Methods of Accelerating Re-Vegetation at Bay of Fundy Salt Marsh Restoration Sites: A Practical Comparison

By
Tasha Rabinowitz

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Approved:	Dr. Jeremy Lundholm Supervisor
Approved:	Dr. Danika van Proosdij Committee Member
Approved:	Dr. Allison Walker Committee Member
Approved:	Mr. Tony Bowron Committee Member
Approved:	Dr. Myriam Barbeau External Examiner
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Abstract

Tidal wetlands provide important coastal protection, and interest in their restoration is growing in response to climate change. In Atlantic Canada, tidal wetland restoration has focused on restoring tidal flow, without planting vegetation. I evaluated five methods of planting eight native species at Bay of Fundy restoration sites by comparing growth and health of plants over two years. Planting potted seedlings facilitated the most growth of desired species and had 75% survival while plants transplanted from adjacent sites had higher mortality. Growth, health, and winter survival were all more strongly related to site than treatment. Important differences in elevation, inundation, salinity and soil nutrients may explain these differences in performance.

These techniques show promise for accelerating re-vegetation at recovering sites, and my results highlight the need for an understanding of site conditions to inform planting schemes. Depending on budget, some combination of the tested planting techniques may be appropriate.

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This work was conducted on the unceded territory of Mi'kma'ki, which I am grateful to have called my home these past years. With this acknowledgement, I am making a commitment to taking conscious action towards restoring balance between Indigenous people and colonizers.

"All flourishing is mutual."

- Robin Wall Kimmerer, Braiding Sweetgrass

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Chapter 1: General Introduction

Canada has the world's longest coastline (Lemmen & Warren, 2016), with 38% of the human population living within 20 km of the coast (Manson, 2005). Nova Scotia's 7,600 km of coastline (along the Atlantic Ocean) is home to over half of its population and infrastructure, and the entirety of the Province is no further than 67 km from the coast (Chesworth, 2016). Coastal areas are highly dynamic and climate change is altering many natural coastal processes (Lemmen & Warren, 2016). Erosion, storm surge and associated flooding, and sea-level-rise are some of the main processes with the potential to damage infrastructure and displace coastal residents. Current coastal management takes a "hard engineering" approach to coastlines where these issues are managed by building seawalls, dykes, breakwaters, and other structures unable to adapt in response to changing conditions. Coastal erosion on the East coast of Canada is projected to increase along with rising sea-levels, and increasing frequency and intensity of storm surge (Lemmen & Warren, 2016). These processes can cause structural damage to coastal roads, buildings and adjacent natural systems. These impacts are further exacerbated by hard engineered coastal structures that reflect wave energy, often simply deflecting erosional action (Bozek & Burdick, 2005; National Research Council, 2007), and prevent sediment supply to adjacent systems. Hard infrastructure also contributes to coastal squeeze, limiting the ability of natural systems to adapt to changing conditions.

Salt marshes (a type of tidal wetland) are an important part of the coastal landscape that have experienced great historical loss as a result of human engineered barriers to tidal flow. In contrast to hard engineered structures, these ecosystems are naturally adapted to dynamic coastal processes and are known to provide excellent

coastal protection (Gittman et al., 2014; Narayan et al., 2017; Shepard et al., 2011) as well as other beneficial services which will be discussed further in the following literature review. As such, the restoration of these systems is gaining popularity as a component of climate change adaptation strategies on the coast.

In Atlantic Canada, it is estimated that these ecosystems have experienced a loss of roughly 75-90 % of their historical extent (Tiner, 2013), particularly concentrated around the Bay of Fundy in Nova Scotia and New Brunswick where 85% has been lost (Hanson & Calkins, 1996). The Bay of Fundy is a unique system subject to the stresses of the highest tidal range in the world (an average range of 12 m, and occasionally exceeding 16 m at the head of the Bay), and ice scour along the coastline because of its northern latitude (Desplanque & Mossman, 2004). Bay of Fundy marshes are distinct from other temperate coastal marshes based upon their vegetation patterns, as some plants are frequently flooded by deep ocean water (Pratolongo et al., 2019). Most of the salt marsh restoration to date in Nova Scotia has been concentrated in this area.

In the Bay of Fundy region there are many constructed tidal barriers including causeways, improperly sized or placed culverts and bridges, and dykes. Dykes are earthen berms with one-way gates preventing tidal inundation yet allowing freshwater drainage which are constructed to convert large swaths of salt marsh to agricultural fields through cutting off their natural hydrological regime. These dykes were initially built beginning in the 1600s by Acadian farmers but have since been updated by Nova Scotia Department of Agriculture (NSDA) (Milligan, 1987). In these dyked systems there is a unique opportunity to remove or "realign" dykes (managed realignment – when dykes are stepped back), and this type of project can include some component of salt marsh

restoration. With increasing frequency over the last 20 years, salt marsh restoration and managed realignment has been occurring in Nova Scotia (e.g., Van Proosdij et al., 2010; Virgin et al., 2020) mainly as an alternative to fixing failing dykes, and because marsh restoration can act as compensation for wetland or fish habitat loss elsewhere in the province. When managed realignment projects include salt marsh restoration, there are added benefits of re-instating some of the ecosystem services that salt marshes can provide and creating a more resilient coastline in the face of climate change.

Restoring a site's natural hydrological regime typically produces a more natural ecological state; however, longstanding deficits in vegetation diversity have been noted both locally and globally. The flora in salt marsh systems naturally form distinct zonation patterns as a result of abiotic stressors, physical factors (e.g., tidal inundation, salinity, topography, soil nutrients), and competition (Pennings & Bertness, 2001). However, the full diversity of plants that would be expected in natural marshes is not always seen at restoration sites. Particularly, restoration sites will often remain dominated by pioneer communities with low abundances of upper marsh species (Bowron et al., 2011b; Byers & Chmura, 2007). Many of the services provided by salt marshes are specifically mediated by the presence of healthy vegetation communities (Shepard et al., 2011), and these deficits in diversity may influence the quality of services and overall health of restored sites. Altered physical characteristics at restoration sites may partially explain deficits in vegetative recovery and in these cases, it may be necessary to take a more active approach to re-establishing proper vegetative diversity.

Some form of adding plants is commonly undertaken in salt marsh restoration projects in other parts of the world (e.g., Broome et al., 1988; O'Brien & Zedler, 2006) to

accelerate re-vegetation and to promote sustainability of restored sites. There have, however, been no planting components to salt marsh restoration projects in the Bay of Fundy region to date, and very few in Atlantic Canada at all (e.g., Wrathall, 2016). My study represents the first attempt at active planting in the context of salt marsh restoration in the Bay of Fundy region where extreme tidal conditions and winter ice activity may uniquely influence plant re-establishment. Further, comparisons of methodological approaches to planting vegetation are usually made between sites, and vegetation is typically planted in grid-style formations. This study takes a smaller-scale approach where treatments are replicated in clusters across sites because of new evidence suggesting that planting in tight clusters may maximize facilitation, whereby interactions of individuals benefit one-another, and increase survival and growth of plantings (Silliman et al., 2015). Planting small clusters across a site also allows performance of planting techniques to be examined in relation to within-site variability in abiotic conditions. The investigation of these approaches to re-vegetation is important to provide the foundation for management of these systems.

My thesis will focus on two recovering restoration sites where tidal flow was restored within one year of starting the project (project began in 2019) and will compare methods of accelerating re-vegetation. The main objective of this study was to establish whether active re-vegetation efforts will accelerate plant re-establishment and enhance vegetative diversity in recovering salt marshes where tidal flow has been returned. Specifically, this study evaluated different methods of re-introducing plants to restoration sites in the Bay of Fundy. Main research questions were: 1) Does planting vegetation accelerate vegetation recovery? 2) Do certain treatments, or species, have higher plant

performance (e.g., survival, growth)? 3) Is performance associated with abiotic

conditions?

