Evaluating the Invasive Potential of South American Spongeplant, *Limnobium laevigatum* (Humboldt and Bonpland ex Willdenow) Heine, in California's Sacramento-San Joaquin Delta

Matthew J. Perryman

ABSTRACT

My project sought to rank the competitive ability of spongeplant among two resident floating plants, water hyacinth and pennywort. I harvested all three plants from Big Break in Oakley, California and then grew the plants in a greenhouse in Berkeley, California. I ranked each plant according to their ability to inhibit the growth of others and their ability to vegetatively reproduce. Additionally, I evaluated the importance of density on growth rates. To account for future conditions, arising from a change in water management or through natural processes, I then ran a similar experiment under elevated salinity. I hypothesized that the South American invaders, spongeplant and water hyacinth, would outperform the native pennywort; but that that pennywort would receive the biggest boost from a return to more natural conditions to which it has evolved. None of the plants were able to inhibit the growth of others ($p > 0.05$) and density had no impact on growth rate ($F_{(4, 44)} = 1.146$, ns). Water hyacinth was the superior competitor in the first experiment followed by spongeplant, with pennywort in last ($F_{(2, 44)} = 3.48$, $p < 0.05$). I was surprised to find that the newest invasive, spongeplant, became the superior competitor under elevated salinity ($F_{(2, 15)} = 15.82$, $p < 0.001$). This project validates the state's rush to eradicate spongeplant before it becomes established. Future conditions on the Delta will promote a successful invasion by spongeplant.

KEYWORDS

Hydrocotyle umbellata, *Eichhornia crassipes*, salinity, competition, Relative Competitive Intensity Index (RCI)

INTRODUCTION

Nationally, mitigation of invasive aquatic weeds such as Brazilian elodea, *Egeria densa* (Planchon), and water hyacinth, *Eichhornia crassipes* (Mart.) (Solms), costs US taxpayers roughly $100 million per year (Pimentel et al. 2000). Although most introductions do not result in establishment, each invader brings with it the possibility of causing great ecological and economic harm. California's Sacramento-San Joaquin Delta and the San Francisco Bay is one of the most invaded estuaries in the world (Cohen and Carlton 1998). A recent invader in the Delta is South American spongeplant, *Limnobium laevigatum* (Humboldt and Bonpland ex Willdenow) Heine. Spongeplant is a common freshwater pond plant which is available and used in pond and aquariums worldwide. Prior to 2010, spongeplant was also available for purchase in California; an aquarium or pond enthusiast is the presumed source of introduction (Anderson 2011).Spongeplant was first identified in small agricultural ponds in Redding and Arcata, California in 2003. By 2007, it was spotted along several miles of the Sacramento River, reaching the Delta in 2008 (Anderson 2011). In January of 2012, California State Assembly Bill 1540 was presented to add spongeplant to the list of invasive aquatics that must be eradicated by the Department of Boating and Waterways (DBW) (Buchanan 2012). In September of 2012, the bill was signed into law. Spongeplant is listed as an "A" rated, noxious weed by the California Department of Food and Agriculture. The "A" rating signifies that the plant is known to cause economic and environmental harm, and that it is not yet established in California which allows for eradication or successful containment when found. Eradication methods employed by the DBW include mechanical removal and application of herbicides. The Delta ecosystem's ability to resist the invasion has been ignored by the state in their rush to eradicate spongeplant before the plant becomes established.

Human alterations of the Delta flow regime affect the biotic and abiotic factors that determine invasion success or failure. The Delta, which prior to western intervention was seasonally inundated with salt water, is currently managed by the state as a freshwater water conveyance system by maintaining a hydrologic barrier (Figure 1) using upstream dam discharges (Moyle 2008). The lack of salt water intrusion creates persistent freshwater conditions that favor non-native species (Cohen and Carlton 1998).The niche the spongeplant is attempting to invade is not vacant; it is currently occupied by natives such as water pennywort, *Hydrocotyle umbellata* (Linnaeus), which was previously invaded by water hyacinth. However, the future of the Delta is uncertain. Due to structural, political, and environmental issues, the Delta's days as a freshwater conveyance system are coming to an end. Factors that are driving Delta management changes include: sea level rise, land subsidence, earthquakes, climate change, floods, and continued declines in native species (Suddeth et al. 2010). Physical forces, such as sea level rise and flooding, will raise the salinity in the Delta over time (Lund et al. 2007). Because increases in salinity eastward past the hydrologic barrier will shut down water transport, the state's plans to build a peripheral tunnel that would draw water from the Sacramento River above the Delta are gaining scientific favor (Lund et al. 2008). While a peripheral tunnel will not solve many of the issues in the Delta, it removes the Delta from statewide water conveyance. The peripheral tunnel could, also, allow management agencies to vary flows, and by extension salinity, to better mimic natural variation. These seasonal variations may allow native species to recover by reintroducing disruptions to which they have evolved. This change in flow regime management will create a new ecological era in the Delta that will force reassessments of invasive and non-native species and their competitive ability.

