Coastal dune invasion and restoration at Point Reyes: the ecology of European sea rocket, *Cakile maritima*

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**ABSTRACT**

California coastal dune ecosystems are prime targets for conservation and restoration efforts due to their high native plant diversity and rates of endemism. Invasive dune species such as European sea rocket (*Cakile maritima*) may disrupt key ecosystem processes by altering dune physical processes and outcompeting native species, decreasing the success of the endangered species beach layia (*Layia carnosoides*) and Tidestrom’s lupin (*Lupinus tidestromii*) at Point Reyes National Seashore in Marin County, California. We investigated potential abiotic and biotic stressors that may inhibit the success of *C. maritima*. We found that elevation did not affect *C. maritima* growth patterns, while topography played a larger role. The backdune community featured greater growth and less investment in belowground competition than the foredune and distal valley site. Competition with non-nitrogen-fixing plants was found to limit *C. maritima* growth and result in greater allocation of resources to root growth, though the number of native competitors did not affect performance. Conversely, native nitrogen-fixer presence (but not abundance) was associated with increased biomass and less investment in root growth, indicating that nitrogen may be one of multiple stressors limiting *C. maritima* success. Further understanding of these environmental stressors may aid in future prediction of susceptibility of coastal dune microhabitats to invasion and the prioritization of restoration project locations.

**INTRODUCTION**

Maritime areas of California’s Central Coast represent some of the most species-rich regions in California, and host particularly high rates of plant endemism (Raven & Axelrod 1978). Endemic species generally have higher risk of extinction due to restricted geographic distribution and limited population sizes, and consequently are prioritized in many conservation and restoration strategies (Myers et al. 2000). Coastal dune ecosystems are particularly vulnerable to human use, pollution, and invasion by non-native
plants. Coastal land is particularly targeted for residential development and recreational use because of its aesthetic value and proximity to the ocean. A complex and difficult biotic threat to control, however, is the introduction of invasive species. Invasive species supplant natives, alter dune physical processes and local topography, and disrupt the foraging and nesting behaviors of dune animals (Young 2017). Consequently, California’s coastal dunes have been an area of interest for many conservation and restoration projects.

Alterations to dune topography and vegetation composition caused by invasive species degrade coastal dunes as habitat for native species. Two of the most extensive invasive species on the California coast, highway ice plant (*Carpobrotus edulis*) and European beach grass (*Ammophila arenaria*), were purposefully introduced to stabilize dunes. By creating a higher and steeper foredune via sand accumulation and restricting sand from flowing to interior dunes, these soil-stabilizing species change the natural topography and successional conditions often required for native species. Many areas of California’s coast are carpeted with ice plant, further limiting the space available for endemic and endangered native plant species. The changes to local topography and vegetation composition in coastal dunes negatively impact the animals that rely on the habitat for foraging and nesting, like the endangered Western Snowy Plover (*Charadrius nivosus nivosus*) (Pickart 1997). The far-reaching consequences of invasions in a relatively fragile ecosystem make restoration efforts critical to the continued existence of many threatened and endangered native species, including many endemic species.

Restoration efforts in dune habitats have been notoriously unsuccessful, however, due to a lack of physiological understanding of the invading species, as demonstrated by the case of early efforts to remove *A. arenaria* from California coastal dunes. Initial attempts at removal included burying patches of *A. arenaria*, but the grass reemerged from where it was buried and spread further throughout the surrounding area, instead amplifying the percent cover of the species (Young 2017). Additionally, restoration is difficult due to the ability of other invasive species to succeed the landscape when one dominant species is suddenly removed, decreasing competition for water and nutrients while increasing open stretches of sand. In one case of *A. arenaria* removal, the grass was manually removed when burial only progressed the spread of the species. While the grass population was severely diminished, European sea rocket (*Cakile maritima*) was readily able to colonize the recently cleared landscape (Michael Spaeth, personal communication). Going forward, physiological limits and responses to biological stressors of an invasive species should be studied extensively and utilized to establish effective and species-specific removal strategies to ensure cost-effective and efficient restoration.
Point Reyes National Seashore in California provides an excellent system with which to explore the abiotic and biotic factors that affect a plant’s ability to invade. Point Reyes has seen intensive efforts at coastal restoration dating back decades. In 2009, Point Reyes National Seashore reported that over 60% of the park’s coastal dunes had been invaded by European beach grass and ice plant (Muldoon 2009). Manual removal of *A. arenaria* has proven to be an effective restoration technique (Pickart 1997). Recent dune restoration projects at Point Reyes have implemented this technique with much success, but a secondary invasive, European sea rocket (*Cakile maritima*) has been noted as taking over restored areas of the dune (Boyd 1988; Michael Spaeth, personal communication). Like *A. arenaria*, *C. maritima* stabilizes dunes and inhibits the progression of dune disturbance and succession cycles. This alteration of ecosystem function decreases the abundance of the endangered endemic species *Layia carnosa* (beach layia) and *Lupinus tidestromii* (Tidestrom’s lupine), which thrive in early successional stages with unstabilized dunes; the same effect is associated with population declines of the endangered shorebird *Charadrius nivosus nivosus* (western snowy plover) due to its utilization of open sand for mating and reproduction (Pardini *et al.* 2015).

