# AN ABSTRACT OF THE DISSERTATION OF

Vanessa Constant for the degree of Doctor of Philosophy in Integrative Biology presented on December 6, 2019.

Title: Coastal Dunes as Meta-Ecosystems: Connecting Marine Subsidies to Dune Ecosystem Functions on the U.S. Pacific Northwest Coast.

Abstract approved:

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Ecological communities are connected in space and time through the transfer of energy, materials, and organisms, together known as ecological subsidies. These ecological subsidies can have substantial effects on community structure, function, and services, especially when the connections are between communities with contrasting productivity. At the ocean-land interface, low productivity coastal beaches and dunes are regularly exposed to subsidies from the ocean. These marine subsidies likely provide an important nutrient source for dune vegetation that might otherwise be nutrient-limited. Given that dune vegetation plays a key role in dune formation and stabilization, it is imperative to understand the role of marine subsidies to the nutrient dynamics and plant productivity patterns of these coastal systems.

In this dissertation, I investigate the role of marine subsidies to dune ecosystem functions from local to meta-ecosystem scales along the U.S. Pacific Northwest coast. Coastal beaches and dunes make up approximately 45% of the Oregon and Washington coasts and are adjacent to many highly productive estuaries

and rocky reefs. The plant communities at these sites experience variable ocean productivity, marine subsidies, and coastal sediment supply. The most common plant species are two non-native invasive grasses, the European beachgrass, *Ammophila arenaria,* and the American beachgrass, *Ammophila breviligulata*. Since their introduction in the early 1900's, the *Ammophila* congeners have spread and rapidly transformed what was once an open, shifting, and sparsely vegetated habitat into one with continuous, stable, and densely vegetated foredunes. Despite this ecosystem-level transformation over the last century, little is known about the role of marine subsidies to the nutrient dynamics and primary production of dune grass communities.

Here I use a combination of observations, laboratory analyses, and experiments to understand the role of ecological subsidies to dune grass production at local to regional scales along the U.S. Pacific Northwest coast. In Chapter 2, I explore the role of marine subsidies to dune grass production at 15 dune-backed beach sites in Washington and Oregon and over three years (2015-2017). Specifically, I ask 1) Is there a relationship between ocean upwelling, distance to wrack source habitat, and beach width to macrophyte wrack amount and composition across large regional (meta-ecosystem) spatial scales and over time (2015-2017)?, 2) Is there a relationship between ocean upwelling, sand supply, and/or marine macrophyte wrack and the marine nutrient dynamics at local and regional scales and over time?, and 3) Is there a relationship between marine nutrients and dune grass production at local to regional spatial scales and over time? I provide evidence that marine subsidies are common and predictable sources of nutrients to these beaches and dunes and that they influence dune grass ecosystems in significant ways. Specifically, I found that macrophyte wrack and sand nitrates, which were positively related to ocean upwelling and sand supply, were important determinants of dune grass production across sites and foredune profile locations. Beaches with more macrophyte wrack and greater sand supply had greater dune grass shoot density and biomass, especially at the toe of the dune where sand nitrate concentrations were high. Beaches with lower macrophyte wrack and sand supply had greater shoot density and biomass of dune grasses at the crest of the dune, where sand deposition and nitrate concentrations were high. Taken together, these results suggest that marine subsidies are important contributors to the nutrient dynamics and productivity of dune grasses, potentially influencing the sand capture and dune building capabilities of these ecosystem engineering grass species.

In Chapter 3, I determine whether dune plant species in the U.S. Pacific Northwest use marine subsidies, and if so, how this use varies at local to regional spatial scales. In particular, I ask 1) Does the amount (%N) and marine source ($\delta^{15}N$) of nitrogen in four dune plant species (two non-native invasive beachgrass species *Ammophila arenaria* and *A. breviligulata*, the native dune grass, *Elymus mollis,* and the native shrub *Cakile edentula*) vary across sites (coast-scale) and foredune profile locations (dune-scale)? and 2) Does the amount (%N) and marine source ($\delta^{15}N$) of nitrogen of beachgrasses correlate with measures of marine subsidies (macrophyte wrack and sand nitrates) and/or beach and foredune geomorphology (beach width and foredune crest height) on coastal foredunes? I found that marine nutrients were an important source of nitrogen for dune plants in the U.S. Pacific Northwest, and that the amount and source of nitrogen in these plants varied among species, sites, and foredune profile locations. Regression analyses showed that, for the most part, macrophyte wrack biomass and sand nitrate concentrations were unrelated to %N or $\delta^{15}N$ of the grasses. However, I did find that wider beaches and shorter foredunes had beachgrasses with slightly lower %N tissue content across foredune profile locations but the source of that nitrogen at the crest and heel had a higher marine signature. The results presented in this chapter corroborate earlier studies that beach nutrients, especially those with marine origin, are an important source of nitrogen for foredune plants.

Finally, in Chapter 4, I test whether beachgrasses in the U.S. Pacific Northwest are nutrient limited and whether this potential limitation varies along foredune profile locations and sites with different sand nitrate conditions. Specifically, I used two manipulative experiments to ask: (1) How does nutrient addition affect dune grass production at sites and foredune profile locations that vary in natural sand nitrate concentrations? and (2) Does dune grass production and plant tissue elemental composition vary with increasing nitrogen additions and do dune grasses experience nitrogen and phosphorous co-limitation? I found that dune grasses were nutrient-limited, with nutrient additions positively affecting dune grass production at sites and foredune profile locations that have higher wrack deposition and background sand nitrate concentrations. I also found that increased nitrogen and phosphorous increased grass shoot density, total biomass, and plant tissue %N. However, grass shoot biomass and shoot length either did not change, or declined, with phosphorus additions suggesting that there was no phosphorus co-limitation.

These results suggest that U.S. Pacific Northwest dune grasses are nutrient limited, especially at the foredune crest and heel, where background sand nitrate concentrations are lower.

In summary, my dissertation fills a critical gap in our understanding of beach and dune nutrient dynamics and the role of nutrients to coastal dune plant community production from a meta-ecosystem perspective. By considering local and regional relationships, this meta-ecosystem approach provides an ideal framework to understanding the role of marine subsidies to dune grass production. This approach also allows us to better understand how coastal dune systems might change under varying climate so that we may better manage their functions and services in the future.

# Coastal Dunes as Meta-Ecosystems: Connecting Marine Subsidies to Dune Ecosystem Functions on the U.S. Pacific Northwest Coast

by
Vanessa Constant

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APPROVED:

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Head of the Department of Integrative Biology

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Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

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Vanessa Constant, Author

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# CONTRIBUTION OF AUTHORS

Chapter 2: Dr. Sally Hacker contributed to the conception of the study, fieldwork design and execution, and writing and editing of the manuscript. Dr. Francis Chan developed the sediment analysis protocol, provided technical guidance with laboratory analyses, and reviewed and edited the manuscript.

Chapter 3: Dr. Sally Hacker contributed to the conception of the study, fieldwork collections, and writing and editing of the manuscript. Dr. Francis Chan provided technical guidance with laboratory analyses and reviewed and edited the manuscript. Ms. Patricia Gonzalez Cruz processed the plant samples for elemental composition.

Chapter 4: Dr. Sally Hacker contributed to the conception of the study, experimental design, and writing and editing of the manuscript. Dr. Francis Chan assisted with the experimental design and reviewed and edited the manuscript. Ms. McKenzie Barker helped with fieldwork and with processing of the plant samples for production measures and elemental composition.

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# DEDICATION

This dissertation is dedicated with love and gratitude
to my parents, Karen Sadock and Bob Constant.

# Coastal Dunes as Meta-Ecosystems: Connecting Marine Subsidies to Dune Ecosystem Functions on the U.S. Pacific Northwest Coast

# Chapter 1 – General Introduction

Ecological communities are shaped by environmental and biological processes operating over multiple spatial and temporal scales. However, it has only been in the last few decades that community ecologists have begun to focus on the ways in which communities are connected at larger spatial scales through the transfer of ecological subsidies, not only in terms of organisms but also energy and materials, across environmental boundaries (e.g., classic studies include Polis and Hurd 1995, 1996, Polis et al. 1997, Rose and Polis 1998). This meta-ecosystem approach (Loreau et al. 2003, Massol et al. 2011) integrates perspectives of community and landscape ecology, providing an opportunity to explore the relationship between ecosystem function and spatial dynamics (Gouhier et al. 2010, Hessing-Lewis and Hacker 2013, Menge et al. 2015, Leibold et al. 2017, Guichard 2017). By examining ecological subsidies and uncovering the mechanisms behind community responses, we can improve our understanding of how communities will respond to large-scale threats such as species invasions, climate change, and other human-caused disturbances.

Since the inception of the meta-ecosystem concept, ecologists have focused on theoretical (e.g., Holt 2004, Loreau and Holt 2004, Leroux and Loreau 2008, Massol et al. 2011) and observational studies (e.g., Polis and Hurd 1995, 1996, Polis et al. 1997, Rose and Polis 1998, Hessing-Lewis and Hacker 2013, Menge et al. 2015, Hayduk et al. 2019) that consider reciprocal subsidy flows (e.g., Nakano and Murakami 2001, Baxter et al. 2005, Bartels et al. 2012, Piovia-Scott et al. 2016). However, some meta-ecosystems show asymmetrical subsidy flows, where one community is the donor and the other is the recipient of these subsidies. Interface habitats, where two difference ecosystems meet, are ideal for evaluating these dynamics because the subsidy flows can be strong and are typically unidirectional. This is especially true in ecosystems with contrasting productivity such as high productivity marine waters and low productivity sandy beaches and dunes (Anderson and Polis 1998, Dugan et al. 2003, Rodil et al. 2019). These inherently low-nutrient settings are subsidized with nutrients in seawater and macrophyte biomass from coastal waters and a variety of nearshore habitats including rocky shores and estuaries (e.g., Orr et al. 2005, Colombini and Chelazzi 2003, Barreiro et al. 2011, Dugan et al. 2011, Reimer et al. 2018). By adding to the food resources and nutrients of sandy beaches, macrophyte wrack supports animal and plant communities on beaches and dunes (Polis and Hurd 1995, 1996, Polis et al. 1997, Rose and Polis 1998, Dugan et al. 2003, Lastra et al. 2008, Barreiro et al. 2011).

Dune vegetation is foundational to the formation and stability of coastal dunes (Hesp 1989, Murray et al. 2008, Hacker et al. 2012, 2019, Zarnetske et al. 2012, 2015, Durán and Moore 2013, Biel et al. 2019). As wind blows across the beach, sand grains are transported up the beach where they are captured by dune vegetation (e.g., Hesp 1981, Wolfe and Nickling 1993, Wiggs et al. 1994, 1995). The plants then compensate for the increased sand burial by increasing growth, which then allows them to capture more sand, producing a positive feedback between vegetative growth and sand accretion. This vegetation-supported positive feedback, and the complex root system of these plants, ultimately results in foredunes, which provide a multitude of ecosystem services from coastal protection to carbon sequestration to habitat for animals and plants (Barbier et al. 2011).

Despite many of the essential ecosystem services provided by coastal dunes (Barbier et al. 2011), few studies explore the mechanisms underlying vegetation growth and production in what is generally considered a nutrient poor and high stress environment. The goal of this dissertation is to investigate the role of marine subsidies to dune ecosystem functions from local to regional meta-ecosystem scales. In particular, I determine the relationship between ocean upwelling, marine nutrients, sediment supply, and dune grass production on beaches and dunes along the U.S. Pacific Northwest coast.

Coastal beaches and dunes of the U.S. Pacific Northwest make up approximately 45% of the Oregon and Washington coasts and are adjacent to many highly productive estuaries and rocky reefs. The plant communities in this region experience variable ocean productivity (e.g., Hickey and Banas 2003, Checkley and Barth 2009, Menge et al. 2015), marine subsidies (e.g., Reimer et al. 2018, Chapter 2 of this thesis), and sediment supply and coastal geomorphology (e.g., Ruggiero et al. 2013, Biel et al. 2019).

In this region, the most common dune plant species are the two invasive grasses, the European beachgrass *Ammophila arenaria* and the American beachgrass *Ammophila breviligulata*, which overlap in their distribution in the north but not the south (Hacker et al. 2012). First introduced in the early 1900's, *A. arenaria* was the dominant beachgrass species (Cooper 1958, Seabloom and Wiedemann 1994) along the entire US Pacific coast. However, in 1935, the intentional planting of *A.*

*breviligulata* around the Columbia River led to the subsequent invasion of this species in the northern part of the study region (Seabloom and Wiedemann 1994, Hacker et al. 2012). Today, *A. breviligulata* is dominant in northern dune sites while *A. arenaria* is dominant in southern sites. These non-native species introductions rapidly transformed what was once open, shifting, and sparsely vegetated dunes into continuous, stable, and densely vegetated coastal dunes. Despite this unique history, and the prolific spread of *Ammophila* along the US Pacific coast, little is known about the mechanisms underlying beachgrass production, particularly the role of marine subsidies. To consider these factors, it is important to understand the oceanographic, geographic, and geomorphic context that underlies the generation of marine subsidies.

Nearshore and estuarine coastal ecosystem productivity is mediated by the California Current System (CCS) (Barth et al. 2007, Hacker and Hessing-Lewis 2013, Menge et al. 2015). The CCS is characterized by seasonal, wind-driven upwelling, an oceanographic process that brings deep, cold, nutrient-rich water to the surface of the ocean and supports macrophyte growth. Upwelling is an important driver of local rocky intertidal and estuarine production and community structure (e.g., Menge et al. 2003, Nielsen and Navarrete 2004, Hessing-Lewis and Hacker 2013, Fenberg et al. 2015, Reddin et al. 2015, Hacker et al. 2019, Hayduk et al. 2019). Rocky headlands are exposed to the strongest ocean upwelling, with nutrients delivered to these locations supporting large macroalgal communities (Menge et al. 2015). Pacific coast estuaries are also influenced by large-scale upwelling processes (Hickey and Banas 2003, Brown and Ozretich 2009). However, eelgrass productivity is greatest in estuaries exposed to lower intensity ocean upwelling (Hessing-Lewis and Hacker

2013, Hayduk et al. 2019). Previous research conducted along the U.S. Pacific Northwest coast concluded that macrophyte wrack deposition patterns on Pacific coast beaches were driven by a combination of ocean upwelling, distance of the beach to macrophyte source habitat (i.e., distance to nearest estuary or rocky reef), and beach morphology (Reimer et al. 2018). In the north, where upwelling is weaker and large estuaries are common, the beaches are dominated by eelgrass wrack. Here estuaries release eelgrass and green macroalgae to coastal waters via outwelling. In the south, where stronger upwelling fuels macroalgal productivity and rocky habitats are more common, the beaches are dominated by kelp wrack. Further, wider and more gently sloping beaches were more conducive to wrack stranding than narrower and steeper beaches.

Here, I build on earlier wrack and dune research by considering the role of marine nutrients to dune ecosystem function in the U.S. Pacific Northwest coastal sand dune system. While studies have experimentally examined the connection between marine subsidies and dune plant production at local scales (e.g., Cardona and Garcia 2008, Williams and Feagin 2010, Del Vecchio et al. 2013 and 2017, van Egmond et al. 2019), observational and experimental studies that link *in situ* nutrient concentrations, via marine subsidies, to dune plant production across space and time do not exist. My dissertation addresses this gap by exploring the dynamics of coastal dunes through observations and experiments designed to understand the role of ecological subsidies, processes of nutrient delivery, and mechanisms of dune grass growth at a meta-ecosystem scale.

In Chapter 2, I explore the role of marine subsidies to dune grass production at 15 dune-backed beach sites in Washington and Oregon over three years (2015-2017). Using observational data, I explore the patterns of environmental factors (ocean upwelling and sand supply), marine subsidies (macrophyte wrack and sand nitrate), and dune grass production at local (across the foredune) and regional (across sites) scales and over time. I then use regression models to determine how much variation in these patterns is attributable to ocean productivity, marine subsidies, sand supply, and beach and foredune geomorphology. Specifically, I ask 1) Is there a relationship between ocean upwelling, distance to wrack source habitat, and beach width to macrophyte wrack amount and composition across large regional (meta-ecosystem) spatial scales and over time (2015-2017)?, 2) Is there a relationship between ocean upwelling, sand supply, and/or marine macrophyte wrack and the marine nutrient dynamics at local and regional scales?, and 3) Is there a relationship between marine nutrients and dune grass production at local to regional spatial scales?

In Chapter 3, I determine whether dune plant species in the U.S. Pacific Northwest use marine subsidies, and if so, how this use varies at local to regional spatial scales. To assess nitrogen natural abundance and quantify the contribution of marine nutrients to dune vegetation, I evaluate the nitrogen content (%N) and source (foliar $\delta^{15}N$) present in common Pacific Northwest dune plant species and relate these patterns to patterns of marine subsidies and measures of coastal geomorphology across sites and foredune profile locations. In particular, I ask 1) Does the amount (%N) and marine source ($\delta^{15}N$) of nitrogen in four dune plant species (two non-native invasive beachgrass species *Ammophila arenaria* and *A. breviligulata*, the native dune grass, *Elymus mollis,* and the native shrub *Cakile edentula*) vary across profile locations (dune-scale) and sites (coast-scale)? and 2) Does the amount (%N) and marine source ($\delta^{15}N$) of nitrogen of beachgrasses correlate with measures of marine subsidies (macrophyte wrack and sand nitrates) and/or beach and foredune geomorphology (beach width and foredune crest height) on coastal foredunes?

In Chapter 4, I test whether beachgrasses in the U.S. Pacific Northwest are nutrient limited and whether this potential limitation varies along foredune profile locations and sites with different sand nitrate conditions. Specifically, I ask (1) How does nutrient addition affect dune grass production at sites and foredune profile locations that vary in natural sand nitrate concentrations? and (2) Does dune grass production and plant tissue elemental composition vary with increasing nitrogen additions and do dune grasses experience nitrogen and phosphorous co-limitation? I examine dune grass production in response to nutrient additions, leveraging the natural variability in marine subsidies and coastal geomorphology. I conduct two experiments, one at the dune scale and one at the coast scale. At the coast scale, plots with fertilizer addition were compared to control plots across the foredune toe, crest, and heel of three sites exposed to variable nutrient subsidies. At the dune scale, five nutrient treatments of increasing concentration were applied to beachgrass plots on the foredune toe, crest, and heel of a single site on the U.S. Pacific Northwest Coast. In both experiments, beachgrass production response to nutrient additions was measured as shoot density, shoot length, shoot biomass, and total plant biomass.

Overall, my dissertation research answers the question, “does ocean productivity contribute to dune grass production?” with a resounding “yes.” Each chapter addresses a different aspect of the connection between nutrient subsidies and beachgrass production. Much of this work employs long-standing field surveying methodologies and experimental techniques, building on previous coastal dune research. However, by exploring multi-scale cross-ecosystem dynamics, new insights are gleaned about the processes that drive the production of coastal vegetation to better understand the structure, function, and services of coastal dunes. This is particularly relevant given the potential shifts in marine subsidies to dune plant communities with changes in ocean productivity, chronic and extreme storm events, and other climate driven nearshore processes.

# Chapter 2 – Does ocean productivity contribute to dune ecosystem function? Connecting marine subsidies to dune grass production on the U.S. Pacific Northwest coast

Vanessa Constant, Francis Chan, and Sally D. Hacker

## Abstract

Communities are connected at large spatial scales via “ecological subsidies” (energy, materials, and/or organisms), influencing their community structure, functions, and services. In systems of contrasting productivity, such as high productivity marine waters and low productivity sandy environments, subsidy flows and their influence can be highly asymmetrical. Coastal dunes are shaped by the positive feedback between wind-blown sand and vegetation. As physical barriers between the ocean and coastal communities, these settings provide coastal protection from extreme storms and coastal flooding. However, even though dune habitats are considered nutrient poor, resulting in nutrient limitation for vegetation, the role of marine subsidies to the nutrient dynamics and primary production of coastal dune plant communities remains understudied. In a previous study, Reimer et al. (2018) found that the amount and type of macrophyte wrack on sandy beaches was dependent on ocean upwelling, proximity of the beach to wrack source habitat (i.e., rocky reef or estuary), and beach morphology. In this study, we extend those results to ask 1) How do environmental factors, marine subsidies, and dune grass production vary at local (beach and foredune profile location) to regional (meta-ecosystem) spatial scales and over time (2015-2017)?, 2) Is there a relationship between ocean upwelling, sand supply, and/or marine macrophyte wrack and the marine nutrient dynamics at local and regional scales?, and 3) Is there a relationship between marine nutrients and dune grass production at local to regional spatial scales? We determined the patterns of environmental factors and marine subsidies on beaches, and dune grass production on dunes along a 550 km stretch of the U.S. Pacific Northwest coast, and evaluated the potential mechanisms contributing to these patterns. Evidence showed that macrophyte wrack on beaches and nitrates bound to sand, which are positively related to ocean upwelling and sand supply, were important determinants of dune grass production across sites and foredune profile locations. Beaches with more macrophyte wrack and greater sand supply had greater dune grass shoot density and biomass at the foredune toe, where sand nitrate concentrations were high. In contrast, beaches with lower macrophyte wrack and sand supply had greater dune grass shoot density and biomass at the crest of the dune, where sand deposition and nitrate concentrations were highest. Our results suggest that marine subsidies and sand supply, two factors that connect ocean productivity to dune plant productivity, are important in shaping local dune sites across the Pacific Northwest. These meta-ecosystem dynamics are particularly relevant given the potential shifts in marine subsidies with changes in ocean productivity, chronic and extreme storm events, and other climate driven nearshore processes that influence beaches and dunes.

## 2.1 Introduction

Over the last few decades, community ecologists have explored the ways in which communities are connected across spatial scales and the effects those connections have on community structure, functions, and services (Leibold et al. 2017, Guichard 2017). This meta-ecosystem approach considers how energy, materials, and/or organisms (known as ecological subsidies) connect communities across environmental boundaries (*sensu* Loreau et al. 2003, Massol et al. 2011). These community connections through subsidies can be strong, mediating key ecological functions such as primary production and food web dynamics (e.g., Polis and Hurd 1995, 1996, Polis et al. 1997, Nakano and Murakami 2001, Menge et al. 2003, 2015, Witman et al. 2010, Hessing-Lewis and Hacker 2013, Kristensen et al. 2014, Vinueza et al. 2014, Uno and Power 2015, Hacker et al. 2019, Hayduk et al. 2019, Montagano et al. 2019) and their associated services (e.g., Lundberg and Moberg 2003, Tscharntke et al. 2005, Kremen et al. 2007, Semmens et al. 2011). Some meta-ecosystems show strongly asymmetrical subsidy flows, where one community is the donor and the other is the recipient. This unidirectionality can be particularly important to communities that have low internal productivity (e.g., Polis and Hurd 1996, Spiller et al. 2010).

By exploring the relationships between ecosystem functions and spatial dynamics, these studies demonstrate that the meta-ecosystem framework as a useful tool for investigating the processes important to community structure. Specifically, the meta-ecosystem perspective helps us understand the novel properties that arise from spatially coupled local ecosystems, gain insights into ecosystem dynamics and functioning across multiple scales, and ultimately enhance our ability to predict the consequences of environmental change on the provision of subsidy-mediated ecosystem services.

A number of studies on the role of ecological subsidies have focused on marine nearshore communities, where the delivery of ocean-derived subsidies to coastal interface habitats is substantial (e.g., ocean-island systems: Polis and Hurd 1995, 1996, Barrett et al. 2005, Spiller et al. 2010, Bassett et al. 2014, Kenny et al. 2017; ocean-coastal systems: Varpe et al. 2005, Hessing-Lewis and Hacker 2013, Menge et al. 2015, Liebowitz et al. 2016, Hacker et al. 2019, Hayduk et al. 2019).

Although some of the early studies considered the material exchanges at local scales (e.g., Oliver and Legović 1988, Polis and Hurd 1995, 1996, Wallace et al. 1997, Rose and Polis 1998), a number of the recent studies have examined the contribution of multiple ecological subsidies at larger, meta-ecosystem scales (e.g., Menge et al. 2015, Gounand et al. 2018, Hacker et al. 2019, Montagano et al. 2019, Hayduk et al. 2019). In one such study, Menge and colleagues (2015) used a comparative approach to explore the scale-dependent controls on rocky intertidal community structure within the California Current System of the U.S. Pacific coast. They found that differences in community structure were driven primarily by external factors (e.g., environmental factors and ecological subsidies), and that this variation was more strongly explained at regional compared to local scales. Later, using species interaction experiments, Hacker and colleagues (2019) determined that community structure in the low intertidal was driven largely by external factors at the regional scale compared to the more secondary role of local, biotic interactions. The influence of local versus regional dynamics has been further explored in coastal estuaries where subsidy variability with space and time influenced macrophyte community structure (Hessing-Lewis and Hacker 2013, Hayduk et al. 2019) and associated animal communities (Hayduk et al. 2019). These studies found, similar to Hacker et al. (2019), that local processes were less important to community structure than subsidies contributed at regional spatial scales.

Despite the strong empirical evidence that cross-ecosystem subsidy transfer at regional scales contributes to coastal ecosystem functions, we know much less about the role of marine subsidies to coastal beach and dune communities. Although sandy environments are generally considered nutrient limited and relatively unproductive (e.g., Willis and Yemm 1961, Willis 1963, 1965, Kachi and Hirose 1983, Hesp 1991, Kooijman et al. 1998, Jones et al. 2004), the role of marine subsidies on the nutrient dynamics and primary production of coastal dune plant communities remains understudied (except see Cardona and García 2008, Del Vecchio et al. 2013, 2017, van Egmond et al. 2019). Coastal plant communities capture and stabilize sand, thereby shaping foredune geomorphology (e.g., Hesp 1989, Murray et al. 2008, Hacker et al. 2012, Zarnetske et al. 2012, 2015, Durán and Moore 2013, Biel et al. 2019) and associated services such as coastal protection (e.g., Seabloom et al. 2013, Biel et al. 2017, Ruggiero et al. 2019), carbon sequestration (Jones et al. 2008, Drius et al. 2016, Bonito et al. 2017), and other ecosystem services including recreation (Barbier et al. 2011).

The role of marine subsidies to beach and dune communities has mostly focused on macrophyte wrack and its role as food and nutrients to animals and plants (Colombini and Chelazzi 2003). For example, multiple studies show that macrophyte wrack can have positive effects on coastal food webs, including beach invertebrates and their predators (e.g., Polis and Hurd 1996, Dugan et al. 2003, Jaramillo et al. 2006, Ince et al. 2007, Lastra et al. 2008). In addition, macrophyte wrack can provide nutrients to dune vegetation, promoting primary production in these systems (Cardona and García 2008, Williams and Feagin 2010, Del Vecchio et al. 2013, 2017, van Egmond et al. 2019). For example, along Mediterranean foredunes, seagrass wrack was found to enhance the nutrient pools in sand and plant tissue, resulting in increased plant size and growth rate as well as plant species richness (Cardona and Garcia 2008, Del Vecchio et al. 2013, 2017).

Detailed analyses show that once wrack becomes stranded, it begins to release nutrients through bacterial decomposition, a process enhanced by drying and wetting events, physical fragmentation, and consumption by macroinvertebrates (Robertson and Mann 1980, Newell et al. 1996, Vähätalo et al. 1998, Ochieng and Erftemeijer 1999, Columbini and Chelazzi 2003, Mateo et al. 2003, Orr et al. 2005, Mews et al. 2006, Cardona and García 2008, Dugan et al. 2011, Del Vecchio et al. 2013, Rodil et al. 2019). Decomposition rate can vary among macrophyte wrack species as a consequence of its composition and morphology as well as aspects of the food web. For example, the preferential consumption and decomposition of *Palmaria decipiens* was seemingly related to its lack of chemical defenses, its palatability, and its overall abundance onshore compared to *Desmarestia menziesii* (Lastra et al. 2014). Nutrients resulting from macrophyte decomposition, and any remaining particles of wrack debris, can be adsorbed to beach sand and then transported further inland to the upper beach and dune by wind and wave action (Cardona and García 2008, Oldham et al. 2014). Seawater from tidal exchange and wave runup can also influence the nutrient condition of beach sand by marine nutrients adsorbing to the sand grains themselves (Eagle 1983, McLachlan et al. 1985, McLachlan and Turner 1994, Hwang et al. 2008, Dugan et al. 2011). Together, sand coated with macrophyte wrack and seawater present two direct pathways for marine nutrient delivery to coastal beaches and dunes.

The limited research exploring the relationship between marine subsidies and dune plant community structure has typically focused at local spatial scales and short time scales. However, it stands to reason that marine nutrients and their effects on primary production will vary among sites given the nature of these subsidies, which are dependent on a number of site and regional scale factors. Here we report on a comparative observational study that considers the role of marine subsidies to dune ecosystem function at a meta-ecosystem scale. In particular, our goal was to determine the relationship between ocean upwelling, marine nutrients (i.e., macrophyte wrack and sand), sand supply and coastal geomorphology, and dune grass production (i.e., shoot density and biomass) on foredunes along a 550 km stretch of the U.S. Pacific Northwest coast. In this study, we ask whether there is a strong connection between marine nutrient conditions and coastal dune vegetation, an important mediator of dune geomorphology.

The expansive coastal dune ecosystem of the U.S. Pacific Northwest (approximately 45% of the Oregon and Washington coasts), along with its close proximity to many highly productive estuaries and rocky reefs, is an ideal study system for exploring the role of marine subsidies to dune plant community structure. In the early 20th century, two non-native beachgrasses, *Ammophila arenaria* L. (European beachgrass) and *Ammophila breviligulata* Fern. (American beachgrass), were intentionally introduced to facilitate dune building and stabilization (Cooper 1958, Wiedemann 1984). The rapid proliferation of the beachgrasses transformed what was once an open, shifting sand habitat with sparse vegetation (including the native, American dune grass, *Elymus mollis* (Trin.) Pilg.), to a continuous, stable foredune system with dense vegetation (Wiedemann and Pickart 1996, Hacker et al. 2012). A recent study, which explored the relative role of geomorphic factors and invasive beachgrass density to foredune height variability across the U.S. Pacific Northwest coast, found that ~50% of the variability in dune height was explained by beach sediment supply and ~10% of the variability was explained by beachgrass density (Biel et al. 2019). In addition, differences in sand capture between the two invasive beachgrass species were found, corroborating previous research showing that *A. arenaria*, because of its denser shoots, captures more sand and builds taller dunes than its congener, *A. breviligulata* (Hacker et al. 2012, Zarnetske et al. 2012, 2015). However, despite research that suggests dune grass density and morphology are important to sand capture and dune building, little is known about the environmental factors important to dune grass production, particularly the role of marine nutrients. To consider these factors, it is important to understand the oceanographic and geological context that underlies the generation of marine subsidies.

Past research along the West Coast of the U.S. has shown that nearshore coastal ecosystem production is mediated by the California Current System (CCS) (Menge et al. 2015), which is characterized by seasonal, wind-driven ocean upwelling. Upwelling—the oceanographic process that brings deep, cold, nutrient-rich water to the nearshore environment—is an important driver of local rocky intertidal and estuarine primary production and community structure (e.g., Menge et al. 2003, Nielsen and Navarrete 2004, Fenberg et al. 2015, Hacker et al. 2019, Hayduk et al. 2019). Rocky headlands are exposed to strong ocean upwelling, where nutrients delivered to these locations support large macroalgal communities (Menge et al. 2015). Estuaries in the U.S. Pacific Northwest are also influenced by ocean upwelling with both nutrients and primary production of eelgrass and macroalgae being more strongly driven by large scale oceanic processes (i.e., upwelling) rather than local or watershed processes (i.e., nutrient runoff) (Hickey and Banas 2003, Brown and Ozretich 2009, Hessing-Lewis and Hacker 2013, Hayduk et al. 2019).

Ocean upwelling has different consequences for primary producers growing in estuaries compared to rocky shore habitats. Estuaries exposed to more persistent upwelling have greater ulvoid macroalgae production, but lower eelgrass production, while those estuaries experiencing less intense upwelling have lower macroalgae production but greater eelgrass production (Hessing-Lewis et al. 2011, Hessing-Lewis and Hacker 2013). In one of the most extensive macrophyte wrack surveys conducted along any coastline (see also Orr et al. 2005, Liebowitz et al. 2016), Reimer and colleagues (2018) found that these upwelling-influenced macrophyte production patterns were evident in wrack deposition patterns on beaches along the U.S. Pacific Northwest coast. In the north, where upwelling is less intense and large estuaries are common, the process of outwelling moves eelgrass and macroalgae from estuaries to the nearshore, where it is deposited on beaches nearby. In the south, where upwelling is stronger and fuels macroalgal productivity and rocky habitats are more common, the wrack on nearby beaches are mostly kelps and other brown macroalgae. The Reimer et al. (2018) results suggest that these differences in macrophyte wrack deposition patterns, and exposure to variable ocean upwelling, sand supply, and beach and dune geomorphology, could have important influences on the nutrient dynamics and dune grass production of this meta-ecosystem. Thus, in this study, we build on Reimer et al. (2018) by considering the role of marine nutrients to dune ecosystem function in the U.S. Pacific Northwest coastal sand dune system. In particular, we surveyed beaches and foredunes along the Washington and Oregon coast for the spatial and temporal patterns of oceanography, sand supply and geomorphology, marine subsidies, and dune grass production. To understand the role of marine subsidies to dune ecosystem function, we present three questions, with their associated hypotheses, below:

1) Is there a relationship between ocean upwelling, distance to wrack source habitat, and beach width to macrophyte wrack amount and composition across large regional (meta-ecosystem) spatial scales and over time (2015-2017)? We hypothesize, similar to Reimer et al.'s (2018) results, that at northern sites, where ocean upwelling is less intense and large estuaries are common, macrophyte wrack will be common and consist mostly of eelgrass. At the southern sites, where upwelling is stronger and rocky habitats are more common, macrophyte wrack will also be common and consist mostly of kelps and other brown macroalgae. In central regions, where rocky reefs and estuaries are less common, macrophyte wrack will be sparse and consist of both eelgrass and brown macroalgae
2) Is there a relationship between ocean upwelling, sand supply, and/or marine macrophyte wrack to sand nutrient content at local and regional scales and over time (2015-2017)? We predict that sand nitrate content at

our beach and dune sites will be positively related to ocean upwelling, sand supply, and macrophyte wrack. Sites and profile locations nearer to strong ocean upwelling, high sediment supply, and large quantities of macrophyte wrack will have greater sand nitrate content than sites and profile locations exposed to weak ocean upwelling, low sediment supply, and lower macrophyte wrack biomass.

3) Is there a relationship between marine subsidies (i.e., macrophyte wrack and sand nitrate concentrations) and dune grass production at local to regional spatial scales and over time (2015-2017)? We hypothesize that macrophyte wrack and sand nitrate concentrations are contributing to dune grass production at local and regional scales, and that these grass production patterns will follow marine subsidy changes through time. Sites and profile locations with higher sand nitrate concentrations and total wrack biomass will have greater grass production than sites with lower sand nitrate concentrations and total wrack biomass.

## 2.2 Methods

### 2.2.1 Study Site Characteristics

We studied fifteen dune-backed beach sites that were exposed to the open coast and adjacent to prominent estuaries (Grays Harbor, Willapa Bay, WA; Netarts Bay, Yaquina Bay, and Coos Bay, OR) and major headlands (Cape Disappointment, WA; Cape Meares, Tillamook Head, Cape Foulweather, Cape Perpetua, Cape Arago, Cape Blanco, OR) along a 550 km stretch of the U.S. Pacific Northwest coast. The fifteen sites included Grays Harbor (GH), Leadbetter Point (LBP), and Long Beach

(LB) in Washington and Fort Stevens (FS), Nehalem Bay (NB), Cape Lookout (CL), Sand Lake (SL), Pacific City (PC), South Beach (SB), Siltcoos River (SILT), Dunes Overlook (DO), Umpqua Dunes (UD), North Spit (NS), Bandon (BAN), and Floras Lake (FL) in Oregon Appendix A Table A1). The sites were located within distinct littoral cells, or areas along the coast containing the same sediment sources, transport pathways, and sinks (Inman and Frautschy 1965). The sites have been used in previous dune and wrack research (Hacker et al. 2012, Reimer et al. 2018, Biel et al. 2019).

### 2.2.2 Environmental Factors: Geographic, Oceanographic, and Geomorphic Measurements

We measured five environmental variables at each transect location and/or each site (Appendix A Table A1), depending on the variable: distance to nearest wrack source habitat (estuary or rocky reef), distance to the Columbia River, ocean upwelling, shoreline change rate, and foredune crest height. The distances between each of our transect locations and the nearest wrack source habitat, estuary and rocky reef headland, were estimated using Google Earth (version 7.1.2.2041). Rocky reefs were verified using the “Rock” layer of the Surficial Geologic Habitat Map for the Oregon Territorial Sea (http://www.activetectonics.coas.oregonstate.edu/data.htm#2). We also determined the distance of each transect location from the center of the mouth of the Columbia River, as another measure of potential marine nutrients, given evidence of elevated nitrates in Columbia River plume seawater (Lohan and Bruland 2006).

Ocean upwelling is a measure of the influence of ocean conditions on seawater nutrients and macrophyte production (see Menge et al. 2015). Daily Bakun upwelling index values (cross-shore transport in units of $m^3 s^{-1}$ per 100 m of coastline; Bakun 1990) were obtained for each of the sites (within a 0.5° radius) and for each of the survey years (2015-2017) from the NOAA Pacific Fisheries Environmental Laboratory database (http://coastwatch.pfeg.noaa.gov/erdd-ap/griddap/erdlasFnTran6.html). We calculated the average Bakun index values for each site and year using daily measurements over the macrophyte growing season (April to October for 2015, 2016, and 2017).

Shoreline change rate (SCR) is an integrated measure of the gains or losses of beach sediment over various time scales, used here as a proxy for sand supply to the beach and foredune. We used short-term SCR data (m/year) for each of our transect locations from Ruggiero et al. (2013). The SCR values were measured as an annualized rate of shoreline change between 1967 and 2002 in Oregon and 1986 and 2002 in southwest Washington (Ruggiero et al. 2013).

Finally, in 2017, we conducted topographic surveys to determine the foredune crest height at each transect location. We surveyed the center transect at each transect location (Appendix A Table A1) to determine beach and dune elevations between the mean higher high water (MHHW) mark and the foredune heel using network real time kinematic differential GPS. Elevations were captured every five meters and foredune crest heights (m above local mean sea level, LMSL) were extracted from the resulting cross-shore profiles.