There is no scientific consensus on spongeplant's competitive ability. The California Department of Food and Agriculture assert the plant is a vigorous competitor that has the potential to have more impact than water hyacinth (Anderson 2011). In South America, spongeplant is found far less frequently than water hyacinth; suggesting that in the native habitat, water hyacinth outcompetes spongeplant (Murphy et al. 2003). In a survey of occurrences outside South America, spongeplant is only recorded in Japan. Like many countries, Japan suffers from an overabundance of water hyacinth; spongeplant, on the other hand, is only occasionally seen, but not in significant densities (Kadono 2004). While the impact of water hyacinth on the Delta ecosystem has been well studied (Finlayson 1983, Agami and Reddy 1991, Toft et al. 2003, Spencer and Ksander 2005) little is known about the Delta biology and ecology of spongeplant. Yet, it has been branded by the state as a vigorous competitor without any published support of the assertion.

In an effort to inform management decisions and validate the state's reaction, my project assesses spongeplant's invasive potential in the Delta by examining its competitive ability against that of water hyacinth and native pennywort in both ideal and anticipated field conditions in the future. I hypothesize that under ambient conditions spongeplant will be less competitive than the globally invasive water hyacinth, but that spongeplant will be more competitive than the native pennywort. My hypothesis is based on the lack of evidence of spongeplant's global invasive history. I believe spongeplant will be more competitive than pennywort because the spongeplant has coevolved with water hyacinth in South America, which is known to be highly competitive. I further hypothesize that in future conditions, with elevated salinity, pennywort will gain a competitive edge because, as a native, it has evolved in the Delta which has historically experienced seasonal fluctuations in salinity.

METHODS

To analyze current and future competitive ability of water hyacinth, pennywort, and spongeplant in the Delta, I ran two related experiments. I harvested the three species from the Big Break flooded tract in Oakley, California, on September 7, 2012 from the same 400 meter stretch (Figure 1).

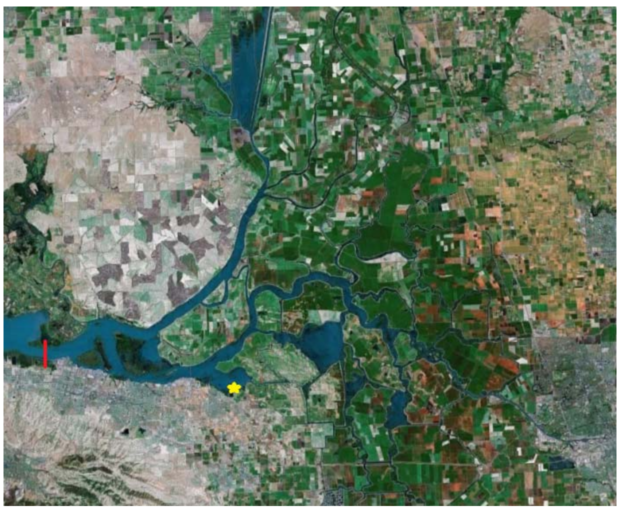

Figure 1. Google satellite image of the California Delta. The gold star indicates the location of the plant harvest. The red line is the location of the hydrobarrier running from Chipp's Island to Pittsburg, California. For scale, the distance between the two is 11 miles.

Mesocosm Information

To simulate the Delta summer growing season, I used the greenhouse in Oxford Tract at UC Berkeley in Berkeley, California. The greenhouse provided growing lights which combined with daylight for a daily total of 13 hours of light, 11 dark. I filled the five-gallon buckets with dechlorinated tap water. I removed the chlorine from the water with Wardley's Chlor Out™ (Secaucus, New Jersey) to minimize plant stress and better mimic natural conditions. I fed the plants and topped off water levels weekly. For the second experiment, I used Petco's™ Premium Marine Salt Mix (San Diego, California) to elevate salinity and mimic estuarine conditions. With the exception of the aquarium salt, the conditions of the two experiments were as similar as possible.

Data Collection

To record changes in growth, I photographed each bucket and analyzed using ImageJ (Rasband 1997). I used the weekly digital photographs to measure area covered, and how it changed over the course of both trials. Temporal trends were particularly important in the second trial, when plants endured salinity related stress. I calculated Relative Competitive Intensity Index (RCI) using the area covered. RCI can be infinitely negative with any number less than 0 indicating the performance of the target plant has been facilitated by the presence of the other. A RCI of 0 indicates there is no effect on growth due to competition. A RCI greater than 0 signifies that neighbors have had a negative effect on the target plant, the larger the RCI value the greater the impact on the target plant performance due to competition (Vila and Weiner 2004).

The equation for RCI is:

$$RCI = (P_{mono} - P_{mix}) / P_{mono},$$

P is performance (Grace 1995)

I calculated performance as:

$$P = (\text{Area}_{\text{final}} - \text{Area}_{\text{initial}}) / \text{Area}_{\text{initial}}$$

Data Analysis

To determine the significant differences in the plants' RCI, I ran various ANOVAs and tukey tests using R (i386 2.15.1) (R Core Team 2012) and Rcommander (Fox et al. 2009). In the Competitor/Density experiment, I inspected each plant's RCI with respect to the other two (Table 2). In the future invasion experiment, I used two-way ANOVA to inspect differences between the plants' performance under increased salinity in monoculture and polyculture. I considered differences significant at the 5% level ($p < 0.05$). I managed my data and created figures using R and Microsoft's Excel (2007).