The following literature review gives more details about concepts introduced here

and provides an overview of salt marsh restoration with respect to vegetation recovery.

First, I outline the importance of salt marshes by way of the services that these

ecosystems provide humans and the crucial role vegetation plays in providing those

services. Then, I discuss the historical and political context into which salt marsh

restoration fits in Atlantic Canada. Lastly, I review the information relevant to the design

of active planting schemes in salt marsh restoration.

Chapter 2: Literature Review

2.1 Ecosystem Services and the Role of Vegetation

Intact salt marshes provide a range of functions that are beneficial to humans,

called ecosystem services. Ecosystem services fit into four broad categories: provisioning

(e.g., food), regulating (e.g., climate), cultural (e.g., recreation), and supporting (e.g.,

biodiversity) (Millennium Ecosystem Assessment, 2005). These services can be a result

of underlying processes, or components of the ecosystem (Rendón et al., 2019).

Vegetation is an ecosystem component that mediates many of the key processes in salt

marshes without which ecosystem services in all categories may be degraded or lost. In

restoration, vegetation recovery alone may not completely restore ecosystem services

(Brisson et al., 2014); however, it is a crucial component to providing these services. Salt

marsh services in which vegetation plays a critical role are discussed in this section, with

details on how vegetation provides or enhances those services.

One of the most important services directly impacting coastal communities and infrastructure is wave and floodwater attenuation. This is a regulating service well-documented from salt marshes (Shepard et al., 2011). Whereas hard infrastructure simply reflects wave energy, salt marshes slow the flow, reducing or preventing flooding and damage from high-impact waves. Vegetation is a critical part of this process since it reduces flow rates (Möller et al., 2014) and vegetation characteristics such as density and height have been cited as the most important factors determining wave attenuation capacity (Shepard et al., 2011). This capacity for marshes to dissipate wave energy has been confirmed even in storm surge conditions (Barbier et al., 2013; Knutson et al., 1982; Möller et al., 2014). This service is very important to mitigate coastal flood risks and risk of damage from storm surge.

While hard infrastructure exacerbates erosional processes, salt marshes are created through depositional processes. Accretion describes the process by which sediment deposited in salt marshes is buried over time, allowing the marsh soils to grow both horizontally and vertically. It is worth noting that marshes can grow when sediment supply or belowground production exceeds erosion and there is no development that presents a barrier to landward migration of the upper marsh edge. Vegetation mediates accretion and shoreline stabilization in a number of ways: roots bind the soil and increase stability (Van Eerdt, 1985), plants contribute organic matter to soil (Feagin et al., 2009), and stems increase sedimentation both through particle capture (deposited onto plant surface) and as a result of increased particle settling due to decreased flow velocity through the plant canopy (Mudd et al., 2010). Marshes with vegetation in comparison to unvegetated coastal areas have an increased capacity for accretion (Shepard et al., 2011)

and accretion has been shown to increase with increasing stem density (Duggan-Edwards et al., 2020; Peng et al., 1979). A key implication of these processes is that healthy marshes can adapt to sea-level-rise and combat erosion induced by hard engineering, making them a resilient long-term climate change adaptation strategy (Erwin, 2009; Singh et al., 2007).

The high productivity and relatively low decomposition rates in salt marshes make them particularly effective at sequestering carbon (Brevik & Homburg, 2004; McLeod et al., 2011; Taillardat et al., 2018). Carbon captured by coastal systems – termed 'blue carbon' – represents a very large global store of carbon despite being significantly smaller by area than other ecosystems (McLeod et al., 2011). Carbon sequestration is an important climate regulatory service that has potential to be part of climate change mitigation strategies. Sources of blue carbon in the marsh can be both external and internal: carbon can be trapped through burial of sediment (external source) which is enhanced by vegetation as per above, and through burial of organic matter (internal source) where carbon is captured locally through photosynthesis. Evidence is growing that restored salt marshes can sequester large amounts of carbon and therefore represent a sink in the global carbon budget (Andrews et al., 2006; Santini et al., 2019; Wollenberg et al., 2018). While one study in the UK indicated that carbon stores at a salt marsh restoration site were not equivalent to a natural site after 15 years (Burden et al., 2013), another study in the Bay of Fundy indicated that 6 years after restoration the salt marsh was sequestering carbon at a rate five times that of a nearby reference salt marsh that would be subjected to the same conditions (Wollenberg et al., 2018). It is possible that the discrepancy between the UK and Bay of Fundy sites may be due to the extremely

high sediment concentrations in the Bay of Fundy and may indicate that restored marshes in the Fundy region have a higher potential for carbon storage than marshes elsewhere. This ability to act as a long-term carbon sink makes salt marshes an important component of climate change mitigation measures.

Salt marshes are also high-quality habitat for many species (some rare and endangered) of fish, birds, invertebrates, mammals and amphibians. As an ecosystem service, this is considered a supporting service. Species of shorebirds and waterfowl are known to use salt marshes throughout their life cycles (Hicklin, 1987; McAloney, 1981; Roberts & Robertson, 1986; Tiner, 2013). Fish, including a large proportion of the world's economically important fishery species, also rely on salt marshes for food, as nursery and for refuge from predators (Boesch & Turner, 2006; Jänes et al., 2020; Tiner, 2013; Whitfield, 2017). Vegetation plays a critical role in the quality of fish habitat through providing refuge and food for fishes. The restoration of salt marsh structural components can cause fish to return in similar density and richness to natural marshes (Burdick et al., 1997; Dionne et al., 1999; Minello & Webb, 1997). Use of restored marshes by fish and other fauna, such as birds and benthic invertebrates, has been seen to the rapidly return upon restoration (Able et al., 2008; Atkinson et al., 2004; Bowron et al., 2015; Dionne et al., 1999; Roman et al., 2002).

The services described here are just some of the reasons why salt marsh restoration is beneficial and current motivation for salt marsh restoration includes the enhancement or re-instatement of the services discussed here. Vegetation plays a crucial role in salt marsh health, and specifically mediates many of these beneficial functions of

salt marshes. The geographical and political context into which this project fits will be discussed further in the next section.

2.2 Salt Marsh Restoration: Political Motivation in Nova Scotia

In Atlantic Canada, salt marshes have been manipulated by humans to create, protect, and connect farmland and settlements for hundreds of years (Milligan, 1987). There are three main ways through which salt marshes have been lost in Atlantic Canada that present an opportunity for restoration: through dyking, through the construction of road infrastructure (e.g,. improperly sized culverts, causeways), and through coastal development. A dyke is an earthen berm with a one-way gate, called an aboiteau, which prevents tidal inundation while allowing outgoing freshwater to drain. These structures eliminate the natural hydrological regime of tidal wetlands, and prevent sedimentation, ultimately creating terrestrial habitat. Milligan (1987) describes that starting in the 1600s, the Acadians built dykes throughout the Maritimes to expose highly fertile agricultural land. Since about 1970 the Nova Scotia Department of Agriculture (NSDA) has been charged with dyke creation and maintenance in the province (Milligan, 1987). Since the oversight of the dykes was transferred to NSDA, all of the dykes in the province have been updated and some newly built. Today, roughly 75-90 % of the historical wetlands in Atlantic Canada have been lost as a result of this dyking process (Tiner, 2013) with over half of the salt marsh in Nova Scotia being dyked (Tiner, 2013). The restoration of dyked sites are the focus of this thesis.