### 2.2.3 Marine Subsidies: Macrophyte Wrack and Sand Nutrient Measurements

We conducted surveys of the abundance and species composition of macrophyte wrack deposited on beaches from southern Washington to southern Oregon for three years (2015-2017). Surveys were conducted from early August through mid-September (August 3 – September 18, 2015; August 8 – September 20, 2016; August 1 – September 20, 2017), a time of year when wrack deposition to the beach was greatest (see seasonal patterns of wrack deposition in Appendix B). Surveys were conducted at three transect locations at each site (except LBP, which had 2 transect locations) that were chosen based on previous dune and wrack surveys (Hacker et al. 2012, Reimer et al. 2018, Biel et al. 2019). Within each transect location, we sampled along three replicate shore perpendicular transects spaced 50 meters apart and extending landward from the mean higher high water (MHHW) mark to the base of the foredune [3 locations (except LBP) x 3 transects x 15 sites = 132 total transects/year] (Appendix A Figure A1). The center transect at each transect location was the same transect surveyed in the aforementioned dune and wrack studies (Hacker et al. 2012, Reimer et al. 2018, Biel et al. 2019).

The transect surveys involved two measurements. First, we counted the total number of individual wrack patches within a 10 m swath around each of the transect lines (Appendix A Figure A1). Patches were visually surveyed as discrete piles of macrophytes that were separate from one another. Second, more detailed wrack patch surveys were conducted along the central transect using 1 $m^2$ quadrats placed adjacent to each other (Appendix A Figure A1). Within each quadrat, the number of patches were recorded, and patches were individually collected and brought back to the laboratory where they were frozen for later analysis. To determine the biomass of each species, patch samples were sorted by species (see species list in Appendix A Table A2), dried to a constant mass at 45°C, and then weighed.

To evaluate the nitrogen content in beach sand, we collected sand samples along each of the transects in conjunction with the wrack surveys. Sand samples were collected at five locations from the beach to dune profile (MHHW, mid-beach, foredune toe, foredune crest, and foredune heel) along each transect, frozen, and subsequently dried at 40°C prior to processing. For each year, equal amounts of sand from the three transects at each of five profile locations were combined, resulting in one sand sample per profile location per transect location per year.

We analyzed the sand samples for inorganic nitrate using the potassium chloride (KCl) extraction method (modified from Mulvaney 1996). Sample analyses were conducted on 2 M KCl extracts with nitrate concentration determined as the amount of nitrate obtained following cadmium reduction in a solution buffered with ammonium chloride and sodium hydroxide ($NH_4Cl$ + 1M NaOH). Nitrate concentrations were determined colorimetrically by measuring the absorbance of the solution at 540 nm wavelength following the addition of an azo dye reagent (sulfanilamide and N-(1-naphyl) ethylenediamine dihydrochloride solution) with an Ocean Optics USB2000 spectrophotometer fitted with a T300 1-cm pathlength transmission dip probe. Standards were prepared from Sodium Nitrate dissolved in 2 M KCl solution. If the absorbance was too high, the samples were diluted with deionized water and re-measured with the spectrophotometer.

### 2.2.4 Dune Grass Production Measurements

In this system, all three dune grass species (the non-native European beachgrass *Ammophila arenaria*, the non-native American beachgrass *Ammophila breviligulata*, and the native American dune grass *Elymus mollis*) overlap in their distribution north of Pacific City, OR, but only *A. arenaria* and *E. mollis* are present to the south (Figure 2.1; Hacker et al. 2012). Moreover, *A. breviligulata* is dominant north of the Columbia River and both species are co-dominant between the Columbia River and Pacific City. The native grass, *E. mollis*, has low abundances across the sites and tends to be more common at the toe and heel of the foredune. For this reason, our dune grass production measurements include a mixture of dune grass species depending on the site, transect location, and profile location.

We surveyed dune grass production metrics at each transect location at the fifteen sites in 2015–2017. Within each transect location, we extended the three transects used for the beach surveys into the foredune (Appendix A Figure A1). At three profile locations along each transect (toe, crest, and heel of the foredune), we counted the number of shoots of each of the three dune grass species (*A. arenaria*, *A. breviligulata*, and *E. mollis*), when present, within 0.25 $m^2$ quadrats. Near each quadrat, we haphazardly collected at least one plant "individual" (defined as the shoot or shoots attached to one rhizome) of each grass species, when present, for a total of at least three plants per species per profile location. In the laboratory, the plants were air-dried and measured for the number of shoots per plant, shoot biomass (g/shoot), and shoot length (cm). For each quadrat, we multiplied shoot density of each species by the average shoot biomass of each species to estimate the biomass of each species per 0.25 $m^2$ quadrat.

### 2.2.5 Statistical Analyses

Data were analyzed using R version 3.5.3 (R Development Core Team 2019). Data were checked visually for normality using residual plots against predicted values, and the data met these assumptions in all cases.

*Spatial and temporal variability in environmental factors*

One-way ANOVAs and Tukey HSD post hoc tests were used to determine how distance to the nearest wrack source habitat (estuary and rocky reef), short-term shoreline change rate, and foredune crest height varied across sites. A two-way ANOVA was used to determine how ocean upwelling varied across sites and years.

*Spatial and temporal variability in marine subsidies and dune grass production*

Two- and three-way ANOVAs were used to test for the differences in macrophyte wrack metrics [wrack patch density (number/m$^2$), wrack patch biomass (g/patch), total wrack biomass (g/transect)], sand nitrate (µmol N/g), and dune grass production metrics [shoot density (number/0.25 m$^2$) and total biomass (g/0.25 m$^2$) for all three dune grass species included and shoot density (number/0.25 m$^2$), total biomass (g/0.25 m$^2$), shoot biomass (g/shoot), and shoot length (cm) for *A. breviligulata* and *A. arenaria* alone] among sites, years, and/or beach and dune profile locations, and their interactions, where applicable. Tukey HSD post hoc tests were conducted on significant factors unless interactions were found, in which case one-way ANOVAs and Tukey HSD post hoc comparisons were conducted between levels of each factor (Underwood 1997).

We also examined the composition of wrack by placing each species into one of nine functional groups: kelp, other brown algae (excluding kelp), green algae, red algae, surfgrass, eelgrass, other estuarine plants (excluding eelgrass), dune vegetation, and freshwater vegetation (Appendix A Table A2). We used PERMANOVA non-multidimensional scaling (Bray-Curtis similarity, RStudio, vegan; Oksanen et al. 2019) to determine how wrack functional group community structure changes across sites and years using the proportion of total wrack biomass per functional group per transect location.

### *Relationships among environmental factors, marine subsidies, and dune grass production*

We used multiple regression analyses (RStudio, car; Fox 2019) to evaluate the relationships between the various environmental factors, marine subsidy variables, and dune grass production metrics. Data were pooled across years and model selection was conducted using AIC. To determine the relative contribution of each individual predictor to the overall association between the outcome and the set of predictors, we calculated partial $R^2$ values, or the variance explained, using the R package 'heplots' and the 'etasq' function (Fox et al. 2018).

We first tested whether three wrack response variables [proportion of wrack, wrack biomass (g/m$^2$), and total wrack biomass (g/transect)], for eelgrass and kelp separately, were correlated with distance to the nearest estuary (eelgrass) or rocky reef (kelp), ocean upwelling, and their interaction. For sand nitrate concentration, we first divided the data by profile location (MHHW, mid-beach, foredune toe, foredune crest, and foredune heel) and combined some profile locations (mid-beach/foredune toe and foredune crest/foredune heel). Depending on the profile location(s) of interest, we tested whether sand nitrate concentration was correlated with multiple environmental factors (ocean upwelling, distance to the Columbia River, short-term shoreline change rate, and foredune crest height) and marine subsidies (total wrack biomass and sand nitrate concentrations at profile locations seaward to the location).

Finally, we tested whether the six response variables for beach grass production [shoot density (number/0.25 $m^2$) and total biomass (g/0.25 $m^2$) for all three dune grass species included, and shoot density (number/0.25 $m^2$), total biomass (g/0.25 $m^2$), shoot biomass (g/shoot), and shoot length (cm) for *A. breviligulata* and *A. arenaria* alone] were correlated with marine subsidies (total wrack biomass and sand nitrate concentrations at profile locations seaward to the location) and a measure of foredune geomorphology (foredune crest height). As with sand nitrate concentration, we divided the dune grass production response variable data by profile location (foredune toe, foredune crest, and foredune heel) and combined some profile locations (mid-beach/foredune toe and foredune crest/foredune heel) in our analyses.

## 2.3 Results

### 2.3.1 Spatial and Temporal Variability in Environmental Factors

We found significant variability in the geographic, oceanographic, and geomorphic factors important to our Pacific Northwest beach and dune sites (Figure 2.1). Distance to the nearest wrack source habitat (estuary and rocky reef), ocean upwelling, short-term shoreline change rate, and foredune crest height all varied across our sites (Figure 2.1, Appendix C Tables C1–C4). The relationships between the distance to the nearest wrack source habitat across sites showed that most northern sites (i.e., GH, LBP, LB, FS, NB) were close to estuaries and far from rocky reefs and some southern sites (i.e., BAN, FL) were close to rocky reefs and far from estuaries (Figure 2.1A, Appendix C Table C1). Some sites (i.e., CL, PC, SB, and NS) were close to both estuaries and rocky reefs.

Ocean upwelling varied across sites and years with no interaction detected (Figure 2.1B, Appendix C Table C2). Upwelling was more intense at southern sites compared to northern sites, and in 2015 compared to 2016 and 2017, which did not differ.

Short-term SCR, taken here as a proxy for sand supply to the beach and foredune, varied across our study region (Figure 2.1C, Appendix C Table C3). Sites in the north had the highest shoreline change rates (i.e., LBP, GH, LB, and FS) compared to all central and some southern sites, where shoreline change rates were neutral or negative. BAN had the only SCR that was positive in the central and southern regions.

Foredune crest height varied across sites (Figure 2.1D, Appendix C Table C4) with the majority of short dunes (i.e., < 10 m LMSL including LBP, GH, LB, and BAN) corresponding to positive SCRs and all the tallest dunes (i.e., > 10 m LMSL including SL, PC, SB, NB, CL, SILT, DO, NS, and UD) corresponding to neutral or negative SCRs. FL was an outlier with both short dunes (~ 7.65 m LMSL) and negative or neutral SCRs.

### 2.3.2 Spatial and Temporal Variability in Marine Subsidies and Dune Grass Production

*Marine subsidies: macrophyte wrack and nutrients*

Wrack patch density (number/m$^2$), wrack patch biomass (g/patch), and total wrack biomass (g/transect) varied among sites, but not years, and there was an interaction for wrack patch density and total wrack biomass (Figure 2.2, Appendix D Table D1). In addition, there was a positive correlation between total wrack biomass and beach width (as measured using beach transect length) (Appendix D Figure D1). With the exception of CL, wrack patch density was highest in the north (Figure 2.2A), where the patches were intermediate in biomass (Figure 2.2B). The total overall wrack biomass per transect was high (Figure 2.2C), likely in part, because northern beaches were wider (Appendix A Table A1) and thus accumulated a greater total amount of macrophyte wrack (Figure 2.2C, Appendix D Figure D1). In the south, though wrack patch density was low, and biomass per patch was high, beaches were narrower resulting in intermediate total wrack biomass per transect compared to the other sites. In the central region, wrack patch density and patch biomass were both low, and beaches were narrow to intermediate in width, resulting in lower total biomass compared to the northern and southern beaches.

Wrack functional group composition, measured as the proportion of total biomass, varied among sites but not years (Figure 2.3, Appendix D Table D2). Generally, there were higher proportions of eelgrass and kelp at the northern sites and southern sites, respectively. For example, the proportion of eelgrass was highest at GH and CL and lowest at FL (Figure 2.3). The proportion of kelp was highest at BAN and FL and lowest at PC. Following eelgrass and kelp wrack, other brown algae besides kelp, surfgrasses, and dune vegetation were in the highest proportions across the study region. Red algae, green algae, other estuarine plants besides eelgrass, and freshwater vegetation were present at most sites in low quantities.

Nitrate concentration in the sand varied across sites, years, and profile locations, and there was a site x year x profile location interaction (Figure 2.4, Appendix D Table D3). To explore these patterns in more detail, we used two-way ANOVAs to test for the differences in sand nitrate concentration among sites and years at the MHHW mark, mid-beach/toe combined, foredune crest, and foredune heel. Sand nitrate concentration varied among years, sites, and there was a site x year interaction, at the MHHW mark and mid-beach/toe profile locations (Appendix D Table D4). Sand nitrate concentrations at the foredune crest and heel locations varied among sites but not years. Post hoc tests showed that, with the exception of FS, sand nitrate concentrations at the MHHW mark and the mid-beach/toe profile locations of the study sites either did not differ among years or were highest in 2015 and lowest in 2016 or 2017. In addition, sand nitrate concentration at MHHW and mid-beach/toe profile locations was generally highest at FS, FL, DO, and GH and lowest at NB, UD, and SL, depending on the year. The sand nitrate concentration on the crest showed no significant site variability using the post hoc tests but the heel concentrations were highest at SB and SILT and lowest at FL.

### *Dune grass production*

The patterns of production for all dune grass species showed that shoot density (number/0.25 $m^2$) and total biomass (g/0.25 $m^2$) varied across sites and profile locations, and there were interactions between site and profile location (Figures 2.5 and 2.6, Appendix E Table E1). These grass production variables either did not vary by year or did so weakly. Post hoc tests show that, for most sites, there was a general pattern that shoot density and total biomass was greatest at the foredune toe and crest, and lower at the foredune heel (Appendix E Table E1). Moreover, shoot density and total biomass at the foredune toe were generally higher at the northern sites (i.e., GH, LBP, LB, FS, NB, and CL) and lower in the central and southern sites (e.g., PC, SL, SB, SILT, DO, UD, NS, BAN, and FL) (Appendix E Table E1). The opposite was true for the foredune crest and heel locations; here shoot density and total biomass tended to be greater at the central and southern sites and lower at the northern sites, although the pattern was not absolute.

The patterns of production for the two *Ammophila* congeners showed similar patterns to those when the native *E. mollis* was present (Appendix E Figures E1–E2, Table E2). For example, the shoot density (number/0.25 m$^2$) and total biomass (g/0.25 m$^2$) of the two species varied across sites and profile locations, but not years, and there were interactions between site and profile location (Appendix E Table E2A, B). Post hoc tests show that for most sites there was a general pattern for shoot density and total biomass to be greater at the foredune toe and crest and lower at the foredune heel (Appendix E Table E2A, B). Shoot density and total biomass at the foredune toe were generally higher at the northern sites (i.e., GH, LBP, LB, FS, NB, and CL) and lower at the central and southern sites (e.g., PC, SL, SB, SILT, DO, UD, NS, BAN, and FL) and the opposite was true for the foredune crest and heel locations.

Finally, shoot biomass (g/shoot) and shoot length of the two *Ammophila* species differed across sites and profile locations, and there were interactions between site and profile location (Appendix E Figures E3–E4, Table E2C, D). The shoots at the foredune crest and heel were heavier and taller than those at the toe of the dune

(Appendix Table E2C, D). In addition, sites in the north tended to have heavier and taller shoots than those in the central and southern regions.

### 2.3.3 Relationships among Environmental Factors, Marine Subsidies, and Dune Grass Production

*Factors important to marine subsidies: macrophyte wrack and nutrients*

Our analyses showed that the patterns of macrophyte wrack distribution and abundance were correlated with distance to the source habitat (either rocky reefs for kelp or estuaries for eelgrass) and ocean upwelling (Appendix F Table F1, Figure F1). For kelp wrack, the proportion, wrack biomass (g/m$^2$), and total wrack biomass (g/transect) were higher on beaches near rocky reefs that had more intense ocean upwelling conditions (Appendix F Table F1). Moreover, for eelgrass wrack, the proportion, wrack biomass, and total wrack biomass increased on beaches close to estuaries that experienced less intense ocean upwelling conditions.

We found that sand nitrate concentrations at the MHHW mark on our beach sites was positively correlated with ocean upwelling and negatively correlated with distance to the Columbia River (Appendix F Table F2). The sand nitrate concentration from the mid-beach to the toe of the foredune was correlated with the distance to the Columbia River, MHHW sand nitrate, total wrack biomass, and short-term shoreline change rate, with MHHW sand nitrate concentration and distance to the Columbia River, explaining the most variability (13.6% and 5%, respectively) (Appendix F Table F3). Finally, the sand nitrate concentrations at the foredune crest and foredune heel were correlated with increased sand nutrients immediately seaward to the profile location of interest and foredune crest elevation (Appendix F Table F4).

For example, the foredune crest nitrate concentration was positively correlated with the mid-beach/toe sand nitrate concentration and the foredune heel nitrate concentration was positively correlated with the foredune crest nitrate concentration. Taller foredunes were positively correlated with greater crest nitrate concentrations and suggestively correlated with greater heel nitrate concentrations.

### *Factors important to dune grass production*

Dune grass production metrics (i.e., shoot density and total biomass) were correlated with measures of marine subsidies (i.e., wrack abundance and sand nitrate concentration) and foredune geomorphology (i.e., foredune crest height) but the relative importance of these factors depended on foredune profile location. For example, shoot density and total biomass of dune grasses at the foredune toe were positively correlated with beach-related marine subsidies, including total wrack biomass and sand nitrate concentration at the mid-beach and toe (Appendix F Tables F5). This was the case whether we analyzed the data including all dune grass species together (Appendix F Table F5A, B) or just the two *Ammophila* congeners alone (Appendix F Table F5C, D). In addition, shoot density and total biomass of dune grasses at the foredune crest were correlated with dune-related processes, including nitrate concentration of sand at the crest of the dune and the foredune crest height (Appendix F Table F6). Taller foredunes, and those with higher crest nitrate concentrations, had higher shoot densities and greater total biomass. Finally, shoot density and total biomass of dune grasses at the foredune heel were not related to the sand nitrate concentrations at the crest/heel or foredune crest height (Appendix F

Table F7). However, total grass biomass was positively correlated with taller foredunes.

We also found correlations between the shoot characteristics of the two *Ammophila* species and measures of marine subsidies (i.e., wrack abundance and sand nitrate concentration) and foredune crest height. At the foredune toe, shoot biomass and shoot length were positively correlated with the nitrate concentrations on the mid-beach and toe of the foredune but not with total wrack biomass (Appendix F Table F8). At the foredune crest, shoot biomass was not related to crest nitrate concentration or foredune crest height, and shoot length was positively correlated with foredune crest height (Appendix F Table F9). Finally, at the foredune heel, shoot biomass was not related to the sand nitrate concentration at the heel or foredune crest height and shoot length was positively correlated with both heel sand nitrate concentration and foredune crest height (Appendix F Table F10).

## 2.4 Discussion

In this study, we surveyed sandy beaches and dunes along the U.S. Pacific Northwest coast to evaluate the role of marine derived nutrients to dune ecosystem functions by (1) assessing the patterns of oceanographic and geological factors, marine subsidies, and dune grass production, and (2) evaluating the mechanisms contributing to these patterns. We provide strong evidence that marine subsidies are common and predictable sources of nutrients to Pacific Northwest beaches and that they influence dune grass ecosystems in significant ways. Our findings provide support for the connectedness among marine subsidies, sandy beaches, and coastal dunes documented in previous studies (e.g., seawater to grass/dunes: Greaver and

Sternberg 2006; wrack to sand: Koop et al. 1982, Griffiths et al. 1983, Barreiro et al. 2013, Dugan et al. 2011, Rodil et al. 2019; wrack to grass/dunes: Cardona and Garcia 2008, Del Vecchio et al. 2013, Del Vecchio et al. 2017, van Egmond et al. 2019) and suggest that meta-ecosystem scale marine subsidy dynamics are important to dune ecosystem function.

In particular, we found relationships between marine subsidies and dune grass production across large spatial scales and over time. We found that macrophyte wrack and sand nitrate concentrations, which are positively related to ocean upwelling and sand supply, were important determinants of dune grass production across sites and foredune profile locations. Beaches with more macrophyte wrack and greater sand supply had greater shoot density and biomass of dune grasses, especially at the toe of the dune, where sand nitrate concentrations were high compared to other locations along the beach to dune profile. Our results suggest that marine subsidies and sand supply, two factors that connect ocean productivity to dune plant productivity, are important in shaping local dune communities across the Pacific Northwest.

Below we describe in greater detail the patterns and drivers of marine subsidies, and their effects on the nutrient dynamics and dune grass production in this coastal dune meta-ecosystem. In addition, we discuss the potential consequences of changes in marine subsidies to coastal foredunes and their important ecosystem services along the U.S. Pacific Northwest Coast.

### 2.4.1 Importance of oceanographic, geographic, and geomorphic factors to marine subsidies on coastal beaches and dunes

Our results show that a combination of oceanographic, geographic, and geomorphic factors at meta-ecosystem scales are important to the delivery of marine nutrients to the beaches and foredunes of our study sites. Marine subsidies, ultimately measured as the nitrate concentration in beach sand, have the potential to come from two basic sources in this system: macrophyte wrack and seawater. Our data suggest that both sources of marine subsidies are important determinates of nutrient dynamics on the beaches, and ultimately foredunes, of our study sites.

The first source of marine subsidies, macrophyte wrack, showed a distribution and abundance pattern similar to that observed by Reimer et al. (2018) who surveyed many of the same sites along the Pacific Northwest coast. There was a strong latitudinal pattern in macrophyte wrack deposition abundance and species composition (Figures 2.2, 2.3, Appendix D Table D1, D2) that was correlated with proximity of the beaches to wrack source habitat (estuaries for eelgrass wrack and rocky reefs for kelp wrack) and ocean upwelling (Appendix F Table F1). At northern beach sites, where there are more estuaries and ocean upwelling is weaker and more intermittent (Figure 2.1, Appendix C Tables C1, 2), we found wrack patches were numerous and intermediate in size, and primarily composed of eelgrass (Figures 2.2, 2.3). At southern sites, where there are more rocky reefs and ocean upwelling is stronger (Figure 2.1, Appendix C Tables C1, 2), we found wrack patches were sparse and large in size, and primarily composed of kelp (Figures 2.2, 2.3). At central sites, which are exposed to both estuaries and rocky reefs and where ocean upwelling is intermediate in strength (Figure 2.1, Appendix C Tables C1, 2), we found wrack patches were sparse and small in size, and composed of multiple macrophyte species (Figures 2.2, 2.3).

Interestingly, the relative differences we see in wrack deposition patterns across our study sites were remarkably similar through time, suggesting predictability in the factors important to these patterns. The strong influence of proximity to macrophyte wrack source and ocean upwelling to the patterns of wrack deposition we document here, and in a previous study (Reimer et al. 2018), are a consequence of ocean upwelling and its indirect effects on estuarine outwelling. It is well-documented that ocean upwelling has differential consequences for aquatic primary producers in the Pacific Northwest; eelgrass is more productive in northern estuaries, where they are exposed to less persistent upwelling, whereas macroalgae are more productive in southern regions, where upwelling is stronger and more persistent (e.g., Fenberg et al. 2015, Menge et al. 2015, Reddin et al. 2015, Hacker et al. 2019, Hayduk et al. 2019). Thus, estuarine outwelling is an important process contributing to the substantial eelgrass wrack produced and deposited on beaches located near large estuaries in the north. For example, one site, Cape Lookout (CL), OR, had unusually high wrack patch densities compared to all the other sites, especially in 2015, when upwelling intensity was nearly double that of the subsequent two years. This site is close to Netarts Bay, a highly marine-dominated estuary that is known to have high eelgrass production (Hessing-Lewis and Hacker 2013). Likewise, ocean upwelling strength is an important factor contributing to the production of macroalgae and the large patches of kelp wrack deposited in beaches to the south. There, rocky reefs are more common and kelp and other brown macroalgae thrive.

Other factors could be important to the wrack deposition patterns we document here. Wave action and macrophyte dislodgement associated with extreme weather and climate may generate more macrophyte wrack on beaches such as we saw at Cape Lookout (CL) in 2015. For example, in U.S. Pacific Northwest, climate cycles such as El Niño significantly intensify wave conditions (Kaminsky et al. 1998, Barnard et al. 2015, 2017), which could dislodge more macrophytes and result in higher wrack deposition on nearby beaches. In addition, beach morphology has been correlated with wrack deposition patterns (Barreiro et al. 2011, Reimer et al. 2018). Wider, more gently sloping beaches have greater potential for wrack accumulation than narrow, steep beaches.

Once wrack is deposited on the beach, it undergoes fragmentation and decomposition, eventually coating grains of sand with inorganic nitrogen and nitrogen-rich organic matter (e.g, Dugan et al 2011). We found that sand nitrate concentrations at our beach sites were positively correlated with the patterns of wrack deposition we documented at the meta-ecosystem scale (Figure 2.4, Appendix F Table F3). For example, sand nitrate concentration was greatest at both the northern and southern sites (Figure 2.4, Appendix D Table D3, D4), where eelgrass and kelp wrack biomass are also high. We also found that, predictably, sand nitrate concentration was highest at the upper end of the beach (mid-beach/foredune toe profile location, Appendix D Table D4), where macrophyte wrack and sand eventually accumulate as a consequence of wave action and aeolian processes. At these locations, macrophyte wrack fragments and decomposes, coating grains of sand that are transported up the beach to the foredune, where they are eventually captured by dune grasses. This relationship between nitrate concentration and wrack abundance and distribution is similar to that observed by Dugan et al. (2011), who found that sand nitrogen concentration was highest at the high tide line of beaches, where wrack accumulates.

The second source of marine subsidies, seawater, was also consistent with the nitrate concentrations on the beaches in this meta-ecosystem. We found that sand nitrate concentration on the upper beach was positively correlated with sand nitrate concentration on the lower beach, specifically at the mean higher high water (MHHW) mark (Appendix F Table F3). The MHHW mark experiences daily tides that wash over the beach, coating sand grains with nutrient-laden seawater. Some beach sites, both in the north and south coast, had high MHHW sand nitrate concentrations (Figure 2.4, Appendix D Table D4), which were, in turn, positively related to increasing ocean upwelling intensity and negatively related to proximity to the Columbia River plume (i.e., as distance from the Columbia River plume increased, MHHW sand nitrate concentration decreased; Appendix F Table F2). The Columbia River itself provides very little nitrate to coastal waters but, under tidal mixing with nutrient-rich subsurface coastal waters, the Columbia River produces a plume of nitrate-rich seawater that extends over a ~17 km alongshore distance from the north and south sides of the river mouth (Lohan and Bruland 2006, Bruland et al. 2008). One site near the Columbia River, Fort Stevens, had elevated sand nitrate concentrations across the beach despite low total wrack biomass (Figure 2.4, Appendix D Table D4), thus obscuring the relationship between macrophyte wrack and sand nitrate that was observed at the other beach sites. Taken together, these results suggest that beside differences in wrack accumulation on beaches, seawater itself contributes significantly to the input of marine subsidies to beaches.

Finally, upper beach sand nitrate concentrations were positively related to SCR, a measure of sand supply to the beach, and foredune height (Appendix F Table F3). Previous work in this system shows that SCRs shape the local geomorphology of beaches and dunes, with positive SCRs producing wider beaches and shorter and wider foredunes, and neutral or slightly negative SCRs producing shorter beaches and taller and narrower foredunes (e.g., Hacker et al. 2012, Komar et al. 2012, Ruggiero et al. 2013, Biel et al. 2019, Ruggiero et al. 2019). For a couple of reasons, SCR is likely an important mitigating factor to the marine subsidy differences among beach sites shown here. First, wider beaches tend to have greater total wrack biomass (Appendix D Figure D1) and greater intertidal area over which tides will deliver seawater. Second, wider beaches have more sand, which may eventually be transported to the back beach and foredune, producing higher nitrate concentrations as a result.

Marine subsidies across the beach sites were largely defined by how large-scale regional processes such as wrack delivery, ocean upwelling, and SCRs were manifested at local scales. On the foredune itself, sand nitrate concentrations were positively correlated with sand nitrate concentrations immediately seaward to the profile location of interest and the geomorphology of the dune (Appendix F Table F4). For example, elevated mid-beach/toe sand nitrate concentrations and taller foredunes were positively correlated with foredune crest sand nitrate concentration. The relationship between sand nitrate concentration and foredune elevation across the study region is likely related to the beach-dune sediment dynamics associated with SCR and foredune geomorphology (Psuty 1988). At almost neutral SCRs, sand accumulates on the foredune crest, resulting in taller and narrower foredunes. These taller dunes could be intercepting nutrient-coated sand at the dune crest and blocking it from reaching the foredune heel.

Finally, our sand nitrate concentrations were high relative to other systems. For example, in a study from Glacier Bay, Alaska, soil nitrate concentrations had values as high as 0.81 μmol N/g soil (Hobbie et al. 1998), a roughly 100-fold decrease in N relative to some of our mid-beach and toe sand nitrate values. Similarly, in a beech forest in Germany, soil nitrate concentrations in unamended soil had a maximum value of 0.06 μmol N/g soil (Limmer and Drake 1998). Our findings also suggest that the nutrient loads of Pacific Northwest beaches, though highly variable in space and time, are high relative to other dune systems. For example, Cain et al. (1999) show that, across coastal dunes of all ages, soil nitrogen concentrations are low and highly variable.

### 2.4.2 Importance of marine subsidies to dune grass production

Our analyses show that most dune grass production metrics were positively correlated to marine subsidies, but the relationships depended on foredune profile locations and sites (Appendix F Table F5–F7). For example, at the foredune toe, dune grass density and total biomass were positively related to sand nitrates present on the beach and dune toe, and some were positively and directly associated with total wrack biomass as well (Appendix F Table F5). In particular, many sites in the northern regions of the coast (i.e., Grays Harbor, Leadbetter Point, Long Beach, Fort Stevens, and Nehalem Bay), where macrophyte wrack biomass and sand nitrates were high (Figures 2.2, 2.4), had greater dune grass shoot density and total biomass at the toe of the dune compared to the crest or heel profile locations (Figures 2.5, 2.6, Appendix E Figures E1, E2). These northern sites generally have wider and gently sloping beaches and short and wide foredunes, a result of decades of sand deposition as indicated by positive SCRs measured at these sites (Figure 2.1; Kamisky et al. 2010, Hacker et al. 2012, Ruggiero et al. 2013, 2018, Biel et al. 2019). In addition, these sites are dominated or co-dominated by *Ammophila breviligulata*, a species with fewer, but more robust, shoots per plant compared to *A. arenaria* (Hacker et al. 2012, 2019). *Ammophila breviligulata* also tends to produce more lateral rather than vertical rhizomes (underground stems), which results in better horizontal growth and sand capture, especially at the leading edge of the foredune toe (Hacker et al. 2012, Biel et al. 2019). Thus, at sites in the north, where sand deposition and toe nitrate concentrations are high, it makes sense that dune grass density and total biomass are higher as well, especially compared to the foredune crest and heel at the same sites.

Similar to the foredune toe profile location, dune grass production metrics at the foredune crest were positively related to nutrients and sand deposition; shoot density and total biomass both increased with crest sand nitrate concentration and dune crest height (Appendix F Table F6). Our analyses showed that crest shoot densities and total biomass were highest at most of the central coast sites (i.e., Cape Lookout, Sand Lake, Pacific City, South Beach, Siltcoos, Dunes Overlook, Umpqua Dunes, and North Spit; Figures 2.5, 2.6, Appendix E Figures E1, E2), where dunes were tall and crest sand nitrate concentrations were high (Figures 2.1, 2.4). These central sites are characterized by relatively taller but narrower foredunes, a result of sand deposition concentrated at the foredune crest, a pattern that tends to be produced when SCRs are neutral or slightly negative (Figure 2.1; Psuty 1988, Hacker et al. 2012, Biel et al. 2019). These sites are also dominated by *Ammophila arenaria*, which produces more shoots and vertical rhizomes per plant, resulting in better vertical growth and sand capture particularly at the crest of the foredune (Hacker et al. 2012, 2019, Biel et al. 2019). Thus, at most sites in the central region, where sand deposition and nitrate concentrations at the foredune crest are high, dune grass density and total biomass are high as well, especially compared to the foredune toe and heel at the same sites.

Finally, at the foredune heel, where dune grass shoot densities and total biomass were lowest (Figures 2.5, 2.6, Appendix E Figures E1, E2), we found that sand nitrate concentrations, either at the heel itself or at other foredune profile locations, were not correlated with dune grass production (Appendix F Table F7). From a nutrient delivery perspective, our data suggest that sand nitrate concentration at the foredune heel is positively correlated with nitrate concentrations at profile locations seaward to the heel. Thus, even though sand nitrate from the beach appears to be delivered to the foredune heel, the variability in the amount or flux of marine nutrients appears to have little effect on heel dune grass production differences among sites. It may be that the grasses in the back dune are nutrient limited, a possibility supported by the fact that they have the lowest shoot density and biomass of all the profile locations.

In fact, a nutrient addition experiment conducted in this system showed that dune grass production metrics varied along the foredune profile and among sites (Chapter 4). For example, dune grass shoot density and total biomass responded most strongly to nutrient additions at the foredune crest and heel and much less so at the foredune toe. In addition, nutrient additions at sites across the region revealed that sites with less macrophyte wrack and lower sand nitrate concentrations had a more elevated response to nitrate additions than sites with greater access to marine subsidies. The difference in nutrient availability suggests that dune grass access to marine nutrients may vary. These results were further explored in Chapter 3 using nitrogen stable isotope analysis, a measure of the uptake of nitrogen sources. This study showed that dune grasses are using marine nitrogen, especially at the foredune toe, where we measured the highest sand nitrate concentrations. Plant nitrogen isotope signatures decreased precipitously over the foredune profile as the distance from the beach and marine nutrient subsidy increased. Together, these findings suggest that dune grass production is the result of marine nutrient availability and benefits from nutrient inputs.

### 2.4.3 Implications of marine subsidies for dune grass production, dune geomorphology, and dune ecosystem services

The Pacific Northwest coast has extensive dune habitat (nearly 45% of the coast), is exposed to one of the most extreme wave climates in the world, and experiences high, upwelling-driven, ocean productivity (Allan and Komar 2006, Seymour 2011, Menge et al. 2015, Wang et al. 2015). Given the strong connections between ocean upwelling, marine wrack subsidies, sediment supply, and dune grass production, it is important to consider how changes in those factors could affect dune geomorphology and coastal vulnerability in this region.

Within the California Current System of the Pacific Northwest coast, ocean upwelling is expected to increase, bringing nutrient rich and high pCO2 seawater to coastal and estuarine systems and fueling macrophyte productivity (Checkley and Barth 2009, Chavez et al. 2011, Doney et al. 2012, Chan et al. 2017). Such predicted shifts in ocean productivity are likely to influence the physiology and ecology of macrophytes. For example, nutrient enrichment and elevated pCO2 have variable but often positive effects on kelps (Harley et al. 2012) and seagrasses (Hurd et al. 2009, Koch et al. 2013), though expected outcomes are sensitive to species and regionally specific factors (Harley et al. 2012). These changes in ocean productivity could result in more marine subsidies to beaches and dunes, which in turn could increase the shoot density and biomass of dune grasses and their ability to capture sand and build taller and wider dunes (Zarnetske et al. 2012, Biel et al. 2019).

As physical barriers from extreme storms and sea level rise, densely vegetated and tall and wide foredunes play a key role in coastal protection and other ecosystem services such as recreation, carbon sequestration, and biodiversity conservation (Barbier et al. 2011). Along the U.S. Pacific Northwest, these services are particularly relevant given the expected increase in intense wave events (Seymour 2011, Allan and Komar 2006, Ruggiero 2013) and sea level rise, both of which could increase beach and dune erosion (Holgate and Woodworth 2004, Ruggiero et al. 2010, Ruggiero 2013) and coastal community vulnerability.

We found that coastal dunes are shaped by patterns and processes interacting over multiple temporal and spatial scales. By reconciling the relationships between within-ecosystem ecosystem functions and across-ecosystem spatial dynamics, the meta-ecosystem approach provides an ideal framework for understanding dune ecosystems and the role of marine subsidies to dune grass production. Armed with the knowledge from this study and others, our improved understanding can be used to inform predictive models. For example, using statistical (e.g., Biel et al. 2019) and process-based (e.g., Cohn et al. 2019) models, one could predict changes in dune geomorphology under variable beach nutrient and dune grass production regimes. As the study of our coastal environments becomes more complex, and the issues more demanding, it is important that we continue to explore the processes and functional relationships between beaches and dunes and the nearshore environment across larger spatial and temporal scales. With this approach, we can improve our understanding of how coastal dune functions might change under varying climate scenarios so that we may consider effective strategies that maintain ecosystem integrity and enhance coastal protection management into the future.

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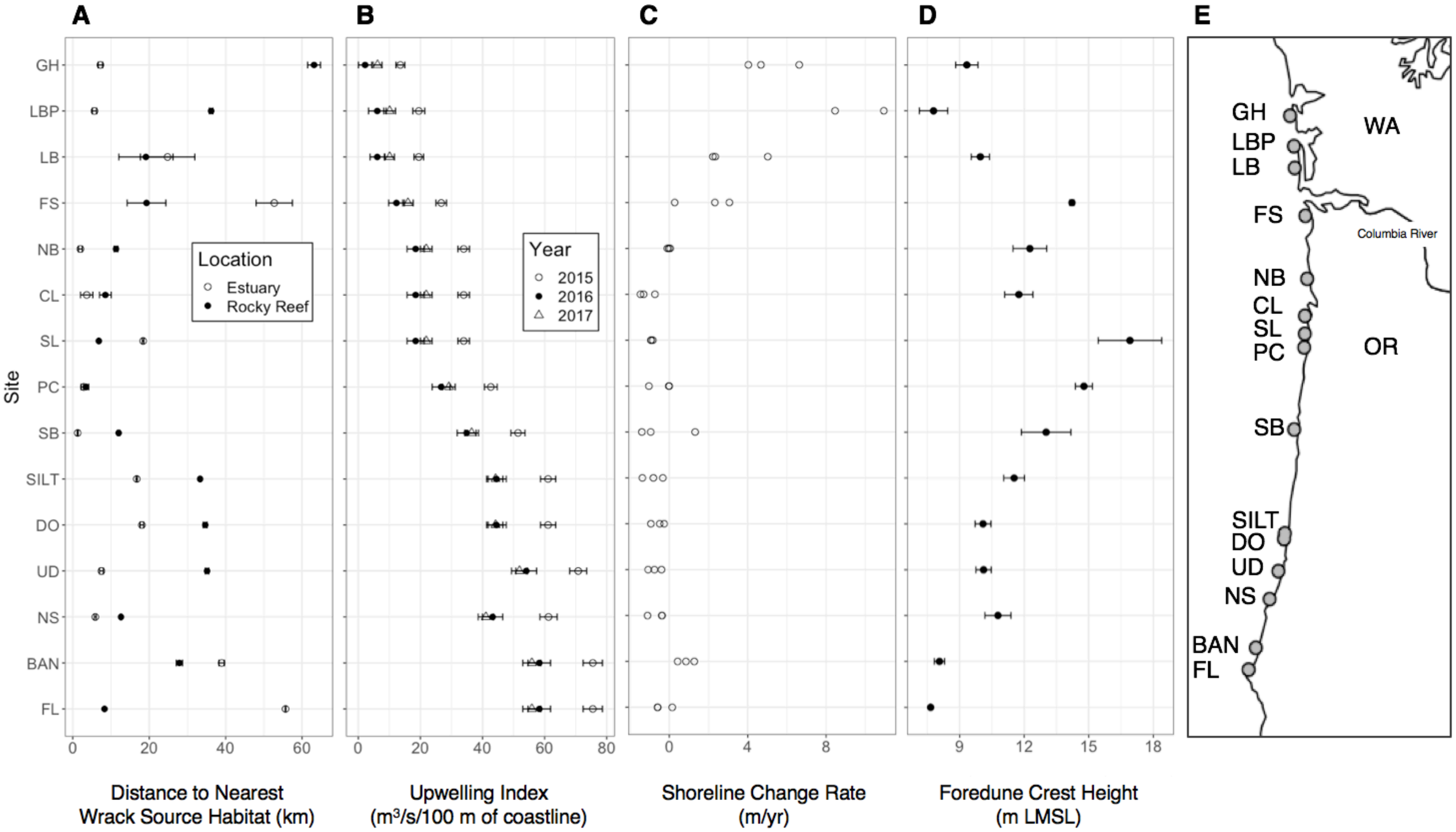

**Figure 2.1.** Mean (± SE) (A) distance to nearest wrack source habitat (estuary and rocky reef; km), (B) ocean upwelling (Bakun upwelling index; $m^3/s/100$ m of coastline) for 2015-2017, (C) short-term shoreline change rate (m/yr) across transects, and (D) foredune crest height (m above local mean sea level, LMSL) across (E) sites (listed north to south) along the US Pacific Northwest coast. See Appendix A Table A1 for site abbreviations and locations.