Competitor/Density experiment

The first experiment inspects each plant's ability to compete with the other plants and the impact of increasing initial density. This trial included a maximum of two species in each bucket. By growing a plant against both of its competitors separately, the first experiment will determine if any of the plants inhibit or facilitate the growth of its cohabitants. I grew varying ratios of similarly-sized plant units in five gallon buckets for six weeks (Table 1). Monocultures of each plant offer a reference to the plant's performance in polyculture.

Table 1. Initial plant unit ratios in treatments for the Performance experiment.
SP is spongeplant, PW is pennywort, WH is water hyacinth.

SP:WH	0:1	1:3	1:2	1:1
SP:PW	1:0	1:3	1:2	1:1
WH:PW	0:1	1:3	1:2	1:1

Future Invasion experiment

In the second experiment, I sought to examine the competitive ability of each plant under elevated salinity. Because there is variety in different individuals' ability to compete, I selected the most productive spongeplant from the first experiment to be replanted and used in the second experiment. My interest in evaluating the invasive potential of the plant leads me to be more concerned with the more resilient individuals that pose the biggest threat of becoming established in the Delta. Instead of two species per bucket like the first experiment, I grew all three plants together in equal ratios, in addition to the monocultures as reference. These four groups (three monoculture and one mixed) received three treatments: no salinity added or 0 parts per thousand (ppt), 5 ppt, and 10 ppt. I selected these salinity values to mimic the salinity levels that could infiltrate the Delta under different possible future flow regimes (Lund et al 2007). I ran three replicates per treatment which totaled 36 buckets in each experiment.

RESULTS

Competitor/Density Experiment

I did not run any statistical tests on the plants in monoculture because their performance is captured in the RCI calculation; I present their performance to illustrate the highly variable growth found in pennywort, the overall high performance of water hyacinth, and the poor performance of the spongeplant monocultures (Figure 2).

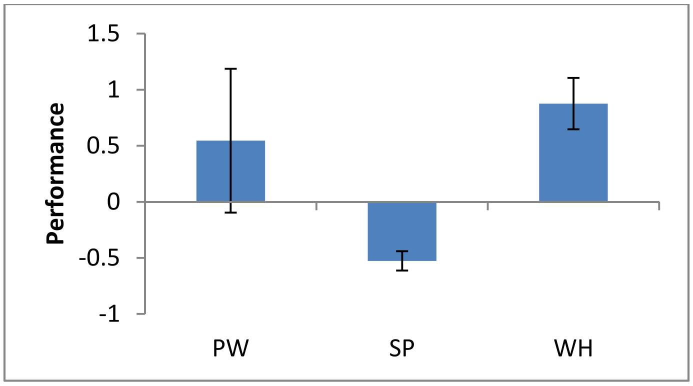

Figure 2. Performance of plants in monoculture for Competitor/Density Experiment. n=3. Error bars demarcate 1 SD.

Among the mixed plants, a one-way ANOVA revealed no difference in performance due to the competitor (Appendix A). Additionally, I found no significant difference in the performance of plants due to the varied initial densities, F (4, 44) =1.146, ns. The performance of water hyacinth was significantly higher than pennywort (Figure 3), F (2,44) = 14.13, $p < 0.001$, I could not include spongeplant in the ANOVA because the results were too skewed for any parametric test. I have included spongeplant in the box plot to highlight the outlying high performance spongeplant that I used in the second experiment (Figure 3). However, RCI controls for the skew and returns more normally distributed data that can be used in ANOVA and tukey tests.