In this study, we examine both abiotic and biotic factors that may limit the growth of *C. maritima* along a coastal stretch of Point Reyes National Seashore in Marin County, California. Abiotic factors included water table accessibility, salinity, and nutrient availability, which were estimated using the proxies of elevation, distance from the ocean, and site topography, respectively. Biotic factors were those associated with competition from or facilitation by surrounding plants of three guilds: native nitrogen fixers, native non-nitrogen-fixer competitors, and invasive competitors. Biomass and root:shoot ratio were used to evaluate the growth performance and resource allocation by *C. maritima*. This study provides a basic insight on *C. maritima* physiology in relation to resource allocation and growth and may be used to prepare effective restoration strategies both in terms of *C. maritima* control and assessment of the relative susceptibility of dunes to its colonization and spread.

**METHODS**

**Natural History**

The study was conducted at Point Reyes National Seashore in Marin County, CA, located northwest of San Francisco. Predominantly covered by Douglas fir (*Pseudotsuga menziesii*) and Bishop pine (*Pinus muricata*) forests covering well over 34,000 acres, Point Reyes spans over 70,000 acres of coastal wilderness area (Sansing & Chapman 1978). In 1962, United States President John F. Kennedy established Point Reyes as a National Seashore protected by the National Forest Service, allowing the continued operation of the 26 ranches established in the area beginning in the 1850s. It is also the most recent site to be added to the University of California Reserves in partnership with the U.S. National Park as of August 2017.
With the establishment of this site, rangers have been able to adopt practices that help preserve both floral and faunal endangered species. Currently, Point Reyes is focusing on preserving and improving the habitats of the threatened Western Snowy Plover on coastal beaches and the restoration of coastal dunes. Coastal dunes are prone to plant invasion due to the low richness of native species adapted to harsh coastal conditions and frequent disturbance by strong wind (Boyd 1992). European sea rocket (Cakile maritima) is one such invasive plant that has disrupted the population of silver lupine (Lupinus albus) as well as many other native species. There is very little accessible information regarding how C. maritima interacts with other plant species in North America, which makes physiology-based restoration strategies for the species difficult to establish.

**Research Design**

This study aims to understand the abiotic and biotic factors that may limit the growth of C. maritima. We measured total biomass and root:shoot ratio by mass to reflect the growth and belowground resource stress of C. maritima by uprooting individuals with roots intact. Total biomass acts as an indicator of overall growth; root:shoot ratio indicates the allocation of resources between belowground resource acquisition for survival and reproductive ability, as root:shoot ratios are more responsive to belowground pressures than those aboveground (Wilson 1988). Total biomass was measured with spring scales in grams. Root mass and shoot mass were separated upon excavating an individual plant and measured separately.

The root:shoot ratio was calculated using the following equation:

\[
\text{Root: shoot ratio} = \frac{\text{root mass (g)}}{\text{shoot mass (g)}}
\]

Measurements were taken between August 3rd and August 6th, 2017 at three distinct sites along Great Beach with an area of 5.7 acres in the coastal dune habitat located south of Abbott’s Lagoon.