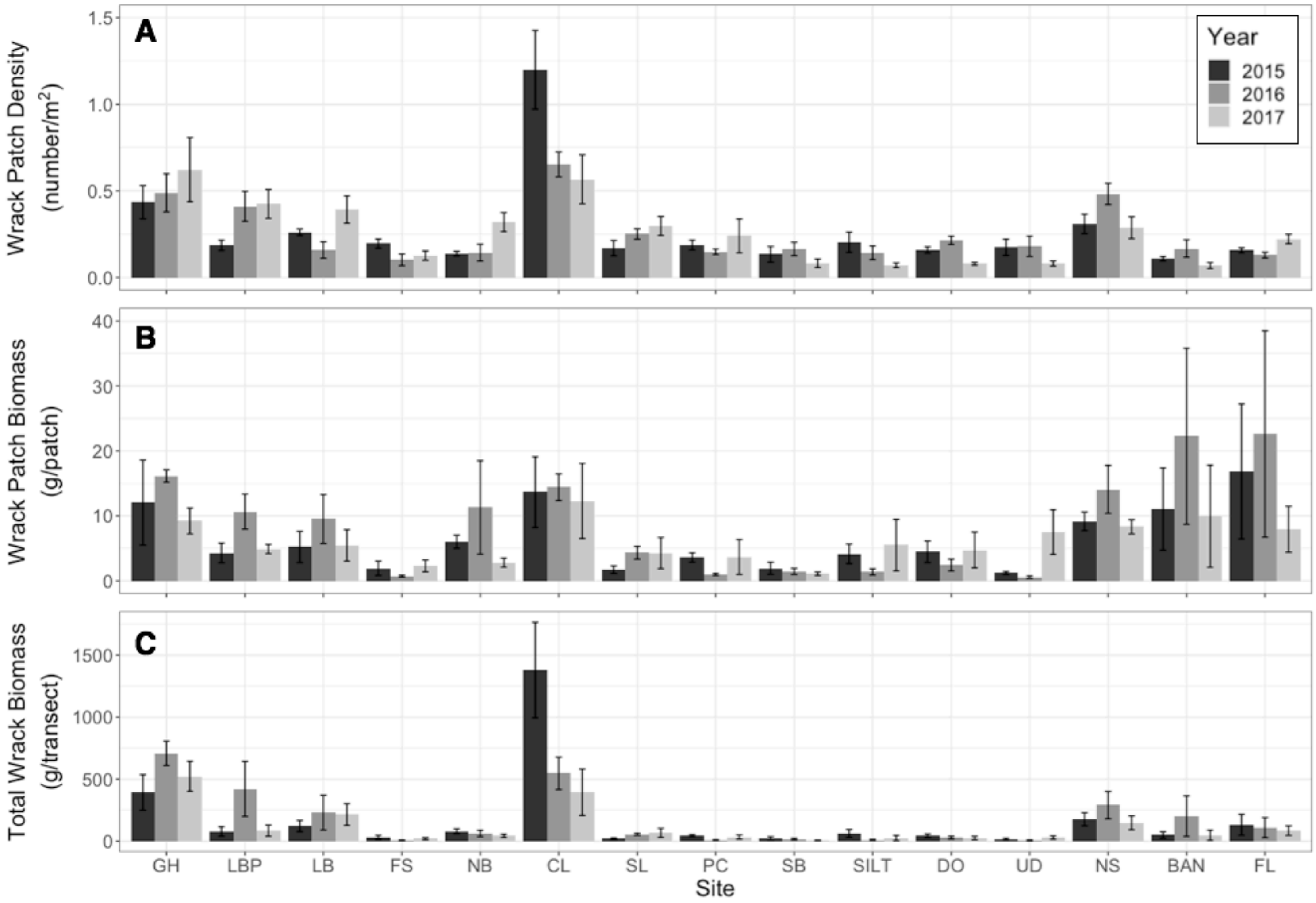

**Figure 2.2.** Mean (± SE) macrophyte (A) wrack patch density (number/m$^2$), (B) wrack patch biomass (g/patch), and (C) total wrack biomass (g/transect) across sites (listed north to south; Figure 2.1) and years (2015-2017). See Figure 2.1, Appendix A Table A1 for site abbreviations and locations (listed north to south).

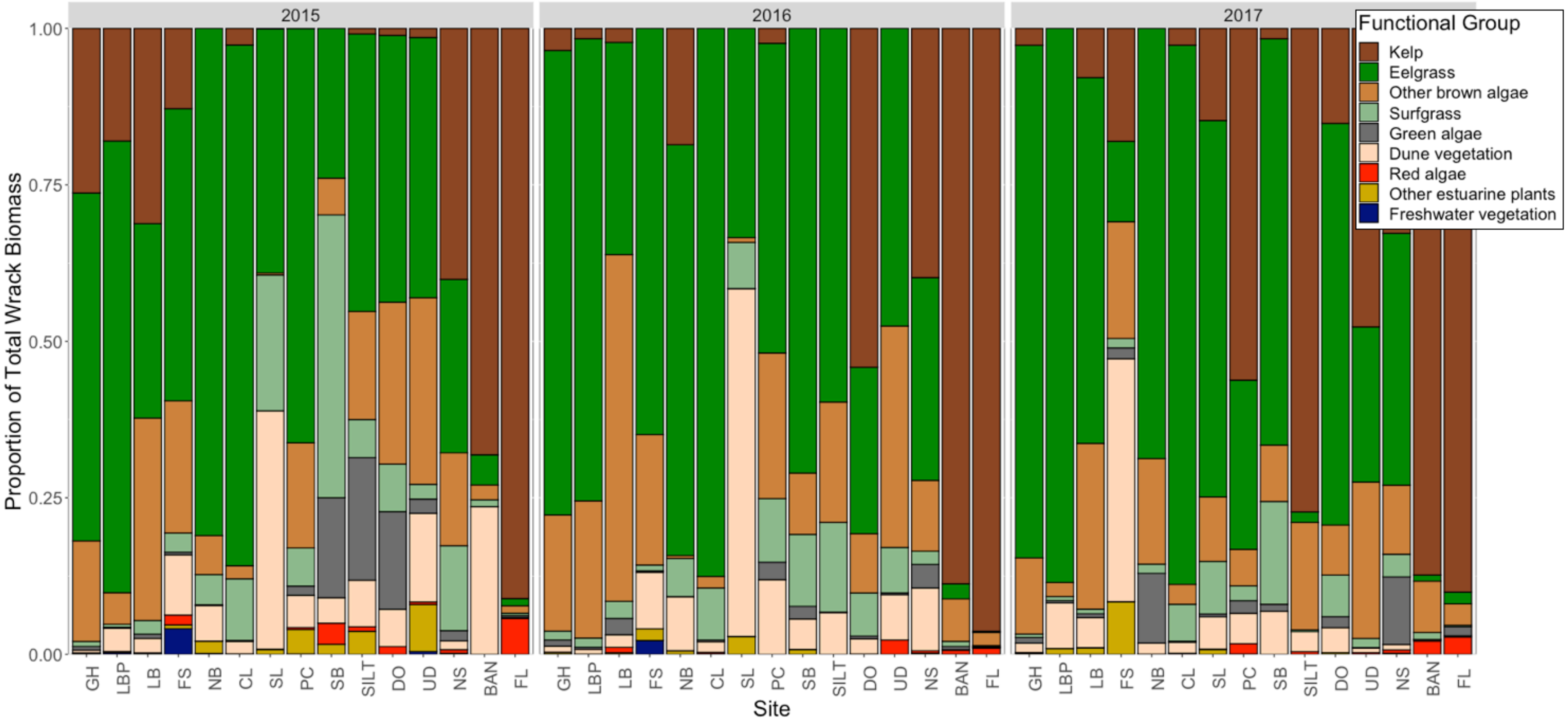

**Figure 2.3.** Proportional biomass of macrophyte wrack functional groups across sites (listed north to south; Figure 2.1) and years (2015-2017). Proportions were calculated from the total biomass of each functional group found in the wrack samples collected at each site. Species within each functional group are listed in Appendix A Table A2. See Figure 2.1, Appendix A Table A1 for site abbreviations and locations (listed north to south).

**Figure 2.4.** Mean (± SE) sand nitrate concentration (µmol N/g sand) across sites (listed north to south; Figure 2.1) and years (2015–2017). Profile locations are listed landward across the beach [mean higher high water (MHHW) and mid-beach] and foredune (toe, crest, and heel). See Figure 2.1, Appendix A Table A1 for site abbreviations and locations (listed north to south).

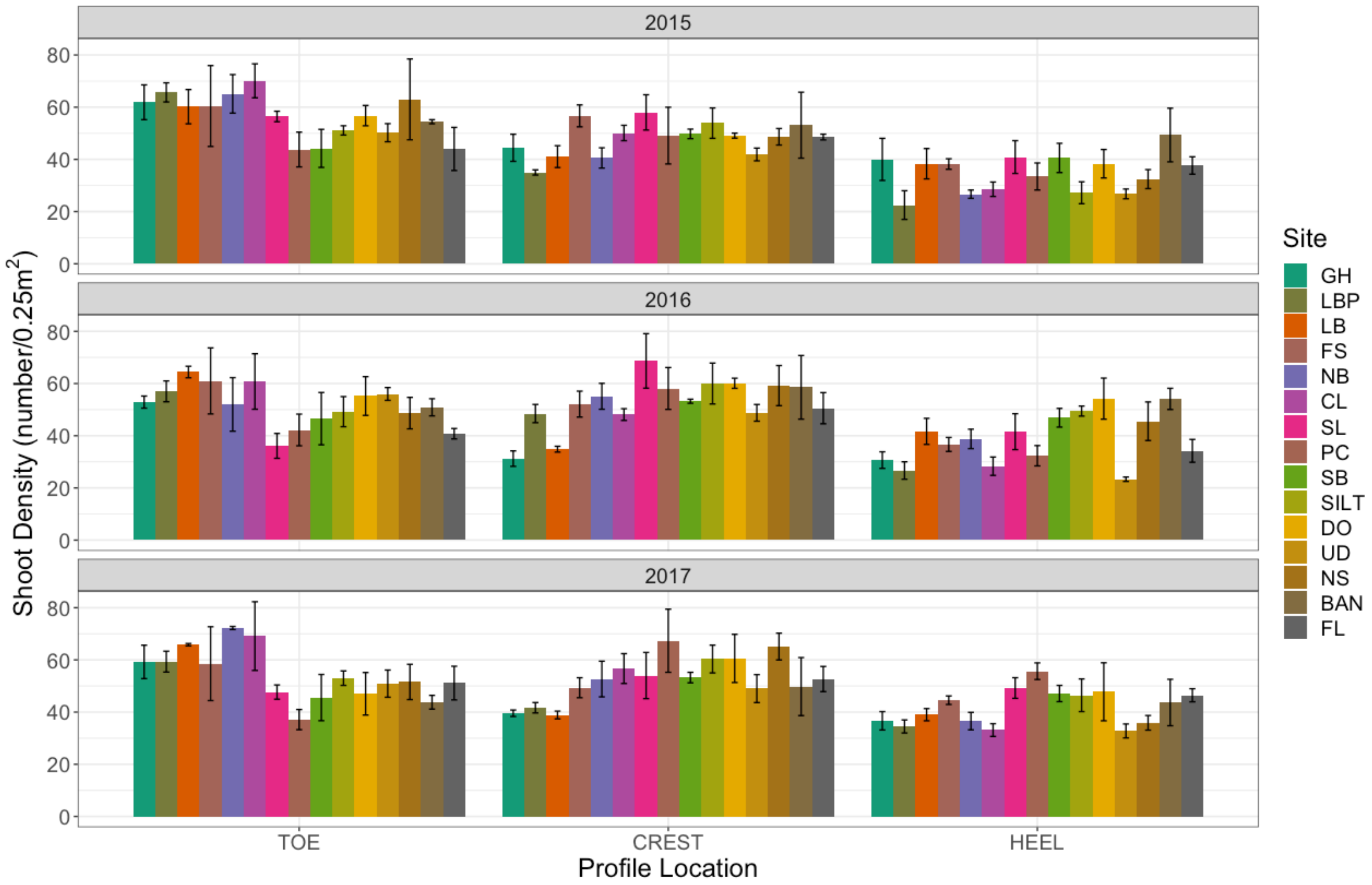

**Figure 2.5.** Mean (± SE) shoot density (number/0.25 $m^2$) for all grass species (*A. arenaria*, *A. breviligulata*, and *E. mollis*) across sites (listed north to south; Figure 2.1) and years (2015–2017). Profile locations are listed landward across the foredune (toe, crest, and heel). See Figure 2.1, Appendix A Table A1 for site abbreviations and locations (listed north to south).

**Figure 2.6.** Mean (± SE) total biomass (g/0.25 m$^2$) for all grass species (*A. arenaria*, *A. breviligulata*, and *E. mollis*) across sites (listed north to south; Figure 2.1) and years (2015–2017). Profile locations are listed landward across the foredune (toe, crest, and heel). See Figure 2.1, Appendix A Table A1 for site abbreviations and locations (listed north to south)

# Chapter 3 – Do dune plants use marine nutrients? Evidence from local to regional spatial scales across the US Pacific Northwest coast

Vanessa Constant, Francis Chan, Patricia Gonzalez Cruz, and Sally D. Hacker

## Abstract

Plants play an important role in dune geomorphology, but the factors important to plant growth, and thus sand deposition and dune building, are understudied. Dune ecosystems have historically been considered nutrient poor, in part, because of the lack of soil formation on actively building dunes and the leaching of nutrients given the high porosity of sand. Taken together, these environmental constraints on nutrient resources suggest a system that is likely reliant on marine nutrient sources. Here we ask whether dune plant nitrogen composition (%N) and source ($\delta^{15}N$) are reflective of the patterns of marine subsidies and coastal beaches and dune morphology across a 550 km of the U.S. Pacific Northwest coast. In particular, we asked 1) Does the composition (%N) and source ($\delta^{15}N$) of nitrogen in four dune plant species (two non-native invasive beachgrass species *Ammophila arenaria* and *A. breviligulata*, the native dune grass, *Elymus mollis,* and the native shrub *Cakile edentula*) vary across sites (coast-scale) and foredune profile locations (dune-scale)? And 2) Does the nitrogen composition (%N) and source ($\delta^{15}N$) of beachgrasses correlate with measures of marine subsidies (macrophyte wrack and sand nitrates) and/or beach and dune morphology (beach width and foredune crest height) on coastal foredunes? We hypothesized that the composition and source of nitrogen will vary across species, sites, and profile locations. Plants will have higher foliar %N and enriched $\delta^{15}N$ signatures at sites with greater macrophyte wrack and at profile locations closest to these sources on the beach (foredune toe). We also predict that plants at sites with wider beaches will have lower $\delta^{15}N$ content at the foredune toe and plants at sites with

taller foredunes will have lower $\delta^{15}N$ content at the foredune crest and heel. We found that marine nutrients are an important source of nitrogen for dune plants in the U.S. Pacific Northwest, and that the composition and source of nitrogen in plants varies among species, sites, and foredune profile locations. At the foredune toe, the %N and $\delta^{15}N$ composition was highest for *Cakile edentula* and lowest for *Elymus mollis*, *Ammophila breviligulata*, and *A. arenaria,* which did not differ. At the foredune crest and heel profile locations, there were no differences in %N composition for the three dune grass species and the $\delta^{15}N$ signature was lower there compared to the foredune toe. Across sites, there were some differences in %N and $\delta^{15}N$ composition of the beachgrasses but these were restricted to a few sites. Our regression analyses showed that, for the most part, macrophyte wrack biomass and sand nitrate concentrations were unrelated to %N or $\delta^{15}N$ of the grasses. However, we did find that beach width and foredune crest height were both important to beachgrass nitrogen composition and nitrogen source. Shorter beaches and taller foredunes had beachgrasses with slightly higher %N tissue content across the foredune profile, but the $\delta^{15}N$ of those grasses declined at the crest and heel, suggesting that these plants were more isolated from marine derived nitrogen. The results suggest that beachgrasses use marine nutrients at the foredune toe, where sand nitrate concentrations are high, and that the use of this source declines further from the beach, especially at sites with taller foredunes. Given the role of vegetation in dune formation and stability, and the protection services that dunes provide to coastal communities, understanding these nutrient dynamics are important to ecosystem functions and services.

### 3.1 Introduction

Coastal habitats such as salt marshes, eelgrass beds, rocky shores, and sandy beaches and dunes provide important ecosystem services to coastal communities including coastal protection, recreation, raw materials, and carbon sequestration (Barbier et al. 2011). One such habitat, sandy beaches and associated dunes, act as natural barriers from intense wave action and coastal flooding, providing significant protective services to coastal communities (e.g., Seabloom et al. 2013, Biel et al. 2017, Ruggiero et al. 2019). The dune portion of this habitat is largely shaped by a positive feedback between wind-blown sand and dune vegetation, resulting in stabilized, vegetated hills of sand parallel to the shoreline, also known as foredunes (e.g., Hesp 1989, Murray et al. 2008, Hacker et al. 2012, Zarnetske et al. 2012, 2015, Durán and Moore 2013).

Despite the important role of plants to dune geomorphology, the factors important to plant growth, and thus sand deposition and dune building, are understudied. Dune ecosystems have historically been considered nutrient poor, in part, because of the lack of soil formation on actively building dunes and the leaching of nutrients given the high porosity of sand (e.g., Kachi and Hirose 1983, Zhang 1996, Kooijman et al. 1998). Despite the potential for stressful nutrient conditions, the biomass, growth rates, and nutrient content of dune plants are similar or higher than similar plants in other coastal communities, suggesting that dune ecosystems are more productive than their inherent nutrient conditions might suggest (Willis and Yemm 1961, van der Valk 1974, Pavlik 1983, Ripley and Pammenter 2004). For example, published values of net primary production values of dune plants range from 250 g $m^2$ per year for *Ammophila arenaria* (Scotland; Deshmukh 1977), 380 g $m^2$ per year for *Ipomoea pes-caprae* (east coast of South America; Ripley and Pammenter 2004), and 540 g $m^2$ per year for *Scaevola plumieri* (east coast of South America; Ripley and Pammenter 2004). This range is comparable to net primary production in salt marshes (e.g., *Spartina alterniflora* 280–500 g $m^2$ per year), one of the most productive coastal ecosystems. Taken together, these comparisons suggest that dune plant communities are likely donor controlled, with their production dependent on outside nutrient sources.

A potential primary nutrient source to sandy beaches and dunes comes in the form of marine subsidies, particularly macrophyte wrack, which is supplied from nearby habitats including estuaries and rocky reefs (Orr et al. 2005, Barreiro et al. 2011, Dugan et al. 2011, Reimer et al. 2018, Chapter 2). Macrophyte wrack can alter food web dynamics, community structure, and ecosystem productivity via inputs of food and nutrients (e.g., Dugan et al. 2003, Jaramillo et al. 2006, Ince et al. 2007). This source is particularly relevant to dune plant communities, where research has shown that beaches with high wrack biomass (either naturally varying or experimentally modified) have more productive and diverse dune plant communities with greater foliar nitrogen content and enriched nitrogen substrate pools (Cardona and Garcia 2008, Williams and Feagin 2010, Del Vecchio et al. 2013, 2017, van Egmond et al. 2019). Nutrients resulting from macrophyte decomposition, and any remaining particles of wrack debris, can be adsorbed to beach sand and then transported further inland to the upper beach and dune by wind and wave action (Cardona and García 2008, Dugan et al. 2011, Oldham et al. 2014). Seawater from tidal exchange and wave runup can also influence the nutrient conditions of beach sand by the nutrients from seawater adsorbing to the sand grains themselves (Eagle 1983, McLachlan et al. 1985, McLachlan and Turner 1994, Hwang et al. 2008, Chapter 2). This nutrient-laden sand can then be delivered via wave or wind induced sediment transport to higher beach elevations and the foredune, where dune plants may then utilize these nutrients.

Despite the evidence that marine subsidies may serve as a source of nitrogen for dune plants, few studies have explored the assimilation of marine nutrients (but see Cardona and Garcia 2008), and none have explored these relationships at local (across foredune profile location) and regional (across sites) scales. In Chapter 2, we showed that there is a positive relationship between marine macrophyte wrack subsidies, sand nitrate concentrations, and dune grass productivity (two non-native invasive beachgrass species *Ammophila arenaria* and *A. breviligulata*, and the native dune grass, *Elymus mollis*) for U.S. Pacific Northwest beach and dune sites spanning 550 kilometers of the coast. We found that there was considerable variability in marine subsidies among sites and beach and foredune profile locations as a result of ocean upwelling, proximity to subsidy source, and beach and foredune sand supply and geomorphology. Dune grass production was connected to this variability in predictable ways. For example, we found that dune grass production was greatest at the foredune toe or crest, dependent on where sand deposition and nitrate concentrations were greatest, and lowest at the foredune heel, where sand deposition and nitrate concentrations were lowest.

Building on these patterns, we explore whether dune grasses use marine nitrogen, and whether the incorporation of marine derived nitrogen varies at local (across the foredune profile) and regional (across sites). We know that the nitrogen content and source in the environment is generally reflected in the nitrogen composition (%N and $\delta^{15}N$) of plant tissue (Sterner and Elser 2002). Because of this variation, naturally occurring stable isotopes of nitrogen ($^{14}N$, light and $^{15}N$, heavy) can be employed to distinguish between nitrogen sources (Sterner and Elser 2002, Craine et al. 2015). In terrestrial environments, the majority of fixed nitrogen contributing to vegetation production comes from the atmosphere and is isotopically light. In marine environments, isotopically light isotopes are preferentially used by primary producers. As coastal sand dunes exist at the interface of these two habitats, the nitrogen isotopic signature in dune grasses using more marine sources of nitrogen should have more of the heavy isotope, leading to a more enriched $\delta^{15}N$ isotopic signature. Comparitively, the nitrogen isotopic signature in dune grasses using more atomspheric sources of nitrogen should have more of the light isotope, leading to a less enriched $\delta^{15}N$ isotopic signature. In a study exploring the effects of seagrass debris on coastal dune plants, Cardona and Garcia (2008) found the $\delta^{15}N$ of select foredune vegetation was usually higher than atmospheric nitrogen and not statistically different from the $\delta^{15}N$ of the seagrass itself. Conversely, the authors found the $\delta^{15}N$ of select hinddune vegetation (collected further from the sea) was not statistically different from that of atmospheric nitrogen and usually lower than the $\delta^{15}N$ of the seagrass itself. Their results support the hypothesis that seagrass, and marine nutrients more generally, are an important source of nitrogen for foredune vegetation.

Here we measured dune plant nitrogen composition (%N) and source ($\delta^{15}N$) across the beaches and dunes of the U.S. Pacific Northwest at both local (foredune profile) and regional (sites) spatial scales. This chapter builds on the results of Chapter 2, where we established the patterns of marine nutrient subsidies on coastal beaches, beach and foredune morphology, and dune grass production on foredunes and determined the factors important to these patterns. Specifically, in Chapter 2, we report that sand nitrate concentration varied at large and small spatial scales: at the coast level, macrophyte wrack and sand nitrate concentrations were greatest at sites in both the north and south of the study region and lowest at sites in the central region. Moreover, at the foredune level, sand deposition rate and nitrate concentration was generally highest at the foredune toe and decreased towards the heel. Dune grass production was positively correlated with these patterns: grass production was greatest at the foredune toe or crest, dependent on where sand deposition rates and nitrate concentrations were greatest, and lowest at the foredune heel, where sand deposition rates and nitrate concentrations were lowest. In this chapter, we ask two questions, with their associated hypotheses:

1) Does the composition (%N) and source ($\delta^{15}N$) of nitrogen in four dune plant species (two non-native invasive beachgrass species *Ammophila arenaria* and *A. breviligulata*, the native dune grass, *Elymus mollis,* and the native shrub *Cakile edentula*) vary across sites (coast-scale) and

foredune profile locations (dune-scale)? We hypothesize that the composition and source of nitrogen will vary across species, sites, and profile locations.

2) Does the nitrogen composition (%N) and source ($\delta^{15}N$) in beachgrasses correlate with measures of marine subsidies (macrophyte wrack and sand nitrate concentration) and/or beach and foredune geomorphology (shoreline change rate, beach width, and foredune crest height) on coastal foredunes? We expect both marine subsidies and beach and foredune geomorphology to be important predictors of beachgrass composition and source because both influence the potential access to and accumulation of marine nutrient sources on beaches. We hypothesize that wide beaches with high marine subsidies and short foredunes will have higher %N and $\delta^{15}N$ in beachgrass tissue. Conversely, we hypothesize that narrow beaches with low marine subsidies and tall foredunes will have lower %N and $\delta^{15}N$ in beachgrass tissue.

## 3.2 Methods

### 3.2.1 Study system

Coastal beaches and dunes of the U.S. Pacific Northwest make up approximately 45% of the Oregon and Washington coasts and are adjacent to many highly productive estuaries and rocky reefs. These sites experience variable ocean productivity (e.g., Hickey and Banas 2003, Checkley and Barth 2009, Menge et al.

2015), marine subsidies (e.g., Reimer et al. 2018, Chapter 2), and coastal geomorphology (e.g., Hacker et al. 2012, Ruggiero et al. 2013, Biel et al. 2019).

In this system, the most common dune plant species are two non-native, invasive dune grasses, the European beachgrass *Ammophila arenaria* (L.) Link and the American beachgrass *Ammophila breviligulata* Fernald, which co-occur in some regions of the coast, but not in others (Hacker et al. 2012). First introduced in the early1900's, *A. arenaria* was the dominant beachgrass species (Cooper 1958, Weidemann and Pickart 2004) along the U.S. Pacific coast. However, in 1935, the intentional planting of *A. breviligulata* led to the subsequent invasion of this species in the northern part of the study region, previously dominated by *A. arenaria* (Seabloom and Wiedemann 1994, Hacker et al. 2012). Today, *A. breviligulata* is generally restricted to northern dune sites while *A. arenaria* dominates more southern sites (Hacker et al. 2012). These non-native species' introductions rapidly transformed what was once open, shifting, and sparsely vegetated dunes (including the native dune grass *Elymus mollis* (Trin.) Pilg., and the native forb *Cakile edentula* (Bigelow) Hook., a species that occurs exclusively at the foredune toe) into continuous, stable, and densely vegetated coastal dunes.

### 3.2.2 Field sites

We sampled dune plants at fifteen dune-backed beach sites that were exposed to the open coast and adjacent to prominent estuaries (Grays Harbor, Willapa Bay, WA; Netarts Bay, Yaquina Bay, and Coos Bay, OR) and major headlands (Cape Disappointment, WA; Cape Meares, Tillamook Head, Cape Foulweather, Cape Perpetua, Cape Arago, Cape Blanco, OR) along a 550 km stretch of the U.S. Pacific

Northwest coast. The fifteen sites included Grays Harbor (GH), Leadbetter Point (LBP), and Long Beach (LB) in Washington and Fort Stevens (FS), Nehalem Bay (NB), Cape Lookout (CL), Sand Lake (SL), Pacific City (PC), South Beach (SB), Siltcoos River (SILT), Dunes Overlook (DO), Umpqua Dunes (UD), North Spit (NS), Bandon (BAN), and Floras Lake (FL) in Oregon Appendix A Table A1). The sites were located within distinct littoral cells, or areas along the coast containing the same sediment sources, transport pathways, and sinks (Inman and Frautschy 1965). The sites have been used in previous dune and wrack research (Hacker et al. 2012, Reimer et al. 2018, Biel et al. 2019, Chapter 2).

### 3.2.3 Plant sample collections and processing

To assess the contribution of marine nutrient sources to dune vegetation, we measured dune plant nitrogen composition (%N) and source ($\delta^{15}N$) in the shoot tissue of four focal dune plant species, *Ammophila arenaria*, *A. breviligulata*, *Elymus mollis, and Cakile edentula*. Dune plants were sampled in summer 2015 at each transect location at the fifteen sites above using the sampling design and methods of Chapter 2 (Chapter 2 Appendix A Figure A1). Briefly, at each transect location, we sampled along three transects that extended from the beach across the foredune (Chapter 2 Appendix A Figure A1). At three profile locations along each transect (toe, crest, and heel of the foredune), we haphazardly collected at least one plant "individual" (defined as the shoot or shoots attached to one rhizome) of each dune plant species, when present, for a total of at least three plants per species per profile location. Note that *Cakile edentula* was only present at the foredune toe.

In the laboratory, the plants were air-dried and three tissue samples were taken from the middle section of the shoot of each plant. Individual plant samples were combined with others based on species, transect location, and foredune profile location at each site. The plant tissue samples were ground to a fine, homogenous powder using a Spex Sigma Prep 8000D Mixer/Mill plant grinder. Powdered samples were then weighed on a micro-balance and run through an element analyzer in the Stable Isotope Laboratory at Oregon State University, Corvallis, OR, using continuous flow isotope ratio mass spectrometry to measure the %N and $\delta^{15}N$ composition of the plant tissue of each sample.

Stable isotope abundances were expressed in delta notation—which indicates the deviation of the sample-measured isotopic composition from the standard—using the following equation:

$$\delta^{15}N = \left(\left(\frac{R_{sample}}{R_{standard}}\right) - 1\right) * 1000$$

in which *R* represents the ratio of the heavy to the light isotope in each sample (i.e., $^{15}N/^{14}N$). The internationally accepted calibration standard, $R_{standard}$, for nitrogen is atmospheric air. A higher or more positive delta value is indicative of a sample enriched in the heavy isotope, $^{15}N$. A lower or more negative delta value reflects a sample depleted in the heavy isotope.

### 3.2.4 Statistical analyses

Data were analyzed using R version 3.5.3 (R Development Core Team 2019). Data were checked visually for normality using residual plots against predicted values, and the data met these assumptions in all cases.

We used one-way ANOVAs to test for differences in nitrogen composition (%N) and source ($\delta^{15}N$) among the four dune plant species (*Cakile edentula*, *Elymus mollis*, *Ammophila breviligulata*, and *A. arenaria*) at the foredune toe, where all the species co-occurred. In addition, at the foredune crest and heel, we compared a subset of three species (*Elymus mollis*, *Ammophila breviligulata*, and *A. arenaria*) that co-occurred at these profile locations. For the two beachgrass species, we combined the data and used two-way ANOVAs to test for differences in nitrogen composition (%N) and source ($\delta^{15}N$) among sites, foredune profile locations, and their interactions. We also used one-way ANOVAs to consider whether nitrogen composition (%N) and source ($\delta^{15}N$) of the native dune grass *Elymus mollis* and the native forb *Cakile edentula* varied across sites, focusing specifically at the foredune toe where they are distributed. Tukey HSD post hoc tests were conducted on significant factors unless interactions were found, in which case one-way ANOVAs and Tukey HSD post hoc comparisons were conducted between levels of each factor (Underwood 1997).

We used multiple regression analyses to evaluate whether the nitrogen composition (%N) and source ($\delta^{15}N$) of beachgrasses were correlated with marine subsidies and geomorphic factors obtained from Chapter 2. These explanatory variables included total wrack biomass (g/transect), sand nitrate concentration (µmol/g sand), beach width (m), and foredune crest height (m). We partition the nitrogen composition (%N) and source ($\delta^{15}N$) data by profile location (foredune toe, crest, and heel) before conducting the regression analyses.

## 3.3 Results

### 3.3.1 Patterns of dune plant nitrogen composition and source by species, site, and foredune profile location

We found that dune plant nitrogen composition (%N) and source ($\delta^{15}N$) varied by dune plant species, but the results depended on foredune profile location (Figure 3.2). For example, at the foredune toe, where the four plant species were present, the %N and $\delta^{15}N$ composition was highest for *Cakile edentula* and lowest for *Elymus mollis*, *Ammophila breviligulata*, and *A. arenaria,* which did not differ (Figure 3.2). At the foredune crest and heel profile locations, there were no differences in %N composition for the three dune grass species (i.e., *E. mollis*, *A. breviligulata*, and *A. arenaria*). However, the $\delta^{15}N$ composition did differ across the three grass species at the crest and heel profile locations. *C. edentula* was only present at the foredune toe so it was not included in the foredune crest and heel analyses.

The %N composition of *A. arenaria* and *A. breviligulata* varied by site, but not profile location, and there was no site by profile location interaction (Figure 3.3, Table 3.1). For the majority of sites, %N composition did not vary but outlier sites included high values for Fort Stevens and low values for Grays Harbor and Long Beach. In contrast, $\delta^{15}N$ composition varied by site, by profile location, and there was a site by profile location interaction (Figure 3.3, Table 3.1). Generally, the $\delta^{15}N$ composition of the beachgrasses was greatest at the foredune toe and decreased the farther away the grasses were from the foredune toe (Figure 3.3, Table 3.1). For example, the beachgrasses at the foredune toe had the highest $\delta^{15}N$ composition, although there were only slight differences among sites. The $\delta^{15}$N composition of the beachgrasses collected from the foredune crest and heel declined precipitously, with the heel plants having the lowest values, but this pattern was dependent on coastal region (Figure 3.3, Table 3.1). In particular, plants at the crest profile locations in the northern (i.e., GH, LBP, LBP, FS, and NB) and southern (i.e., BAN and FL) sites had higher $\delta^{15}$N composition than the central sites. This pattern generally carried through to the foredune heel but $\delta^{15}$N composition was incrementally lower.

Finally, the %N and $\delta^{15}$N composition of *E. mollis* and *C. edentula* at the foredune toe (where we had sufficient data to analyze with statistics) either weakly differed, or did not differ, across dune sites (Figures 3.4 and 3.5, Table 3.2).

### 3.3.2 Relationships among geomorphic factors, marine subsidies, and nitrogen composition of beachgrasses

Our analyses showed that the patterns of nitrogen composition (%N) and source ($\delta^{15}$N) of beachgrasses were correlated with geomorphic and marine subsidy variability across foredune profile locations and sites. We found that %N composition was positively correlated with foredune crest height and that $\delta^{15}$N composition was positively correlated with beach width and negatively correlated with foredune crest height (Table 3.3A). Comparing the grasses from the foredune toe alone, %N composition was unrelated to any explanatory variable but $\delta^{15}$N composition increased as beach width increased. At the foredune crest and heel, %N and $\delta^{15}$N of the grasses was negatively correlated with increasing dune crest height (Table 3.3C, D). At the foredune crest, %N was positively correlated with sand nitrate concentration at the foredune crest (Table 3.3C).

## 3.4 Discussion

Our findings are consistent with the hypothesis that marine nutrients are an important source of nitrogen for dune plants in the US Pacific Northwest. We found that the composition and source of nitrogen in plants varies among species, sites, and foredune profile locations. Our results suggest that some of this spatial variability is attributable to marine subsidies and geomorphic factors including beach and foredune morphology. Below, we describe in greater detail the composition and source of nitrogen for the four common dune plants used in this study. We explore the potential factors important in determining these patterns and consider some possible consequences of the incorporation of marine nitrogen into dune vegetation along the U.S. Pacific Northwest coast.

### 3.4.1 Species-specific differences in %N and $\delta^{15}$N of dune plants

Previous research has found that, generally, plant elemental composition is dependent on soil elemental composition (Sterner and Elser 2002). For example, nutrient-poor sites are dominated by slow-growing plant species with low leaf nutrient concentrations (e.g., Monk 1966, Aerts 1995). As nutrient availability increases, these species are replaced by rapidly-growing species with higher leaf nutrient concentrations (e.g., Aerts and Berendse 1988, Aerts 1995). However, some plants have the ability to keep their element composition relatively stable regardless of changes in nutrient availability, via various physiological mechanisms (Sterner and Elser 2002, Morgan and Connolly 2013). Because of this equilibrium, leaf nutrient concentration in plants—specifically nitrogen, for the purposes of this chapter—may not always reflect the nutrient availability of growth soil.

Moreover, the ratio between the two nitrogen stable isotopes ($^{15}N$ and $^{14}N$) varies in ecosystems as a result of isotope fractionation in physical, chemical, and biological processes (Hogberg 1997). Because of this, when stable isotopes of nitrogen are used, they can provide insights into the nitrogen source. However, this $\delta^{15}N$ source approach can be confounded by the fact that plant $\delta^{15}N$ signature can also reflect site productivity. For example, plant leaf $\delta^{15}N$ generally reflects not only the available N sources, but also rates of N cycling, plant-fungal associations, and other physiological mechanisms within the plant, all of which influence N isotopic fractionation (Hogberg 1997, Evans 2001, Morris et al. 2005). Thus, the relationships between tiller N and marine subsidies within and across sites may be determined by other factors besides marine subsidies, such as site productivity, coastal geomorphology, and nitrogen fixing bacteria.