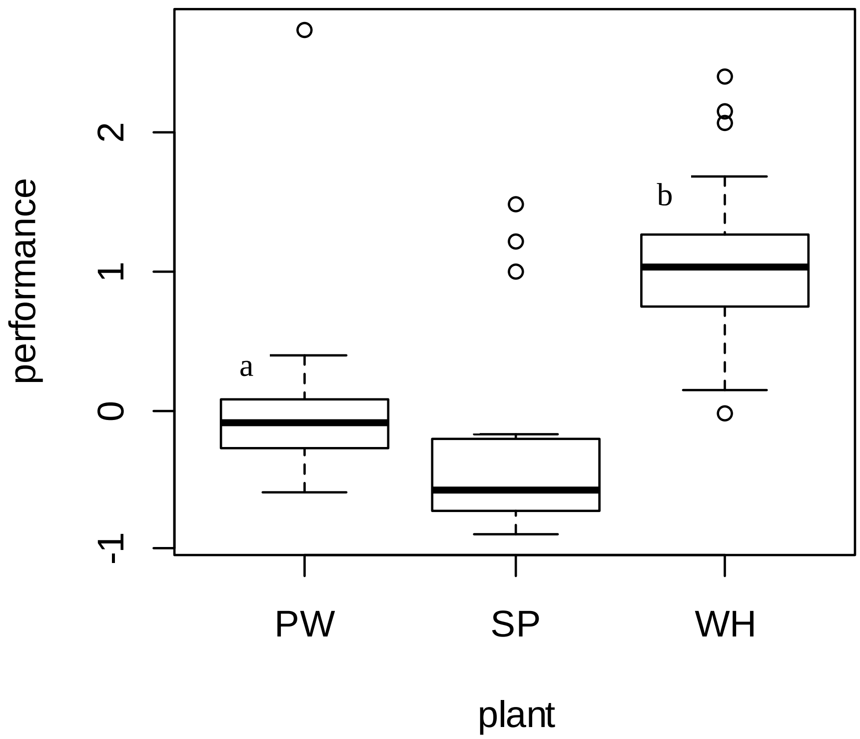

Figure 3. Performance of competing plants in all densities in the first trial. WH (b) is significantly higher than PW (a). n_{pw}= 16, n_{sp}= 16, n_{wh}= 17

The one-way ANOVA results for the Relative Competitive Intensity Index (RCI) as a function of the different plants reveals that pennywort's RCI is significantly greater than water hyacinth, with spongeplant between the two (Figure 4), $F(2, 44) = 3.48$, $p < 0.05$.

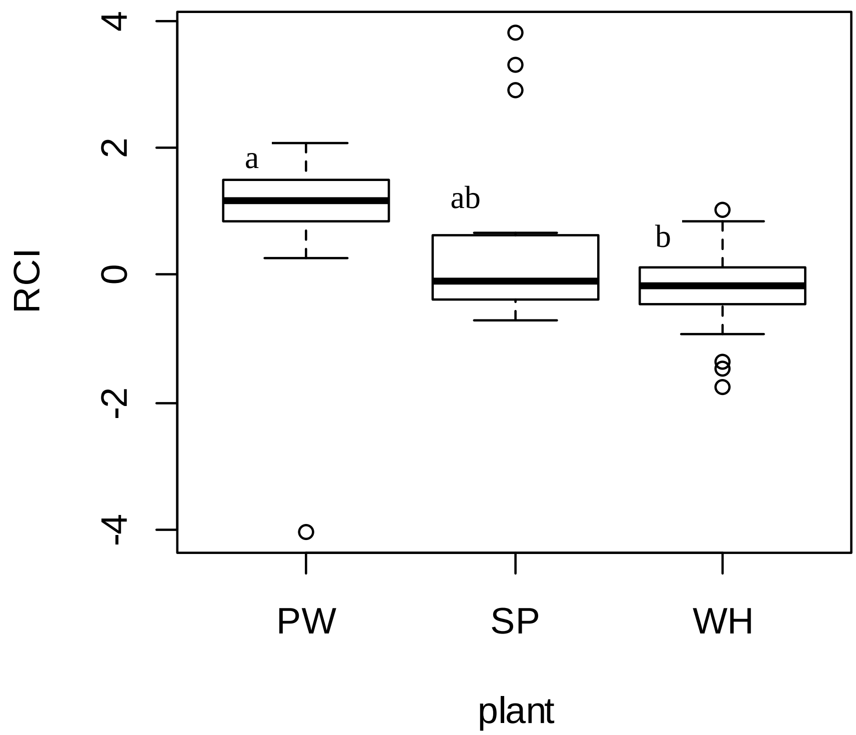

Figure 4. Relative Competitive Intensity Index (RCI) for plants from the Competitor/Density Trial. PW (a) is significantly higher than WH (b), while SP (ab) is not significantly different than either ($p < 0.05$) n_{pw}= 16, n_{sp}= 16, n_{wh}= 17

Future Invasion experiment

In the future invasion experiment, I found all plants' average performance was significantly lower under high salinity compared to ambient salinity, $F (2, 51) = 6.31$, $p < 0.01$ (Figure 5, Figure 6). I found no statistically significant differences in performance due to the presence of competitors (mixed vs mono) under all treatment groups, however monoculture treatments in ambient salinity are nearly significantly better than mixed plants (Figure 5, Figure 6; high salinity: $F (1, 12) = 0.5652$, ns; medium salinity: $F (1, 12) = 1.7684$, ns; ambient salinity: $F (1, 12) = 2.2398$, nearly significant, $p< 0.1$).