Salt marsh restoration projects (in any case where tidal flow has been restricted or stopped) and managed realignment projects (whereby a dyke is moved back, sometimes

restoring salt marsh) have been occurring with increasing frequency over the past 20 years in this region (e.g., Bowron et al., 2011b, 2012; Sherren et al., 2019; Van Proosdij et al., 2010) mainly as a result of legislative compliance (Bowron et al., 2012). These restoration projects have been mostly concentrated in the Bay of Fundy region (Bowron et al., 2012). Legislative requirements for wetland compensation at the provincial level, and fish habitat compensation at the federal level have been the motivation for Nova Scotia Department of Transport and Infrastructure Renewal (NSTIR) to fund many of these projects to date. In addition to legislative compliance, these projects present an opportunity for NSDA to reduce the amount of dyke infrastructure they have to manage (which can cut costs e.g., Sherren et al., 2019). The 241 kilometers of dykes and 252 aboiteaux in the province are costly to maintain, especially as rising sea levels increase the risk of failure and the need for creating solutions for long term sustainability of the province's dykeland systems. In situations where dykes are failing or the protected land (dykeland) is no longer in use, managed realignment and salt marsh restoration can help cut costs while restoring the ecosystem services salt marshes have to offer.

2.3 Research Problem

The most critical component of salt marsh restoration is the return of a more natural hydrological regime. Sediment inputs, soil biogeochemistry, and flora and fauna communities are all intrinsically linked to tidal flooding and are altered when tidal flooding is restricted (Burdick et al., 1997). Restoration projects to date in the Fundy region have been focused solely on removing barriers to tidal flow and allowing natural processes to drive plant re-establishment (Bowron et al., 2012). The restoration trajectory

typically begins with a die-back of freshwater and terrestrial species and an influx of sediment, followed by the recolonization of halophytic species (Bowron et al., 2011b; Burdick et al., 1997; Lemieux, 2012; Van Proosdij et al., 2010; Virgin et al., 2020). While this typically produces a more natural ecosystem, longstanding deficits in vegetation recovery have been noted both locally and globally (e.g., Bowron et al., 2011; Brooks et al., 2014; Burdick et al., 1997; Byers & Chmura, 2007; Chang et al., 2016). Restoration sites may have persistent freshwater and upland species (Bowron et al., 2013) or remain dominated by pioneer communities with low abundances of upper marsh species (discussed further below) for anywhere from 7 to 55+ years (Bowron et al., 2011b; Brooks et al., 2014; Burdick et al., 1997; Byers & Chmura, 2007; Chang et al., 2016).

Restored marshes at managed realignment sites have been seen to have lower creek density, lower rugosity, and more concave features when compared to natural salt marsh reference sites (Lawrence et al., 2018). This issue is highly persistent over time (Brooks et al., 2014; Lawrence et al., 2018), and this altered topography has been found to lead to poorly vegetated areas (Brooks et al., 2014; Haltiner et al., 1997). Factors such as distance to creek have been shown to be important determinants of the development of upper marsh vegetation communities (Chang et al., 2016). These altered physical characteristics at restored marshes may partially explain deficits in vegetative diversity at restoration sites and in these cases it may be necessary to take a more active approach to re-establishing proper vegetative diversity and abundance.

2.4 Plant Zonation: Choosing Appropriate Locations and Species

Salt marshes are a highly dynamic environment, influenced by a wide range of abiotic factors (Table 1). As a result of these physical stresses and the tolerance and competitive ability of vegetation species, the flora form distinct zonation patterns created by a predictable strata of plant associations (Anastasiou & Brooks, 2003; Batzer & Baldwin, 2012; Bertness, 1991; Pennings et al., 2005; Pennings & Callaway, 1992; Porter et al., 2015; Stalter & Batson, 1969; Wilson et al., 2015). Elevation mediates most of the conditions leading to these patterns – flooding and salinity in particular – and zonation patterns are well-known to follow elevational gradients in the salt marsh (Broome, 1989; Broome et al., 1988; Konisky & Burdick, 2004; Seneca et al., 1985). Species are excluded from lower elevations by unsuitable conditions and excluded from higher elevations due to relative lack of competitive ability against species adapted to less saline conditions (Bertness, 1991; Pennings et al., 2005; Pennings & Callaway, 1992). Flooding, salinity, and elevation are often taken as the three main abiotic variables determining salt marsh zonation and are discussed further in this section in relation to zonation patterns seen in Nova Scotia. Understanding these patterns and the conditions that underlie them can inform the appropriate species and locations for planting in restoration projects.

In Nova Scotia, there are seven distinct plant associations found in natural marshes across a range of tidal magnitudes and salinity ranges (depending on distance from the ocean). These are described by Porter et al. (2015), and will be discussed in depth in this section. This study included mainly Fundy sites, with two sites in other parts of the province. Similar zonation patterns have been well described by other researchers

in Nova Scotia, and elsewhere in the world with some variation in specific species (Adams, 1963; Bertness, 1991; Bertness & Ellison, 1987; Pennings & Bertness, 2001; Pielou & Routledge, 1976). The zones described here are named after the dominant graminoid species, or according to the relative elevation (i.e. low- mid- high-).

The *Spartina alterniflora* (note: the *Spartina* spp. discussed in this thesis have recently been reclassified to the *Sporobolous* genus; however, for the purposes of this thesis I have retained the name *Spartina*) association in the low marsh zone is characterized by high salinity, low elevation, and long inundation periods. Dominated almost entirely by *S. alterniflora*, *Spartina patens* is the only other species occasionally present in low abundance in this zone (Porter et al., 2015). *S. alterniflora* is known to be a stress tolerant, poor competitor and is therefore refined mostly to high-stress environments where other species are unable to survive (Bertness, 1991; Pennings et al., 2005). *S. alterniflora* is a poor seed producer but is generally viewed as an ecosystem engineer (Bruno, 2000) and is commonly one of the first species to recolonize the marsh. There is evidence that *S. alterniflora* may be able to outcompete *S. patens* in high nutrient environments (Levine et al., 1998; Muench & Elsey-Quirk, 2019), indicating that nutrients may be an important limiting factor in these systems, and competitive dynamics may be altered in early successional systems.

The *S. patens* association in the mid marsh zone was characterized by high salinity, intermediate elevation, and intermediate inundation. This zone had slightly higher diversity and was dominated by *S. patens*, with small amounts of *S. alterniflora*, *Atriplex glabriuscula*, *Limonium carolinianum*, and *Salicornia maritima* (Porter et al., 2015).

Table 1. Main physical stressors acting on plant zonation in salt marshes.

Abiotic Stress	Effect on Vegetation	Reference
Tidal Hydrology	Saturation & Drying	Lyon & Lyon, 2011 Tiner, 2005
	Wave Energy	Bergen et al., 2000
	Anoxic Soils	Anastasiou & Brooks, 2003 Lyon & Lyon, 2011 Tiner, 2005
Salinity	Toxicity	Pennings et al., 2005
	Decreased water availability	Shumway & Bertness, 1992 Bertness et al., 1992
Wrack Deposition	Smothering	Bertness & Ellison, 1987 Hartman et al., 1983 Minchinton, 2006 Valiela & Rietsma, 1995
	Seed Source	Glogowski, 2013 Minchinton, 2006
Edaphic Factors	Nutrient Dynamics	Broome et al., 1988 Levine et al., 1998
Ice (at Northern latitudes)	Smothering & Scouring	Desplanque & Mossman, 2004 Ewanchuk & Bertness, 2003 Pennings & Bertness, 2001
	Propagule Source	Greene, 2009
Topography	Tidal Creeks (flooding)	Chang et al., 2016

There were two different associations found in the high marsh zone: *Juncus gerardii* and *Distichlis spicata* both growing in environments characterized by high salinity, high elevation and short inundation durations. The *J. gerardii* zone had low abundances of *Solidago sempervirens* and *A. glabriuscula.* The *D. spicata* zone had *S. patens*, and *S. alterniflora* also present in low abundance (Porter et al., 2015).