We found that only one of the four common dune plant species we considered varied in their nitrogen tissue composition. The sea rocket, *Cakile edentula*, which exclusively occurs at the foredune toe and is the only forb species (Brassicaeceae) we measured in this study, had greater %N and $\delta^{15}N$ compared to the three dune grass species (native dune grass *E. mollis* and the two non-native beachgrasses *Ammophila arenaria* and *A. breviligulata*), which did not differ from one another. In a study from the British Isles, Davy et al. (2006) found *Cakile maritima* to be particularly responsive to local variation in N, suggesting *Cakile* may have adaptations of exploiting N as it becomes available. Similar species-specific differences in plant N content and $\delta^{15}N$ were observed by Cardona and Garcia (2008), who found that dune forbs had higher nitrogen content compared to $C_3$ dune grasses. The greater %N and $\delta^{15}N$ of *C. edentula* might also be attributed to the slightly lower distribution of this species on the beach/foredune toe. By being closer to the beach, and thus marine subsidies, this species may have slightly better access to marine nutrients compared to the three dune grass species. Finally, the lack of differences in N content among the grasses at all foredune profile locations is counter to one study in northern California, which found that *E. mollis* had slightly higher N content compared to *A. arenaria* when grown in a common garden experiment (Pavlik 1983). This discrepancy suggests that studies of plant N content are likely to vary with geographic context and controlled experimentation.

### 3.4.2 Spatial differences reflected in the %N and $\delta^{15}N$ of *A. arenaria* and *A. breviligulata*

Focusing on the beachgrasses, the regional comparisons of nitrogen composition (%N) and source ($\delta^{15}N$) showed little variation among sites, particularly at the foredune toe. For nitrogen composition, most sites had similar beachgrass nitrogen, except a few outlier sites including high values for Fort Stevens and low values for Grays Harbor and Long Beach. From Chapter 2, we know that Fort Stevens, in particular, has high sand nitrate concentrations as a result of upwelled ocean nutrients mixing with the Columbia River (Lohan and Bruland 2006). The fact that the same site has been found to have exceptionally high sand nitrate concentrations and tissue nitrogen content, suggests that the beachgrasses are responding to differences in sand nitrates in their environment at the site-level.

However, the lack of strong differences in tissue nitrogen content at the profile-level suggest that differences in sand nitrate concentration within sites may be obscured by homeostatic regulation of the beachgrasses. Most plants are able to maintain internal nutrient balance to continue functioning as natural fluctuations in nutrient availability occur. This adaptation could result in a mis-match between available soil nutrients and plant tissue nutrients. For example, in non-forested wetland systems with 10-fold variation in nitrogen additions, there was only 2-3 fold variation in plant nitrogen observed (Güsewell and Koerselman 2003). Further, species from nutrient-poor habitats tend to have low tissue turnover rates (e.g., Aerts et al. 1990, Escuerdo et al. 1992, Ryser and Lambers 1995, Schlapfer and Ryser 1996). Thus, the within site, or profile-level nutrient condition of dune vegetation is more likely to be upheld than the regional, or across site nutrient condition.

Even though beachgrasses did not differ greatly in %N composition among sites or foredune profile locations, the source of that nitrogen did vary among profile locations, with the highest $\delta^{15}N$ in beachgrasses at the foredune toe, where nitrate from marine subsidies are concentrated (Chapter 2). In addition, $\delta^{15}N$ in beachgrasses varied among sites, but this depended on the foredune profile location in which the beachgrasses were sampled. Our stable isotope analysis showed that the marine nitrogen signature in beachgrasses extend to the crest and heel of the foredune in both the extreme northern and southern regions of the coast. Given the spatial differences in beachgrass tissue nitrogen and its source across sites and profile locations, what factors could be important to this pattern?

We explored the role of marine subsidies and beach and foredune geomorphology that might influence the amount and/or transfer of these subsidies along the beach and foredune profile. The factors we used in our analyses included measures of marine subsidies (total wrack biomass and sand nitrate concentration across the beach and dune profile) and measures of beach and foredune geomorphology (beach width and foredune crest height). Our regression analyses showed that, for the most part, macrophyte wrack biomass and sand nitrate concentrations were unrelated to %N or $\delta^{15}N$ of the grasses. The lack of relationship with marine subsidy amount was the case at the level of the site and for each foredune profile locations separately (except for the nitrogen content of the beachgrasses at the foredune crest, where %N composition was positively related to crest nitrate concentration). However, we did find that beach width and foredune crest height were both important to beachgrass nitrogen composition and nitrogen source. Wider beaches and shorter foredunes had beachgrasses with slightly lower %N tissue content across foredune profile locations, but the source of that nitrogen at the crest and heel had a higher marine signature. In contrast, shorter beaches and taller foredunes had beachgrasses with slightly higher %N composition across foredune profile locations, but the source of that nitrogen at the crest and heel had a lower marine signatures. Interestingly, one site, Sand Lake, with a very narrow beach and tall foredune had the lowest beachgrass $\delta^{15}N$ of all the sites, suggesting much lower marine subsidy input. In fact, total wrack biomass and sand nitrate concentrations from marine sources are low at this site (Chapter 2 Figures 2.2, 2.3, 2.4).

How could beach and dune geomorphology affect the content and source of nitrogen in dune plants? In changing the potential area for nutrients to accumulate on the beach and potentially acting as a barrier to nutrient delivery along the foredune profile, beach and dune morphology can impact the nitrogen content and source of nitrogen in dune plants. We found that beach width and foredune height influenced plant tissue $\delta^{15}N$. We argue that while wider beaches have greater potential for wrack accumulation, taller foredunes may inhibit marine nutrients from reaching the foredune heel.

We also found that, depending on foredune profile location, beachgrass %N varied with sand nitrate concentration and foredune height. As noted in Chapter 2, though marine subsidies are greatest at the foredune toe, taller dunes could be capturing higher quantities of marine-nutrient coated beach sand over a shorter area than shorter dunes where nutrient capture could be more spread along the entire dune profile. Greater sand capture by taller foredunes could subsequently result in greater nutrient availability at the foredune crest but, again, create as a physical barrier from marine nutrient resources arriving at the foredune heel.

Finally, the lower $\delta^{15}N$ of beachgrasses at the crest and heel of the foredune could be driven by factors other than marine subsidies and dune geomorphology. Depleted $\delta^{15}N$ signatures are potentially due to increased accumulation of atmospheric nitrogen through deposition and the increased presence of nitrogen fixing plants as distance from the beach increases. Plants further away from the marine nutrient are more reliant on other nutrient sources, like atmospheric nitrogen, and thus have $\delta^{15}N$ values reflective of that source. Likewise, plants fixing nitrogen from the atmosphere tend to have $\delta^{15}$N values of approximately -2 ‰ and +2 ‰, close to the value of atmospheric nitrogen, 0 ‰ (Shearer and Kohl 1986).

### 3.4.3 Implications

The results presented in this paper corroborate an earlier hypothesis that beach nutrients, especially those with marine origin, contribute nitrogen to foredune plants (Cardona and Garcia 2008 ). Specifically, our results support the notion that marine subsidies are a nitrogen source for foredune vegetation along the U.S. Pacific Northwest coast. In this study, marine nitrogen content and source was correlated with measures of beach and foredune geomorphology. From Chapter 2, though, we know there is a correlation between nutrient subsidies on the beach, nitrate in sand, sediment supply, and dune plant production. Together, these studies point to the idea that marine subsidies, in tandem with coastal geomorphology, have important biogeochemical and ecological implications for the coastal dune formation.

Incipient foredunes, or embryo dunes, are formed by the sand trapping ability of early colonizing dune plants such as *Cakile* spp., which can then be colonized by dune building grasses (e.g., *Ammophila* spp.) (Hesp 1984). As sand grains are picked up by wind, they are blown to the foredune where they hit vegetation and are deposited. The plants then respond positively, growing vertically to avoid burial and increasing dune height. Given this feedback and the relationship between marine nutrients and dune plants, it stands to reason that marine nutrient use by dune plants may influence dune formation. As such, potential dune initiation and building could be impacted by shifts in marine subsidies on coastal beaches and subsequent integration of marine nutrients into foredune plants.

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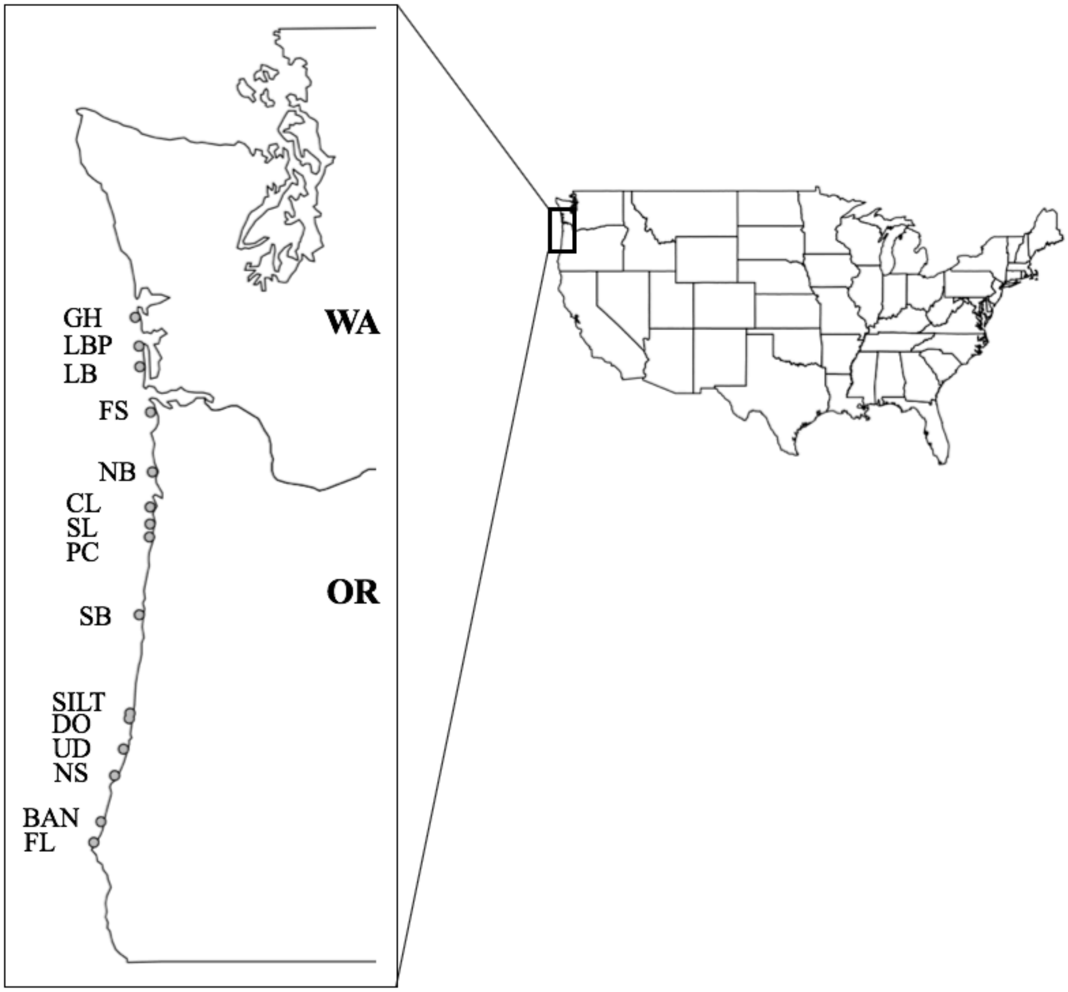

**Figure 3.1.** Map of the site locations used to collect foredune vegetation for nitrogen composition and stable isotope analysis along 550 km of the coast of the U.S. Pacific Northwest. See Chapter 2 Appendix A Table A1 for site abbreviations.

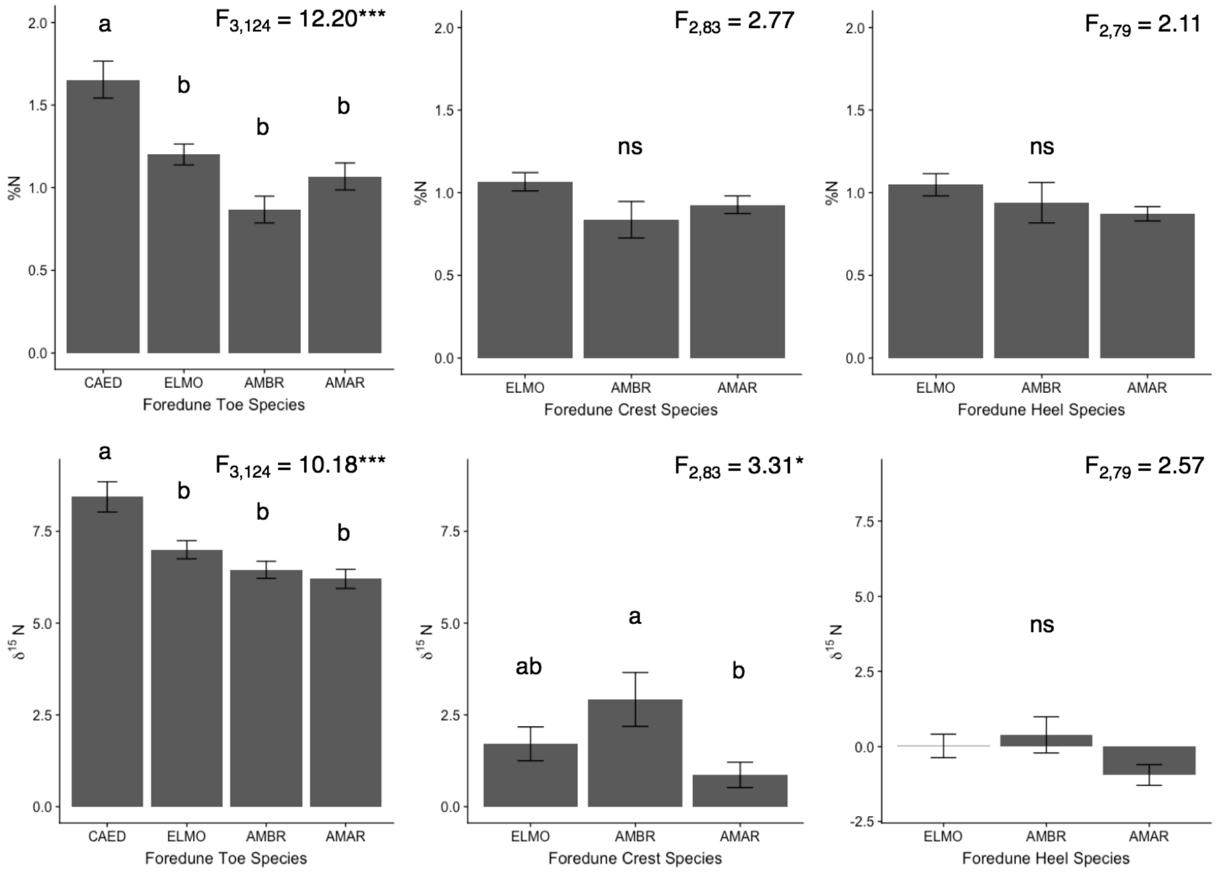

**Figure 3.2.** Comparisons (mean ± SE) of %N and $\delta^{15}N$ for the most common dune plant species (CAED = *Cakile edentula*, ELMO = *Elymus mollis*, AMBR = *Ammophila breviligulata*, AMAR = *Ammophila arenaria*) found at the foredune toe, crest, and heel. One factor ANOVA results are given in plots. Bars that do not share letters are significantly different (Tukey's HSD Test $P \leq 0.05$). *** $P < 0.001$, * $P \leq 0.05$ (ns = no significant difference).

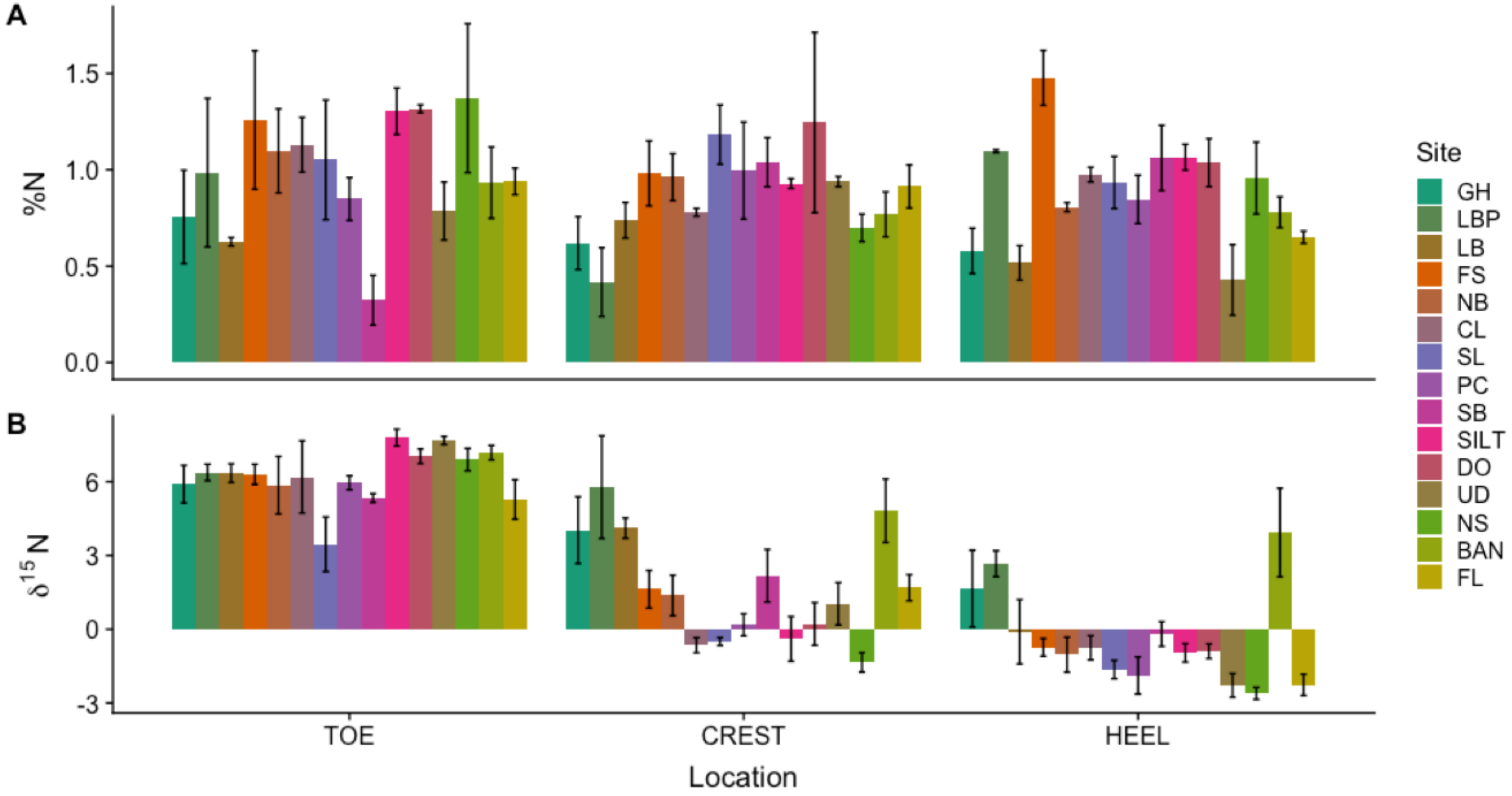

**Figure 3.3.** Mean (± SE) (A) %N and (B) $\delta^{15}$N for the beachgrasses *Ammophila arenaria* and *A. breviligulata* across sites (listed north to south; Figure 3.1) and foredune profile locations (toe, crest, and heel). See Chapter 2 Appendix A Table A1for site abbreviations and locations. See Table 3.1 for statistics.

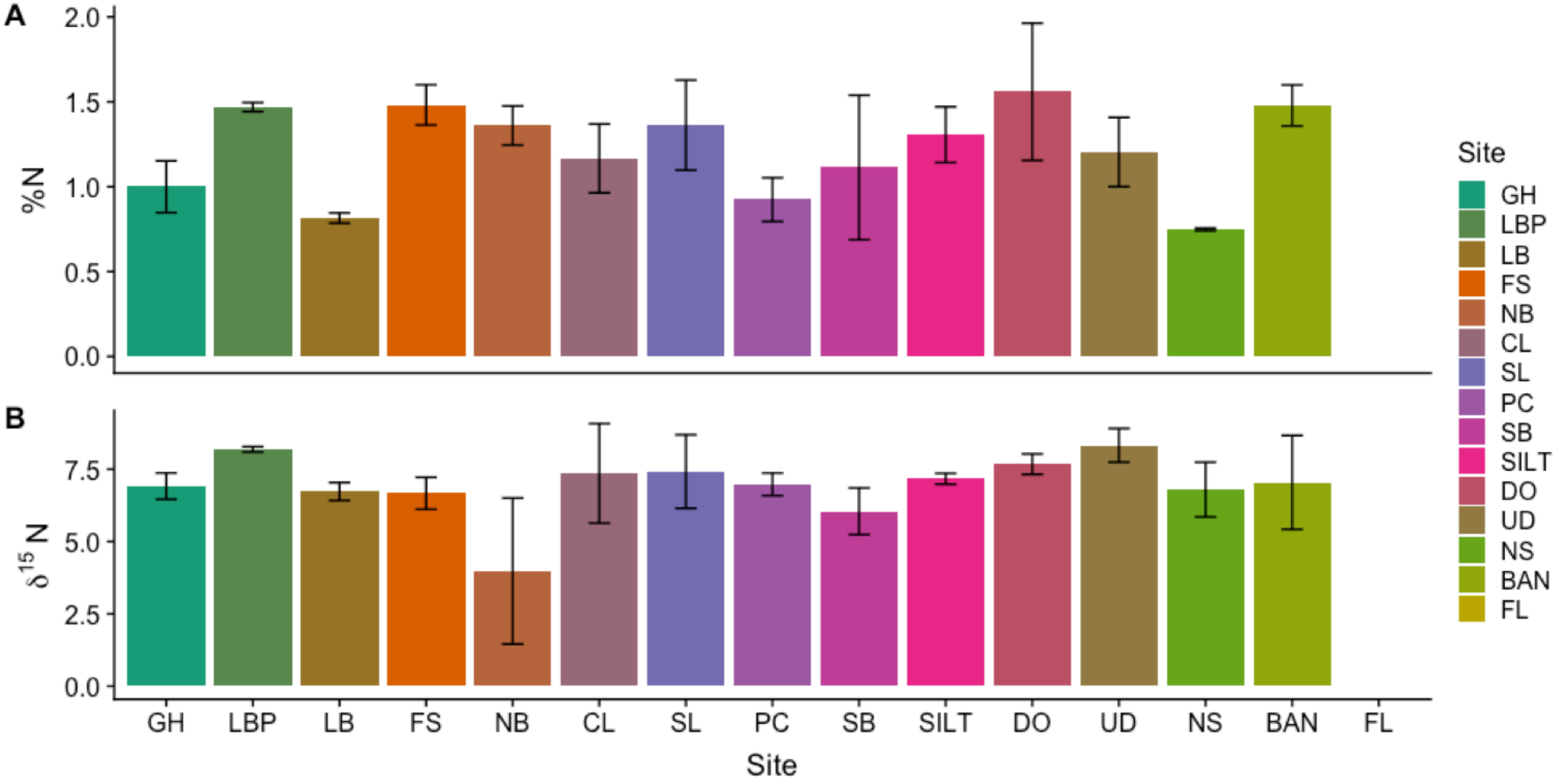

**Figure 3.4.** Mean (± SE) *Elymus mollis* foliar (A) %N and (B) $\delta^{15}$N across sites (listed north to south; Figure 3.1). See Chapter 2 Appendix A Table A1for site abbreviations and locations. See Table 3.2 for statistics.

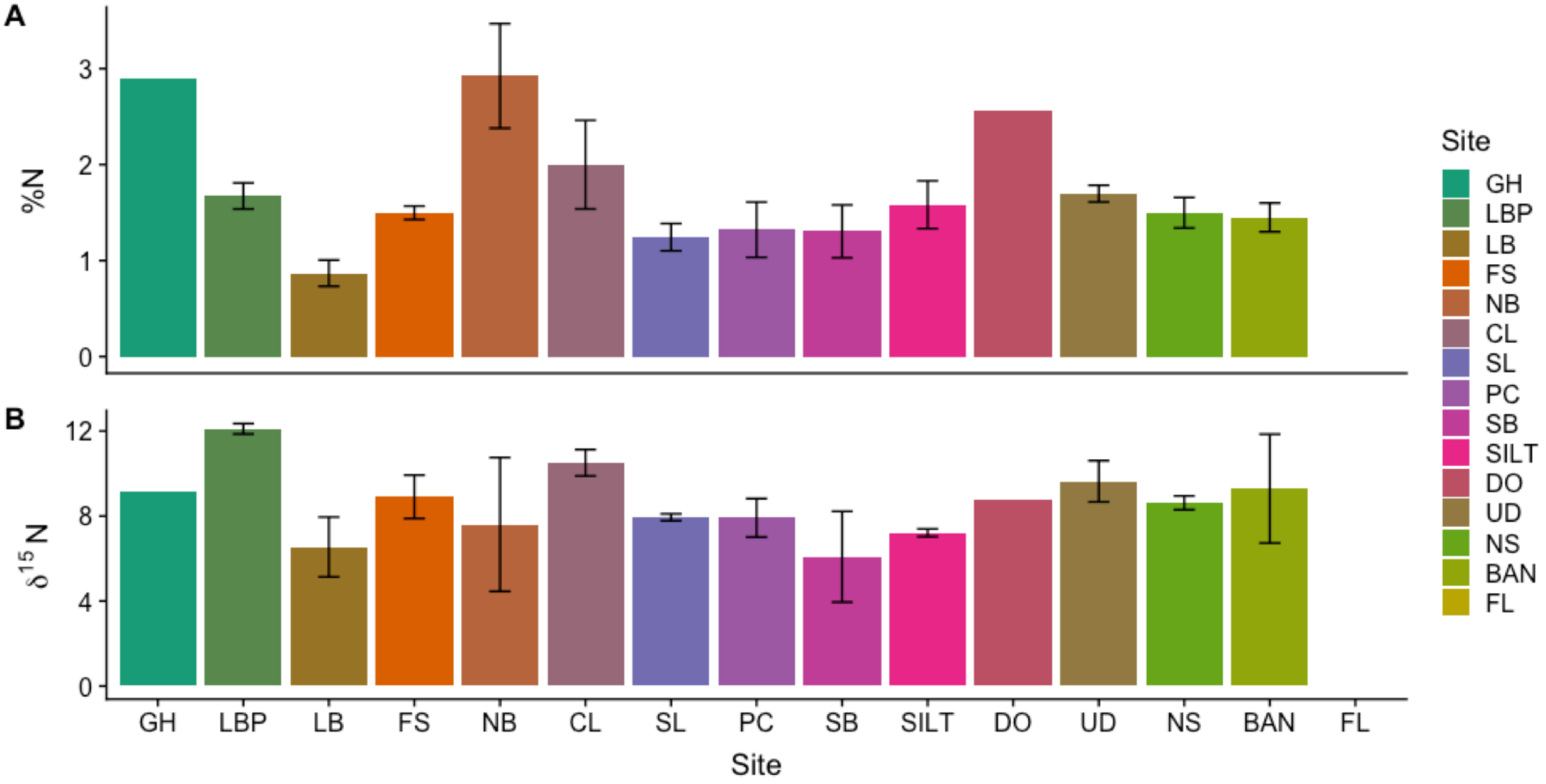

**Figure 3.5.** Mean (± SE) *Cakile edentula* foliar (A) %N and (B) $\delta^{15}N$ across sites (listed north to south; Figure 3.1). See Chapter 2 Appendix A Table A1for site abbreviations and locations. See Table 3.2 for statistics.

**Table 3.1.** Two-way ANOVA results for the foliar %N and $\delta^{15}N$ of both *Ammophila arenaria* and *A. breviligulata* together across sites (see Figure 3.1, Chapter 2 Appendix A Table 2A for site abbreviations and locations) and foredune profile locations (toe, crest, and heel). Significant P values are in bold. Tukey's HSD post hoc tests $P < 0.05$.

| | df | SS | F | Prob > F | Tukey HSD post hoc test |
|---|---|---|---|---|---|
| **%N** | | | | | |
| Site | 14 | 4.27 | 3.41 | **0.0002** | FS ≥ DO ≥ SILT = SL = NS = CL = NB = PC = FL = LBP = BAN = SB ≥ UD ≥ GH = LB |
| Profile location | 2 | 0.29 | 1.61 | 0.2050 | |
| Site*Profile location | 28 | 3.90 | 1.56 | 0.0619 | |
| Residuals | 87 | 7.78 | | | |
| **$\delta^{15}N$** | | | | | |
| Site | 14 | 220.58 | 8.28 | **5.81E-11** | |
| Profile location | 2 | 1063.29 | 279.28 | **< 2.2E-16** | |

**Table 3.1.** (Continued)

| | | | | | | |
|---|---|---|---|---|---|---|
| Site*Profile location | 28 | 148.63 | 2.79 | **0.0001** | **GH, LBP, BAN:** Toe = Crest = Heel<br>**LB:** Toe = Crest > Heel<br>**FS, UD, FL:** Toe > Crest > Heel<br>**NB, CL, SL, PC, SB, SILT, DO, NS:** Toe > Crest = Heel | **TOE:** SILT = UD = BAN ≥ DO = NS = LBP = LB = FS = CL = PC = GH = NB = SB = FL ≥ SL<br>**CREST:** LBP = BAN ≥ LB ≥ GH ≥ SB = FL = FS = NB = UD ≥ DO = PC ≥ SILT ≥ SL = CL = NS<br>**HEEL:** BAN ≥ LBP ≥ GH = LB = SB ≥ FS = CL = DO = SILT = NB = SL = PC ≥ FL = UD = NS |
| Residuals | 87 | 165.62 | | | | |

**Table 3.2.** One-way ANOVA results for the nitrogen composition (%N and $\delta^{15}N$) of A) *Cakile edentula* and B) *Elymus mollis* across sites (see Figure 3.1, Chapter 2 Appendix A Table 2A for site abbreviations and locations) at the foredune toe profile location. Significant P values are in bold. Tukey HSD post hoc tests P < 0.05.

| Component | Source of variation | df | SS | F | Prob > F | Tukey HSD post hoc test |
|---|---|---|---|---|---|---|
| (A) *Cakile edentula* | %N | | | | | |
| | Site | 13 | 10.88 | 3.74 | **0.0032** | NB ≥ GH = DO = CL = UD = LBP = SILT = NS = FS = BAN ≥ PC = SB = SL = LB |
| | Residuals | 22 | 4.92 | | | |
| | $\delta^{15}N$ | | | | | |
| | Site | 13 | 82.35 | 1.06 | 0.4399 | N.S. |
| | Residuals | 22 | 131.99 | | | |
| (B) *Elymus mollis* | %N | | | | | |
| | Site | 13 | 2.39 | 1.27 | 0.2941 | N.S. |
| | Residuals | 25 | 3.63 | | | |
| | $\delta^{15}N$ | | | | | |
| | Site | 13 | 32.08 | 1.03 | 0.4526 | N.S. |
| | Residuals | 25 | 59.68 | | | |

**Table 3.3.** Statistical results from multiple regression analyses for the %N and $\delta^{15}N$ in both *Ammophila arenaria* and *A. breviligulata* together (A) across all foredune profile locations as a function of MHHW sand nitrate concentration, mid-beach/toe sand nitrate concentration, total wrack biomass, beach width, and foredune crest height; at the (B) foredune toe as a function of MHHW sand nitrate concentration, mid-beach/toe sand nitrate concentration, total wrack biomass, and beach width; (C) foredune crest as a function of mid-beach/toe sand nitrate concentration, crest sand nitrate concentration, and foredune crest height; (D) foredune heel as a function of mid-beach/toe sand nitrate concentration, foredune crest/heel sand nitrate concentration, and foredune crest height. Significant P values are in bold.

| Foredune profile component | Source of variation | %N | | | | $\delta^{15}N$ | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | df | SS | F | Prob > F | df | SS | F | Prob > F |
| (A) ALL | MHHW sand nitrate concentration | 1 | 0.01 | 0.10 | 0.7565 | 1 | 1.49 | 0.13 | 0.7204 |
| | Mid-beach/toe sand nitrate concentration | 1 | 0.03 | 0.26 | 0.6137 | 1 | 7.22 | 0.62 | 0.4316 |
| | Total wrack biomass | 1 | 0.00 | 0.00 | 0.9856 | 1 | 7.97 | 0.69 | 0.4087 |
| | Beach width | 1 | 0.24 | 2.04 | 0.1561 | 1 | 42.91 | 3.70 | **0.0567** |
| | Foredune crest height | 1 | 0.76 | 6.41 | **0.0126** | 1 | 57.02 | 4.91 | **0.0284** |
| | Residuals | 126 | 14.91 | | | 126 | 1462 | | |

**Table 3.3.** (Continued)

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| (B) TOE | MHHW sand nitrate concentration | 1 | 0.00 | 0.00 | 0.9995 | 1 | 0.01 | 0.01 | 0.9382 |
| | Mid-beach/toe sand nitrate concentration | 1 | 0.15 | 0.83 | 0.3669 | 1 | 4.69 | 2.30 | 0.1371 |
| | Total wrack biomass | 1 | 0.03 | 0.15 | 0.7005 | 1 | 1.83 | 0.90 | 0.3492 |
| | Beach width | 1 | 0.50 | 2.84 | 0.1002 | 1 | 8.15 | 4.01 | **0.0522** |
| | Residuals | 39 | 6.85 | | | 39 | 79.30 | | |
| (C) CREST | Mid-beach/toe sand nitrate concentration | 1 | 0.22 | 2.62 | 0.1134 | 1 | 1.32 | 0.28 | 0.5991 |
| | Crest sand nitrate concentration | 1 | 0.36 | 4.33 | **0.0438** | 1 | 2.18 | 0.47 | 0.4992 |
| | Foredune crest height | 1 | 0.43 | 5.16 | **0.0286** | 1 | 52.56 | 11.22 | **0.0018** |
| | Residuals | 40 | 3.34 | | | 40 | 187.45 | | |
| (D) HEEL | Mid-beach/toe sand nitrate concentration | 1 | 0.02 | 0.22 | 0.6450 | 1 | 1.85 | 0.43 | 0.5151 |
| | Foredune crest/heel sand nitrate concentration | 1 | 0.15 | 1.76 | 0.1920 | 1 | 2.58 | 0.60 | 0.4422 |
| | Foredune crest height | 1 | 0.40 | 4.58 | **0.0384** | 1 | 26.04 | 6.08 | **0.0181** |
| | Residuals | 40 | 3.50 | | | 40 | 171.39 | | |

# Chapter 4 – Are coastal dune plants nutrient limited? Experimental tests of beachgrass production in the U.S. Pacific Northwest dunes

Vanessa Constant, Francis Chan, McKenzie Barker, and Sally D. Hacker

## Abstract

Sandy beaches and dunes are generally considered low nutrient environments, potentially placing constraints on primary and secondary production. However, marine subsidies can be an important nutrient input, influencing dune plant productivity. On the U.S. Pacific Northwest coast, little is known about the source of nutrients to dune vegetation and whether dune plants are nutrient limited. Here we investigate the effects of nutrient additions on the dune grass production across multiple sites and foredune profile locations. Specifically, we used two manipulative experiments to ask: (1) How does nutrient addition affect dune grass production at sites and foredune profile locations that vary in background sand nitrate concentrations? (2) Does dune grass production and elemental composition vary with increasing nitrogen additions and do dune grasses experience nitrogen and phosphorous co-limitation? We found that dune grasses were nutrient-limited, with nutrient additions positively affecting dune grass production at sites and foredune profile locations that have higher wrack deposition and background sand nitrate concentrations. We also found that nitrogen additions resulted in increased grass shoot density, total biomass, and plant tissue %N and %S, and there was little support for phosphorus co-limitation. However, grass shoot biomass and shoot length either did not change, or declined, with added nitrogen and phosphorus. The study results suggest that, given the variability in marine subsidies, sand supply, and coastal geomorphology of these beaches and dunes, the potential for marine nutrients to influence dune grass production is high. With greater dune grass production,

particularly shoot densities, there is potential for better sand capture and increased dune height, resulting in enhanced ecosystem functions and services.

## 4.1 Introduction

Boundary habitats are strongly linked through the movement of ecological subsidies (i.e., energy, materials, and/or organisms), influencing population and community structure (Polis and Hurd 1995, 1996, Polis et al. 1997, Nakano and Murakami 2001, Menge et al. 2003, 2015, Witman et al. 2010, Hessing-Lewis and Hacker 2013, Kristensen et al. 2014, Vinueza et al. 2014, Uno and Power 2015, Hacker et al. 2019, Hayduk et al. 2019). Ecological subsidies are likely to be particularly important in inherently low productivity systems that interface with highly productive systems (e.g., ocean benthos—Boero et al.1996, Koslow 1997; lava flows—Howarth 1979, Thornton et al. 1988, 1990). Coastal beaches and dunes are generally characterized by low nutrient availability (Kooijman et al. 1998, Zhang 1996) and high nutrient turn-over rates, creating a stressful environment with potential constraints on dune plant production (Willis 1965, Kachi and Hirose 1983, Hester and Mendelssohn 1990, Hesp 1991, Maun 1994). Despite the possibility of low productivity potential, the biomass, growth rates, and nutrient content of dune plants are similar or higher than similar plants in other coastal communities (Deshmukh 1977, Ripley and Pammenter 2004). Findings from these studies and others suggest that dune ecosystems are more productive than their inherent nutrient conditions might imply (Willis and Yemm 1961, van der Valk 1974, Pavlik 1983, Ripley and Pammenter 2004) and that dune plant communities are likely donor controlled, with their production dependent on outside nutrient sources. Specifically, coastal beaches are frequently subsidized with high quantities of allochthounous biomass (e.g., macrophyte wrack) from the coastal ocean, rocky shores, and estuary areas (Colombini and Chelazzi 2003, Dugan et al., 2003, Griffiths et al. 1983, Orr et al. 2005). Macrophyte wrack can increase the nutrient availability (Harrison and Mann 1975, Rice and Tenore 1981, Levinton et al. 1984, Pellikaan 1984, Tenore et al. 1984).

Wrack supply to the beach is variable in space and time with deposition patterns being strongly influenced by ocean productivity, buoyancy characteristics, nearshore hydrodynamic patterns, and coastal geomorphology, among other factors (Orr et al. 2005, Liebowitz et al 2016, Reimer et al 2018). Once stranded, the beach wrack begins to break down and decompose via biotic and abiotic processes (Rossi and Underwood 2002, Mateo et al. 2003, Orr et al. 2005, Mews et al. 2006, Dugan et al. 2011, Rodil et al. 2019,). Nutrients resulting from macrophyte decomposition, and any remaining fragmented wrack debris, can be adsorbed to beach sand and then transported further inland to the upper beach and foredune by wind or large waves (Cardona and García 2008, Oldham et al. 2014).