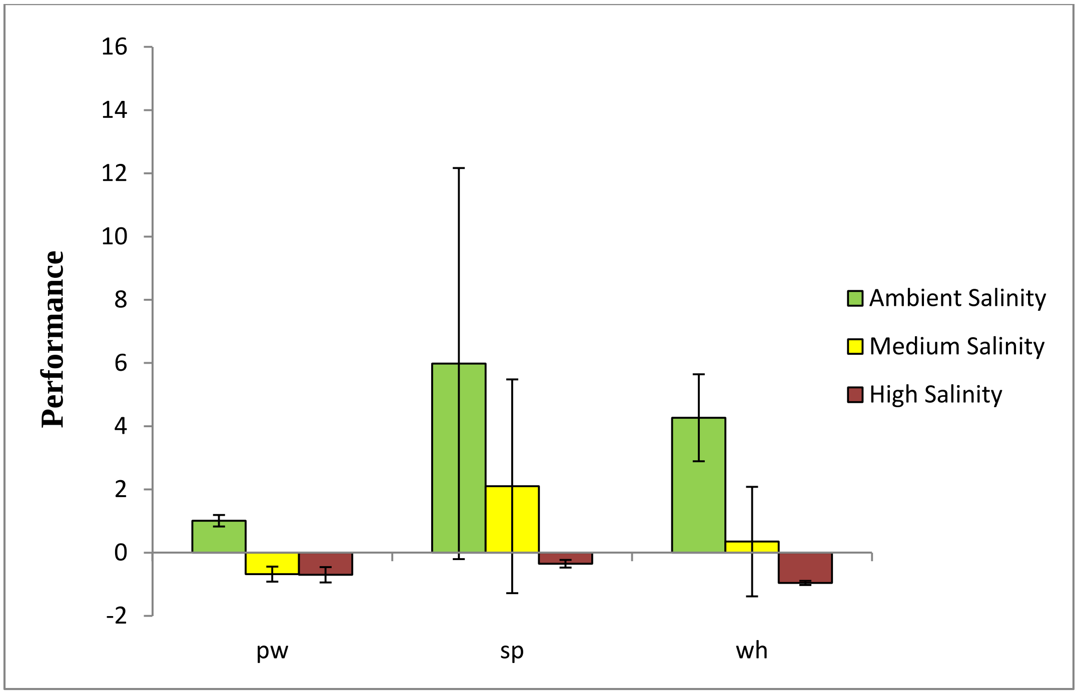

Figure 5. Performance of the monoculture plants in varying salinity. n = 3. Ambient Salinity is no salt added. Medium Salinity is 5 ppt. High Salinity is 10 ppt. Error bars demarcate 1 SD.

The plants' performance was not significantly different under ambient salinity conditions, $F\ (2, 15) = 2.07$, ns (Figure 6). But under medium salinity, spongeplant significantly outperformed pennywort, $F\ (2, 15) = 4.692$, $p < 0.05$, with water hyacinth insignificantly in between the two (Figure 6). And in high salinity, spongeplant significantly outperformed both water hyacinth and pennywort, $F\ (2, 15) = 15.82$, $p < 0.001$ (Figure 6). Mixed spongeplant's high growth in medium salinity breaks the clear pattern in both monoculture and mixed plants' performance declining with increased salinity (Figure 6).

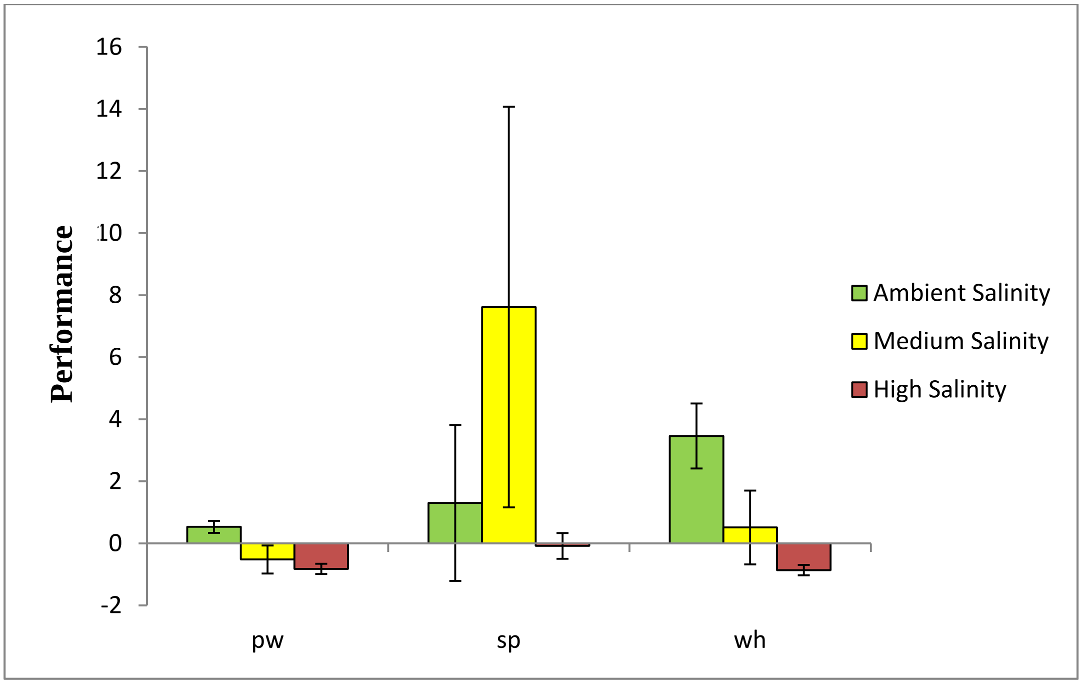

Figure 6. Performance of the mixed plants in varying salinity. n = 3. Ambient Salinity is no salt added. Medium Salinity is 5 ppt. High Salinity is 10 ppt. Error bars demarcate 1 SD.