At sites slightly higher in the tidal frame (farther from the ocean), or with a higher freshwater influence and therefore lower salinity, three distinct zones were found: *Carex paleacea* (intermediate salinity, low elevation, intermediate inundation), *Spartina*

pectinata (intermediate salinity, intermediate elevation, short inundation), and *Juncus balticus – Festuca rubra* (intermediate salinity, high elevation, and intermediate inundation). The *C. paleacea* association commonly had *Agrostis stolonifera*, *F. rubra*, *S. patens, J. gerardii,* and *Argentina anserina* also growing, as well as *S. alterniflora*, and *S. sempervirens* occasionally. The *S. pectinata* association commonly included *C. paleacea*, *Symphiotrichum novi-belgii, A. stolonifera,* and *S. sempervirens*. The *J. balticus – F. rubra* association had a relatively high species richness and within this association *C. paleacea* was the only species found in relatively high abundance (Porter et al., 2015). No research has been completed examining the competitive dynamics in these lower salinity tidal marshes.

As the trajectory of a restoration site is difficult to determine, species that survive in a range of conditions should be chosen. While the literature usually emphasizes that projects are not "one-size-fits-all", graminoids are typically targeted for planting efforts, especially *S. alterniflora* and *S. patens* (e.g., Adnitt et al., 2007; GBF, 2014; MDE, 2008). There has been very little research regarding planting salt marsh forbs, but one study found that planting assemblages with higher species richness contributed to higher biomass and plant tissue nitrogen accumulation (Callaway et al., 2003). These findings indicate that species-rich plantings may increase plant growth in a restoration context. Since the mid- and high- marsh communities with higher forb abundance and diversity typically take longer to come back than the low marsh, my study will use a mixture of species from different zones in high-richness assemblages. Of the species described here, many are found at the paired reference sites for this project. Species targeted for planting in my project are: *S. alterniflora*, *S. patens*, *S. pectinata*, *L. carolinianum, S.*

sempervirens, *Poa palustris, Plantago maritima* and *C. paleacea*. The two target species

not described in a natural zone by Porter et al. (2015), *P. palustris and P. maritima*, are

also native species found in salt marshes in Nova Scotia and due to their availability, they

were chosen as target species.

2.5 Methods of Restoring Vegetation: Considerations and Efficacy

Salt marsh restoration is a relatively common practise worldwide. There is

agreement throughout the literature that the most critical component of restoring a salt

marsh is restoring proper hydrology. This has been shown to return the site to a more

natural ecological state (Burdick et al., 1997). Since vegetation does not always return to

natural conditions, as outlined above, adding vegetative material can be a beneficial next

step to accelerate the return of the proper vegetation.

There are a variety of methods that can be used to add vegetative material or

otherwise accelerate re-vegetation, each with its own set of considerations surrounding

logistics, efficacy and costs. Depending on the goals and budget of a restoration project,

it may be necessary to use a method on its own, or in combination with one or more of

the other methods. Planting schemes carried out by restoration practitioners are not

typically well documented in the literature; however, there is a small group of researchers

that has produced documents comparing methods utilized at different sites and across

time scales (e.g., Broome et al., 1988). While these comparisons are useful, there have

been no practical comparisons of the range of methods represented in this study. The

following section reviews literature relating to five methods of plant re-establishment

used in my project: three commonly used methods and two methods that are novel for

establishing plants in salt marsh restoration in Nova Scotia. These methods fall into three broad categories: adding plants, adding a propagule source, and manipulating rugosity (tilling).

<u>2.5.1 Adding Plants</u>

Planting plants – seedlings grown in a greenhouse (potted seedlings) or transplants dug up from the restoration, or a nearby, site (field transplants) – are the most common ways to actively establish vegetation in restoration projects. These methods are attractive because using plants provides immediate erosion control and allows plants with a well-formed root mass to quickly colonize the site through rhizomal spread or seed production. Plantings can be successful under a wide range of conditions given that appropriate species are used; however, these methods can have high costs associated with sourcing plants, plant transport and labour. Fertilization, plant spacing, timing of planting, and herbivory are all logistical considerations that mediate the efficacy of any method of adding plants.

Salt marshes have been shown to be nitrogen and phosphorus-limited (Broome et al., 1983; Kiehl et al., 1997); however, no research has been conducted investigating nutrient limitations in Fundy systems. In managed realignment projects, past land use is often agricultural, and in these cases legacy nutrient or pesticide pollution may require consideration. Where systems are nutrient-limited, fertilization has been seen to increase growth and establishment of vegetation (Bergen et al., 2000; Broome et al., 1983, 1988; Covin & Zedler, 1988; Darby & Turner, 2008; Kiehl et al., 1997; Langley et al., 2013; O'Brien & Zedler, 2006) making it useful for vegetation restoration. While increased

growth is desirable, broadcast fertilizer application represents a source of pollution and may alter the vegetation community of a site (Covin & Zedler, 1988; Kiehl et al., 1997; Langley et al., 2013; Levine et al., 1998), cause eutrophication, or decrease soil strength through lowering relative root biomass (Turner, 2011). Since the unintended consequences of using fertilizer pose an environmental risk, plants in this project were not fertilized but soil nutrient concentrations and variations were tested at each site.

Vegetation is often added in a grid-style formation, and recommendations for ideal plant spacing range from 30 - 90 cm (Broome et al., 1986; de Blasio & Silver, n.d.; GBF, 2014), depending on wave energy and plant availability. New evidence, however, suggests that planting in tight clusters may be an effective alternative to grid-style plantations, with an emphasis on maximizing facilitation instead of minimizing competition. Silliman et al. (2015) found that survival and growth of *S. alterniflora* (in Florida, USA) and *Spartina angelica* (in Baarland, the Netherlands) outplantings were higher when planted individuals were touching as opposed to 50 cm apart. O'Brien and Zedler (2006) also found that tighter spacing (10 cm compared to 90 cm) of potted seedlings of five salt marsh species (all non-graminoid) increased survivorship; however, this clumping did not affect growth.

Aside from fertilization and plant spacing, a few other considerations are important for insuring planting success. Planting as early as possible in the year is recommended to allow plants to become established before the winter, and to avoid transplant shock from higher water temperatures in the summer (Broome, 1989; de Blasio & Silver, n.d.; GBF, 2014), but exact dates depend on climate. Plantings may be vulnerable to herbivory by wildlife and fencing may be necessary. Bergen et al. (2000)

found that consumption by Canada Goose (*Branta canadensis*) was a major factor controlling the success of *S. alterniflora* plantings at a salt marsh restoration site in New York. These considerations will affect the potential for planting success using either potted seedlings or field transplants. Additional considerations unique to each method and evidence pertaining to relative success of each method are outlined below.

2.5.1.1 Potted Seedlings

This method has been successful in many cases (Anastasiou & Brooks, 2003; Bergen et al., 2000; Broome et al., 1988; O'Brien & Zedler, 2006), typically using graminoid species. It has been found that potted seedlings can initiate marsh revegetation as well as or better than field transplants (Broome et al., 1988) and using potted seedlings has the added benefit that they can be used when there are no available plants in the field. Broome et al. (1988) suggest that potted seedlings are particularly useful at drier sites since the potting medium can retain water. The success of this method may be variable depending on the implementation of the planting scheme with respect to the factors outlined above.