Marine wrack is an important nutrient source for coastal dune vegetation and a critical factor in controlling plant primary productivity in sandy dune ecosystems (Cardona and Garcia 2008, Williams and Feagin 2010, Del Vecchio et al. 2013, 2017). For example, Del Vecchio et al. (2013, 2017) found that the application of macrophyte wrack resulted in a doubling of plant biomass and significant increases in tissue nutrient content. Studies such as these suggest that coastal dune vegetation is likely to be nutrient limited despite the important role of marine subsidies to these systems, but very few studies have tested this possibility. For example, a mesocosm study in Western Europe, van den Berg and colleagues (2005) found that nitrogen addition to dune grass species resulted in significant increases in aboveground plant biomass. Another study in Eastern Asia, conducted by Kachi and Hirose (1983), found that dune grasses were deficient in nitrogen, rather than phosphorous, while a study by Willis (1963) in English dunes found dune grasses were co-limited by nitrogen and phosphorous.

On U.S. Pacific Northwest coast, little is known about the source of nutrients to dune vegetation and whether dune plants are nutrient limited. In this system, nearly 45% of the coast is dune-backed (Cooper 1958) and has become densely vegetated by sediment-stabilizing invasive beachgrasses in the last century (Hacker et al. 2012). Prior to 1900, U.S. Pacific Northwest coastal dunes were highly transient and sparsely vegetated with native plant species, such as American dune grass, *Elymus mollis*. In the early 1900s, dunes in the region were managed to optimize dune stabilization through the planting of two non-native grass species, European beachgrass (*Ammophila arenaria*) and American beachgrass (*Ammophila breviligulata*). The shift in dominance from the native *E. mollis* to the invasive *A. arenaria* dramatically altered coastal dune structure along this coastline (Wiedemann and Pickart 1996). What was previously low-lying, transient, and sparsely vegetated became tall, stable, and densely vegetated.

Here we investigate the effects of nutrient additions on the production of beachgrasses and how these growth patterns vary spatially along foredune profile locations and sites along the U.S. Pacific Northwest coast. The study area lies in a region where ocean productivity and coastal geomorphology gives rise to contrasting marine subsidies for beach and dune communities. In Chapters 2 and 3, we found a positive relationship between marine macrophyte wrack subsidies, sand nitrate concentrations, nitrogen composition, and dune grass (the two non-native invasive beachgrass species *Ammophila arenaria* and *A. breviligulata*, and the native dune grass, *Elymus mollis*) productivity for U.S. Pacific Northwest beach and dune sites spanning 550 kilometers of the coast. We found that there was considerable variability in marine subsidies among sites and beach and foredune profile locations as a result of ocean upwelling, proximity to subsidy source, and beach and foredune sand supply and geomorphology. Dune grass production was connected to this variability in predictable ways. For example, we found that dune grass production was greatest at the foredune toe or crest, dependent on where sand deposition and nitrate concentrations were greatest, and lowest at the foredune heel, where sand deposition and nitrate concentrations were lowest. In addition, we found that marine nutrients are an important source of nitrogen for dune plants and that the composition and source of nitrogen in plants varies among species, sites, and foredune profile locations. Here we extend these findings by asking whether dune grasses are nutrient limited at sites and foredune profile locations that vary in their marine subsidy input.

Previous research has shown that nitrogen, phosphorous, and potassium can limit plant production in dune systems (Brown and Hafenrichter 1948, Willis and Yemm 1961, Augustine et al. 1964, Willis 1965, van der Valk 1974, Pavlik 1983) but can be increased with nutrient additions. The focus of the present study is to understand the growth response of beachgrasses to nutrient additions (both nitrogen and phosphorus), and to determine if nutrient use and production varies across the coast and along foredune profile locations. Specifically, we used two manipulative experiments to ask: (1) How does nutrient addition affect dune grass production at sites and foredune profile locations that vary in natural sand nitrate concentrations? (2) Does dune grass production and elemental composition vary with increasing nitrogen addition and do dune grasses experience nitrogen and phosphorous co-limitation? We hypothesize that dune plants will show greater plant production with nutrient additions but the magnitude of the response will differ depending on background sand nitrate concentrations. Moreover, we expect grass production and nitrogen elemental composition to increase with increasing nitrogen concentration and with phosphorus addition.

## 4.2 Methods

To determine how nutrient addition affects beachgrass production along a natural nutrient gradient, we conducted an experiment at three sites along the U.S. Pacific Northwest Coast that differed in their ambient nutrient availability: Long Beach, WA, Fort Stevens, OR, and South Beach, OR (Experiment 1) (Figure 4.1). To more explicitly test the degree to which dune vegetation is nutrient limited, we manipulated nutrient concentrations of nitrogen and phosphorous in a single-site experiment at Long Beach, WA (Experiment 2). The Long Beach site is located on the Long Beach Peninsula, a coastal barrier spit between the Pacific Ocean and the Willapa Bay estuary, north of the Columbia River mouth in southern Washington. In Oregon, the Fort Stevens site is located south of the Columbia River mouth and the South Beach site located south of Yaquina Bay estuary. Each of these dune-backed sites vary in their dune vegetation, subsidy exposure, and sand nutrient condition (Chapter 2). While the dominant beachgrass species on the Long Beach Peninsula is *Ammophila breviligulata*, *A. arenaria* is the dominant beachgrass species at South Beach, and both species co-occur at Fort Stevens. The native *E. mollis* is present at all sites in low densities.

The geographic position and nearshore dynamics of the study sites result in varying nutrient conditions from marine subsidies. In Chapter 2, we found that sand nitrate concentration was greatest at Long Beach and Fort Stevens and decreased at South Beach and that nitrate concentration was greatest at the foredune toe and decreased across the foredune. Long Beach had the highest wrack biomass, followed by Fort Stevens and South Beach, which did not differ. The Fort Stevens site had relatively high sand nitrate concentrations because it is located near the Columbia River plume where, under upwelling conditions, nitrate concentrations are elevated due to tidal mixing with nutrient-rich coastal seawater (Lohan and Bruland 2006, Bruland et al. 2008).

### 4.2.2 Experimental Design and Dune Grass Measurements

#### *Experiment 1*

In June 2016, thirty 0.25 $m^2$ permanent plots were established at the foredune toe, crest, and heel profile locations at the three sites described above: Long Beach, WA, Fort Stevens, OR, and South Beach, OR (Figure 4.1). At each foredune profile location, five blocks of two treatment plots were established. Paired treatments within a block were spaced approximately 1 m apart and blocks were spaced approximately 3 m apart for independence.

The two treatments applied were (1) no added nutrients (control) and (2) macronutrient addition. To each nutrient addition plot, 15 g of the macronutrient fertilizer, Lily Miller's Ultra Green (10% total N, 10% $P_2O_5$, 10% $K_2O$), was added in dry prill form. The 15 g of fertilizer is equivalent to 60 kg N:P:K/ha, and was applied to all nutrient addition quadrats twice over the course of the study for a total of 120 kg N:P:K/ha/yr. As a point of reference, mature temperate forest stands and many agricultural systems have an annual nitrogen requirement of approximately 100 kg N/ha/yr (Kreutzer et al. 2009, Butterbach-Bahl et a. 2011).

The experiment lasted until June 2017 for a total of twelve months. A number of grass response variables were measured at the start and end of the experiment. In the field, shoot densities (number/0.25m$^2$) were counted. In addition, to estimate total biomass (g/0.25 m$^2$), shoot biomass (g/shoot) and shoot length (cm), "individual" plants (defined as the shoot or shoots attached to one rhizome) of each dune grass species were collected at the start (near each of the plots) and end (in the plots themselves) of the experiment. The grass samples were air-dried and measured for shoot biomass (g) and shoot length (cm). These samples allowed for starting and ending measurements of dune grass production so that experimental changes could be determined.

*Experiment 2*

In March 2018, ninety 0.25 m$^2$ permanent plots were established at the foredune toe, crest, and heel profile locations at the Long Beach, WA site. Each profile location had six blocks with five nutrient treatment plots, including (1) no added nutrients (control), (2) low nitrogen addition (N1), (3) medium nitrogen addition (N2), (4) high nitrogen addition (N3), and (5) high nitrogen plus high phosphorous addition N3+P). Each block was spaced 3 m apart, and within a given block, each treatment plots was spaced approximately 1 m apart.

Fertilizer application began in March 2018 and took place every four months until March 2019, for a total of three fertilizer applications per year. Relatively high levels of nitrogen fertilizer were used to compensate for potential nutrient loss in this highly dynamic system. The fertilized plots received applications of nitrogen fertilizer in the form of calcium nitrate (15.5 – 0 – 0) and phosphorous fertilizer in the form of Treble Super Phosphate (0 – 45 – 0). For the nitrogen only treatments, 4.83 g, 9.67 g, and 19.35 g of fertilizer was applied for the low, medium, and high concentrations, respectively. These additions were equivalent to 29.9 kg N/ha (87.7 kg N/ha/yr), 59.9 kg N/ha (179.7 kg N/ha/yr), and 119.97 kg N/ha (359.91 kg N/ha/yr), respectively. For the high nitrogen plus high phosphorous treatment, 19.35 g of nitrogen fertilizer and 6.6 g of phosphorous fertilizer was added, equivalent to 119.97 kg N/ha (359.91 kg N/ha/yr) and 118.8 kg P/ha (356.4 kg P/ha/yr). Phosphorous was added to the highest nitrogen concentration treatment to test for phosphorous co-limitation, especially in high nitrogen addition treatments.

The same grass response variables were measured at the start and end of Experiment 2 as were measured in Experiment 1. In addition, the grass samples in Experiment 2 were analyzed for elemental composition at the end of the experiment. Leaf blade clippings of the grasses from the same species, treatment, block, and profile location were combined and ground to a fine, homogenous powder using a Spex Sigma Prep 8000D Mixer/Mill plant grinder. Sampled were then analyzed for nutrient content (%N, %C, and %S) in the Crop and Soil Science Lab at Oregon State University, Corvallis, OR.

### 4.2.3 Statistical Analyses

Data were analyzed using R version 3.5.3 (R Development Core Team 2019). Data were checked visually for normality using residual plots against predicted values, and the data met these assumptions in all cases.

For Experiment 1, we used 3-way ANOVAs to test for the difference in dune grass production [shoot density (no./0.25m$^2$), total biomass (g/0.25m$^2$), biomass per shoot (g), and shoot length (cm)] among sites, nutrient addition treatments, dune profile locations, and their interactions. In this experiment, the data were analyzed irrespective of dune grass species (*A. breviligulata*, *A. arenaria*, and/or *E. mollis*) present in the plots. For Experiment 2, we used 2-way ANOVAs to test for the difference in dune grass production [shoot density (no./0.25m$^2$), total biomass (g/0.25m$^2$), biomass per shoot (g), and shoot length (cm)] among nitrogen addition treatments, foredune profile locations, and their interactions. In this experiment, the data were analyzed for *A. breviligulata,* the only species present in the plots, with the exception of sparse *E. mollis* in the foredune toe plots. Tukey HSD post hoc tests were conducted on significant factors unless interactions were found, in which case one-way ANOVAs and Tukey HSD post hoc comparisons were conducted between levels of each factor (Underwood 1997).

To control for potential differences in the response variables among plots at the start of the experiment, we calculated response ratios (RR) for each treatment/profile location combination of each of the response variables using a

BACI index ([ln ($N_{\text{Final Experimental}}/N_{\text{Initial Experimental}}$)/($N_{\text{Final Control}}/N_{\text{Initial Control}}$)]). Confidence intervals (± 95% CI) were calculated around the RR means and considered statistically significant if the confidence intervals did not overlap zero.

## 4.3 Results

*Experiment 1*

In the nitrogen addition experiment across sites, the shoot density (number/0.25 $m^2$), total biomass (g/0.25 $m^2$), shoot biomass (g/shoot), and shoot length (cm) of dune grasses generally increased with nutrient additions. The extent of grass production increase relative to the control depended on site and foredune profile location (Figure 4.2, Table 4.1). At the site level, South Beach dune grasses had the greatest positive response to nutrient additions compared to Long Beach and Fort Stevens. Fort Stevens showed almost no response to added nutrients. At the profile level, the foredune heel had the greatest positive response to nutrient additions compared to the foredune crest and toe (Figure 4.5). The foredune toe had the most muted response to added nutrients.

*Experiment 2*

In the nitrogen and phosphorus addition experiment, *Ammophila breviligulata* shoot density (number/0.25 $m^2$) and total biomass (g/0.25 $m^2$) generally increased with added nitrogen, especially at the crest and heel foredune profile locations (Figure 4.3, Table 4.2). Interestingly, the increases were mostly incremental except for the highest nitrogen and nitrogen plus phosphorus additions, for which the response was more positive and different from zero compared to the other nutrient treatments

(Figure 4.6). Grass shoot biomass and shoot length either did not change or decreased, especially with the addition of phosphorus (Figure 4.3, 4.6).

The elemental composition of the grasses showed an incremental increase in %N and %S, no change in %C, and a decline in C:N across nitrogen addition treatments (Figure 4.4, 4.7, Table 4.3). Beachgrass treated with N3+P had the highest %N and %S and the control had the lowest %N and %S (Figure 4.6, Table 4.3).

## 4.4 Discussion

In this study, we found that dune grasses along the U.S. Pacific Northwest coast are nutrient limited, with nutrient additions differentially affecting beachgrass production at sites and foredune profile locations that vary in natural sand nitrate concentrations. We found treatment effects across sites and profile locations, particularly at South Beach and the foredune crest and heel, where the effect of nutrient addition was greatest compared to the other sites (Long Beach and Fort Stevens) and profile locations (toe). The differences across sites led us to further explore if dune grass production and elemental composition varies with increasing nutrient additions and the potential of co-limitation with phosphorous. We found that nitrogen additions resulted in increased grass shoot density, total biomass, and plant tissue %N and %S, and there was little support for phosphorus co-limitation. However, grass shoot biomass and shoot length either did not change, or declined, with added nitrogen and phosphorus.

Below, we describe in more detail the reasons behind the observed production response of dune grasses to nutrient addition and consider the implications of these patterns given variability in marine subsidies and dune grass production along the U.S. Pacific Northwest Coast.

*Multi-site dune grass production responses to single treatment nutrient addition*

We showed that the effect of nutrient additions to dune grass production varies among sites along the U.S. Pacific Northwest (Figure 4.2, Table 4.1). These site-specific differences are likely due to differences in the nutrient conditions at these sites, which are correlated with variability in marine wrack subsidies and sand supply (Chapter 2). We showed in Chapter 2 that Long Beach has the greatest macrophyte wrack compared to Fort Stevens and South Beach. In addition, Long Beach and Fort Stevens both have much higher sand nitrate concentrations compared to South Beach. The high sand nitrate values at Fort Stevens are likely the consequence of the Columbia River plume where, under upwelling conditions, nitrate concentrations are elevated due to tidal mixing with nutrient-rich coastal seawater (Lohan and Bruland 2006, Bruland et al. 2008).

In addition to site variability, we found differences in dune grass responses to nutrient additions across the foredune profile locations. We found that the greatest beachgrass production responses to nutrient addition were at the foredune heel and crest. This result makes sense given that nitrate concentrations are greater at the middle of the beach and foredune toe compared to the foredune heel (Chapter 2), thus providing greater nutrient resources at this profile location.

The more northern sites in the study region (Long Beach and Fort Stevens) are also subject to higher shoreline change rates and thus greater sediment supply to the beach (Ruggiero et al. 2013). In Chapter 2, we found that sites with greater sediment supply have higher sand nitrate concentrations at the foredune toe and greater dune grass production as well.

Taken together, the relationships between nutrient addition and dune grass production we observed across sites could be a consequence of differential sand nitrate concentrations, a result of differential macrophyte wrack deposition, ocean conditions, and sand supply. Similarly, the greater treatment effects on dune plant total biomass, biomass per shoot, and shoot length observed at the foredune crest and heel could be associated with the reduction in available marine nutrients at these locations.

### *Beachgrass production responses to multi-treatment nutrient additions*

Our multi-treatment nutrient additions showed that beachgrasses respond incrementally to added nitrogen and phosphorus and that the threshold concentrations are high (Figure 4.3, Table 4.2). In addition, phosphorus increased shoot densities but either neutrally or negatively affected biomass measures and shoot length (Figure 4.6). Thus, our results suggest that foredune grasses along the U.S. Pacific Northwest coast are nitrogen limited but unlikely co-limited with phosphorus.

In both marine and terrestrial environments, supplies of nitrogen and phosphorous—nutrients critical for plant growth—frequently limit the growth of primary producers (Vitousek and Howarth 1991). When vegetation is fertilized with one or all of these essential macronutrients, and increases in plant biomass production are observed (Güsewell et al. 2003), it is likely that the vegetation is nutrient limited. Given this, our grass production and foliar nutrient content results support the hypothesis that foredune vegetation are nitrogen limited. Interestingly, sulfur content mirrored nitrogen content in our treatments, with both increasing with each increase in nutrient concentration, suggesting co-regulation or a regulatory interaction, of nitrate and sulfate uptake. Several studies from other plant systems have established regulatory interactions between sulfate and nitrate (e.g., Reuveny et al. 1980, Cacco et al. 1983, Brunold and Suter 1984).

Nitrogen limitation has also been observed in coastal dune grass species from other parts of the globe (Kooijman et al.1998, Jones et al. 2004). Some studies, however, have shown neutral responses of dune vegetation to nitrogen addition. For example, in a fertilization experiment conducted in the Dutch coastal dunes, ten Harkel and van der Meulen (1996) found that nitrogen addition did not affect vegetation, leading the authors to suggest that after decades of nitrogen deposition, vegetation had become phosphorous limited. Another study in the English dunes found evidence for co-limitation of nitrogen and phosphorous (Willis 1963).

While co-limitation of nitrogen and phosphorous is possible, and suggestively supported by observed increases in shoot density in the N3+P treatment at the foredune heel, beachgrass species could also be experiencing a change in resources allocation from shoot biomass to shoot density with phosphorous additions. Change in biomass allocation in response to nutrient manipulation has been observed in other grassland systems (e.g., Yan et al. 2016, 2019). In a recent study of the dry and warm grasslands of China, Yan and others (2016) found that plants adapted to low nutrient conditions allocated less biomass to individual stems. Similarly, N and N+P fertilization research by Li et al. (2018) found that a species of coniferous tree generally increased biomass allocation to needles under all fertilization conditions, except under P fertilization. As a consequence of their results, the authors suggested that P fertilization caused a nutrient imbalance and subsequent negative effects on resource partitioning within the foliage.

### *Conclusions*

This study suggests that US Pacific coast dune grasses are generally nutrient limited, but this limitation depends on site and foredune location. Given the variability in marine subsidies and geomorphology of these beaches and dunes, the potential for marine nutrients to influence dune grass production is high. With greater dune grass production, particularly shoot density, there is the potential for better sand capture and dune building as a result (Hacker et al. 2012, Zarnetske et al. 2012, Biel et al. 2019). This direct correlation between shoot density and dune building thus has the potential to significantly affect the ecosystem functions and services of dunes should nutrient provisions change.

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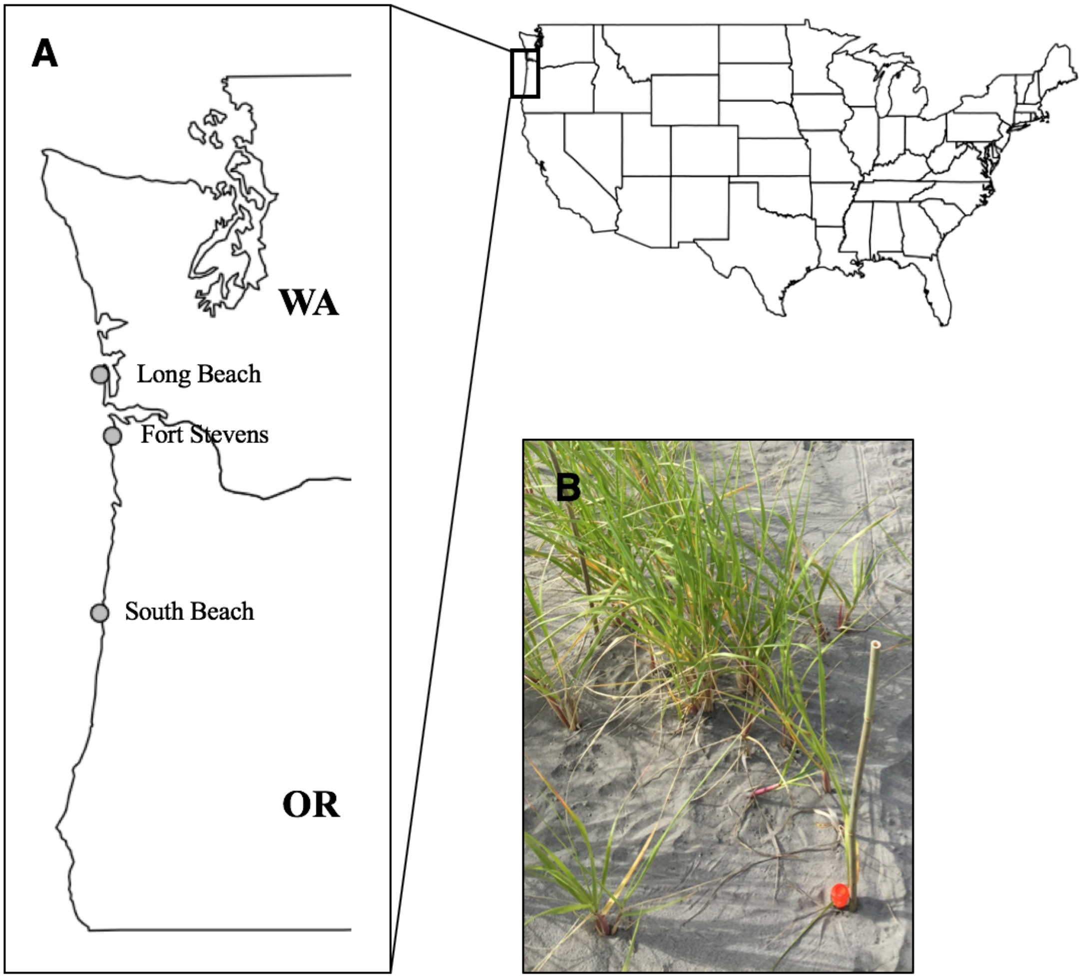

**Figure 4.1.** (A) Map of study sites used to evaluate the response of dune grass species to nutrient addition along the U.S. Pacific Northwest coast. Sites, from north to south, include Long Beach (WA), Fort Stevens (OR), and South Beach (OR). (B) Photo of a nutrient addition plot with the American beachgrass, *Ammophila breviligulata*.

**Figure 4.2.** Mean (± SE) (A) shoot density (number/0.25 m$^2$), (B) total biomass (g/0.25 m$^2$), (C) shoot biomass (g), and (D) shoot length (cm) of dune grasses across treatments (control and nutrient addition), foredune profile locations, and sites. Foredune profile locations are listed, from left to right, with increasing distance from the beach (foredune toe, crest, and heel). Sites are listed from north to south (Long Beach (LB), Fort Stevens (FS), and South Beach (SB))(Figure 4.1). Note that values represent the mean of all grass species for a given site (i.e., LB: *Ammophila breviligulata* and *Elymus mollis*, FS: *Ammophila arenaria*, *A. breviligulata* and *E. mollis*, and SB: *A. arenaria* and *E. mollis*) at the end of the experiment.

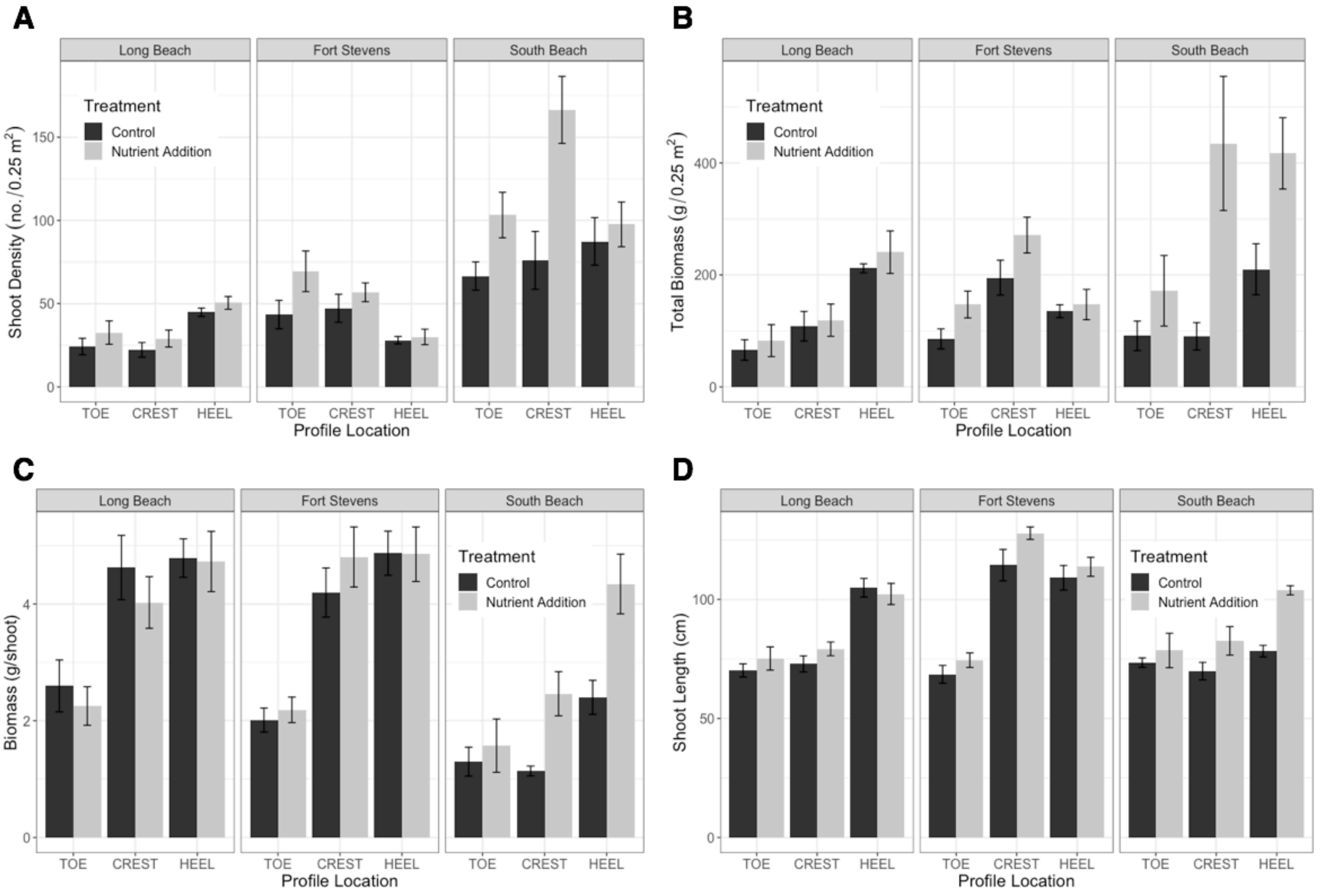
A
Long Beach
Fort Stevens
South Beach
Treatment
Control
Nutrient Addition
Shoot Density (no./0.25 m$^2$)
0
50
100
150
TOE
CREST
HEEL
Profile Location
B
Long Beach
Fort Stevens
South Beach
Treatment
Control
Nutrient Addition
Total Biomass (g/0.25 m$^2$)
0
200
400
TOE
CREST
HEEL
Profile Location
C
Long Beach
Fort Stevens
South Beach
Treatment
Control
Nutrient Addition
Biomass (g/shoot)
0
2
4
TOE
CREST
HEEL
Profile Location
D
Long Beach
Fort Stevens
South Beach
Treatment
Control
Nutrient Addition
Shoot Length (cm)
0
50
100
TOE
CREST
HEEL
Profile Location

**Figure 4.2.**

**Figure 4.3.** Mean (± SE) (A) shoot density (number/0.25 $m^2$), (B) total biomass (g/0.25 $m^2$), (C) shoot biomass (g), and (D) shoot length (cm) for dune grasses across treatments and foredune profile locations at Long Beach, WA (Figure 4.1). Nutrient addition treatments are listed as control (C), increasing nitrogen concentration (N1, N2, N3) and phosphorus addition (N3+P). Foredune profile locations are listed, from left to right, with increasing distance from the beach (foredune toe, crest, and heel). Note that shoot density (A) includes both *Ammophila breviligulata* and *E. mollis* but the other response variables (B-D) are for *A. breviligulata* alone. Measurements presented are from the end of the experiment.

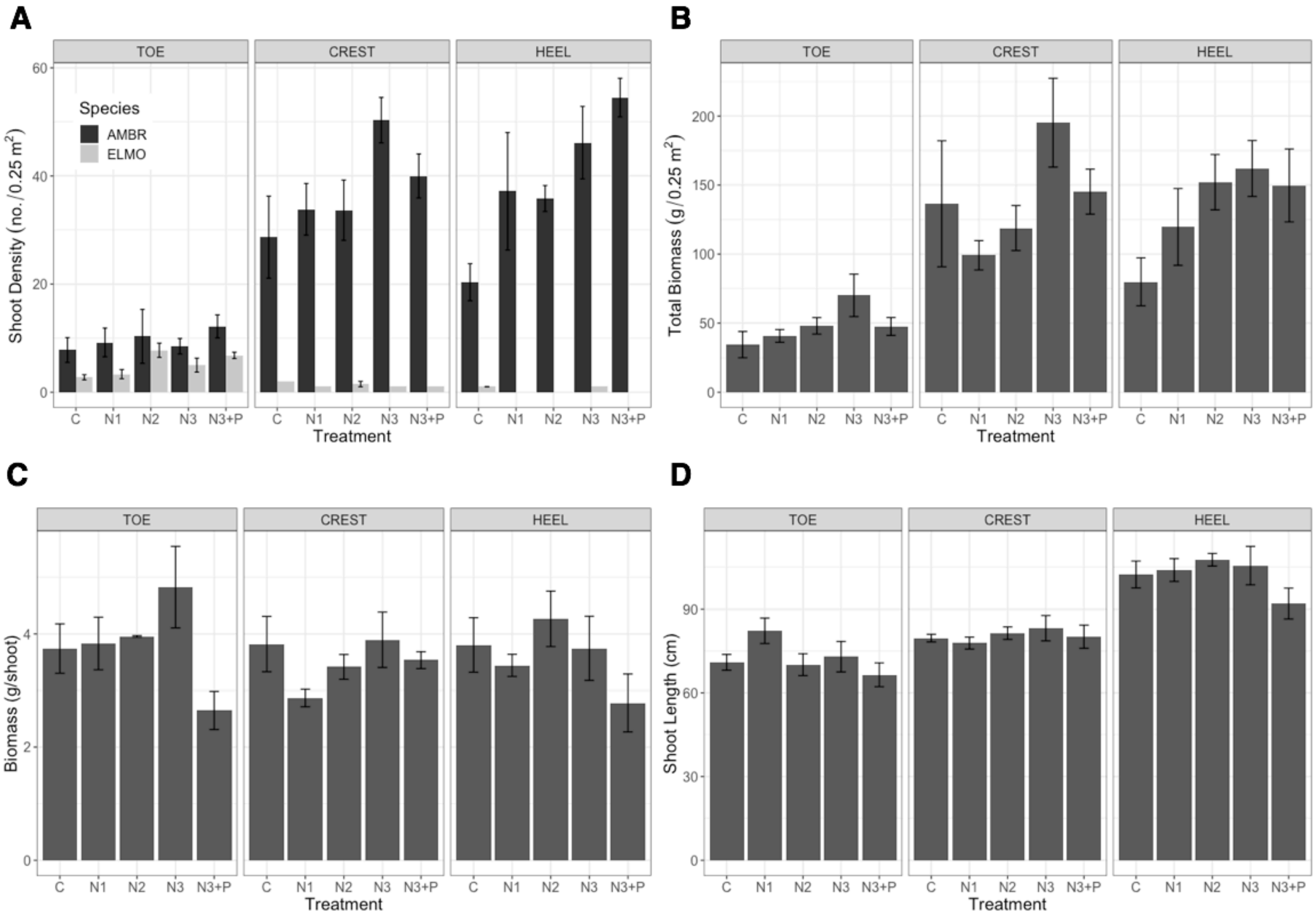
A
TOE
CREST
HEEL
Species
AMBR
ELMO
Shoot Density (no./0.25 m$^2$)
0
20
40
60
C
N1
N2
N3
N3+P
Treatment
B
Total Biomass (g/0.25 m$^2$)
0
50
100
150
200
C
Biomass (g/shoot)
0
2
4
D
Shoot Length (cm)
0
30
60
90

**Figure 4.3.**

**Figure 4.4.** Mean (± SE) (A) % nitrogen, (B) % carbon, (C) % sulfur, and (D) carbon:nitrogen (C:N) ratio in *Ammophila breviligulata* across treatments and foredune profile locations at Long Beach, WA (Figure 4.1). Nutrient addition treatments are listed as control (C), increasing nitrogen concentration (N1, N2, N3) and phosphorus addition (N3+P).. Foredune profile locations are listed, from left to right, with increasing distance from the beach (foredune toe, crest, and heel). Note that values presented are from the end of the experiment.

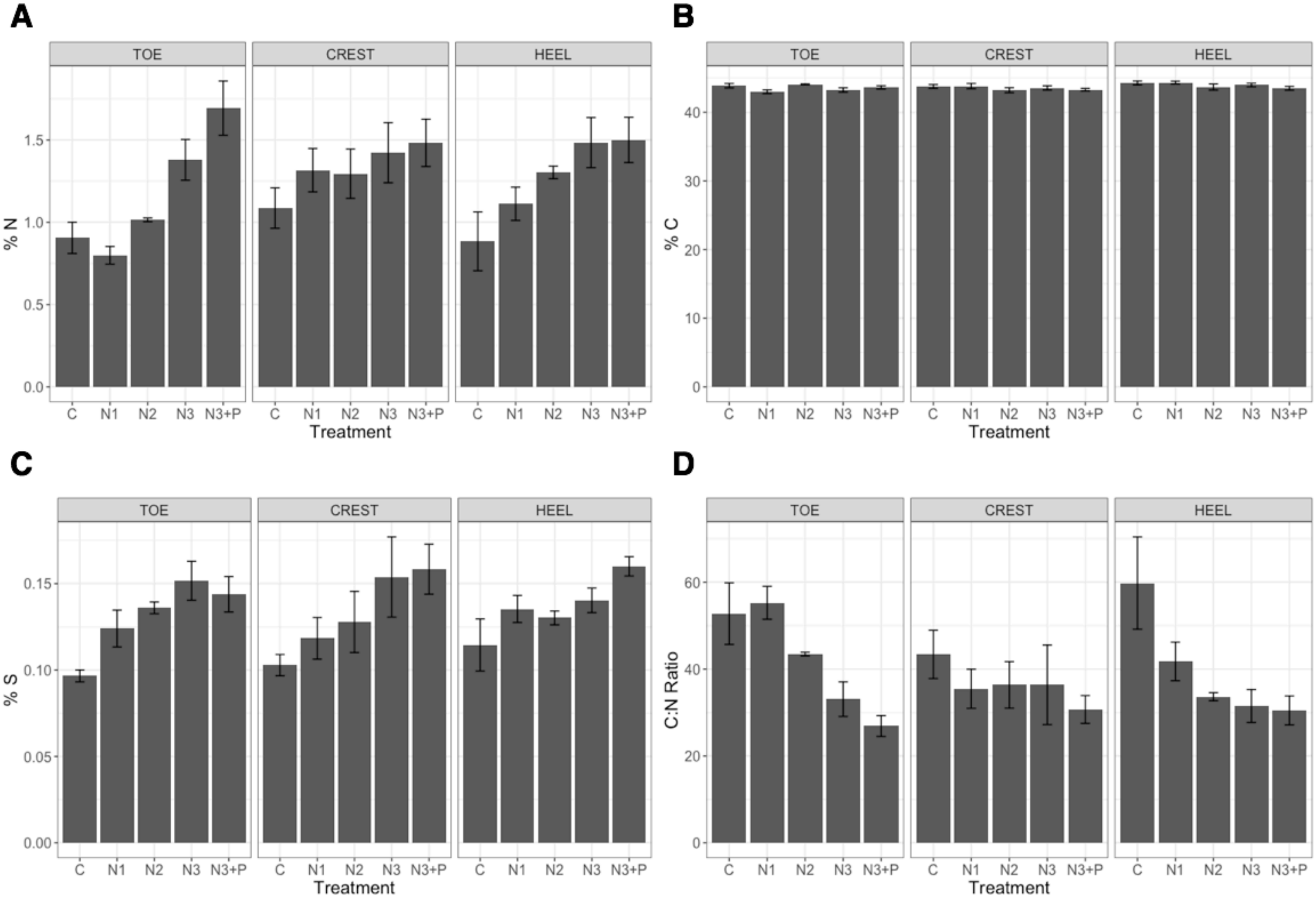
A
TOE
CREST
HEEL
% N
0.0
0.5
1.0
1.5
C
N1
N2
N3
N3+P
Treatment
B
% C
0
10
20
30
40
C
% S
0.00
0.05
0.10
0.15
D
C:N Ratio
0
20
40
60

**Figure 4.4.**

**Figure 4.5.** Mean (± 95% CI) response ratios for (A) shoot density (number/0.25 $m^2$), (B) total biomass (g/0.25 $m^2$), (C) shoot biomass (g), and (D) shoot length (cm) across foredune profile locations and sites. Foredune profile locations are listed, from left to right, with increasing distance from the beach (foredune toe, crest, and heel). Sites are listed from north to south (Long Beach (LB), Fort Stevens (FS), and South Beach (SB))(Figure 4.1). Note that values represent the mean of all grass species for a given site (i.e., LB: *Ammophila breviligulata* and *Elymus mollis*, FS: *Ammophila arenaria*, *A. breviligulata* and *E. mollis*, and SB: *A. arenaria* and *E. mollis*) at the end of the experiment Response ratios were calculated using a Before – After – Control – Impact design such that the final beachgrass variable measured in the experimental treatment was divided by the initial beachgrass variable measured in the experimental treatment (prior to nutrient addition) and then compared with the ratio of change between final and initial in the control treatment [$\ln(N_{\text{Final Experimental}}/N_{\text{Initial Experimental}})/(N_{\text{Final Control}}/N_{\text{Initial Control}})$].