DISCUSSION

My objective is to evaluate spongeplant's invasive potential in the California Delta. I sought to fill in the information gap regarding spongeplant's competitive ability. The state asserts that spongeplant is an aggressive invader (Anderson 2009) without any published support of their assertion. I hypothesized that water hyacinth would outperform both pennywort and spongeplant, and that an increase in salinity levels would favor the native pennywort. My results suggest that in current conditions water hyacinth is clearly a superior competitor to both spongeplant and pennywort. In future conditions, spongeplant may be able to outperform the others under elevated salinity which could promote a successful invasion. This is contrary to most invasive literature that assumes a return to historical/natural regime will favor natives (Moyle and Light 1996, Lund et al. 2008).

Competitor/Density experiment

Invasive theory suggests that an attribute for a successful invader is its ability to outcompete natives (Levine et al. 2003), but journals are littered with examples of native species outcompeting invasive species (Vila and Weiner 2004, Dostal 2011). My results from the Competitor/Density trial are examples of both; spongeplant was outperformed by pennywort which was outperformed by water hyacinth. Water hyacinth was clearly the superior performer, doubling its area in just six weeks. This agrees with several studies and explains water hyacinth's global invasiveness (Agami and Reddy 1991, Toft et al. 2003, Spencer and Ksander 2005). Spongeplant's performance results were extremely skewed with only a handful of plants performing strongly. I was therefore unable to include spongeplant in the ANOVA in which water hyacinth was significantly a better performer than pennywort (Figure 3). However, RCI corrected the skew and allowed spongeplant to be included in the RCI ANOVA which showed that spongeplant is between the significantly different water hyacinth and pennywort (Figure 4). Milne et al. (2007) found that spongeplant grew faster in competition with two other floating aquatic plants than it did in a monoculture, my results do not reflect these findings. However, their results show that spongeplant was not an overall fierce competitor agrees with my findings from the first experiment.

Pennywort was the most impacted by competition, with an RCI significantly higher than water hyacinth (Figure 4). This contradicts Agami and Reddy (1991), who report the growth rates of pennywort and water hyacinth where higher when grown together versus monoculture. They found that, over a 14 week period, the petioles of pennywort in mixed culture were elongated and benefited by the structural support of the water hyacinth. The difference in time accounts for the difference in our findings; if I extended my trial period from 6 to 14 weeks perhaps I, too, would have witnessed the facilitation of pennywort by water hyacinth that Agami and Reddy report.

Future Invasion experiment

Because the statistical outliers are the individuals who are most capable of becoming established, at the conclusion of the first experiment; I selected the highest performing plants to use in the second experiment in varied salinity levels. Selecting these higher performing spongeplant resulted in them performing as well as water hyacinth in the second experiment, whereas in the first experiment on average they languished (Figure 5 and Figure 6).

All three plants in monoculture and two (water hyacinth and pennywort) in mixed growth were stressed by increased salinity, which supports my choice of salinity levels. As in the Competitor/Density trial, most plants performed better in monoculture than in competition. Spongeplant in medium salinity grown in polyculture is the exception, which outperformed spongeplant in low salinity and spongeplant monoculture in medium salinity, suggesting that an increase in salinity would favor a successful invasion. Additionally, spongeplant significantly outperformed both water hyacinth and pennywort in high salinity. It is a bit surprising to see pennywort so clearly stressed by elevated salinity, not only is it contradictory to my hypothesis, it also contrasts Vasey et al. (2012) whose surveys found pennywort in oligohaline waters but only found water hyacinth in freshwater. However, the limited scope of their field surveys should be noted as they found no spongeplant.

My results from the Future Invasion trial suggest that spongeplant will be a stronger competitor in future conditions. I recorded a stronger average performance by spongeplant, almost on par with water hyacinth. Spongeplant performs even better in mixed growth with increased salinity compared to its counterparts. With a change in water management or a natural disaster, brackish, oligohaline conditions will exist in the Delta (Lund et al. 2008). These conditions could enable spongeplant’s expansion in the future.

Limitations

My project attempts to draw conclusions about environmental outcomes based on experimental results; buckets under grow lights are not summer in the Delta, but a greenhouse experiment is the next best substitute. By replicating summer-like conditions, I have excluded the influence of seasonality from my analysis. While the buckets provide a great arena for competition, they also inhibit important environmental factors such as water mixing. Although lentic conditions exist in the Delta, few, if any, places are as stagnant as a bucket in a greenhouse.

Future Direction

The threat of spongeplant invading may become exacerbated with increased salinity. In high salinity, (>10 ppt) all three plants will die out, but salinity fluctuations may aid spongeplant's invasion. These results need to be replicated, ideally in Delta conditions. Biotic resistance is usually less important in invasions than environmental resistance (Moyle and Light 1996); future studies should focus on abiotic factors such as increased nitrates and varied temperatures. There is evidence that pennywort is a cooler weather plant and begins growing earlier in the season compared to water hyacinth (Reddy and DeBusk 1984).

Broader Implications

We often restore an environment with the goal of aiding native species to regain their foothold. I hypothesized that the native, pennywort, would gain a competitive edge with a return to more natural disturbance regime (i.e. increased salinity) which was absolutely incorrect. This can be a big assumption for managers, therefore, we need to treat each situation individually and recognize that there is no "one-size-fits-all" solution.