We assessed the effects on growth and resource allocation of three abiotic factors: elevation, site, and distance from the ocean. Elevation was used as an approximation of the distance from the water table, which serves as rough estimate of groundwater availability. The value was recorded by GPS and calibrated with Google Earth due to equipment error related to thick cloud cover during the study period. Distance away from the ocean was used to describe the salinity, which is proportionally associated with the travel distance of ocean spray. The coordinates of each plant were recorded by GPS and processed by Google Earth to calculate the distance from the ocean for each plant. Three sites were selected to represent topographical variation, sorted into ocean-facing foredunes, inland-facing backdunes, and a flat, distal inland valley (Fig. 1); each site additionally featured a distinct distance from the ocean. Sunlight was not considered as a limiting factor due to high sun exposure in the dunes. In addition, equipment limitations disallowed for direct measurement of nutrients, which were estimated with a biotic proxy.
Plants surrounding *C. maritima* individuals were sorted into three functional guilds: native nitrogen fixers, non-nitrogen-fixing native competitors, and invasive competitors. Nitrogen fixers can convert atmospheric nitrogen (N\textsubscript{2}) into ammonium (NH\textsubscript{4}) or other molecules that can be utilized by a plant and benefit the surrounding plants by leaving remnants of usable nitrogen in the soil. Surrounding plants were defined as plants located within a 1 m radius centered at each individual *C. maritima* root. Each surrounding plant was identified and classified into one of the three categories stated above. In addition, the abundance of each surrounding plant was recorded.

*C. maritima* individuals were selected randomly by generating a direction and distance to travel before assessing the nearest plant.

**Statistical Analysis**

Statistical analyses were performed in the JMP Statistical Software package 13.0. We used two-tailed T-tests and the Bivariate Fit Model to examine the variation in the effects of biotic factors, including both number of individuals and presence or absence of surrounding plant species.

Variation caused by abiotic factors was analyzed using one-factor ANOVAs. Due to large sample size, distance from the ocean was approximated using three site locations; the sites had distinctly different distances from the ocean.

**RESULTS**

Over the course of four days, 228 samples were collected to test total biomass and root:shoot ratios. Elevation showed no significant impact on growth performance (total biomass: $F = 0.48, P > 0.20$; root:shoot ratio: $F=1.00, P > 0.20$). The backdune site with a medium distance away from the ocean showed significantly higher biomass ($F = 3.80, P < 0.05$), and significantly lower root:shoot ratio ($F = 13.57, P < 0.0001$) compared to the other two sites.

For biotic factors, 15 different plant species were found within a 1-meter radius of *C. maritima*, including two nitrogen fixers, nine native competitors, and four invasive competitors. The presence of nitrogen fixers significantly increased biomass ($F = 2.20, P < 0.05$; Fig. 2a) and decreased root:shoot ratios ($F = -3.39, P = 0.001$; Fig. 2b).

![Figure 1. The study system and its three sampling sites.](image-url)
DISCUSSION

The results of our study suggest a correlation between biotic interactions and \textit{C. maritima} performance. The presence of nitrogen fixers, i.e. native yellow bush lupine (\textit{Lupinus arboreus}) and Tidestrom’s lupine (\textit{Lupinus tidestromii}), significantly reduced belowground stress, allowing for higher biomass and a lower root:shoot ratio.

Nitrogen fixers increase the accessible nitrogen near \textit{C. maritima}, thereby reducing the need to develop long, extensive roots and allowing the plant to allocate more resources to shoot growth. Shoot length is crucial to the reproductive success of \textit{C. maritima}; a seed being dispersed more than 1 m away from the mother plant significantly increases survival (Barbour 1970). Nitrogen fixers may thereby facilitate the extension of \textit{C. maritima} invasion by increasing their reproductive success.

Both native and invasive competitors decreased the performance and increased belowground stress of \textit{C. maritima}. The presence of native competitors may cause the plant to have a lower biomass and allocate more resources to the root, but with an increase of the abundance of native competitors, the change in growth performance is not significantly different.
Figure 3. Effects of native competitor presence on (A) total biomass and (B) root:shoot mass ratio. Results showed significantly lower biomass and higher belowground resource allocation (root:shoot ratio) with the presence of native competitors.

Figure 4. Effects of invasive competitor presence on (A) total biomass and (B) root:shoot mass ratio. Greater numbers of invasive competitors surrounding C. maritima were associated with reduced total biomass and greater relative prioritization of belowground resource allocation.
Table 1. Summary of C. maritima biomass and belowground resource allocation (root:shoot) by nearby plant guilds. Belowground resource allocation indicating increased water or nutrient stress is indicated by ln[Root-to-shoot ratio]; total growth is represented by ln[Biomass]. Surrounding plants were classified into native nitrogen-fixers, native competitors, and non-native competitors. Both species presence/absence and species abundance were examined and listed with F/T ratio, P value, and R-square if applicable. Asterisks indicate significance. NA = Not Applicable.