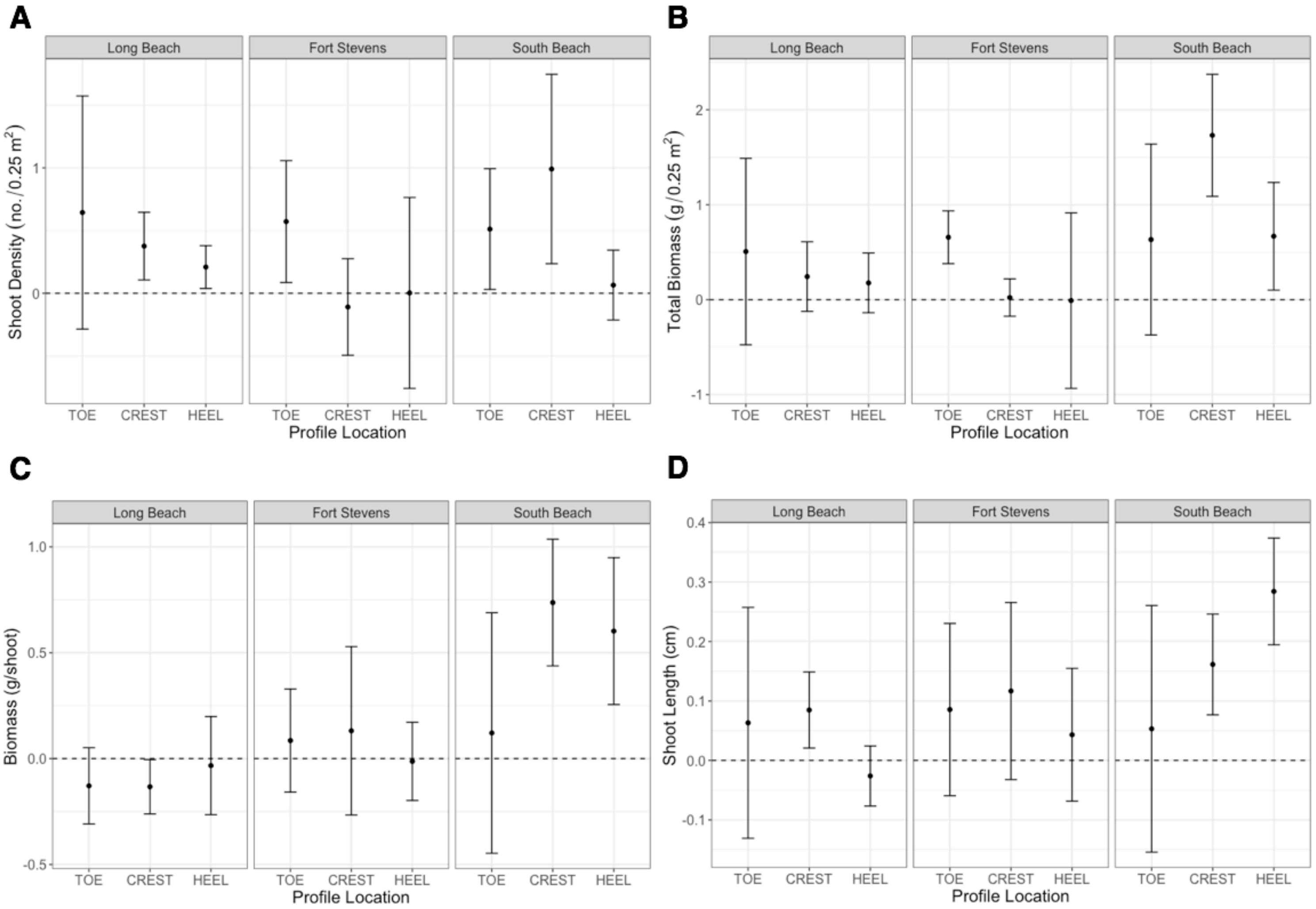
A
Long Beach
Fort Stevens
South Beach
Shoot Density (no./0.25 m²)
1
0
TOE
CREST
HEEL
Profile Location
B
Total Biomass (g/0.25 m²)
2
1
0
-1
C
Biomass (g/shoot)
1.0
0.5
0.0
-0.5
D
Shoot Length (cm)
0.4
0.3
0.2
0.1
0.0
-0.1

**Figure 4.5.**

**Figure 4.6.** Mean (± 95% CI) response ratios of (A) shoot density (number/0.25 $m^2$), (B) total biomass (g/0.25 $m^2$), (C) shoot biomass (g), and (D) shoot length (cm) across treatments and profile locations at Long Beach, WA (Figure 4.1). Nutrient addition treatments are listed as increasing nitrogen concentration (N1, N2, N3) and phosphorus addition (N3+P). Foredune profile locations are listed, from left to right, with increasing distance from the beach (foredune toe, crest, and heel). Note that shoot density (A) includes both *Ammophila breviligulata* and *E. mollis* but the other response variables (B-D) are for *A. breviligulata* alone. Response ratios were calculated using a Control - Impact design such that the final beachgrass variable measured in the experimental treatment was divided by the final beachgrass variable measured in the control treatment [$\ln(N_{\text{Final Experimental}}/N_{\text{Final Control}})$].

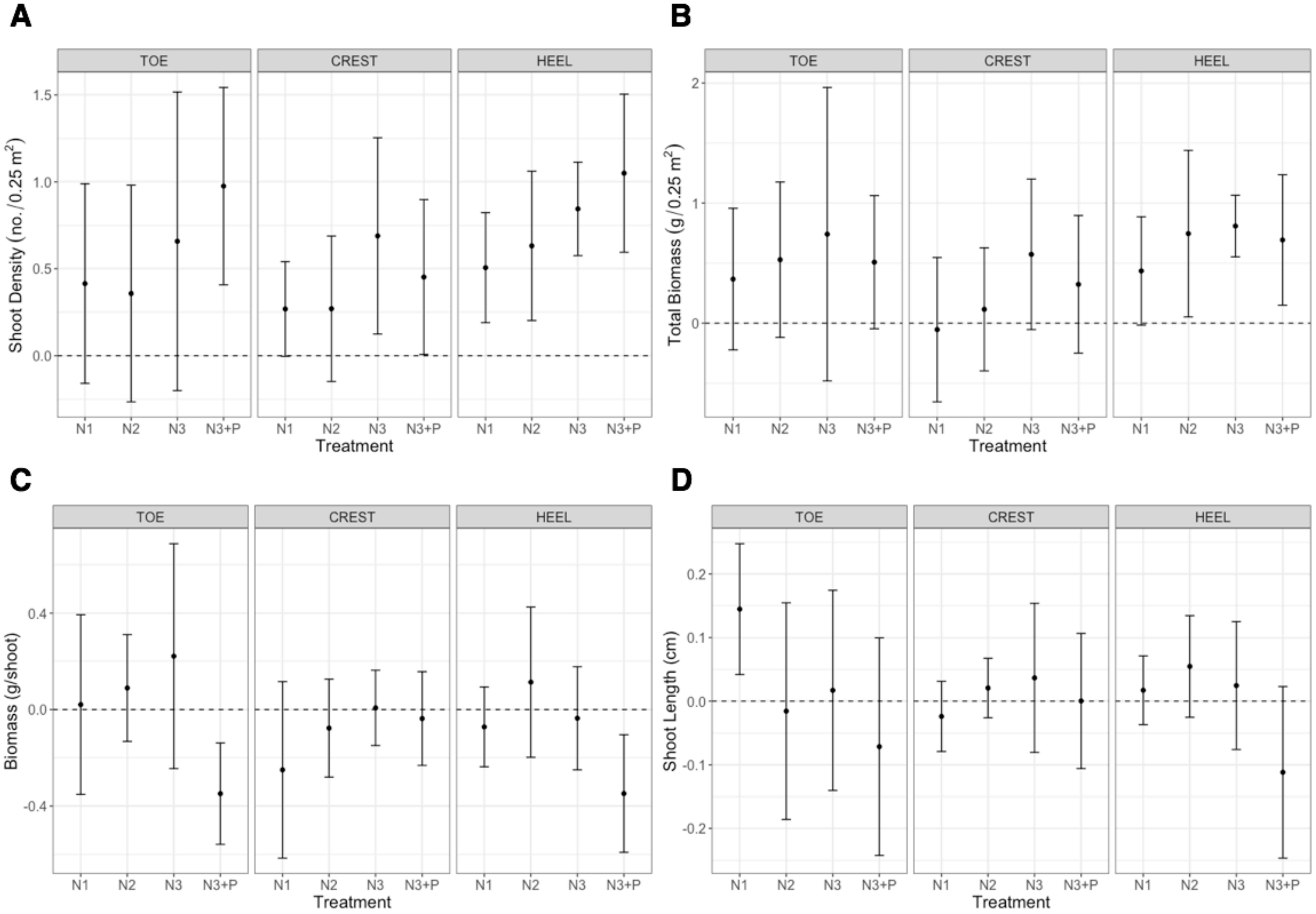
A
TOE
CREST
HEEL
Shoot Density (no./0.25 m²)
1.5
1.0
0.5
0.0
N1
N2
N3
N3+P
Treatment
B
TOE
CREST
HEEL
Total Biomass (g/0.25 m²)
2
1
0
N1
N2
N3
N3+P
Treatment
C
TOE
CREST
HEEL
Biomass (g/shoot)
0.4
0.0
-0.4
N1
N2
N3
N3+P
Treatment
D
TOE
CREST
HEEL
Shoot Length (cm)
0.2
0.1
0.0
-0.1
-0.2
N1
N2
N3
N3+P
Treatment

**Figure 4.6.**

**Figure 4.7.** Mean (± 95% CI) response ratios of A) % nitrogen, (B) % carbon, (C) % sulfur, and (D) carbon:nitrogen (C:N) ratio across treatments and profile locations at Long Beach, WA (Figure 4.1). Nutrient addition treatments are listed as increasing nitrogen concentration (N1, N2, N3) and phosphorus addition (N3+P). Foredune profile locations are listed, from left to right, with increasing distance from the beach (foredune toe, crest, and heel). Note that shoot density (A) includes both *Ammophila breviligulata* and *E. mollis* but the other response variables (B-D) are for *A. breviligulata* alone. Response ratios were calculated using a Control - Impact design such that the final beachgrass variable measured in the experimental treatment was divided by the final beachgrass variable measured in the control treatment [$\ln(N_{\text{Final Experimental}}/N_{\text{Final Control}})$].

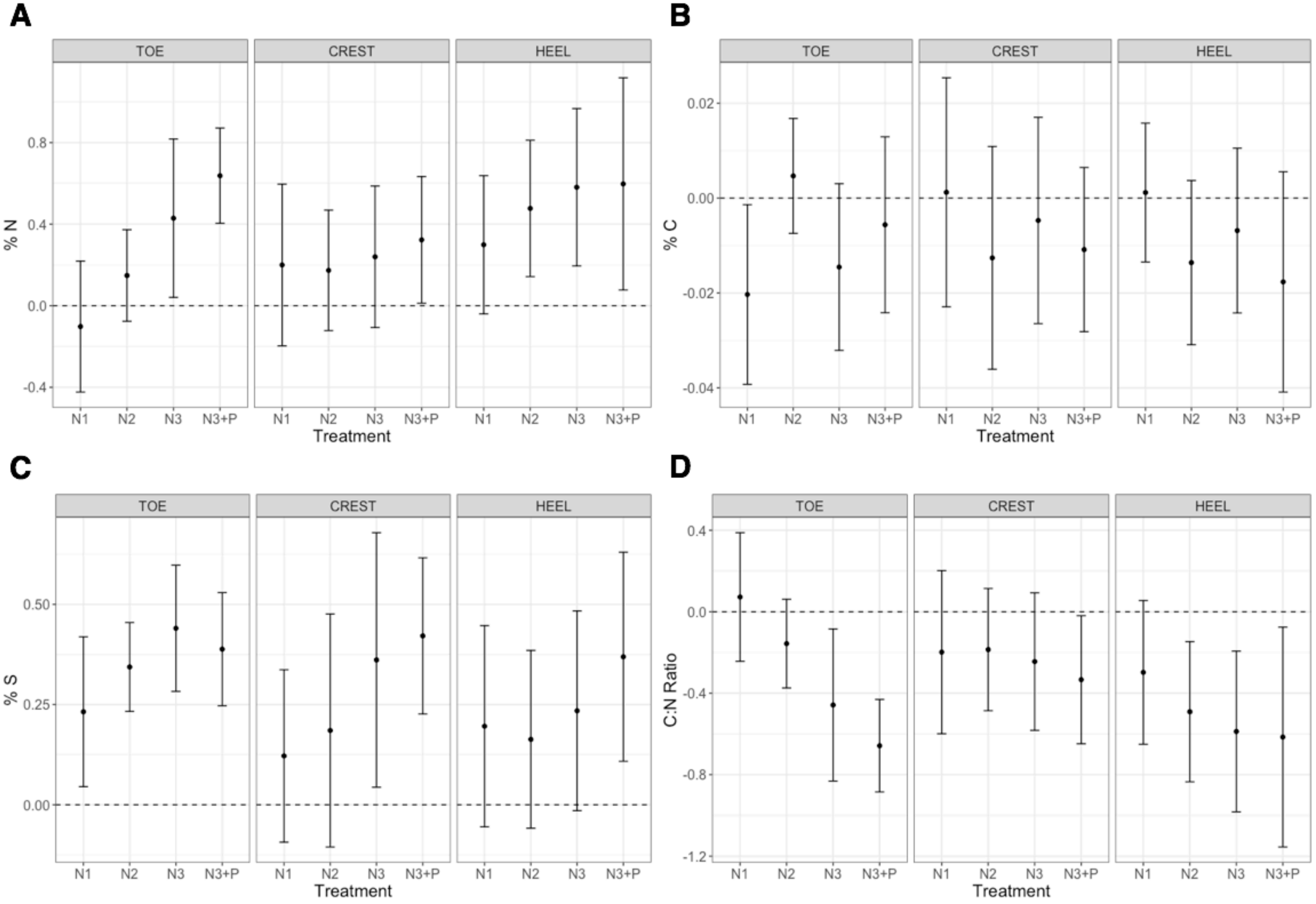
A
B
C
D
TOE
CREST
HEEL
% N
0.8
0.4
0.0
-0.4
% C
0.02
0.00
-0.02
-0.04
% S
0.50
0.25
0.00
C:N Ratio
0.4
0.0
-0.4
-0.8
-1.2
N1
N2
N3
N3+P
Treatment

**Figure 4.7.**

**Table 4.1.** Statistical results using ANOVAs for final (A) shoot density (no./0.25m$^2$), (B) total biomass (g/0.25m$^2$), (C) biomass (g/shoot), and (D) shoot length (cm) of dune grasses across treatments (C, E), foredune profile locations (toe, crest, heel), and sites (Long Beach, Fort Stevens, South Beach) (Figure 4.1). Significant P values are in bold. Tukey HSD post hoc tests P < 0.05.

| **Source of variation** | **df** | **SS** | **F** | **Prob > F** | **Tukey HSD post hoc test** |
|---|---|---|---|---|---|
| **Shoot Density (no./0.25 m$^2$)** | | | | | |
| Site | 2 | 73405 | 48.67 | **1.16E-14** | SB > FS = LB |
| Treatment | 1 | 10622 | 14.09 | **0.0003** | E > C |
| Profile location | 2 | 1920 | 1.27 | 0.2855 | |
| T*PL | 2 | 3342 | 2.22 | 0.1156 | |
| Residuals | 82 | 61837 | | | |
| Model | 7 | | 16.91 | **1.23E-13** | |
| **Total Biomass (g/0.25 m$^2$)** | | | | | |
| Site | 2 | 154577 | 6.15 | **0.0032** | SB > FS = LB |
| Treatment | 1 | 194841 | 15.51 | **0.0002** | E > C |
| Profile location | 2 | 240562 | 9.57 | **0.0002** | Heel = Crest > Toe |
| T*PL | 2 | 32264 | 1.28 | 0.2824 | |
| Residuals | 82 | 1030182 | | | |
| Model | 7 | | 7.08 | **1.33E-06** | |
| **Biomass per shoot (g)** | | | | | |
| Site | 2 | 52.8 | 26.99 | **9.85E-10** | LB = FS > SB |
| Treatment | 1 | 3.0 | 3.10 | 0.08193 | |
| Profile location | 2 | 85.3 | 43.59 | **1.27E-13** | Heel > Crest > Toe |
| T*PL | 2 | 1.3 | 0.69 | 0.50207 | |
| Residuals | 82 | 80.3 | | | |
| Model | 7 | | 20.81 | **8.01E-16** | |
| **Shoot length (cm)** | | | | | |
| Site | 2 | 7161.3 | 18.31 | **2.67E-07** | FS > LB = SB |
| Treatment | 1 | 1607.6 | 8.22 | **0.0053** | E > C |
| Profile location | 2 | 12532.2 | 32.04 | **5.22E-11** | Heel > Crest > Toe |
| T*PL | 2 | 117.7 | 0.30 | 0.7410 | |
| Residuals | 82 | 16035.3 | | | |
| Model | 7 | | 15.65 | **7.30E-13** | |

**Table 4.2.** Statistical results using ANOVAs for final (A) shoot density (no./0.25m$^2$), (B) total biomass (g/0.25m$^2$), (C) biomass (g/shoot), and (D) shoot length (cm) of dune grasses across nutrient treatments (C, N1, N2, N3, N3+P) and foredune profile locations (toe, crest, heel). Significant P values are in bold. Tukey HSD post hoc tests P < 0.05.

| Source of variation | df | SS | F | Prob > F | Tukey HSD post hoc test |
|---|---|---|---|---|---|
| **Shoot Density (no./0.25 m$^2$)** | | | | | |
| Treatment | 4 | 4179.2 | 7.36 | **4.72E-05** | N3+P = N3 ≥ N1 = N2 ≥ C |
| Profile location | 2 | 13581.4 | 47.80 | **4.12E-14** | Heel = Crest > Toe |
| T*PL | 8 | 1631.6 | 1.44 | 0.1958 | |
| Residuals | 75 | 10654 | | | |
| Model | 14 | | 9.75 | **6.74E-12** | |
| **Total Biomass (g/0.25 m$^2$)** | | | | | |
| Treatment | 4 | 40953 | 3.78 | **0.0074** | N3 ≥ N3+P = N2 ≥ N1 = C |
| Profile location | 2 | 154346 | 28.51 | **6.19E-10** | Crest = Heel > Toe |
| T*PL | 8 | 21489 | 0.99 | 0.4491 | |
| Residuals | 75 | 203042 | | | |
| Model | 14 | | 5.72 | **2.14E-07** | |
| **Biomass per shoot (g)** | | | | | |
| Treatment | 4 | 15.1 | 3.49 | **0.0114** | N3 ≥ N2 = C = N1 ≥ N3+P |
| Profile location | 2 | 1.3 | 0.61 | 0.5439 | |
| T*PL | 8 | 10.6 | 1.23 | 0.2956 | |
| Residuals | 75 | 81.1 | | | |
| Model | 14 | | 1.79 | 0.0564 | |
| **Shoot length (cm)** | | | | | |
| Treatment | 4 | 836.6 | 1.98 | 0.1068 | |
| Profile location | 2 | 14301.3 | 67.56 | **<2E-16** | Heel > Crest > Toe |
| T*PL | 8 | 992.2 | 1.17 | 0.3274 | |
| Residuals | 75 | 7938.3 | | | |
| Model | 14 | | 10.89 | **5.55E-13** | |

**Table 4.3.** Statistical results using ANOVAs for final nutrient content (%N, %C, %S, C:N) of dune grasses across nutrient treatments (C, N1, N2, N3, N3+P) and foredune profile locations (toe, crest, heel). Significant P values are in bold. Tukey HSD post hoc tests P < 0.05.

| **Source of variation** | **df** | **SS** | **F** | **Prob > F** | **Tukey post hoc test** |
|---|---|---|---|---|---|
| **Percent N** | | | | | |
| Treatment | 4 | 4.40 | 11.04 | **4.30E-07** | N3+P ≥ N3 ≥ N2 ≥ N1 = C |
| Profile location | 2 | 0.40 | 2.01 | 0.1417 | |
| T*PL | 8 | 1.08 | 1.36 | 0.2294 | |
| Residuals | 75 | 7.47 | | | |
| Model | 14 | | 4.22 | **2.08E-05** | |
| **Percent C** | | | | | |
| Treatment | 4 | 2.48 | 1.21 | 0.3153 | |
| Profile location | 2 | 3.29 | 3.20 | **0.0464** | N.S. |
| T*PL | 8 | 7.18 | 1.74 | 0.1022 | |
| Residuals | 75 | 38.58 | | | |
| Model | 14 | | 1.80 | **5.45E-02** | |
| **Percent S** | | | | | |
| Treatment | 4 | 0.0278 | 8.70 | **7.95E-06** | N3+P ≥ N3 = N2 ≥ N1 ≥ C |
| Profile location | 2 | 0.0005 | 0.31 | 0.7327 | |
| T*PL | 8 | 0.0032 | 0.50 | 0.8538 | |
| Residuals | 75 | 0.0599 | | | |
| Model | 14 | | 2.82 | **2.00E-03** | |
| **C:N** | | | | | |
| Treatment | 4 | 5713.1 | 8.51 | **1.03E-05** | C ≥ N1 ≥ N2 = N3 ≥ N3+P |
| Profile location | 2 | 511.4 | 1.52 | 0.2247 | |
| T*PL | 8 | 1969.2 | 1.47 | 0.1841 | |
| Residuals | 75 | 12593.3 | | | |
| Model | 14 | | 3.49 | **2.19E-04** | |

# Chapter 5 – General Conclusion

In an age of environmental change, the challenges of pursuing ecological studies are becoming increasingly daunting. These challenges are compounded by the interaction of biological and environmental processes operating at multiple spatial and temporal scales. As environmental change becomes more complex and issues more pressing, “deep dives” into the connectivity of ecosystems become even more essential to improve our understanding and preparedness for the future. In this dissertation, I used a meta-ecosystem approach to explore the importance of cross-ecosystem connectivity of U.S. Pacific Northwest coastal dunes. Coastal beaches and dunes make up approximately 45% of the Oregon and Washington coasts and are adjacent to many highly productive estuaries and rocky reefs. The plant communities at these sites experience variable ocean productivity, marine subsidies, and coastal sediment supply. The most common plant species are two non-native invasive grasses, the European beachgrass, *Ammophila arenaria,* and the American beachgrass, *Ammophila breviligulata*. Since their introduction in the early 1900’s, the *Ammophila* congeners have spread and rapidly transformed what was once an open, shifting, and sparsely vegetated habitat into one with continuous, stable, and densely vegetated foredunes. Despite this ecosystem-level transformation over the last century, little is known about the role of marine subsidies to the nutrient dynamics and primary production of dune grass communities.

In the past, most coastal dune research explored the role of marine subsidies to dune plant community structure at local spatial scales and short time scales (e.g., Cardona and Garcia 2008, Del Vecchio et al. 2013, van Egmond et al. 2019). However, multiple scale theory suggests that ecological patterns, such as primary production, are the result of local and regional scale processes (Guichard 2005, Gotelli et al. 2010, Gouhier et al. 2010). Thus, studying these ecosystems across large meta-ecosystem spatial and temporal scales is critical to understand dune ecosystem function and services. Here I used a combination of observations, laboratory analyses, and experiments to determine how nutrient subsidies and coastal geomorphology interact to influence dune plant production at local to regional scales along the U.S. Pacific Northwest coast.

In Chapter 2, I set out to answer if there is a connection between ocean productivity, in the form of marine subsidies, and dune ecosystem function, through dune grass production. I provide evidence that marine subsidies are common and predictable sources of nutrients to Pacific Northwest beaches and that they influence dune grass ecosystems in significant ways. Using extensive field surveys and plant and sand collections, I determined the patterns of oceanographic and geological factors, marine subsidies, and dune grass production and assessed the processes contributing to these patterns using multiple regression analyses. I found that patterns of macrophyte wrack across 15 beach sites were driven by ocean upwelling and distance from macrophyte source. Patterns of sand nitrate concentration were driven by the nutrient source immediately seaward to the profile location of interest, metrics of sand supply, and the geomorphology of the foredune. Finally, macrophyte wrack biomass and metrics related to sand supply were both important to dune grass production. These results suggest a strong connection between marine nutrients, sediment delivery, and vegetation production in US Pacific Northwest dunes. This study, conducted at a meta-ecosystem scale, suggests that changes in ocean productivity or sediment supply could have important implications to dune ecosystem structure, function, and services.

In Chapter 3, I asked whether dune plant species are using marine nutrients and whether this varied among sites and dune profile locations. Universally, plant species at the foredune toe were enriched with marine nitrogen compared to plants further away from the beach. A focus on beachgrasses (*Ammophila* spp.) showed that foliar $\delta^{15}N$ and nitrogen content varied among sites but nitrogen content did not vary across foredune profile locations. Regression models revealed that, for the most part, macrophyte wrack biomass and sand nitrate concentrations were unrelated to %N or $\delta^{15}N$ composition of the grasses. However, I did find that wider beaches and shorter foredunes had beachgrasses with slightly lower %N tissue content across foredune profile locations but the source of that nitrogen at the crest and heel had a higher marine signature. The results presented in this chapter corroborate earlier studies that beach nutrients, especially those with marine origin, are an important source of nitrogen for foredune plants.

Finally, the goal of Chapter 4 was to determine if beachgrasses in the U.S. Pacific Northwest are nutrient limited and whether nutrient use varies among sites and foredune profile locations. I found that dune grasses were nutrient-limited, with nutrient additions positively affecting dune grass production at sites and foredune profile locations that have higher wrack deposition and background sand nitrate concentrations. I also found that increased nitrogen and phosphorous increased grass shoot density, total biomass, and plant tissue %N. However, grass shoot biomass and shoot length either did not change, or declined, with phosphorus additions, suggesting that there was no phosphorus co-limitation. These results suggest that U. S. Pacific Northwest dune grasses are nutrient limited, especially at the foredune crest and heel, where background sand nitrate concentrations are lower.

Taken as a whole, my dissertation fills a critical gap in our understanding of coastal dune plant communities from a meta-ecosystem perspective, where I explicitly consider the role of marine subsidies from estuaries and nearshore coastal rocky reefs. These findings shed new light on the nutrient dynamics of Pacific Northwest beaches and dunes, important coastal interface habitats that provide critical ecosystem services such as coastal protection (e.g., Seabloom et al. 2013, Biel et al. 2017, Ruggiero et al. 2019). Moreover, coastal beaches and dunes sequester carbon (Jones et al. 2008, Drius et al. 2016, Bonito et al. 2017), provide essential wildlife habitat, and provide recreation services (Barbier et al. 2011). Such services are strengthened by marine subsidy-supported dune plant communities, which capture and stabilize sand, thereby shaping foredune morphology (e.g., Hesp 1989, Murray et al. 2008, Hacker et al. 2012, Zarnetske et al. 2012, 2015, Durán and Moore 2013, Biel et al. 2019). However, subsidy provisions may vary with predicted changes in ocean productivity, wave climates, and sea level rise. Thus, by way of vegetation production, changes in soil fertility can significantly impact ecosystem functions and services and should not be overlooked when considering coastal dune ecology.  It is important to explore these systems at larger meta-ecosystem scales.

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# Appendices

# Appendix A Chapter 2 Supplemental Tables and Figures for Methods

**Table A1.** Site and transect names and locations sampled in the study, including the length [measured from mean higher high water (MHHW) mark on the beach to the foredune toe; m] of the center transects (Appendix A Figure A1; for years 2015–2017) and their latitude and longitude (decimal degrees). The center transects are the same as those surveyed in Hacker et al. (2012), Reimer et al. (2018), and Biel et al. (2019).

| Site name and abbreviations | Transect location name | Center transect length (MHHW to foredune toe, (m)) | | | Latitude | Longitude |
|---|---|---|---|---|---|---|
| | | 2015 | 2016 | 2017 | | |
| Washington | | | | | | |
| Grays Harbor (GH) | GH18 | 71.9 | 72.1 | 58.4 | 46.8523 | -124.1134 |
| | GH09 | 109.5 | 174.9 | 78.7 | 46.8380 | -124.1084 |
| | GH05 | 97.5 | 65.0 | 225.0 | 46.7992 | -124.0993 |
| Leadbetter Point (LBP) | LB49 | 96.0 | 96.5 | 61.1 | 46.6191 | -124.0699 |
| | LBP8 | 92.9 | 77.1 | 20.5 | 46.6087 | -124.0691 |
| Long Beach (LB) | LB1020 | 115.0 | 101.9 | 103.5 | 46.5529 | -124.0616 |
| | LB05 | 98.4 | 159.9 | 148.0 | 46.4893 | -124.0584 |
| | LB36A | 77.2 | 130.5 | 85.1 | 46.3370 | -124.0663 |
| Oregon | | | | | | |
| Fort Stevens (FS) | FS02 | 64.5 | 65.3 | 50.3 | 46.2057 | -123.9983 |
| | FS03 | 100.0 | 92.6 | 77.8 | 46.1017 | -123.9434 |
| | FS01 | 76.2 | 81.3 | 72.3 | 46.0522 | -123.9316 |
| Nehalem Bay (NB) | NB03 | 90.5 | 59.9 | 55.0 | 45.6826 | -123.9400 |
| | NB02 | 100.4 | 57.2 | 47.8 | 45.6708 | -123.9404 |
| | NB01 | 91.8 | 62.4 | 39.5 | 45.6651 | -123.9409 |
| Cape Lookout (CL) | CL03 | 87.8 | 50.7 | 78.6 | 45.4273 | -123.9604 |
| | CL02 | 94.6 | 61.3 | 68.3 | 45.4217 | -123.9603 |
| | CL01 | 93.5 | 57.6 | 37.8 | 45.3810 | -123.9665 |
| Sand Lake (SL) | SL02 | 78.4 | 78.0 | 76.2 | 45.2859 | -123.9635 |
| | SL01 | 49.2 | 34.4 | 38.6 | 45.2823 | -123.9635 |
| | SL03 | 59.4 | 55.6 | 46.9 | 45.2809 | -123.9629 |
| Pacific City (PC) | PC03 | 55.0 | 48.0 | 87.8 | 45.1943 | -123.9687 |
| | PC01 | 83.4 | 70.7 | 40.2 | 45.1899 | -123.9690 |
| | PC02 | 70.6 | 50.3 | 55.2 | 45.1741 | -123.9706 |

**Table A1.** (Continued)

| | | | | | | |
|---|---|---|---|---|---|---|
| South Beach (SB) | SB03 | 80.8 | 58.6 | 40.9 | 44.6078 | -124.0683 |
| | SB02 | 43.4 | 69.4 | 82.2 | 44.6045 | -124.0670 |
| | SB01 | 45.6 | 59.5 | 104.7 | 44.5996 | -124.0669 |
| Siltcoos River (SILT) | SILT01VC | 59.2 | 62.9 | 43.9 | 43.8705 | -124.1572 |
| | SILT02 | 69.0 | 38.6 | 40.6 | 43.8676 | -124.1575 |
| | SILT03 | 67.4 | 49.3 | 54.4 | 43.8643 | -124.1582 |
| Dunes Overlook (DO) | DO01 | 57.3 | 46.4 | 60.6 | 43.8354 | -124.1634 |
| | DO02 | 62.5 | 62.4 | 65.3 | 43.8250 | -124.1658 |
| | DO03 | 78.0 | 52.8 | 63.8 | 43.8212 | -124.1663 |
| Umpqua Dunes (UD) | UD03 | 71 | 38.7 | 39.5 | 43.6084 | -124.2183 |
| | UD02 | 55.6 | 52.8 | 51.5 | 43.597 | -124.2215 |
| | UD01 | 62.1 | 43.8 | 46.5 | 43.5937 | -124.2226 |
| North Spit (NS) | NS01 | 58.7 | 35.1 | 48.5 | 43.4039 | -124.3049 |
| | NS02 | 55.6 | 46.2 | 63.5 | 43.4022 | -124.3056 |
| | NS03 | 65.2 | 41.4 | 61.8 | 43.3977 | -124.3089 |
| Bandon (BAN) | BAN-NR3 | 58.0 | 44.6 | 57.5 | 43.0646 | -124.4382 |
| | BAN-NR2 | 64.4 | 48.9 | 51.3 | 43.0584 | -124.4398 |
| | BAN-NR1 | 38.6 | 62.2 | 51.0 | 43.0444 | -124.4433 |
| Floras Lake (FL) | FL01 | 51.5 | 45.5 | 54.9 | 42.9034 | -124.5087 |
| | FL02 | 48.8 | 34.9 | 53.3 | 42.9006 | -124.5106 |
| | FL03 | 53.4 | 37.0 | 46.1 | 42.8985 | -124.5122 |

**Table A2.** List of the macrophyte genus and/or species identified in wrack samples collected across the study region (Figure 2.1) and over time (2015–2017), sorted by functional group.

| Functional Group | Species | |
|---|---|---|
| Kelp | *Alaria marginata* | *Macrocystis* sp. |
| | *Egregia menziesii* | *Nereocystis luetkeana* |
| | *Laminaria* spp. | *Postelsia palmaeformis* |
| | *Lessoniopsis littoralis* | |
| Eelgrass | *Zostera japonica* | *Zostera marina* |
| Other brown algae | *Analipus japonicus* | *Leathesia difformis* |
| | *Coilodesme californica* | *Melanosiphon intestinalis* |
| | *Colpomenia bullosa* | *Pelvetiopsis limitata* |
| | *Cystoseira geminata* | *Petalonia fascia* |
| | *Cystoseira osmundacea* | *Sargassum* sp. |
| | *Desmarestia* spp. | *Scytosiphon lomentaria* |
| | *Fucus* spp. | *Silvetia compressa* |
| | *Hesperophycus californicus* | *Soranthera ulvoidea* |
| Surfgrass | *Phyllospadix* spp. | |
| Green algae | *Acrosiphonia* sp. | *Derbesia marina* |
| | *Bryopsis corticulans* | *Enteromorpha* sp. |
| | *Chaetomorpha* sp. | *Kornmannia leptoderma* |
| | *Cladophora* sp. | *Ulva* spp. |
| | *Codium fragile* | |
| Dune vegetation | *Ammophila arenaria* | *Elymus mollis* |
| | *Ammophila breviligulata* | *Lathyrus japonicus* |
| | *Cakile* spp. | |
| Red algae | *Ahnfeltia* sp. | *Macstocarpus* spp. |
| | *Bossiella* spp. | *Mazzaella* spp. |
| | *Calliarthron tuberculosum* | *Microcladia* spp. |
| | *Callophyllis* sp. | *Nemalion elminthoides* |
| | *Ceramium* sp. | *Neorhodomela* spp. |
| | *Chondracanthus* spp. | *Odonthalia floccosa* |
| | *Corallina* sp. | *Palmaria palmata* |
| | *Cryptopleura* spp. | *Pikea californica* |
| | *Cryptosiphonia woodii* | *Plocamium* sp. |
| | *Cumagloia andersonii* | *Polyneura latissima* |
| | *Dilsea californica* | *Polysiphonia* sp. |

**Table A2.** (Continued)

| | | |
|---|---|---|
| | *Endocladia muricata* | *Porphyra* sp. |
| | *Euthora cristata* | *Prionitis lanceolata* |
| | *Gastroclonium subarticulatum* | *Pterocladia* sp. |
| | *Gelidium coulteri* | *Ptilota plumosa* |
| | *Gracilaria pacifica* | *Sarcodiotheca gaudichaudii* |
| | *Gracilariopsis andersonii* | *Schizymenia* sp. |
| | *Gymnogongrus griffithsiae* | *Serraticardia macmillanii* |
| | *Halosaccion glandiforme* | *Smithora naiadum* |
| | *Hymenena flabelligera* | *Sparlingia pertusa* |
| Other estuarine plants | *Carex deweyana* | *Salicornia* sp. |
| Freshwater vegetation | *Myriophyllum spicatum* | *Potamogeton richardsonii* |

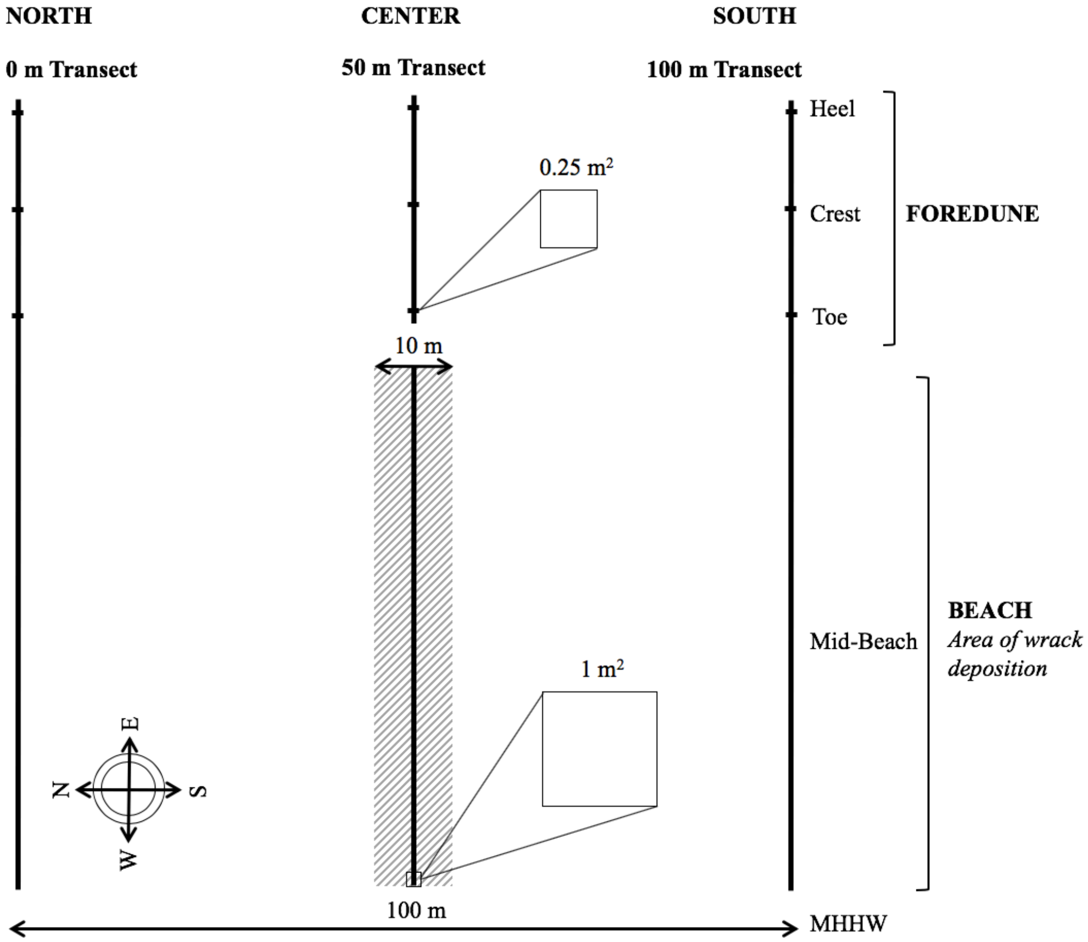

**Figure A1.** Diagram of the sampling design for macrophyte beach wrack, sand nutrients, and dune grass surveys. At each transect location (see Table A1), sampling took place along three replicate shore perpendicular transects spaced 50 meters (m) apart and extending landward from the mean higher high water (MHHW) mark on the beach to the base of the foredune. The total number of individual wrack patches within a 10 m swath around each of the transect lines was counted. More detailed wrack surveys were conducted along the central transect using 1 $m^2$ quadrats placed adjacent to each other. The center transect was the same transect surveyed in Hacker et al. (2012), Reimer et al. (2018), and Biel et al. (2019).