When using plants grown in the greenhouse, pre-treatment to harden the plants to salinity, less water, and outdoor conditions may increase chances of survival; however, there is limited literature supporting this theory. While hardening plants to outdoor conditions and less water are simple, low-cost pre-treatments that are used frequently by gardeners and in plant nurseries, salinity pre-treatments may have little effect on plant performance (Brancaleoni et al., 2018) and are higher-cost. Pre-treatment necessity may

depend on the conditions of the site (i.e. position in tidal frame and therefore salinity levels).

Practitioners using this method can partner with local nurseries or grow plants themselves; however, this process is time consuming, expensive and requires facilities. Since these native species are not typically cultivated, information regarding their cultivation is limited and cultivation may be unsuccessful. Plants grown in the greenhouse can be planted at a range of ages with success but there is little literature pointing to the age at which it is most appropriate to transplant. Older and larger plants may establish more quickly; however, there is a trade-off in cost and time for propagation. An additional cost consideration is plant transport to the site.

This method represents a high-efficacy, high-cost methodology for accelerating re-vegetation at restoration sites. Further research is required directly comparing its efficacy to the other methods of re-vegetation outlined in this section and using a wider range of species. Additionally, pre-treatments and age of planting are variables that may affect success but have been seldom investigated.

2.5.1.2 Field Transplants

Transplants of various sizes can be dug up from the field, either single shoots or larger turfs, and transplanted soon after digging. Both options have been used in the past with success (Bergen et al., 2000; Broome et al., 1988; Konisky & Burdick, 2004); however, *S. alterniflora* and *L. carolinianum* transplants have had high mortality upon planting (Stalter & Batson, 1969). This discrepancy may be a result of techniques used, or site conditions. In a restoration project that used both field transplants and potted

seedlings, after rapid initial growth of the potted seedlings, field transplants were taller and produced more flowers consistently over the course of 4 years (Bergen et al., 2000), which may indicate pre-acclimatization to site conditions that may enhance growth, for example through mycorrhizal associations (d'Entremont et al., 2018).

As a lower-cost alternative to potted seedlings, transplantation is attractive. Transplanting vegetation from on-site can cut costs associated with transporting plants and can easily incorporate species that may not have grown well in the greenhouse. Despite these benefits, its use is limited when field transplants are not available and can have high associated labour costs (labour will vary by species and depending on the sediment type (i.e. easier in sandy soils)). This method also causes direct damage to existing marshes. Since most salt marsh species are hardy, they may be able to withstand this disturbance but there is no literature examining the impact of digging transplants from the salt marsh. This type of transplanting is typically limited to graminoid species and additional research is required to examine the survival of a wider range of species using this method of transplanting.

2.5.2 Adding a Propagule Source

Adding propagules, such as seed or rhizome, to a site is another way of establishing plant cover. Two potential methods of adding propagules to the site will be outlined here: directly sowing seed of native species and using wrack as a propagule source. Wrack refers to mats of dead vegetation that are washed onto salt marshes with the tide. These mats can contain a variety of species and promote diversity in marshes through shading out patches beneath them and starting new successional trajectories

(Hartman et al., 1983; Tolley & Christian, 1999; Valiela & Rietsma, 1995). Wrack

contains viable seeds and rhizomes (Glogowski, 2013; Minchinton, 2006) and therefore

may be useful as a propagule source for restoration. These methods represent relatively

low-cost alternatives to planting plants whose potential for success is relatively unknown.

Direct seeding has been used with limited success to establish salt marsh vegetation in the

past (Broome et al., 1988), but this method has associated challenges. Wrack has been

used only once in this region in an attempt to establish plants in salt marshes but with no

success (Wrathall, 2016). Additional considerations for these methods are outlined

below.

2.5.2.1 Sowing Seed

Sowing a native seed mix on the site is a method that is commonly outlined in salt

marsh restoration guides. Seeding may be most successful in sheltered sites with low

wave energy to avoid the loss of seeds with flooding or in storms (Broome, 1989;

Broome et al., 1988) and this method eliminates risk of transplant shock or under-

acclimation. Broome et al. (1988) successfully planted *S. alterniflora* seed in spring or

early summer 2 to 3 cm deep at a rate of 100 seed/m^2. Seeding in this manner in the upper

marsh produced comparable biomass to field transplants by the second growing season.

On the Atlantic coast of Nova Scotia, *S. patens* seeds had high germination at one site

with low wave energy, but no germination at another site where seeds were scoured

within a day (Wrathall, 2016). At a managed realignment site in the United Kingdom,

seed of 6 salt marsh forb species were planted at two densities (500 seeds/m^2, and 5000

seeds/m^2) with no germination success (Garbutt et al., 2005). These results suggest that seed germination may be highly variable depending on species and site conditions.

Seeding as a method of re-vegetation is a much lower-cost alternative to planting plants as costs associated with transport and propagation are eliminated. Specific storage requirements for seed of these species (i.e. dormancy periods, wet vs. dry storage) (Heim et al., 2018) may complicate this method; however, these considerations are not unique if practitioners collect and propagate their own seeds for transplanting. Broome (1989) suggests that if seed supply is limited, growing them for potted seedlings may be the best use of resources. Because of the low reliability with this method, seeding may perhaps be best used in conjunction with some other method.

2.5.2.2 Wrack as a Seed Source

A potentially overlooked application of wrack material in salt marsh restoration is its use as a source of seed. One attempt to use wrack as a seed source on the Atlantic Coast of Nova Scotia saw no germination (Wrathall, 2016); however, this was likely due to the 30 cm depth of burial and the small quantities added. Using larger quantities and burying wrack a similar depth as that recommended for seed (5 cm) may prove more successful. Thin wrack mats have also been shown to increase biomass in the high marsh, potentially through decreasing soil salinity (Pennings & Richards, 1998) which may be an added benefit to using wrack in a restoration context.

This treatment method is contingent on wrack availability at time of planting, and success may be variable due to seasonal differences in wrack contents. One study in the Fundy region found that wrack collected in the spring from several sites contained mostly

high marsh seeds (Glogowski, 2013); however, there have been no other similar studies in this region. Variation in wrack viability and contents may influence seed germination potential. Further research on using wrack in this way may point to a viable low-cost method for establishing plant cover at restored marshes.

2.5.3 Manipulating Rugosity

Increasing topographic heterogeneity on a large scale (e.g., adding creeks) can provide a variety of benefits as discussed above; however, manipulating topography at a smaller scale may be a promising method for increasing natural colonization of plants on the salt marsh. This method has been shown to successfully increase seedling recruitment in salt marsh systems (Wang et al., 2018), and to increase species richness and diversity in a coastal plain swamp (Vivian-smith, 1997). As an extension of microtopography, increasing soil rugosity, or roughness, by tilling the soil may increase seed trapping, and increase micro-diversity in abiotic variables. Success of this method may be mediated by wave energy and topographic variables at the large scale as built structures may be compacted or otherwise manipulated by waves. Increasing soil rugosity without adding any plants will help to disentangle the effects of increasing soil rugosity and any facilitative effects that plants may have on seed trapping or otherwise facilitating plant recruitment.