Conclusion

Spongeplant will continue to attempt to establish itself on the Delta and anywhere else environmental factors will allow. As with all new invasions, the state must react with as much fervor as financially reasonable. If the invasion is preventable it will be in these early stages of establishment. As costs to mitigate invasions climb, information about the invaders and their impacts on the ecosystem becomes more valuable to efficiently allocate management resources. This has particular relevance given California's current economic condition. The results of this project are the first step in understanding the invasion potential of spongeplant in the Delta. This information with already present vegetation can aid management agencies in their predictions of potential impacts to the economy and the ecosystem. These potential impacts will determine if current eradication efforts are worthwhile and whether they should continue.

ACKNOWLEDGEMENTS

This project would not have been possible without the support of the entire Environmental Science Team, particularly Patina Mendez, Anne Murray, and my mentor, John Battles. Their ability to ask the right questions at the right time was integral in my maturation as an academic and as a person. Throughout my life, I have been blessed to have the unwavering support of my family. They have continually picked up the slack I have created by indulging myself in academic pursuits. A special thank you to my life partner, she has been my advisor, editor, lab assistant, my rock and my inspiration. I would also like to thank Barb Rotz and the Oxford tract staff for all their help in the greenhouse. Finally, I would like to thank my Environmental Science cohort, their brilliance, passion, and energy is evident in everything they do; they will go on to do amazing things that will change the world, I am honored and humbled to be a member.

REFERENCES

Agami M. and K. Reddy. 1991. Interrelationships between *Eichhornia crassipes* (Mart) Solms and *Hydrocotyle umbellata* L. Aquatic Botany 39:147-157.

Anderson, L. 2011. Spongeplant: A new aquatic weed threat in the Delta. Cal-IPC News 19: 4-5.

Buchanan, J. 2012. Sacramento-San Joaquin Delta: invasive weeds: South American Spongeplant. California Assembly Bill 1540.

Caraco, N., J. Cole, S. Findlay and C. Wigand. 2006. Vascular plants as engineers of oxygen in aquatic systems. Bioscience 56:219-225.

Cohen, A.N., and J.T. Carlton. 1998. Accelerating invasion rate in a highly invaded estuary. Science 279:555-558.

Dostal, P. 2011. Plant competitive interactions and invasiveness: Searching for the effects of phylogenetic relatedness and origin on competition intensity. The American Naturalist 177:655-667.

Ellison, A.M., M.S. Bank, B.D. Clinton, E.A. Colburn, K. Elliot, C.R. Ford, D.R. Foster, B.D. Kloeppel, J.D. Knoepp, G.M. Lovett, J. Mohan, D.A. Orwig, N.L. Rodenhouse, W.V. Sobczak, K.A. Stinson, J.K. Stone, C.M. Swan, J. Thompson, B.V. Holle, and J.R. Webster. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 9:479-486.

Finlayson, B.J. 1983. Water hyacinth: threat to the Delta? Outdoor California 44:10-14.

Fox, John, L. Andronic, M. Ash, T. Boye, S. Calza, A. Chang, P. Grosjean, R. Heiberger, G.J. Kerns, R. Lancelot, M. Lesnoff, U. Ligges, S. Messad, M. Maechler, R. Muenchen, D. Murdoch, E. Neuwirth, D. Putler, B. Ripley, M. Ristic and P. Wolf. 2009. Rcmdr: R Commander. R package version 1.5-4. http://CRAN.R-project.org/package=Rcmdr.

Grace, James B. 1995. On the measurement of plant competition intensity. Ecology 76:305-308.

Kadono, Y. 2004. Alien aquatic plants naturalized in Japan: History and present status. Global Environmental Research 8:163-169.

Levine, J. M., M. Vila, C. M. D'Antonio, J.S. Dukes, K. Garigulis and S. Lavorel. 2003. Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal Society B: Biological Sciences 270:775-781.

Lund, Jay, Ellen Hanak, William Fleenor, Richard Howitt, Jeffrey Mount and Peter Moyle. 2007. Envisioning futures for the Sacramento-San Joaquin Delta. Public Policy Institute of California, San Francisco, California, USA.

Lund, J., E. Hanak, W. Fleenor, W. Bennett, R. Howitt, J. Mount, and P. Moyle. 2008. Comparing Futures for the Sacramento-San Joaquin Delta. Public Policy Institute of California. San Francisco, California, USA.

Madani, K. and J.R. Lund. 2012. California's Sacramento-San Joaquin Delta Conflict: From Cooperation to Chicken. Journal of Water Resources Planning and Management 138:90-99.

Milne, Judith, Pauline Lang and Kevin Murphy. 2007. Competitive interactions between *Salvinia auriculata* Aubl., *Limnobium laevigatum* (Humb. And Bonpl.ex Willd.) Heine, and other free-floating aquatic macrophytes under varying nutrient availability. Fundamental and Applied Limnology 169:169-176.

Moyle P.B. and T. Light. 1996. Biological invasions of fresh water: Empirical rules and assembly theory. Biological conservation 78:149-161.