# Appendix B Chapter 2 Supplemental Text, Tables, and Figures for Seasonal Surveys of Macrophyte Wrack along the Pacific Northwest Coast

## Background

Marine subsidies (i.e., nutrients and organic matter) are important drivers of coastal food web dynamics, community structure, and ecosystem productivity (e.g., Polis and Hurd 1995, 1996, Kirkman and Kendrick 1997, Dugan et al. 2003, Lastra et al. 2008, Spiller et al. 2010, Piovia-Scott et al. 2013). Research in sandy beach ecosystems shows that variability in macrophyte wrack deposition patterns is attributable to multiple factors including ocean upwelling, macrophyte production, proximity to wrack source habitat, ocean currents, wave exposure, and coastal geomorphology (e.g., Orr et al. 2005, Jaramillo et al. 2006, Barreiro et al. 2011, Gómez et al. 2013, Liebowitz et al. 2016, Reimer et al. 2018). Macrophyte wrack deposition can vary seasonally, particularly in temperate regions where macrophyte productivity responds to variability in light and nutrients (e.g., Alcoverro et al. 1995, Orr et al. 2005, Barreiro et al. 2011, Jiménez et al. 2015). Seasonality in macrophyte wrack production, in particular, could affect the delivery of wrack to beaches and dunes and thus the nutrient pools available to primary and secondary producers living on beaches and dunes (e.g., Jędrzejczak 2002, Schlacher and Connolly 2009, Dugan et al. 2011, Nicastro et al. 2012, Lavery et al. 2013).

In this survey, our goal was to measure the seasonal variability in macrophyte wrack deposition on the U.S. Pacific Northwest dune-backed beaches used in the study (Appendix A Table A1). We wanted to know whether the abundance and distribution patterns of macrophyte wrack deposition varies over time in this region.

In particular, we asked (1) whether the abundance and species composition of macrophyte wrack deposition varies seasonally and (2) whether those seasonal patterns are similar at different sites over the study region. We hypothesized that macrophyte wrack abundance is strongly correlated with macrophyte production in estuaries and rocky reefs. We expect beaches have the greatest amount of macrophyte wrack in the late summer months, when macrophyte production from rocky reef and estuary sources is greatest (Hessing-Lewis and Hacker 2013, Menge et al. 2015). Concurrent with these seasonal fluctuations in production, we expected macrophyte wrack functional group diversity to increase from winter to summer and vary regionally, with eelgrass wrack dominating the northernmost site that is nearer to large estuaries, and kelp dominating the southernmost site that is nearer to large rocky reefs (Reimer et al. 2018).

## Methods

We surveyed three dune-backed beach sites, located in the northern, central, and southern regions spread across 550 km distance of the Pacific Northwest coastline (Figure 2.1E), for the abundance and species composition of macrophyte wrack. The three sites included Grays Harbor (GH) in Washington and Cape Lookout (CL) and Bandon (BAN) in Oregon (see Appendix A Table A1 for locations). All sites were located on the open coast but varied in their distance to nearest wrack source habitat (estuary and rocky reef), their exposure to ocean upwelling, and their shoreline change rates (Figure 2.1A-C). The northern site, GH, is located near multiple estuaries (Grays Harbor and Willapa Bay), is exposed to less intense upwelling, and has high and positive shoreline change rates. The central site, CL, is located adjacent to both an estuary (Netarts Bay) and rocky reef (Cape Lookout), is exposed to greater upwelling intensity, and has slightly negative shoreline change rates. The southern site, BAN, is located near multiple rocky reefs (e.g., Cape Perpetua, Cape Arago, Cape Blanco), is exposed to the greatest upwelling intensity, and has low but positive shoreline change rates.

At the three study sites, seasonal surveys of macrophyte wrack were conducted at three time periods, winter (January/February), spring (May/June), and summer (August/September) of 2016. Each site had three transect locations and within each transect location we placed three replicate shore perpendicular transects spaced 50 meters apart and extending landward from the mean higher high water (MHHW) mark to the base of the foredune (Appendix A Figure A1).

The transect surveys involved two measurements. First, we counted the total number of individual wrack patches within a 10 m swath around each of the transect lines (Appendix A Figure A1). Patches were visually surveyed as discrete piles of macrophytes that were separate from one another. Second, more detailed wrack patch surveys were conducted along the central transect using 1 $m^2$ quadrats placed adjacent to each other (Appendix A Figure A1). Within each quadrat, the numbers of patches were recorded, and patches were individually collected and brought back to the laboratory where they were frozen for later analysis. To determine the biomass of each species, patch samples were sorted by species (see species list in Appendix A Table A2), dried to a constant mass at 45°C, and then weighed.

Data were analyzed using R version 3.5.3 (R Development Core Team 2019). We used two-way ANOVAs and Tukey HSD post hoc tests to determine if there was a difference in macrophyte wrack on beaches [using the response variables: wrack patch density (number/$m^2$), wrack patch biomass (g/patch), total wrack biomass (g/transect)] over sites and seasons. We examined the composition of wrack by placing each species into one of nine functional groups: kelp, other brown algae (excluding kelp), green algae, red algae, surfgrass, eelgrass, other estuarine plants (excluding eelgrass), dune vegetation, and freshwater vegetation (Appendix A Table A2). We used PERMANOVA non-multidimensional scaling (Bray-Curtis similarity, RStudio, vegan; Oksanen et al. 2019) to determine how wrack functional group community structure changes across sites and seasons using the proportion of total wrack biomass per functional group per transect location.

## Results

Wrack patch density (number/$m^2$), wrack patch biomass (g/patch), and total wrack biomass (g/transect) all varied with site and/or season but there were no site x season interactions (Figure B1, Table B1). Comparison of the study sites showed that wrack patch density was least abundant at BAN and most abundant at CL and GH, which did not differ. Across all sites within the survey region, we found that wrack patch density and both measures of wrack biomass were greatest in the summer compared to the spring and winter, which did not differ (Table B1).

Macrophyte wrack functional group composition varied with site and season but there was no site x season interaction (Figure B2, Table B1). The functional group richness and composition varied from winter to summer, but the patterns depended on site (Figure B2). Macrophyte wrack at GH and CL increased in functional group richness from winter to summer, with eelgrass as the dominant functional group in the spring and summer. Likewise, BAN increased in functional group richness from winter to summer, with kelp as the dominant functional group by summer. Interestingly, dune vegetation, particularly beachgrass, was a common constituent of wrack patches in the winter (GH and CL) and spring (BAN).

## Discussion

The seasonal and site patterns of wrack deposition on beaches that we report here are consistent with the seasonal variability in macrophyte production seen along the Pacific Northwest coast (Hessing-Lewis and Hacker 2013, Menge et al. 2015) and in other regions of the world (e.g., Duarte 1989, Sfriso and Ghetti 1998, Barriero et al. 2011, Orr et al. 2011, Włodarska-Kowalczuk et al. 2014, Kokubu et al. 2019). As macrophyte production increased from its lowest values in the winter months to its highest values in the summer months, this pattern was reflected in the macrophyte wrack that washed ashore on beaches of the Pacific Northwest. Likewise, as seen in this study and a previous one (Reimer et al. 2018), there was regional variability in wrack abundance and composition over sites and seasons. Across all sites, the greatest wrack abundance and species composition diversity was observed in summer, compared to winter and spring. In summer, GH and CL had high densities of low biomass wrack patches, resulting in higher total wrack biomass per transect; BAN had low densities of high biomass wrack patches, resulting in lower total wrack biomass per transect. Interestingly, there was a high proportion of dune vegetation in winter beach-cast wrack relative to other sampling periods. This increase was likely the result of foredune erosion associated with greater wave action from winter storms.

While seasonal fluctuations in macrophyte wrack abundance are universal among the sites, macrophyte wrack abundance and species composition varies with latitude, coastal geomorphology, and distance to macrophyte wrack source habitat (Reimer et al. 2018). In the northern part of our study region, where upwelling intensity is weak (Figure 2.1A), large estuaries are common, and outwelling moves eelgrass from estuaries to the nearshore, wrack deposits can be large and dominated by eelgrass. In the southern part of our study region, where upwelling is strong and fuels macroalgal productivity and rocky habitats are more common, the wrack on nearby beaches can also be large and mostly dominated by kelp and other macroalgae.

Wrack functional group traits may further influence seasonal and regional variation in macrophyte wrack abundance and distribution (Orr et al. 2005, Oldham et al. 2014). For example, we found that the many, eelgrass dominated wrack deposits at GH and CL compared to the few, kelp dominated wrack deposits at BAN, resulted in similar total biomass of wrack at GH and CL compared to BAN. Such patterns could be attributed to species biomass differences, with eelgrass wrack having much lower biomass than kelp or other macroalgae.

In this system, and across sandy beaches worldwide, the amount, distribution, and type of macrophyte wrack deposited on beaches over seasonal timescales has important implications for ecosystem functions (e.g., Lastra et al. 2008, Spiller et al. 2010, Gonçalves and Marques 2011, Rodil et al. 2015). In particular, because of the key role macrophyte wrack plays as a nutrient subsidy across ecosystem boundaries, significant changes in wrack abundance and composition with seasons, such as we see in temperate systems worldwide, likely poses interesting consequences for dune vegetation. Studies have found that when marine subsidies are abundant and diverse, beach and foredune sand nutrients are enhanced (e.g., Dugan et al. 2011, Rodil et al. 2019, Chapter 2). As nutrient availability increases, dune plant production can increase, resulting to higher grass densities (e.g., Cardona and Garcia 2008, Del Vecchio et al. 2013, 2017, van Egmond et al. 2019, Chapter 2). Because of the potential relationship between nutrient availability and beachgrass production, the location and seasonality of nutrients available from beach-cast wrack should not be overlooked.

**Table B1.** Statistical results using ANOVA for the difference in (A) wrack patch density (number/m$^2$), (B) wrack patch biomass (g/patch), and (C) total wrack biomass (g/transect) across sites (see Figure 2.1) and seasons (Winter, Spring, and Summer 2016). Significant P values are in bold. Tukey HSD post hoc tests P < 0.05.

| Component | Source of variation | df | SS | MS | F | Prob > F | Tukey HSD test |
|---|---|---|---|---|---|---|---|
| (A) Wrack Patch Density (number/m$^2$) | Site | 2 | 0.30 | 0.15 | 11.0 | **0.001** | CL = GH > BAN |
| | Season | 2 | 0.50 | 0.25 | 19.0 | **7.6E-05** | Su 2016 > Sp 2016 = W 2016 |
| | Site x Season | 4 | 0.11 | 0.03 | 2.0 | 0.123 | |
| | Residuals | 15 | 0.20 | 0.01 | | | |
| (B) Wrack Patch Biomass (g) | Site | 2 | 23 | 11 | 0.15 | 0.863 | |
| | Season | 2 | 1169 | 584 | 7.5 | **0.005** | Su 2016 > Sp 2016 = W 2016 |
| | Site x Season | 4 | 143 | 35 | 0.46 | 0.763 | |
| | Residuals | 15 | 1162 | 77 | | | |
| (C) Total Wrack Biomass (g/transect) | Site | 2 | 149165 | 74582 | 3.34 | 0.063 | |
| | Season | 2 | 1188015 | 594007 | 26.6 | **1.1E-05** | Su 2016 > Sp 2016 = W 2016 |
| | Site x Season | 4 | 178492 | 44623 | 2.0 | 0.146 | |
| | Residuals | 15 | 334674 | 22312 | | | |

**Table B2.** Statistical results from the multivariate permutational analysis (PERMANOVA) using a Bray-Curtis similarity matrix of differences in wrack community composition (proportional species biomass) between sites (see Figure 2.1) and seasons (Winter 2016 – Summer 2016). Significant P values are in bold.

| Source of variation | df | SS | MS | F | Prob > F | Variance explained |
|---|---|---|---|---|---|---|
| Site | 2 | 0.88 | 0.44 | 1.80 | 0.16 | 0.37 |
| Season | 2 | 0.49 | 0.25 | 1.01 | 0.40 | 0.21 |
| Residuals | 4 | 0.98 | 0.24 | | | 0.42 |
| Total | 8 | 2.35 | | | | 1.00 |

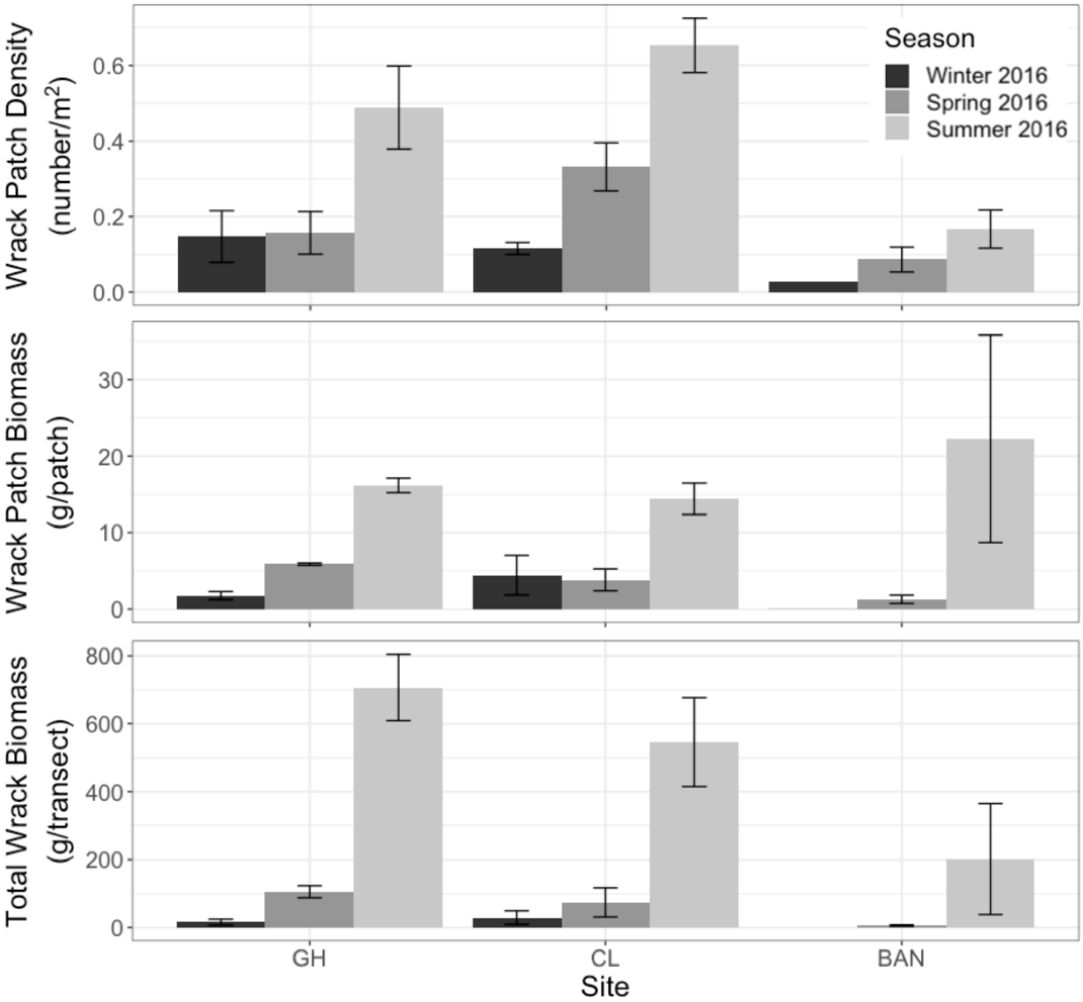

**Figure B1.** Mean (± SE) seasonal wrack patch density (number/m$^2$), wrack patch biomass (g/patch), and total wrack biomass (g/transect) over the 2016 season (winter: January/February, spring: May/June, and summer: August/September) and across sites (listed north to south; Figure 2.1) along the U.S. Pacific Northwest coast. See Appendix A Table A1 for site abbreviations and locations.

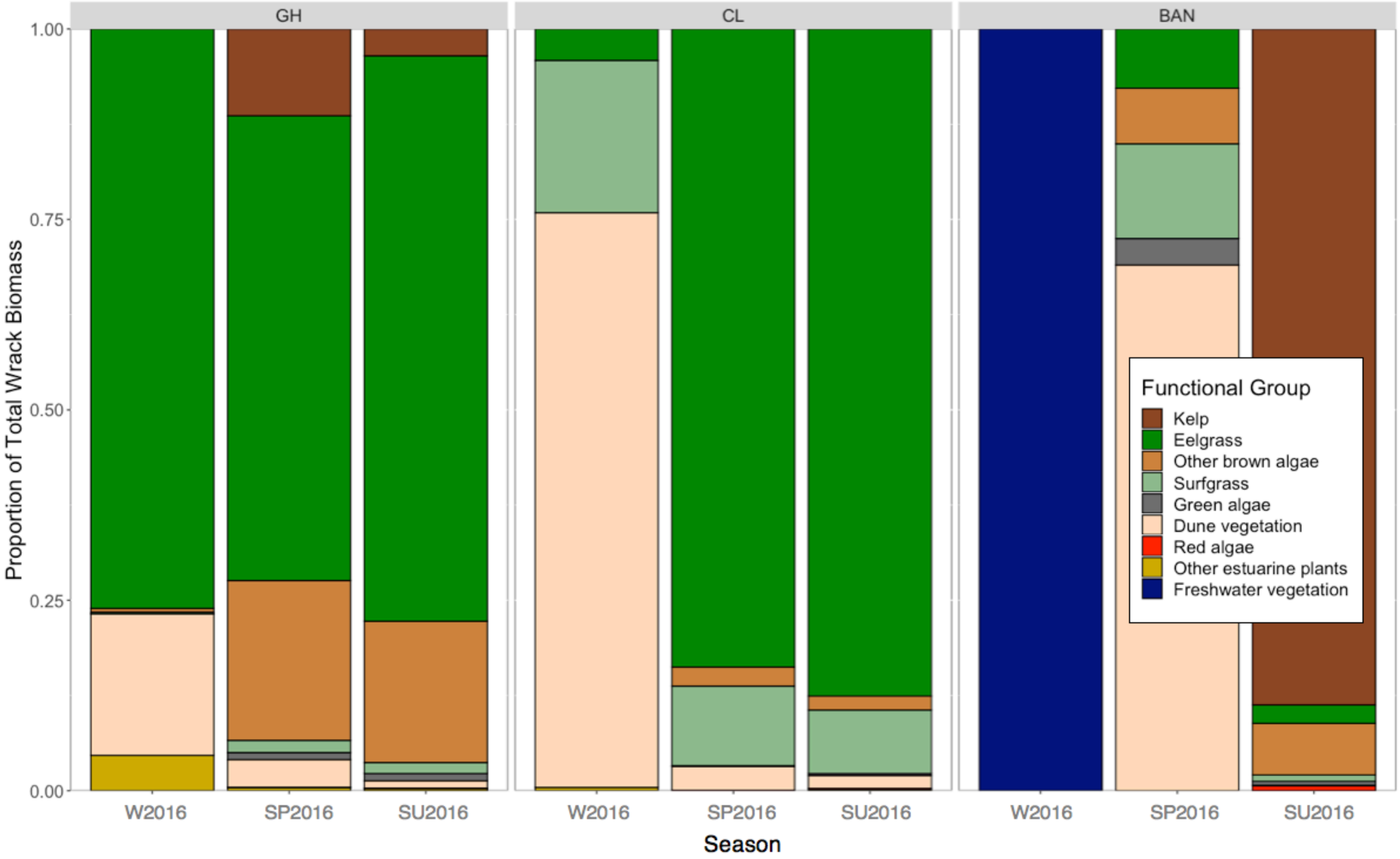

**Figure B2.** Proportional biomass of macrophyte wrack functional groups over the 2016 season (winter: January/February, spring: May/June, and summer: August/September; see Appendix A Table A2) and across sites (listed north to south; Figure 2.1) along the U.S. Pacific Northwest coast. Proportions were calculated from the total biomass of each functional group found in the wrack samples collected at each site. See Appendix A Table A1 for site abbreviations and locations.

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# Appendix C Chapter 2 Supplemental Tables for Spatial and Temporal Variability in Environmental Factors

**Table C1.** Results of one-way ANOVAs for the distances to (A) nearest estuary and (B) rocky reef across sites along the U.S. Pacific Northwest coast (see Figure 2.1A, Appendix A Table A1 for sites and abbreviations). Significant P values are in bold. Tukey HSD post hoc tests P < 0.05.

| Source of variation | df | SS | MS | F | Prob > F | Tukey HSD test |
|---|---|---|---|---|---|---|
| (A) Estuary | | | | | | |
| Site | 14 | 13670 | 976.4 | 60.2 | **< 2E-16** | FL = FS > BAN > LB > SL = DO > SILT > UD = GH > NS = LBP > CL = PC = NB = SB |
| Residuals | 29 | 470 | 16.2 | | | |
| (B) Rocky Reef | | | | | | |
| Site | 14 | 10749 | 767.8 | 44.6 | **8.5E-16** | GH > LBP = UD = DO = SILT > BAN > FS = LB > NS = SB = NB = CL = FL = SL > PC |
| Residuals | 29 | 499 | 17.2 | | | |

**Table C2.** Results of a two-way ANOVA for ocean upwelling (Bakun index) across sites and years (2015-2017) along the U.S. Pacific Northwest coast (see Figure 2.1B, Appendix A Table A1 for sites and abbreviations). Significant P values are in bold. Tukey HSD post hoc tests P < 0.05.

| Source of variation | df | SS | MS | F | Prob > F | Tukey HSD test |
|---|---|---|---|---|---|---|
| Site | 14 | 9765961 | 697569 | 174.8 | **< 2E-16** | BAN = FL = UD > DO = SILT = NS > SB > PC > CL = NB = SL > FS > LB = LBP > GH |
| Year | 2 | 1419757 | 709879 | 177.9 | **< 2E-16** | 2015 > 2017 = 2016 |
| Site*Year | 28 | 81981 | 2928 | 0.7 | 0.844 | |
| Residuals | 28230 | 112514431 | 3989 | | | |

**Table C3.** Results of a one-way ANOVA for short-term shoreline change rates across sites along the U.S. Pacific Northwest coast (see Figure 2.1C, Appendix A Table A1 for sites and abbreviations). Significant P values are in bold. Tukey HSD post hoc tests $P < 0.05$.

| Source of variation | df | SS | MS | F | Prob > F | Tukey HSD test |
|---|---|---|---|---|---|---|
| Site | 14 | 296.1 | 21.1 | 26.3 | **9.81E-13** | LBP > GH > LB > FS > BAN > NB = SB = FL = PC = DO = NS = UD > SILT = SL = CL |
| Residuals | 29 | 23.3 | 0.8 | | | |

**Table C4.** Results of a one-way ANOVA for foredune crest height across sites along the U.S. Pacific Northwest coast (see Figure 2.1D, Appendix A Table A1 for sites and abbreviations). Significant P values are in bold. Tukey HSD post hoc tests P < 0.05.

| Source of variation | df | SS | MS | F | Prob >F | Tukey HSD test |
|---|---|---|---|---|---|---|
| Site | 14 | 291.3 | 20.8 | 16.1 | **4.76E-10** | SL > PC = FS > SB > NB = CL = SILT > NS = UD = DO = LB > GH > BAN = LBP = FL |
| Residuals | 29 | 37.4 | 1.3 | | | |

## Appendix D Chapter 2 Supplemental Tables for Spatial and Temporal Variability of Macrophyte Wrack and Nutrient Subsidies

**Table D1.** Two-way ANOVAs for macrophyte (A) wrack patch density, (B) wrack patch biomass, and (C) total wrack biomass across sites (see Figure 2.1, Appendix A Table 1A for sites and abbreviations) and years (2015-2017). Significant P values are in bold. Tukey HSD post hoc tests P < 0.05.

| Component | Source of variation | df | SS | MS | F | Prob > F | Variance explained | Tukey HSD test | |
|---|---|---|---|---|---|---|---|---|---|
| (A) Wrack Patch Density (number/m$^2$) | Site | 14 | 4.39 | 0.31 | 22.52 | **< 2E-16** | 0.784 | | |
| | Year | 2 | 0.01 | 0.00 | 0.27 | 0.7610 | 0.006 | | |
| | Site x Year | 28 | 1.21 | 0.04 | 3.09 | **3.14E-05** | 0.499 | **2015:** CL > GH = NS = LB = SILT = FS = PC = LBP = UD = SL = DO = FL = NB = SB = BAN<br>**2016:** CL > GH = NS > LBP > SL = DO > UD = BAN = SB = LB = PC = NB = SILT = FL > FS | **GH, LBP, LB, FS, NB, CL, SL, PC, SB, SILT, UD, NS, BAN:** N.S.<br>**DO:** 2016 = 2015 > 2017<br>**FL:** 2017 ≥ 2015 ≥ 2016 |

**Table D1.** (Continued)

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | **2017:** GH > CL > LBP = LB = NB = SL = NS = PC > FL > FS = SB = UD = DO = SILT = BAN | |
| | Residuals | 87 | 1.21 | 0.01 | | | | | |
| | Model | 44 | | | 9.15 | **< 2E-16** | 0.732 | | |
| (B) Wrack Patch Biomass (g/patch) | Site | 14 | 3078 | 219.89 | 3.42 | **0.0002** | 0.355 | FL > BAN = CL = GH = NS = LB = NB = LBP = DO = SILT = SL = UD = PC > FS = SB | |
| | Year | 2 | 194 | 97.21 | 1.51 | 0.2260 | 0.034 | | |
| | Site x Year | 28 | 901 | 32.19 | 0.50 | 0.9798 | 0.139 | | |
| | Residuals | 87 | 5591 | 64.26 | | | | | |
| | Model | 44 | | | 1.48 | 0.1379 | 0.138 | | |
| (C) Total Wrack Biomass (g/transect) | Site | 14 | 5975039 | 426789 | 17.23 | **< 2E-16** | 0.735 | | |
| | Year | 2 | 104722 | 52361 | 2.11 | 0.1270 | 0.046 | | |

**Table D1.** (Continued)

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Site x Year | 28 | 2004483 | 71589 | 2.89 | **0.0001** | 0.482 | **2015:** CL > GH = NS = FL = LB = NB = LBP = SILT = BAN = PC = DO = FS = SB = SL = UD<br>**2016:** GH > CL > LBP = NS > LB = BAN = FL > NB = SL = DO = SB = SILT = PC = FS = UD<br>**2017:** GH > CL > LB > NS = LBP = FL = SL = BAN = NB > PC = UD = SILT = DO = FS = SB | **GH, LBP, LB, FS, NB, CL, SL, PC, SB, SILT, DO, UD, NS, BAN, FL:** N.S. |
| | Residuals | 87 | 2155251 | 24773 | | | | | |
| | Model | 44 | | | 7.42 | 1.45E-15 | 0.683 | | |

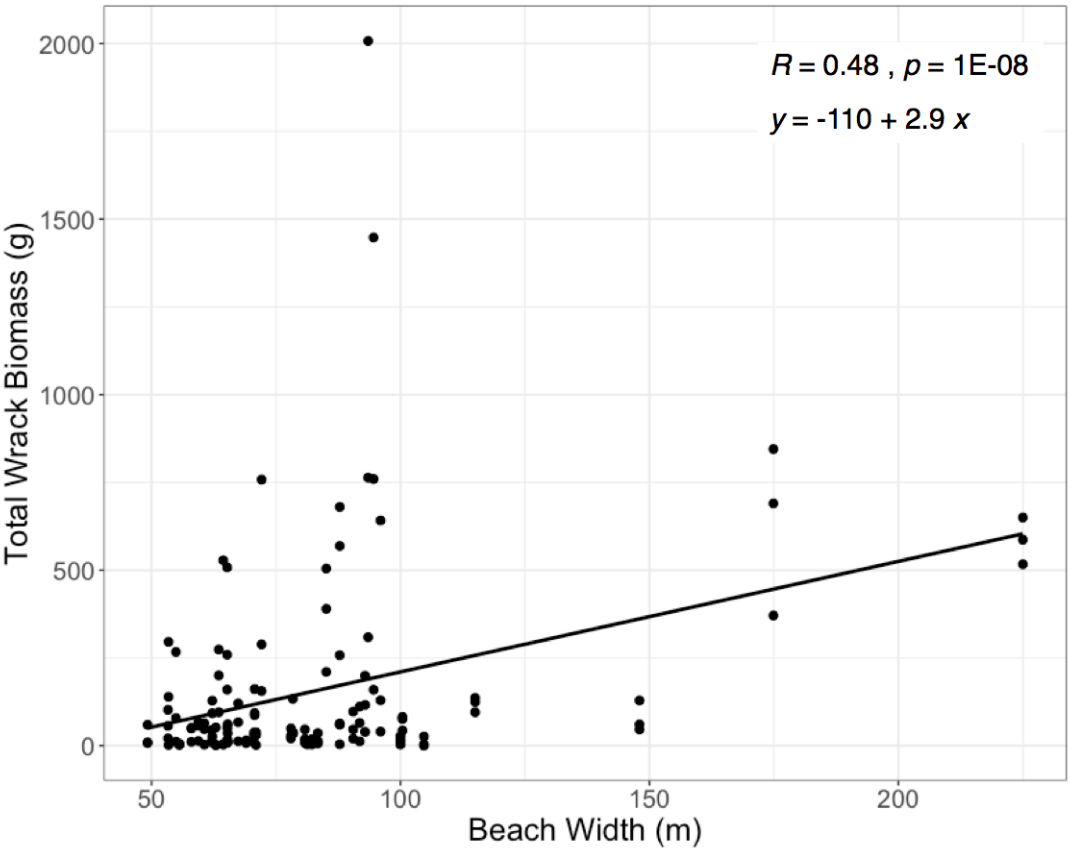

**Figure D1.** Plot of the relationship between total wrack biomass (g) as a function of beach width (measured as the longest beach transect; m) for all central transect locations (Appendix A Table A1) and years (2015 – 2017). The analysis excludes two outlying biomass values from CL01 and CL02 in 2015.

**Table D2.** Statistical results from the multivariate permutational analysis (PERMANOVA) using Bray-Curtis similarity matrix of differences in wrack community composition (proportional species biomass) between sites (see Figure 2.1) and years (2015-2017). Significant P values are in bold.

| Source of variation | df | SS | MS | F | Prob > F | Variance explained |
|---|---|---|---|---|---|---|
| Site | 14 | 4.79 | 0.34 | 5.63 | **0.001** | 0.72 |
| Year | 2 | 0.16 | 0.08 | 1.31 | 0.263 | 0.02 |
| Residuals | 28 | 1.71 | 0.06 | | | 0.26 |
| Total | 44 | 6.66 | | | | 1.00 |

**Table D3.** Three-way ANOVA results for sand nitrate concentration across sites (see Figure 2.1, Appendix A Table A1 for site abbreviations and locations), years (2015-2017), profile locations [mean higher high water (MHHW) mark, mid-beach, foredune toe, foredune crest, foredune heel], and their interaction. Significant P values are in bold.

| Source of variation | df | SS | MS | F | Prob > F | Variance explained |
|---|---|---|---|---|---|---|
| Site | 14 | 49213 | 3515 | 10.58 | **< 2E-16** | 0.254 |
| Year | 2 | 10892 | 5446 | 16.39 | **1.38E-07** | 0.070 |
| Profile Location | 4 | 74523 | 18631 | 56.06 | **< 2e-16** | 0.340 |
| S x Y x PL | 112 | 55956 | 500 | 1.50 | **0.0022** | 0.279 |
| Residuals | 435 | 144578 | 332 | | | |
| Model | 224 | | | 4.103 | **< 2E-16** | 0.513 |

**Table D4.** Two-way ANOVA results for sand nitrate concentration at each profile location [mean higher high water (MHHW) mark, mid-beach/foredune toe combined, foredune crest, and foredune heel] across sites (see Figure 2.1, Appendix A Table A1 for site abbreviations and locations) and years (2015-2017). Significant P values are in bold. Tukey HSD post hoc tests P < 0.05.

| Component | Source of variation | df | SS | MS | F | Prob > F | Variance explained | Tukey HSD test | |
|---|---|---|---|---|---|---|---|---|---|
| (A) MHHW Mark | Site | 14 | 5574 | 398.2 | 3.35 | **0.0003** | 0.350 | | |
| | Year | 2 | 3576 | 1787.8 | 15.03 | **2.48E-06** | 0.257 | | |
| | Site x Year | 28 | 5819 | 207.8 | 1.75 | **0.0263** | 0.360 | **2015:** N.S.<br>**2016:** FS = FL > DO = GH = NS = LBP = SB = PC = NB = CL = SILT = BAN = LB = UD > SL<br>**2017:** FS > DO > FL = GH = NS = LB = BAN = LBP = UD = NB = SILT > SB = PC = SL = CL | **GH, LBP, LB, NB, SB, SILT, DO, UD, NS, BAN, FL:** N.S.<br>**FS:** 2017 > 2016 = 2015<br>**CL, PC:** 2015 > 2016 = 2017<br>**SL:** 2015 > 2017 = 2016 |
| | Residuals | 87 | 10352 | 119 | | | | | |

**Table D4.** (Continued)

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Model | 44 | | | 2.86 | **1.49E-05** | 0.384 | | |
| (B) Mid-Beach/Foredune Toe | Site | 14 | 40936 | 2924 | 11.40 | **2.46E-14** | 0.647 | | |
| | Year | 2 | 7116 | 3558 | 13.87 | **5.91E-06** | 0.242 | | |
| | Site x Year | 28 | 15630 | 558 | 2.18 | **0.0033** | 0.412 | **2015:** FS = LB > FL = GH = NS > CL = SL = LBP = NB = DO = PC = BAN > SB > SILT = UD<br>**2016:** FS > LB > LBP = GH > DO = BAN = FL = SILT = CL = NS = SB = UD > PC > SL > NB | **GH, LBP, LB, FS, CL, PC, SB, SILT, DO, UD, BAN:** N.S.<br>**NB, NS, FL:** 2015 > 2016 = 2017<br>**SL:** 2015 > 2017 > 2016 |

**Table D4.** (Continued)

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | **2017:** FS > LB > GH = SB > DO = SL = BAN = FL = LBP = NS > CL = PC = UD = SILT = NB | |
| | Residuals | 87 | 22319 | 257 | | | | | |
| | Model | 44 | | | 5.64 | **3.57E-12** | 0.609 | | |
| (C) Foredune Crest | Site | 14 | 7341 | 524.4 | 1.82 | **0.0475** | 0.227 | SL = FS = SB = DO = CL = NS = UD = BAN = FL = LBP = LB = SILT = GH = PC = NB (N.S.) | |
| | Year | 2 | 700 | 349.8 | 1.22 | 0.3013 | 0.027 | | |
| | Site x Year | 28 | 11654 | 416.2 | 1.45 | 0.0992 | 0.318 | | |
| | Residuals | 87 | 25020 | 287.6 | | | | | |
| | Model | 44 | | | 1.56 | **0.0402** | 0.158 | | |
| (D) Foredune Heel | Site | 14 | 16841 | 1202.9 | 2.80 | **0.0017** | 0.311 | SB > SILT > SL = CL = LB = GH = NS = UD = FS = BAN = DO > PC = LBP = NB > FL | |

**Table D4.** (Continued)

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Year | 2 | 44 | 22 | 0.05 | 0.9501 | 0.001 | |
| | Site x Year | 28 | 15967 | 570.2 | 1.33 | 0.1598 | 0.300 | |
| | Residuals | 87 | 37333 | 429.1 | | | | |
| | Model | 44 | | | 1.74 | **0.0143** | 0.199 | |

# Appendix E Chapter 2 Supplemental Tables and Figures for the Spatial and Temporal Patterns of Dune Grass Production

**Table E1.** Statistical results using two-way ANOVAs for (A) shoot density (number/0.25 $m^2$) and (B) total biomass (g/0.25 $m^2$) of all dune grass species across sites (see Figure 2.1), years (2015-2017), and foredune profile locations (toe, crest, heel). Significant P values are in bold. Tukey HSD post hoc tests $P < 0.05$.

| Component | Source of variation | df | SS | MS | F | Prob > F | Variance explained | Tukey HSD test | |
|---|---|---|---|---|---|---|---|---|---|
| (A) Shoot Density (number/0.25 $m^2$) | Site | 14 | 3355 | 239.6 | 2.15 | **0.0095** | 0.0792 | | |
| | Year | 2 | 676 | 338.2 | 3.03 | **0.0497** | 0.0171 | | |
| | Profile location | 2 | 17231 | 8615.3 | 77.14 | **< 2.2E-16** | 0.3065 | | |
| | Site x Profile location | 28 | 15048 | 537.4 | 4.81 | **5.06E-13** | 0.2785 | **TOE:** CL ≥ LB = NB ≥ LBP = FS = GH = NS = DO = UD = SILT = BAN ≥ SL = SB = FL ≥ PC<br>**CREST:** SL = PC = SILT = NS = DO ≥ | **GH:** Toe > Crest = Heel<br>**LBP, NB, CL:** Toe > Crest > Heel<br>**LB:** Toe > Heel = Crest<br>**FS:** Toe ≥ Crest ≥ Heel |

**Table E1.** (Continued)

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | BAN = FS = SB = CL = FL = NB = UD = LBP ≥ GH = LB<br>**HEEL:** BAN = DO ≥ SB = SL ≥ SILT = PC = FS = LB = FL = NS = GH = NB ≥ CL = LBP ≥ UD | **SL, SILT, FL:** Crest ≥ Toe ≥ Heel<br>**PC:** Crest ≥ Toe = Heel<br>**SB, DO, BAN:** N.S.<br>**UD:** Toe = Crest > Heel<br>**NS:** Crest = Toe > Heel |
| | Residuals | 349 | 38980 | 111.7 | | | | | |
| | Model | 46 | | | 7.07 | **< 2.2E-16** | 0.4140 | | |
| (B) Total Biomass (g/0.25 m$^2$) | Site | 14 | 332759 | 23769 | 5.06 | **1.22E-08** | 0.1686 | | |
| | Year | 2 | 18630 | 9315 | 1.98 | 0.1394 | 0.0112 | | |
| | Profile location | 2 | 303164 | 151582 | 32.25 | **1.41E-13** | 0.1560 | | |
| | Site x Profile location | 28 | 311774 | 11135 | 2.37 | **0.0002** | 0.1597 | **TOE:** LBP ≥ LB ≥ GH ≥ NB = FS ≥ NS = | **GH, LB, FS, CL, PC, BAN:** N.S. |