2.6 Synthesis and Objectives

This literature review has provided the necessary context and identified gaps in the research pertaining to active re-vegetation in salt marsh restoration. Salt marsh

restoration projects are occurring with increasing frequency following from motivations including legislative compliance, and motivation to reinstate beneficial ecosystem services. In Atlantic Canada, and especially around the Bay of Fundy in Nova Scotia the historic loss of salt marsh due to dyking provides opportunity to execute managed realignment and salt marsh restoration projects. Until now, salt marsh restoration in Atlantic Canada has largely been focused on reinstating tidal flow, and there have been very few active planting components to restoration and none in the Fundy region. Vegetation cover at managed realignment sites in this region will return rapidly; however, community structure does not always reflect natural conditions. The main objective of my study was to establish whether active re-vegetation efforts will accelerate plant re-establishment and enhance vegetative diversity in two recovering salt marshes where tidal flow has been returned. Specifically, this study will evaluate different methods of re-introducing plants to restoration sites in the Bay of Fundy. Main research questions were: 1) Does planting vegetation accelerate vegetation recovery? 2) Do certain treatments, or species, have higher plant performance (e.g., survival, growth)? 3) Is performance associated with abiotic conditions? Through comparing a range of practical planting methods with a variety of native salt marsh plant species, this project will help to inform restoration best practices in Atlantic Canada.

Chapter 3: Methods

3.1 Study Sites

Treatment techniques were tested at two salt marshes in the Bay of Fundy region where tidal flow had been restored within one year of beginning this project (project

began in 2019). The Bay of Fundy is an extension of the Gulf of Maine and it is bordered by both Nova Scotia and New Brunswick in eastern Canada. It is a macro-tidal estuary with semidiurnal tides with an average tidal range of 5 m at the mouth of the Bay and an average of 12 m at the head of the Bay (Desplanque & Mossman, 2004). There are high suspended sediment concentrations in the Bay that have been measured at < 100 g L^{-1} in the upper Bay (van Proosdij et al., 2006a) with large variation both spatially and temporally (van Proosdij et al., 2006b). These high concentrations of suspended sediment contribute to the minerogenic nature of the marshes in the region, particularly in the upper Bay, whose soils are built mainly through high rates of deposition of inorganic material (Graham et al., 2020; van Proosdij et al., 2006a, 2006b). The marshes in this region are also influenced by ice in the winter.

The first restoration site, Belcher, is located approximately 15 km downstream from Kentville, NS along the Jijuktu'kwejk (Cornwallis) River (45.073237 ˚N, -64.474148 ˚E). The second site, Converse, is located near Amherst, NS on the Chignecto Isthmus (part of the Tantramar marsh system) at the mouth of the Missaguash River (45.843420 ˚N, -64.268710 ˚E) (Figure 1). These are both sites where dykes were realigned (managed realignment) because the existing dyke was failing and there were few engineering options to repair them. By realigning the dykes at these dykes, NSDA was able to reduce the amount of at-risk infrastructure and improve the protection of remaining dykeland. These sites are part of the "Making Room for Wetlands" project spearheaded by TransCoastal Adaptations: Center for Nature-Based Solutions (www.transcoastaladaptations.com) (a center for research and outreach related to nature-based solutions to climate change adaptation) and funded in part by the Department of

Fisheries and Oceans' Coastal Restoration Fund. Making Room for Wetlands is focused on implementation and research related to the "managed realignment" of dykes in Nova Scotia and the restoration of tidal wetlands as approaches to climate change adaptation. There is a suite of ongoing long-term monitoring and research occurring at these sites related to the recovery of these wetlands.
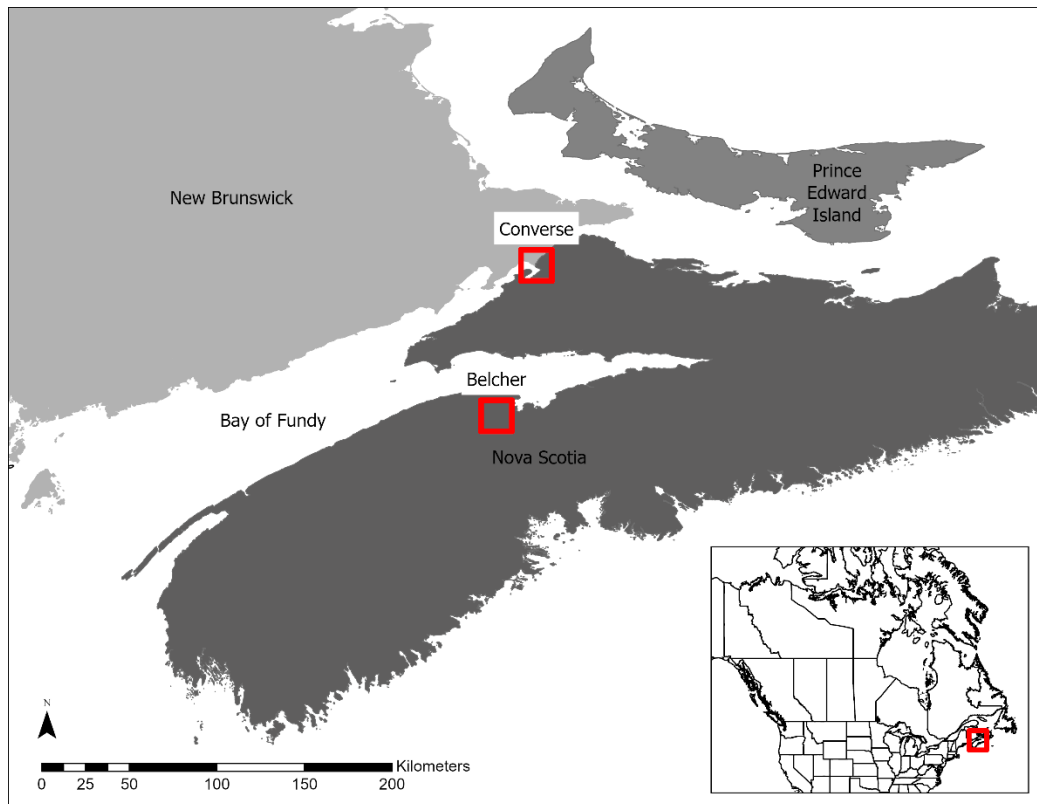
Figure 1. Location of study sites within Nova Scotia, Canada. The southerly site is Belcher, and the northerly is Converse.

The restoration area at Belcher is approximately 9.7 ha. The old dyke was decommissioned by pushing the material from the entire length of the dyke into the interior of the site and levelling it to the elevation of the foreshore marsh. This process was completed in May 2018, before which construction of the new dyke had been