Murphy, K.J., G. Dickinson, S. M. Thomaz, L.M. Bini, K. Dick, K. Greaves, M.P Kennedy, S. Livingstone, H. McFerran, J.M. Milne, J. Oldroyd and R.A Wingfield. 2003. Aquatic plant communities and predictors of diversity in a sub-tropical river floodplain: the upper Rio Parana, Brazil. Aquatic Botany 77:257-276.

Navas, M.L., E. Garnier, M.P. Austin, A. Viaud and R.M. Gifford. 2002. Seeking a sound index of competitive intensity: Application to the study of biomass production under elevated CO_2 along a nitrogen gradient. Austral Ecology 27:463-473.

Pimentel, D., L. Lach, R. Zuniga and D. Morrison. 2000. Environmental and economic costs of nonindiginous species in the United States. Bioscience 50:53-65.

Rasband, W.S. 1997. ImageJ.U. S. National Institutes of Health, Bethesda, Maryland, USA. http://imagej.nih.gov/ij/, 1997-2012.

R Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Reddy, K.R. and W.F. DeBusk. 1984. Growth characteristics of aquatic macrophytes cultured in nutrient-enriched water: I. water hyacinth, water lettuce, and pennywort. Economic Botany 38:229-239.

Spencer D. and G. Ksander. 2005. Seasonal growth of water hyacinth in the Sacramento/San Joaquin Delta, California. Journal of Aquatic Plant Management 43:91-94.

Suddeth, R., J.F. Mount and J.R. Lund. 2010. Levee decisions and sustainability for the Sacramento San Joaquin Delta. San Francisco Estuary Watershed Science 8:1-23.

Toft J., C. Simenstad, J. Cordell, and L. Grimaldo. 2003. The effects of introduced water hyacinth on habitat structure, invertebrate assemblages, and fish diets. Estuaries 26:746-758.

Vasey, M.C., P.V. Thomas, J.C. Callaway, E.R. Herbert and L.M. Schile. 2012. Tidal wetland vegetation in the San Francisco Bay-Delta estuary. San Francisco Estuary and Watershed Science 10:1-16.

Vila, M. and J. Weiner. 2004. Are invasive plant species better competitors than native plant species?: Evidence from pair-wise experiments. Oikos 105:229-238.

APPENDIX A: COMPETITOR PERFORMANCE RESULTS

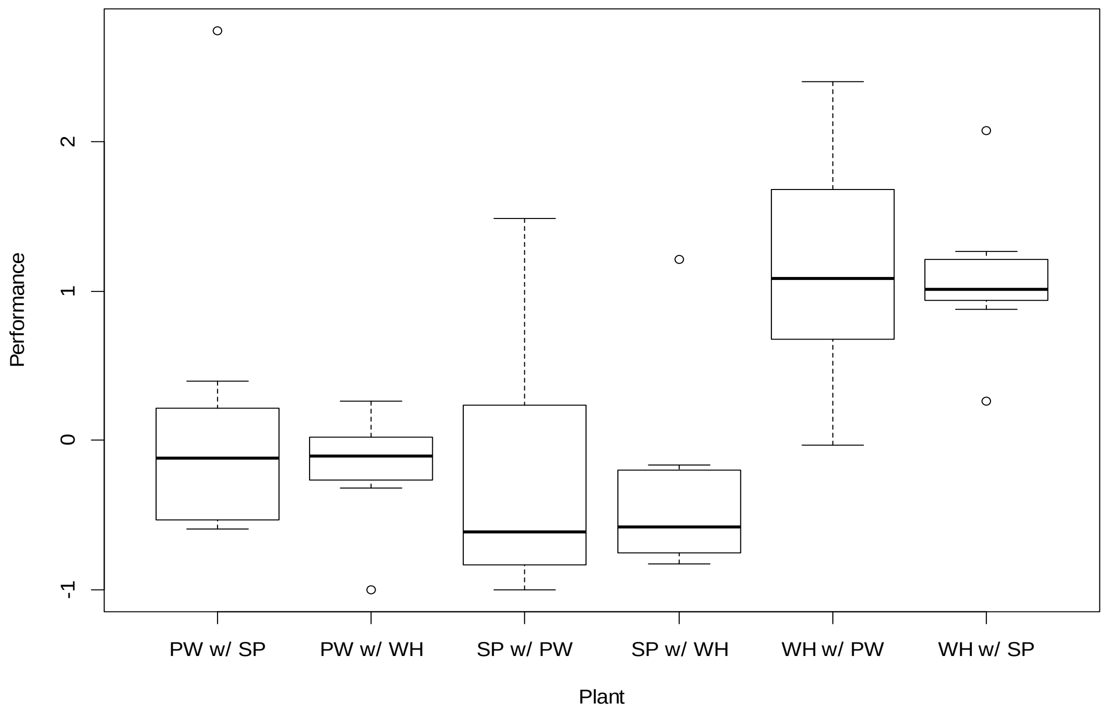

Figure A1. The performance of the plants when grown with each competitor. n = 3. PW w/ SP is the performance of pennywort when grown with spongeplant. Because there is essentially no difference in plants' performance due to competitor, these results were combined to form Figure 3 and in the calculations of RCI in Figure 4.