**Table E1.** (Continued)

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | SILT = UD ≥ SL = CL = SB = PC ≥ BAN = FL = DO<br>**CREST:** N.S.<br>**HEEL:** N.S. | **LBP:** Toe ≥ Crest ≥ Heel<br>**NS:** Crest ≥ Toe ≥ Heel<br>**SL, SB, SILT, DO, FL:** Crest ≥ Heel ≥ Toe<br>**UD, NS:** Crest > Toe = Heel |
| | Residuals | 349 | 1640503 | 4701 | | | | | |
| | Model | 46 | | | 4.47 | 2.49E-16 | 0.2877 | | |

**Table E2.** Statistical results using two-way ANOVAs for (A) shoot density (number/0.25$m^2$), (B) total biomass (g/0.25$m^2$), (C) shoot biomass (g/shoot), and (D) shoot length (cm) of *Ammophila arenaria* and *Ammophila breviligulata* across sites (see Figure 2.1), years (2015-2017), and foredune profile locations (toe, crest, heel). Significant P values are in bold. Tukey HSD post hoc tests P < 0.05.

| Component | Source of variation | df | SS | MS | F | Prob >F | Variance explained | Tukey HSD test | |
|---|---|---|---|---|---|---|---|---|---|
| (A) Shoot Density (number/0.25 $m^2$) | Site | 14 | 3527 | 252 | 2.02 | **0.0156** | 0.0751 | | |
| | Year | 2 | 737 | 369 | 2.96 | 0.0531 | 0.0167 | | |
| | Profile location | 2 | 22473 | 11237 | 90.26 | **< 2e-16** | 0.3409 | | |
| | Site x Profile location | 28 | 13714 | 490 | 3.93 | **6.82E-10** | 0.2399 | **TOE:** CL ≥ LB = NB ≥ LBP = GH = FS = ND = DO = UD =SILT = BAN ≥ SL = FL = SB ≥ PC<br>**CREST:** SL = PC = DO = SILT ≥ BAN = NS = CL = FL = | **GH:** Toe > Crest = Heel<br>**LBP, NB, CL:** Toe > Crest > Heel<br>**LB:** Toe > Heel = Crest<br>**FS, UD, NS:** Toe = Crest > Heel |

**Table E2.** (Continued)

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | FS = NB = SB = UD = LBP ≥ LB = GH<br>**HEEL:** BAN ≥ DO = SL = FL = LB = PC = SILT = GH = NS = NB = SB ≥ CL = LBP = FS = UD | **SL, PC, SB, FL:** Crest ≥ Toe ≥ Heel<br>**SILT:** Crest = Toe > Heel<br>**DO, BAN:** N.S. |
| | Residuals | 349 | 43447 | 124 | | | | | |
| | Model | 46 | | | 7.06 | **< 2.2E-16** | 0.4139 | | |
| (B) Total Biomass (g/0.25 m$^2$) | Site | 14 | 297461 | 21247 | 4.51 | **1.72E-07** | 0.1533 | | |
| | Year | 2 | 19044 | 9522 | 2.02 | 0.1339 | 0.0115 | | |
| | Profile location | 2 | 328270 | 164135 | 34.87 | **1.57E-14** | 0.1665 | | |
| | Site x Profile location | 28 | 289964 | 10356 | 2.20 | **5.80E-04** | 0.1500 | **TOE:** LBP ≥ LB ≥ GH ≥ NB = FS ≥ NS = SILT = UD ≥ SL | **GH, LB, CL, PC, SB, BAN:** N.S.<br>**LBP:** Toe ≥ Crest ≥ Heel |

**Table E2.** (Continued)

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | = CL = SB = PC ≥ BAN = FL = DO<br>**CREST:** N.S.<br>**HEEL:** N.S | **FS, NB, NS:** Crest ≥ Toe ≥ Heel<br>**SL, SILT, DO, FL:** Crest ≥ Heel ≥ Toe<br>**UD:** Crest > Toe = Heel |
| | Residuals | 349 | 1643020 | 4708 | | | | | |
| | Model | 46 | | | 4.32 | **1.43E-15** | 0.2786 | | |
| (C) Shoot Biomass (g/shoot) | Site | 14 | 175.4 | 12.5 | 8.48 | **8.61E-16** | 0.2537 | LBP = LB = GH ≥ FS ≥ NB ≥ SILT = UD = SL = NS ≥ FL = SB = PC ≥ CL ≥ DO ≥ BAN | |
| | Year | 2 | 8.4 | 4.2 | 2.85 | 0.0592 | 0.0161 | | |
| | Profile location | 2 | 131.1 | 65.5 | 44.34 | **< 2E-16** | 0.2026 | Crest = Heel > Toe | |
| | Site x Profile location | 28 | 35.7 | 1.3 | 0.86 | 0.6704 | 0.0647 | | |

**Table E2.** (Continued)

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Residuals | 349 | 515.8 | 1.5 | | | | | |
| | Model | 46 | | | 5.16 | **< 2.2E-16** | 0.3262 | | |
| (D) Shoot Length (cm) | Site | 14 | 10736 | 767 | 6.12 | **7.06E-11** | 0.1970 | | |
| | Year | 2 | 21267 | 10633 | 84.80 | **< 2E-16** | 0.3270 | | |
| | Profile location | 2 | 17881 | 8941 | 71.30 | **< 2E-16** | 0.2901 | | |
| | Site x Profile location | 28 | 14127 | 505 | 4.02 | **3.28E-10** | 0.2440 | **TOE:** LB ≥ NB = GH = LBP = FS = UD = PC = BAN = SILT = SB = FL = NS = CL = DO ≥ SL<br>**CREST:** SL ≥ FS = NB = SILT = NS = CL = SB = UD = PC = FL = LBP = LB = GH ≥ BAN = DO | **GH, LBP, LB, DO, UD, BAN, FL:** N.S.<br>**FS, SB:** Heel = Crest > Toe<br>**NB:** Crest ≥ Heel ≥ Toe<br>**CL, SL, PC, NS:** Crest = Heel > Toe<br>**SILT:** Heel > Crest > Toe |

**Table E2.** (Continued)

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | **HEEL:** SILT ≥ FS ≥ SB ≥ SL ≥ GH = CL = NS = DO = UD = PC ≥ NB ≥ LB ≥ FL ≥ BAN = LBP | |
| | Residuals | 349 | 43764 | 125 | | | | | |
| | Model | 46 | | | 11.10 | **< 2E-16** | 0.5404 | | |

**Figure E1.** Mean (± SE) shoot density (number/0.25 m$^2$) of *Ammophila arenaria* and *Ammophila breviligulata* across sites (listed north to south; Figure 2.1) and years (2015–2017). Profile locations are listed landward across the foredune (toe, crest, and heel). See Figure 2.1, Appendix A Table A1 for site abbreviations and locations.

**Figure E2.** Mean (± SE) total biomass (g/0.25 m$^2$) of *Ammophila arenaria* and *Ammophila breviligulata* across sites (listed north to south; Figure 2.1) and years (2015–2017). Profile locations are listed landward across the foredune (toe, crest, and heel). See Figure 2.1, Appendix A Table A1 for site abbreviations and locations.

**Figure E3.** Mean (± SE) shoot biomass (g/shoot) of *Ammophila arenaria* and *Ammophila breviligulata* across sites (listed north to south; Figure 2.1) and years (2015–2017). Profile locations are listed landward across the foredune (toe, crest, and heel). See Figure 2.1, Appendix A Table A1 for site abbreviations and locations.

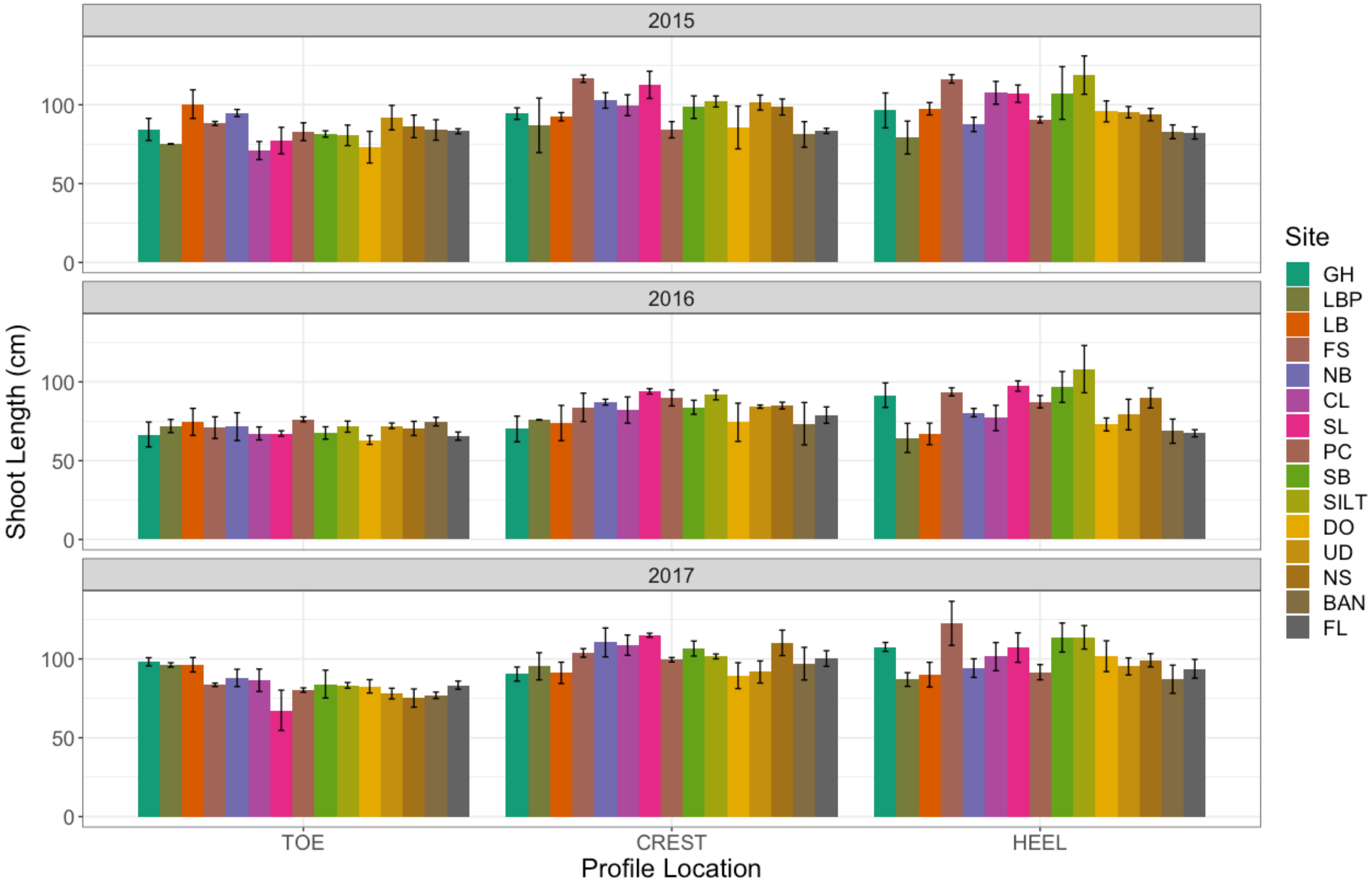

**Figure E4.** Mean (± SE) shoot length (cm) of *Ammophila arenaria* and *Ammophila breviligulata* across sites (listed north to south; Figure 2.1) and years (2015–2017). Profile locations are listed landward across the foredune (toe, crest, and heel). See Figure 2.1, Appendix A Table A1 for site abbreviations and locations.

## Appendix F Chapter 2 Supplemental Tables and Figures for the Relationships between Environmental Factors, Marine Subsidies, and Dune Grass Production

**Table F1.** Statistical results from multiple regression analyses for the proportion, biomass (g/m$^2$), and total biomass (g/transect) of kelp and eelgrass wrack as a function of the distance (D) to the nearest rocky reef (kelp) or estuary (eelgrass), ocean upwelling (U), and their interactions. Significant P values are in bold.

| | | Kelp | | | | | Eelgrass | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Component | Source of variation | df | SS | F | Prob > F | Variance explained | df | SS | F | Prob > F | Variance explained |
| Wrack Proportion | D | 1 | 0.29 | 2.68 | 0.1061 | 0.034 | 1 | 3.17 | 45.66 | **4.77E-10** | 0.268 |
| | U | 1 | 1.64 | 15.07 | **0.0002** | 0.167 | 1 | 1.49 | 21.41 | **9.13E-06** | 0.146 |
| | D x U | 1 | 0.51 | 4.64 | **0.0345** | 0.058 | 1 | 1.00 | 14.47 | **0.0002** | 0.104 |
| | Residuals | 75 | 8.18 | | | | 125 | 8.67 | | | |
| | Model | 3 | | 9.38 | **2.43E-05** | 0.244 | 3 | | 33.32 | **6.78E-16** | 0.431 |
| Wrack Biomass (g/m$^2$) | D | 1 | 39 | 0.50 | 0.4828 | 0.007 | 1 | 252 | 8.28 | **0.0047** | 0.062 |
| | U | 1 | 561 | 7.25 | **0.0087** | 0.088 | 1 | 339 | 11.13 | **0.0011** | 0.082 |
| | D x U | 1 | 409 | 5.28 | **0.0243** | 0.066 | 1 | 149 | 4.88 | **0.0290** | 0.038 |
| | Residuals | 75 | 5798 | | | | 125 | 3809 | | | |
| | Model | 3 | | 5.00 | **0.0036** | 0.133 | 3 | | 9.96 | **6.20E-06** | 0.174 |

**Table F1.** (Continued)

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Total Wrack Biomass (g/transect) | D | 1 | 665 | 0.11 | 0.7417 | 0.001 | 1 | 89691 | 5.54 | **0.0201** | 0.042 |
| | U | 1 | 14799 | 2.43 | 0.1230 | 0.031 | 1 | 501054 | 30.97 | **1.52E-07** | 0.199 |
| | D x U | 1 | 36088 | 5.93 | **0.0172** | 0.073 | 1 | 240976 | 14.89 | **0.0002** | 0.106 |
| | Residuals | 75 | 456053 | | | | 125 | 2022469 | | | |
| | Model | 3 | | 3.02 | **0.0351** | 0.072 | 3 | | 19.86 | **1.37E-10** | 0.307 |

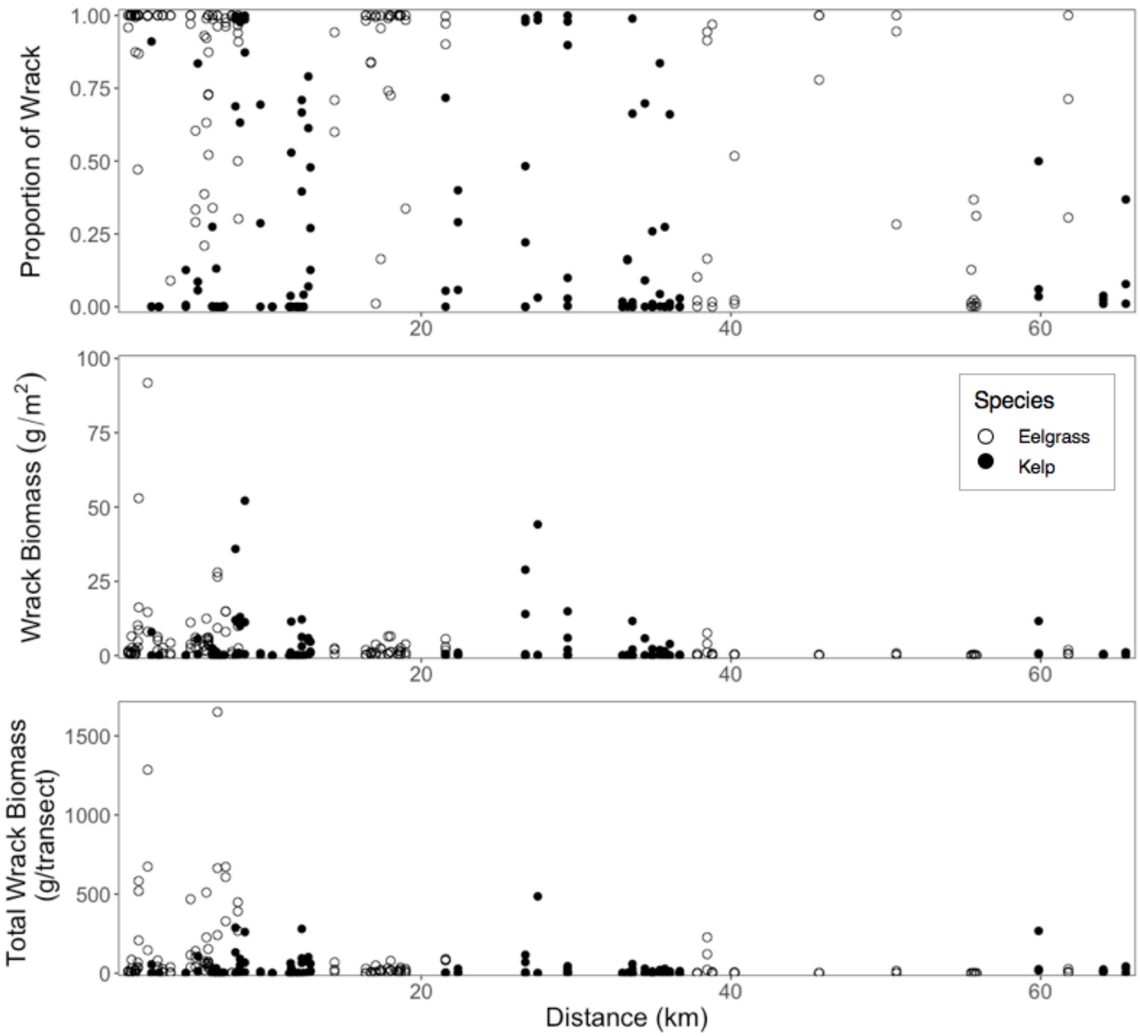

**Figure F1.** Relationships between the proportion, biomass (g/m$^2$), and total biomass (g/transect) for eelgrass or kelp wrack as a function of distance from nearest estuary (eelgrass) or rocky reef (kelp). See Appendix F Table F1 for statistical results.

**Table F2.** Statistical results from multiple regression analyses for sand nitrate concentration at the mean higher high water (MHHW) mark across sites as a function of ocean upwelling and distance to the Columbia River (see Figure 2.1). Significant P values are in bold.

| Source of variation | df | SS | F | Prob >F | Variance explained |
|---|---|---|---|---|---|
| Ocean upwelling | 1 | 2640 | 15.01 | **0.0002** | 0.106 |
| Distance to Columbia River | 1 | 1532 | 8.71 | **0.0038** | 0.064 |
| Residuals | 127 | 22337 | | | |
| Model | 2 | | 7.76 | **0.0007** | 0.095 |

**Table F3.** Statistical results from multiple regression analyses for the sand nitrate concentration at the mid-beach/toe profile location across sites as a function of ocean upwelling, distance to the Columbia River, mean higher high water (MHHW) sand nitrate concentration, total wrack biomass, and short-term shoreline change rate (see Figures 2.1, 2.2, and 2.4). Significant P values are in bold.

| Source of variation | df | SS | F | Prob > F | Variance explained |
|---|---|---|---|---|---|
| Ocean upwelling | 1 | 1088 | 2.38 | 0.1252 | 0.019 |
| Distance to Columbia River | 1 | 3498 | 7.66 | **0.0065** | 0.058 |
| MHHW sand nitrate concentration | 1 | 8909 | 19.52 | **2.15E-05** | 0.136 |
| Total wrack biomass | 1 | 2247 | 4.92 | **0.0283** | 0.038 |
| Short-term shoreline change rate | 1 | 2554 | 5.59 | **0.0196** | 0.043 |
| Residuals | 124 | 56606 | | | |
| Model | 5 | | 12.48 | **8.13E-10** | 0.308 |

**Table F4.** Statistical results from multiple regression analyses for the average sand nitrate concentration at the foredune (A) crest and (B) heel as a function of mid-beach/toe sand nitrate concentration, foredune crest sand nitrate concentration (for foredune heel), and/or foredune crest height. Significant P values are in bold.

| Component | Source of variation | df | SS | F | Prob >F | Variance explained |
|---|---|---|---|---|---|---|
| (A) Foredune crest sand nitrate concentration | Mid-beach/toe sand nitrate concentration | 1 | 2399 | 7.69 | **0.0064** | 0.057 |
| | Foredune crest height | 1 | 1327 | 4.25 | **0.0412** | 0.032 |
| | Residuals | 127 | 39635 | | | |
| | Model | 2 | | 5.30 | **0.0061** | 0.063 |
| (B) Foredune heel sand nitrate concentration | Mid-beach/toe sand nitrate concentration | 1 | 150 | 0.33 | 0.5653 | 0.003 |
| | Crest sand nitrate concentration | 1 | 6856 | 15.24 | **0.0002** | 0.108 |
| | Foredune crest height | 1 | 1238 | 2.75 | 0.0997 | 0.021 |
| | Residuals | 126 | 56695 | | | |
| | Model | 3 | | 7.52 | **1.14E-04** | 0.132 |

**Table F5.** Statistical results from multiple regression analyses for dune grass species production metrics at the foredune toe, as a function of marine subsidies. (A) Shoot density (number/0.25 $m^2$) and (B) total biomass (g/0.25 $m^2$) for all dune grass species. (C) Shoot density (number/0.25 $m^2$) and (D) total biomass (g/0.25 $m^2$) for *Ammophila arenaria* and *Ammophila breviligulata*. Significant P values are in bold.

| Component | Source of variation | df | Sum Sq | F value | Prob > F | Variance explained |
|---|---|---|---|---|---|---|
| (A) Shoot Density (number/0.25 $m^2$) | Total wrack biomass | 1 | 1281 | 7.80 | **0.0060** | 0.057 |
| | Mid-beach/toe sand nitrate concentration | 1 | 798 | 4.86 | **0.0293** | 0.036 |
| | Residuals | 129 | 21210 | | | |
| | Model | 2 | | 7.72 | **0.0007** | 0.093 |
| (B) Total Biomass (g/0.25 $m^2$) | Total wrack biomass | 1 | 433 | 0.06 | 0.8015 | 0.000 |
| | Mid-beach/toe sand nitrate concentration | 1 | 68202 | 9.99 | **0.0020** | 0.072 |
| | Residuals | 129 | 880772 | | | |
| | Model | 2 | | 5.36 | **5.83E-03** | 0.062 |
| (C) Shoot Density (number/0.25 $m^2$) | Total wrack biomass | 1 | 1428 | 7.98 | **0.0055** | 0.058 |
| | Mid-beach/toe sand nitrate concentration | 1 | 510 | 2.85 | 0.0938 | 0.022 |
| | Residuals | 129 | 23097 | | | |
| | Model | 2 | | 6.51 | **0.0020** | 0.078 |

**Table F5.** (Continued)

| | | | | | | |
|---|---|---|---|---|---|---|
| (D) Total Biomass (g/0.25 $m^2$) | Total wrack biomass | 1 | 625 | 0.09 | 0.7641 | 0.001 |
| | Mid-beach/toe sand nitrate concentration | 1 | 58622 | 8.49 | **0.0042** | 0.062 |
| | Residuals | 129 | 890741 | | | |
| | Model | 2 | | 4.61 | **1.17E-02** | 0.052 |

**Table F6.** Statistical results from multiple regression analyses for dune grass species production metrics at the foredune crest, as a function of marine subsidies, foredune dune crest height, and their interaction. (A) Shoot density (number/0.25 $m^2$) and (B) total biomass (g/0.25 $m^2$) for all dune grass species. (C) Shoot density (number/0.25 $m^2$) and (D) total biomass (g/0.25 $m^2$) for *Ammophila arenaria* and *Ammophila breviligulata*. Significant P values are in bold.

| Component | Source of variation | df | Sum Sq | F value | Prob > F | Variance explained |
|---|---|---|---|---|---|---|
| (A) Shoot Density (number/0.25 $m^2$) | Crest sand nitrate concentration | 1 | 902 | 7.42 | **0.0073** | 0.055 |
| | Foredune crest height | 1 | 2652 | 21.81 | **7.51E-06** | 0.146 |
| | Crest sand nitrate concentration x Foredune crest height | 1 | 1003 | 8.25 | **0.0048** | 0.061 |
| | Residuals | 128 | 15568 | | | |
| | Model | 3 | | 9.46 | **1.09E-05** | 0.162 |
| (B) Total Biomass (g/0.25 $m^2$) | Crest sand nitrate concentration | 1 | 23556 | 3.97 | **0.0483** | 0.030 |
| | Foredune crest height | 1 | 69559 | 11.73 | **0.0008** | 0.083 |
| | Residuals | 129 | 764718 | | | |
| | Model | 2 | | 6.96 | 0.0013 | 0.083 |
| (C) Shoot Density (number/0.25 $m^2$) | Crest sand nitrate concentration | 1 | 879 | 7.12 | **0.0086** | 0.053 |
| | Foredune crest height | 1 | 2152 | 17.43 | **0.0001** | 0.120 |
| | Crest sand nitrate concentration x Foredune crest height | 1 | 1012 | 8.20 | **0.0049** | 0.060 |

**Table F6.** (Continued)

| | | | | | | |
|---|---|---|---|---|---|---|
| | Residuals | 128 | 15804 | | | |
| | Model | 3 | | 6.73 | **3.00E-04** | 0.116 |
| (D) Total Biomass (g/0.25 $m^2$) | Crest sand nitrate concentration | 1 | 26154 | 4.48 | **0.0362** | 0.034 |
| | Foredune crest height | 1 | 49203 | 8.43 | **0.0043** | 0.061 |
| | Residuals | 129 | 752801 | | | |
| | Model | 2 | | 5.64 | **0.0045** | 0.066 |

**Table F7.** Statistical results from multiple regression analyses for dune grass species production metrics at the foredune heel, as a function of marine subsidies and foredune crest height. (A) Shoot density (number/0.25 m$^2$) and (B) total biomass (g/0.25 m$^2$) for all dune grass species. (C) Shoot density (number/0.25 m$^2$) and (D) total biomass (g/0.25 m$^2$) for *Ammophila arenaria* and *Ammophila breviligulata*. Significant P values are in bold.

| Component | Source of variation | df | Sum Sq | F value | Prob > F | Variance explained |
|---|---|---|---|---|---|---|
| (A) Shoot Density (number/0.25 m$^2$) | Crest/heel sand nitrate concentration | 1 | 256 | 2.23 | 0.1374 | 0.017 |
| | Foredune crest height | 1 | 144 | 1.26 | 0.2634 | 0.010 |
| | Residuals | 129 | 14788 | | | |
| | Model | 2 | | 2.18 | 0.1170 | 0.018 |
| (B) Total Biomass (g/0.25 m$^2$) | Crest/heel sand nitrate concentration | 1 | 1271 | 0.34 | 0.5584 | 0.003 |
| | Foredune crest height | 1 | 21699 | 5.88 | **0.0167** | 0.044 |
| | Residuals | 129 | 476299 | | | |
| | Model | 2 | | 3.55 | 0.0316 | 0.037 |
| (C) Shoot Density (number/0.25 m$^2$) | Crest/heel sand nitrate concentration | 1 | 30 | 0.22 | 0.6379 | 0.002 |
| | Foredune crest height | 1 | 36 | 0.26 | 0.6088 | 0.002 |
| | Residuals | 129 | 17616 | | | |
| | Model | 2 | | 0.31 | 0.7376 | -0.011 |

**Table F7.** (Continued)

| | | | | | | |
|---|---|---|---|---|---|---|
| (D) Total Biomass (g/0.25 m$^2$) | Crest/heel sand nitrate concentration | 1 | 2778 | 0.76 | 0.3842 | 0.006 |
| | Foredune crest height | 1 | 4709 | 1.29 | 0.2578 | 0.010 |
| | Residuals | 129 | 470221 | | | |
| | Model | 2 | | 0.86 | 0.4254 | -0.002 |

**Table F8.** Statistical results from multiple regression analyses for the (A) shoot biomass (g/shoot) and (B) shoot length (cm) of *Ammophila arenaria* and *Ammophila breviligulata* at the foredune toe, as a function of various environmental factors and marine subsidies. Significant P values are in bold.

| Component | Source of variation | df | Sum Sq | F value | Prob > F | Variance explained |
|---|---|---|---|---|---|---|
| (A) Shoot Biomass (g/shoot) | Total wrack biomass | 1 | 0.80 | 0.50 | 0.4815 | 0.004 |
| | Mid-beach/toe sand nitrate concentration | 1 | 8.80 | 5.51 | **0.0205** | 0.041 |
| | Residuals | 129 | 206 | | | |
| | Model | 2 | | 2.79 | **6.50E-02** | 0.027 |
| (B) Shoot Length (cm) | Total wrack biomass | 1 | 275 | 1.87 | 0.1736 | 0.014 |
| | Mid-beach/toe sand nitrate concentration | 1 | 626 | 4.26 | **0.0409** | 0.032 |
| | Residuals | 129 | 18942 | | | |
| | Model | 2 | | 2.64 | 0.0755 | 0.024 |

**Table F9.** Statistical results from multiple regression analyses for the (A) shoot biomass (g/shoot) and (B) shoot length (cm) of *Ammophila arenaria* and *Ammophila breviligulata* at the foredune crest, as a function of various environmental factors and marine subsidies. Significant P values are in bold.

| Component | Source of variation | df | Sum Sq | F value | Prob > F | Variance explained |
|---|---|---|---|---|---|---|
| (A) Shoot Biomass (g/shoot) | Crest sand nitrate concentration | 1 | 7.86 | 3.71 | **0.0564** | 0.028 |
| | Foredune crest height | 1 | 0.27 | 0.13 | 0.7232 | 0.001 |
| | Residuals | 129 | 273 | | | |
| | Model | 2 | | 1.85 | 0.1607 | 0.013 |
| (B) Shoot Length (cm) | Crest sand nitrate concentration | 1 | 13.2 | 0.07 | 0.7972 | 0.001 |
| | Foredune crest height | 1 | 4337 | 21.85 | **7.33E-06** | 0.145 |
| | Residuals | 129 | 25611 | | | |
| | Model | 2 | | 11.03 | **3.77E-05** | 0.133 |

**Table F10.** Statistical results from multiple regression analyses for the (A) shoot biomass (g/shoot) and (B) shoot length (cm) of *Ammophila arenaria* and *Ammophila breviligulata* at the foredune heel, as a function of various environmental factors and marine subsidies. Significant P values are in bold.

| Component | Source of variation | df | Sum Sq | F value | Prob > F | Variance explained |
|---|---|---|---|---|---|---|
| (A) Shoot Biomass (g/shoot) | Heel sand nitrate concentration | 1 | 0.04 | 0.02 | 0.8875 | 0.0002 |
| | Foredune crest height | 1 | 2.35 | 1.28 | 0.2596 | 0.010 |
| | Residuals | 129 | 236 | | | |
| | Model | 2 | | 0.64 | 0.5272 | -0.005 |
| (B) Shoot Length (cm) | Heel sand nitrate concentration | 1 | 2646 | 11.22 | **0.0011** | 0.080 |
| | Foredune crest height | 1 | 5412 | 22.96 | **4.48E-06** | 0.151 |
| | Residuals | 129 | 30413 | | | |
| | Model | 2 | | 20.72 | 1.57E-08 | 0.2314 |

## Appendix G Chapter 4 Summary tables and statistical results for the spatial variability of dune grass production response to nutrient addition

**Table G1.** Summary data (mean ± SE) and statistical results using ANOVAs for initial (A) shoot density (number/0.25$m^2$), (B) total biomass (g/0.25$m^2$), (C) biomass (g/shoot), and (D) shoot length (cm) for dune grasses across treatments (C, E), foredune profile locations (toe, crest, heel), and sites (Long Beach, Fort Stevens, South Beach). Significant P values are in bold. Tukey HSD post hoc tests $P < 0.05$.

| | **Site** | | | **Site** | | |
|---|---|---|---|---|---|---|
| | Long Beach | Fort Stevens | South Beach | Long Beach | Fort Stevens | South Beach |
| **Profile Location** | **Shoot Density (number/0.25m2)** | | | **Total Biomass (g/0.25m2)** | | |
| Toe | 28 ± 5.13 (C)<br>22 ± 5.87 (E) | 74 ± 15.73 (C)<br>69 ± 14.94 (E) | 81 ± 6.27 (C)<br>83 ± 17.56 (E) | 56 ± 11.18 (C)<br>44 ± 11.60 (E) | 192 ± 28.50 (C)<br>182 ± 33.65 (E) | 80 ± 6.13 (C)<br>79 ± 14.97 (E) |
| Crest | 26 ± 3.65 (C)<br>25 ± 4.50 (E) | 44 ± 5.38 (C)<br>62 ± 7.83 (E) | 73 ± 13.19 (C)<br>67 ± 13.76 (E) | 152 ± 49.49 (C)<br>158 ± 60.86 (E) | 258 ± 44.14 (C)<br>363 ± 61.23 (E) | 74 ± 14.30 (C)<br>71 ± 20.14 (E) |
| Heel | 46 ± 4.44 (C)<br>42 ± 4.73 (E) | 30 ± 4.58 (C)<br>31 ± 4.79 (E) | 60 ± 5.27 (C)<br>64 ± 5.54 (E) | 271 ± 54.30 (C)<br>243 ± 43.59 (E) | 136 ± 29.68 (C)<br>141 ± 37.28 (E) | 137 ± 35.20 (C)<br>145 ± 34.97 (E) |
| | **Biomass per shoot (g)** | | | **Shoot length (cm)** | | |
| Toe | 2 ± 0.15 | 2 ± 0.36 | 1 ± 0.07 | 72 ± 2.04 | 77 ± 3.04 | 71 ± 2.97 |
| Crest | 5 ± 1.13 | 5 ± 0.48 | 1 ± 0.14 | 86 ± 7.79 | 115 ± 5.60 | 68 ± 5.23 |
| Heel | 5 ± 0.74 | 4 ± 0.52 | 2 ± 0.47 | 100 ± 5.19 | 99 ± 2.57 | 80 ± 4.07 |

**Table G2.** Statistical results using two-way ANOVAs for (A) shoot density (number/0.25 $m^2$) and (B) total biomass (g/0.25 $m^2$) for all dune grasses across treatments (C, E), foredune profile locations (toe, crest, heel), and sites (Long Beach, Fort Stevens, South Beach). Significant P values are in bold. Tukey HSD post hoc tests $P < 0.05$.

| **Source of variation** | **df** | **SS** | **F** | **Prob > F** | **Tukey HSD post hoc test** |
|---|---|---|---|---|---|
| **Shoot Density (number/0.25 $m^2$)** | | | | | |
| Site | 2 | 23802 | 23.85 | **6.86E-09** | SB > FS > LB |
| Treatment | 1 | 4 | 0.01 | 0.9250 | |
| Profile location | 2 | 3156 | 3.16 | **0.0475** | Toe ≥ Crest ≥ Heel |
| Treatment*Profile location | 2 | 172 | 0.17 | 0.8423 | |
| Residuals | 82 | 40921 | | | |
| Model | 7 | | 7.77 | **3.46E-07** | |
| **Total Biomass (g/0.25 $m^2$)** | | | | | |
| Site | 2 | 195259 | 9.99 | **0.0001** | FS ≥ LB ≥ SB |
| Treatment | 1 | 1408 | 0.14 | 0.7052 | |
| Profile location | 2 | 107681 | 5.51 | **0.0057** | Crest = Heel > Toe |
| Treatment*Profile location | 2 | 9002 | 0.46 | 0.6326 | |
| Residuals | 82 | 801465 | | | |
| Model | 7 | | 4.58 | **2.34E-04** | |

**Table G3.** Summary data (mean ± SE) and statistical results using ANOVAs for initial (A) stem density (number/0.25$m^2$), (B) total biomass (g/0.25$m^2$), (C) biomass (g/shoot), and (D) shoot length (cm) for *Ammophila breviligulata* across treatments (C, N1, N2, N3, N3+P) and foredune profile locations (toe, crest, heel). Significant P values are in bold. Tukey HSD post hoc tests P < 0.05.

| | **Treatment** | | | | | **Treatment** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | C | N1 | N2 | N3 | N3+P | C | N1 | N2 | N3 | N3+P |
| **Profile Location** | **Shoot Density (number/0.25 $m^2$)** | | | | | **Total Biomass (g/0.25 $m^2$)** | | | | |
| Toe | 6 ± 0.88 | 7 ± 0.54 | 6 ± 0.52 | 7 ± 0.79 | 7 ± 0.58 | 37 ± 6.24 | 41 ± 4.18 | 35 ± 4.77 | 45 ± 5.71 | 40 ± 4.83 |
| Crest | 35 ± 6.31 | 33 ± 6.31 | 34 ± 5.94 | 35 ± 5.30 | 35 ± 4.84 | 95 ± 14.94 | 108 ± 15.15 | 106 ± 12.41 | 107 ± 12.40 | 104 ± 14.67 |
| Heel | 23 ± 3.87 | 26 ± 4.02 | 25 ± 2.85 | 26 ± 3.48 | 25 ± 3.75 | 119 ± 23.59 | 136 ± 26.06 | 131 ± 21.16 | 134 ± 23.00 | 131 ± 25.28 |
| | **Biomass per shoot (g)** | | | | | **Shoot length (cm)** | | | | |
| Toe | 5 ± 0.37 | | | | | 80 ± 3.02 | | | | |
| Crest | 4 ± 0.33 | | | | | 82 ± 3.30 | | | | |
| Heel | 5 ± 0.36 | | | | | 105 ± 5.43 | | | | |

**Table G4.** Statistical results using two-way ANOVAs for (A) shoot density (number/0.25 $m^2$) and (B) total biomass (g/0.25 $m^2$) for for *Ammophila breviligulata* across treatments (C, N1, N2, N3, N3+P) and foredune profile locations (toe, crest, heel). Significant P values are in bold. Tukey HSD post hoc tests $P < 0.05$.

| **Source of variation** | **df** | **SS** | **F** | **Prob > F** | **Tukey HSD post hoc test** |
|---|---|---|---|---|---|
| **Shoot Density (number/0.25 $m^2$)** | | | | | |
| Treatment | 4 | 25.5 | 0.07 | 0.9914 | |
| Profile location | 2 | 12028 | 64.20 | **<2E-16** | Crest > Heel > Toe |
| Treatment*Profile location | 8 | 42.6 | 0.06 | 0.9999 | |
| Residuals | 75 | 7026 | | | |
| Model | 14 | | 9.22 | **2.28E-11** | |
| **Total Biomass (g/0.25 $m^2$)** | | | | | |
| Treatment | 4 | 1554 | 0.25 | 0.9117 | |
| Profile location | 2 | 130516 | 41.17 | **8.56E-13** | Heel > Crest > Toe |
| Treatment*Profile location | 8 | 409 | 0.03 | 1 | |
| Residuals | 75 | 118867 | | | |
| Model | 14 | | 5.97 | **1.04E-07** | |