<table>
<thead>
<tr>
<th>Presence/Absence</th>
<th>Species Abundance</th>
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<th>Presence/Absence</th>
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<tbody>
<tr>
<td>F/T Ratio</td>
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<td>P Value</td>
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<td>0.205</td>
<td>&lt;0.0001*</td>
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<td>R-square</td>
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<td>0.062</td>
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Unlike native competitors, the presence of invasive competitors significantly lowers the biomass but not the root:shoot ratio, while the abundance of invasive competitors significantly impact both variables. Thus, native competitors negatively affect C. maritima by their presence, and invasive competitors negatively affect C. maritima by both presence and abundance. This is likely the result of a decrease in water availability in the soil causing the plant to either increase its resource investment in roots or decrease overall size. Resource investment in longer roots and decreased investment in overall size takes away from the plant’s ability to grow longer shoots and disperse its seeds farther. This suggests that competitors decrease C. maritima reproductive success.

One possible explanation for abundance having little effect on resource allocation or biomass in relation to natives may be that competition from native competitors is limited by their maximum root length, and once C. maritima allocates enough resources to roots to grow beyond the native competition, the native roots are too short to pose an issue at any abundance. More research into the root system structure of the native and non-native competitors is recommended to better understand this relationship.

Abiotic components of coastal dune ecosystems measured by this study had a less reliable correlation with C. maritima performance and belowground resource stress. The backdune site at an intermediate distance from the ocean featured greater biomass and allocated less resources to their roots, indicating the slightly sheltered dune area provided less stress. This result is consistent with an earlier finding that the mortality of American sea rocket (C. edentula) was higher closest to the ocean and farthest from the ocean compared to an intermediate distance. This was previously hypothesized to be due to high wave and wind stress near the ocean and lack of water or nutrients inland, where there is little nutrient-providing detritus carried by waves (Payne & Maun 1984). Ocean salt spray and evaporation explain soil salinity...
gradients within varying distances from the ocean, with the most inland areas being the most saline. According to the study of salinity effects on *C. maritima* by Ahmed Debez et al. in 2004, *C. maritima* requires a moderate salt concentration (Debez et al. 2004). The backdune site, at an intermediate distance from the ocean, exhibited this by having higher biomass and lower root:shoot ratios relative to the other sites. Therefore, future restoration efforts should focus on areas that have an intermediate distance from the ocean.

The results of this study could be used to pinpoint coastal dune sites that are at high risk of *C. maritima* invasion. Sites abundant with nitrogen fixers, low in competitors, and an intermediate distance from the ocean can be targeted for restoration and preventative measures to halt invasion before it becomes unmanageable and spreads to less vulnerable sites.

This study provides some insights on the physiology of *C. maritima* that is needed to construct effective restoration strategies. Our findings are consistent with the history of *C. maritima* in Point Reyes National Seashore: once the non-native competitor *A. arenaria* was removed, the sand previously stabilized and dominated by the grass was open to *C. maritima* invasion. The species was largely free of competition in the newly-restored area; *A. arenaria* had dominated over the natives. *C. maritima* colonized and was able to grow and disperse, likely establishing itself in areas with competitors but faring less well. It is likely that nitrogen fixers aiding reproduction promoted the spread of the species. It is unknown where the species first invaded, but we speculate that the greater growth and reproductive success found on the backdune may have aided in the dispersal of *C. maritima* from the sea to the inland valley. From this perspective, three primary steps to managing the species become apparent: plant native species immediately following the removal of non-native species, prioritize early removal of invaders in backdune areas, and closely monitor areas with nitrogen-fixing species for signs of non-native colonization. When invasion of the species is noticed immediately, manual removal of fruits and seedlings may be sufficient for management of *C. maritima*.

Misunderstanding the life history of an invasive species when planning a restoration project is very costly in terms of both money and time. It is imperative to continue physiological research on invasive species to establish preventative measures and restoration guidelines for early stages of invasion while a species is still manageable and it is possible to extirpate the entire population. Not only will these efforts preserve California’s precious dune ecosystems through preserving their current states, restoration will promote the resumption of traditional successional regimes and assist in the renewal of the endemic and endangered populations that depend on the coastal dune ecosystems.

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**REFERENCES**