completed (Figure 2). Most of the land was fallow agricultural land pre-restoration, with a small portion having been actively farmed. Following the return of tidal flooding, much of the upland plant cover died. Only 3 halophytic species (*J. gerardii*, *S. sempervirens*, and *S. pectinata)* were present on-site pre-breach (Ellis et al., 2018a) and little re-vegetation occurred over the first growing season (summer 2018). Considerable sedimentation occurred during 2018 and the entire site was bare mud at the beginning of summer 2019. During the summer of 2019 green-up was observed over much of the site mainly including annuals such as *Chenopodium* spp., *Atriplex* spp., *Suaeda* spp., and *Spergularia spp.*. The three halophytic species that were present pre-breach were still present on the site after tidal restoration, either having survived salt water intrusion or newly colonizing. There was also new colonization of other perennial halophytes including *S. alterniflora*. Belcher is higher in the tidal frame than Converse and has a strong freshwater influence. The marsh starts to flood at the mean high tide elevation, and the entire site is only flooded on higher spring tides. The center of the western portion of the site is flooded on 75 % of the high tides (see Graham et al., 2020 for flood maps). Due to low elevations and a lack of drainage channels in this half of the site, drainage is slow and inundation times are long (Graham et al., 2020). In the eastern portion of the site the dyke was straightened to restore three river meanders, these areas flood with >25 % of the high tides (Graham et al., 2020).
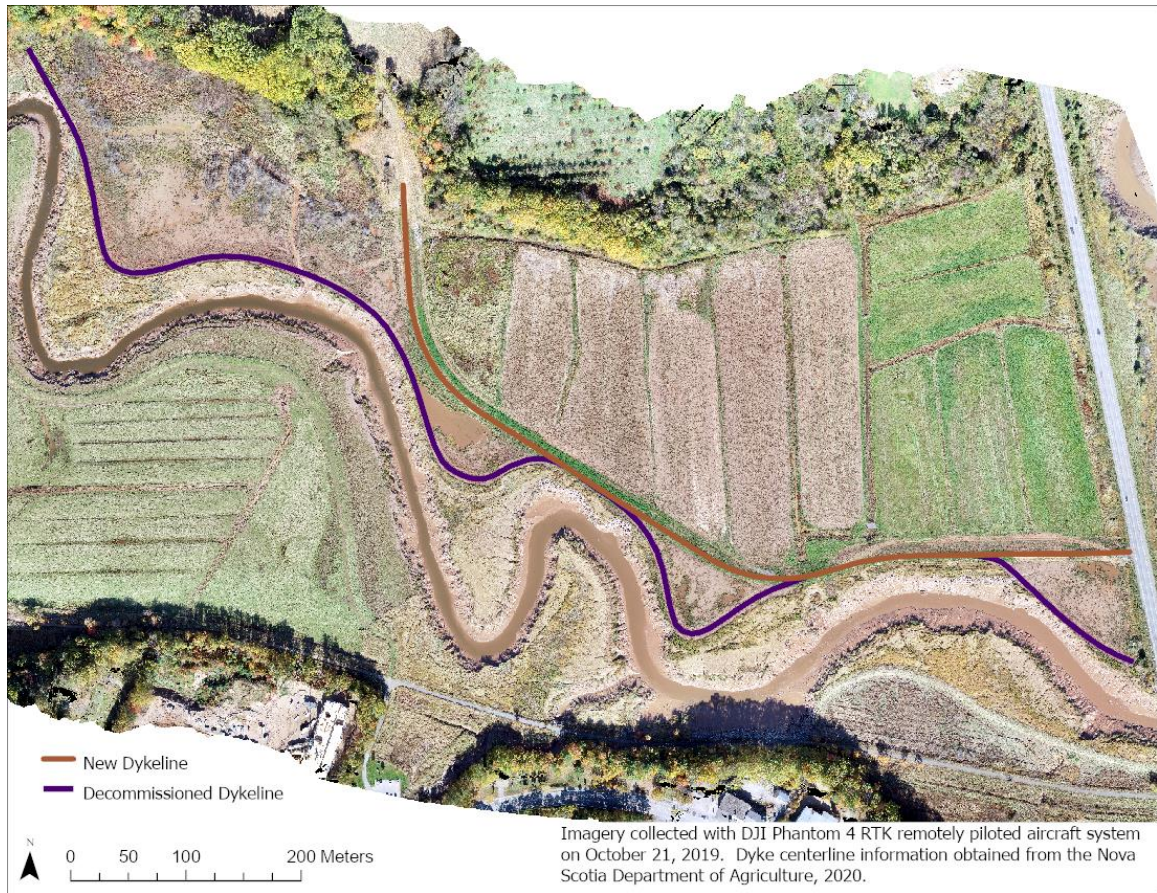
Figure 2. Map of Belcher showing the restoration area where upland vegetation has died back between the locations of old and new dykes. The upland edge of the marsh is delineated by the treeline.

The restoration area at Converse is 15.4 ha. The old dyke was breached in December 2018 after the new dyke was built (Figure 3). Portions of the dyke were removed at this site. Historically, this marsh was used for hay farming and pasture land (Ellis et al., 2018b). Halophytic species richness was low pre-breach (Ellis et al., 2018b). Localized patches of *S. pectinata*, *C. paleacea*, and *Suaeda* spp. were observed over the course of the first growing season (summer 2019), potentially survival from pre-breach or new colonization. Aside from these patches, the site remained mostly bare. Half of the site was mainly covered with dead grass and half was wet with a shallow layer of mud

covering dead tufts of sedge. Converse is more exposed to waves and wind then Belcher

and has considerably higher tidal velocity as tidal waters enter through a single breach

location (site of removed aboiteau) with minimal overbank flow from the adjacent tidal

river. The marsh starts to flood at a level slightly above mean high tide and a large

portion of the site is flooded with 75% of the high tides (see Bowron et al., 2020 for flood

map). Drainage is faster on the eastern portion of the site because of well-developed

drainage ditches, whereas drainage is slower on the western side since the area drains

from a single point (Bowron et al., 2020).

Figure 3. Map of Converse showing the restoration area in which upland vegetation has died back between the locations of old and new dykes.

3.2 Weather

Climate normal data (1981-2010) was obtained from Environment and Climate Change Canada's (ECCC) website for the weather station nearest each site (Belcher: Kentville CDA station, ID: 8202800; Converse: Nappan CDA station, ID: 8203700). Conditions over the first growing season were compared to climate normals to identify any seasonal anomalies.

During the first growing season (2019), daily average temperatures and average maximum temperatures were on par with climate normals at both sites. Monthly total rainfall in June and August at both sites were approximately twice as much as climate normal. This was mainly due to heavy rainfall events (>70 mm) that occurred on June 21, August 7, and August 29. Total rainfall in July at Kentville was approximately half of the climate normal, while Converse was on par. Immediately following planting at Belcher (June 2019), there were 4 days of rain with no extreme temperatures. Following planting at Converse (June 2019), there was about 2 weeks of rain with no extreme temperatures. Leading up to taking final measurements at Belcher (August 2019) was a two-week period with no rain; however, there was some rain during the sampling period. At Converse (August 2019), there were consistent small rainfall events leading up to the final sample period.

3.3 Seed Collection

Seeds were collected from two salt marsh sites: Lawrencetown (Atlantic Coast, 20 km East of Halifax) and Truro (Fundy Coast, 80 km Northeast of Halifax at the head of the Bay of Fundy). All seedstock that was used in this project was from Truro except *L.*

carolinianum in order to match provenance as closely as possible (Table 2). Seeds from

the most common native species found at each collection site were collected by hand in

the Fall of 2018 on three dates from September 23 through October 22. Seed heads were

either placed entire in plastic bags, or seeds were stripped from the seed heads. Spatially,

seeds were collected randomly from clusters of plants across each site and placed in

labelled Ziploc bags for transport. In the lab, seeds were stored with tap water in a

refrigerator (4ºC) in accordance with the findings of Heim et al. (2018) until cleaning and

propagation (2-3 months post-collection). This storage time was consistent with the

stratification time required for *S. alterniflora* (Biber, n.d.).

Table 2. Matrix of species planted in each treatment and site. BEL represents Belcher and CON represents Converse.

	Potted Seedlings		Field Transplants		Seed	
Species	BEL	CON	BEL	CON	BEL	CON
Carex paleacea			x	x		
Juncus gerardii	x	x			x	x
Limonium carolinianum					x	x
Plantago maritima	x	x		x	x	x
Poa palustris	x	x			x	x
Solidago sempervirens	x	x	x	x	x	x
Spartina alterniflora			x	x	x	x
Spartina pectinata	x	x	x	x	x	x

3.4 Experimental Design

Five treatment methods were tested in this project: planting potted seedlings, field

transplants, sowing seed, adding wrack (dead vegetative material), and manipulating soil

rugosity (tilling). These methods were compared with passive restoration reference plots.

