of seed input for future generations and (2) removes the plants before they have had much time in acquiring soil resources which leaves the resources for the native plant community. However, potential native herbivores of Russian thistle in the field are unknown, although one non-native species has been tested for the purpose of a biological control of Russian thistle (Smith et al., 2009).

Herbivory, simulated and natural, can account for significant losses of aboveground plant material but herbivory may not exacerbate competitive interactions as expected. First, we did not observe interactive effects from herbivory and interspecific competition. Because competition is likely occurring more so belowground rather than aboveground, herbivory effects on competition aboveground were possibly moderated by the strong rooting system of the perennial evening-primrose. As long as roots belowground survive to produce new rosettes, the individual plant can continue to compete well with neighboring plants. Second, partial browse of an evening-primrose shoot reduced the intensity of intraspecific competitive interactions and can allow more growth in evening-primrose neighbors. Additionally, complete browse of whole rosettes induced more vegetative growth. Overall, herbivory was not as detrimental to evening-primrose as it was for Russian thistle in our study. However in the field we have noted higher numbers of evening-primrose losses due to herbivory but losses of Russian thistle due to herbivory is unknown.

Protection of roots may be just as important as preventing loss of shoots for reproduction in evening-primrose. Roots are the source of vegetative reproduction. Dozens of new rosettes can form within the first 10 cm of the root crown, waiting underneath the soil surface to fully emerge (personal observations during pilot study). Rabbits that dig for and eat the root crown would be more likely to kill the plant and reduce vegetative growth than rabbits that eat only the shoots. The next steps in gaining a full understanding of the population dynamics of evening-primrose is to study the effect of root loss due to herbivory. Of this herbaceous perennial species, the loss of roots to herbivory or disease may have stronger impacts on plant mortality and thus, population abundance, than loss of shoots to herbivory.

Future Plans

The competition study with leaf-clipping will be repeated with approximately two-year old evening-primrose plants to evaluate if older perennials are stronger competitors against Russian thistle. There is a possibility that older individuals of evening-primrose may compete with Russian thistle in the field. Because we do not have a feasible method to prevent herbivory of Russian thistle competitors in the natural rabbit herbivory treatment, we will not conduct a rabbit herbivory treatment in combination with the competition treatment. Instead we are using evening-primrose plants to conduct another survival analysis, starting them earlier in the growing season to allow time for plants to transition to sexually reproductive stages of the life cycle. This will better inform us of how rabbit herbivory may impact fecundity of individuals of evening-primrose.

References

Albani, M. C., & Coupland, G. (2010). Chapter Eleven-Comparative Analysis of Flowering in Annual and Perennial Plants. Current topics in Developmental Biology, 91, 323-348.

Bernier, G. (1988). The control of floral evocation and morphogenesis. Annual Review of Plant Physiology and Plant Molecular Biology, 39, 175-219.

Cahill, Jr., J. F and Casper, B. B. (2000). Investigating the relationship between neighbor root biomass and belowground competition: field evidence for symmetric competition belowground. Oikos, 90, 311-320.

Casper, B. B., & Jackson, R. B. (1997). Plant competition underground. Annual Review of Ecology and Systematics, 28(1), 545-570.

Chow, E. and Klinger, R. (2013). Brief summary of work conducted on the Eureka Valley evening-primrose (Oenothera californica ssp. eurekensis). Submitted to U.S.F.W.S. 24pp.

Connolly, J. and Wayne, P. (1996). Asymmetric competition between plant species. Oecologia, 108, 311-320.

Crawley, M. J. and May, R. M. (1987). Population dynamics and plant community structure: competition between annuals and perennials. Journal of Theoretical Biology 125:475-489.

DeDecker, M. Personal letter to Bureau of Land Management. August 27, 1988.

Fowler, N. L. (1984). The role of germination date, spatial arrangement, and nighbourhood effects in competitive interactions in linum. Journal of Ecology,72(1), pp. 307-318.

Goldberg, D. E. and Werner, P. A. (1983). Equivalence of competitors in plant communities: A null hypothesis and a field experimental approach. American Journal of Botany, 70(7):1098-1104

Hunt-Joshi, T. R. Blossey, B, and Root, R. R. (2004). Root and leaf herbivory on Lythrum salicaria: implication for plant performance and communities. Ecological Applications, 14(5)2574-1589

Klein, W. M. (1970). The evolution of three diploid species of Oenothera subgenus anogra (Onagraceae). Evolution, 24:578-597.

Loeser, M. R., Crew, T. E., and Sisk, T. D. (2004). Defoliation increased above-ground productivity in a semi-arid grassland. Journal of Rangel Management, 57(5),442-447.

Mckee, R.C. (2011). The impacts and ecology of the non-native plant Cotula coronopifolia in Californian vernal pools. M.S. thesis, Graduate Group of Ecology, University of California at Davis, 179pp.

McNaughton, S. J. (1983). Compensatory plant growth as a response to herbivory. Oikos, 40(3), 329-336.

Notzöld, R, B. Blossey, and E. Newton. (1998). The influence of below ground herbivory and plant competition on growth and biomass allocation of purple loosestrife. Oecología 113:82-93.

Pavlik, B. M. & M. G. Barbour, M. G. (1985). Demography of endemic psammophytes, Eureka Valley, California, I. Seed production, dispersal and herbivory. State of California, Department of Fish and Game, Rare Plant Program, Sacramento, California. 78pp.

Pavlik, B. M. (1979a). A synthetic approach to the plant ecology of desert sand dunes, Eureka Valley, California (unpublished M.S. thesis), University of California at Davis.

Ross, M. A. and Harper, J. L. (1972). Occupation of biological space during seedling establishment. Journal of Ecology, 60(1), 77-88

Smith, L. Cristofaro, M., de Lillo, E., Monfreda, R., and Paolini, A. (2009). Field assessment of host plant specificity and potential effectiveness of a prospective biological control agent, Aceria salsolae, of Russian thistle, Salsola tragus. Biological Control, 48, 237-243.

Tolvanen, A., and Laine, K. (1997). Effects of reproduction and artificial herbivory on vegetative growth and resource levels in deciduous and evergreen dwarf shrubs. Canadian Journal of Botany, 75, 656-666.

Turner, M. D. and Rabinowitz, D. (1983). Factors affecting frequency distributions of plant mass: The absence of dominance and suppression in competing monocultures of Festuca Paradoxa, 64, 469-475.

Vilela, A., Cariaga, R., González-Paleo, L., & Ravetta, D. (2008). Trade-offs between reproductive allocation and storage in species of Oenothera L.(Onagraceae) native to Argentina. *Acta oecologica*, *33*(1), 85-92.

Weiner, J. (1990). Asymmetric competition in plant populations. Trends in Ecology & Evolution, 5(11), 360-364.

Weiner, J., Wright, D. B., and Castro, S. (1997). Symmetry of below-ground competition between Kochia scopari individuals. Oikos, 79, 85-91.

Young, J. A. and Evans, R. A. (1979). Barbwire Russian thistle seed germination. Journal of Range Management. 32:390-394.