Planting potted seedlings, field transplants and sowing seed are methods that are

commonly used in restoration projects with varying degrees of success, as discussed in the introduction. These have not been tested in the Fundy region. Adding wrack and manipulating soil rugosity are both less frequently used restoration methods that have had little-to-no testing in the Fundy region. Further information and justification for these methods can be found in the introduction.

Treatments were established in June 2019. In the field, fifteen clusters of six 1 m^2 plots were established (see Figure 4 for example configuration) at each site. Plots were measured using a 1m^2 quadrat flipped horizontally and vertically into configuration. Plots were marked out using bamboo or metal flags. Configurations were adjusted slightly among clusters to attempt to keep all plots in similar conditions. Clusters ranged across abiotic conditions (i.e. varied distance from river and elevations) within each site (Belcher: Figure 5, Converse: Figure 6) (total n = 30 clusters). One of each treatment method was established, in a randomized configuration, per cluster.
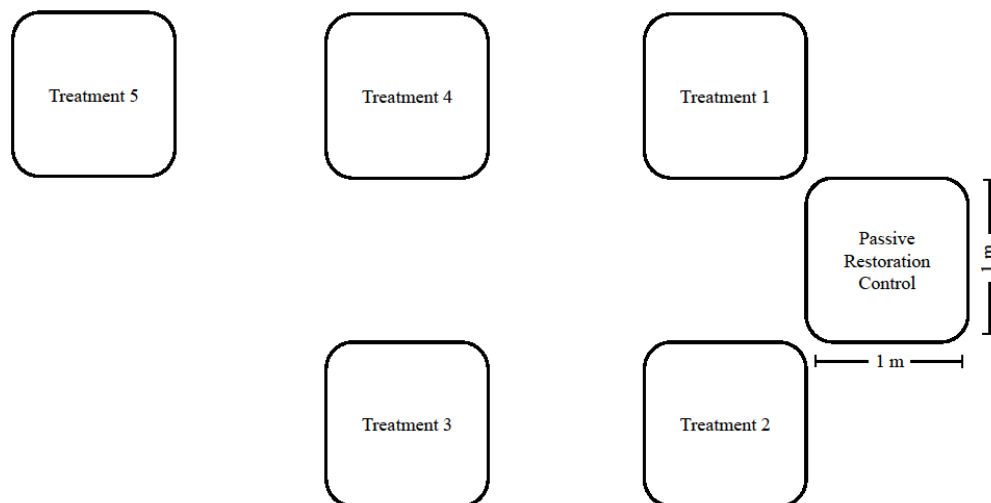
Figure 4. Example arrangement of a plot cluster. Arrangement of treatments types was randomized across the sites.
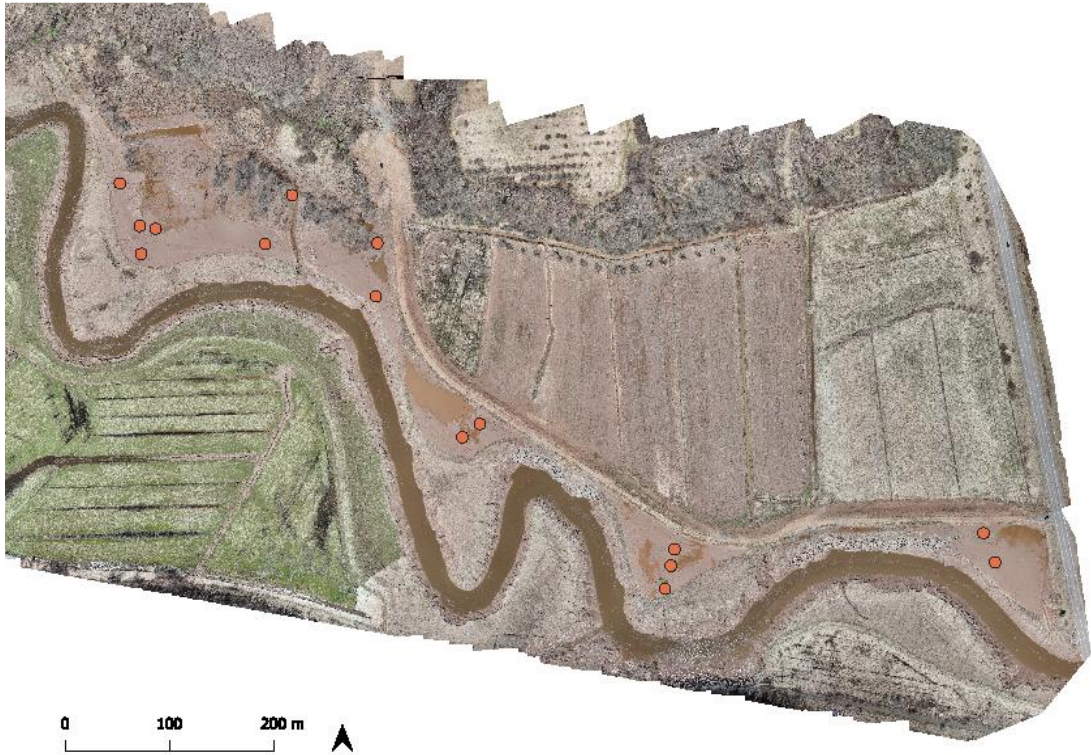
Figure 5. Field layout of plot clusters at Belcher. Each point represents a cluster.

Figure 6. Field layout of plot clusters at Converse. Each point represents a cluster.

<u>3.4.1 Potted Seedlings</u>

Seeds (see Table 2 for species) were cleaned prior to germination by stripping seed heads by hand and rinsing with tap water on an appropriately sized sieve. Plant growing trays were filled with soil (Pro-mix BX Mycorrhizae Growing Medium) and approximately 2000 seeds of a single species were sowed in each tray in January 2019. Trays were then covered with a clear dome, stored at room temperature (20˚C) and kept moist with freshwater until germination (Biber, n.d.; Heim et al., 2018; Walker, 2015). Soils enriched with arbuscular mycorrhizae (AM) were used since some study species are known to associate with AM (Burcham et al., 2012; Koske & Walker, 1984; Rozema et al., 1986). Seeds not used to grow plugs remained in Ziploc bags with ~10 mL of freshwater and stored in a fridge.

Trays were kept at room temperature under full spectrum growth lights (Heim et al., 2018) to germinate at an 18:6 hour light/dark cycle. Once root networks had been sufficiently established for transplanting and/or at least one set of true leaves had matured, seedlings were transplanted into 2.5" pots, each containing one seedling. Seedlings were kept in the greenhouse at Saint Mary's University under full spectrum growth lights (16:8 hour light/dark cycle and 25:18 ˚C day/night temperature) and irrigated with tap water two to three times per week. Beginning April 24, 2019, seedlings were set outside for increasing lengths of time to harden them to the elements when temperatures were above 5°C. In early May, many of the plugs were potted into 4" pots. At the time of planting, potted seedlings were approximately 5 months old.

In the field (June 2019), each plot was cleared of existing live biomass using scissors, tilled, and plants were added in uniform rows, for example in 5-6 rows with 5-7

plants each. Plants were added to each plot (n ≈ 33 per plot; Figure 7, Table A 1) at relatively constant species ratios (Table A 2).

Figure 7. Photo of a freshly planted potted seedling plot (~1m²) at Converse. Taken June 17, 2019.

3.4.2 Field Transplants

Transplants were dug from the existing vegetation in the fringe, or foreshore, marsh on each site in June 2019 (see Table 2 for species). Plants were separated into clumps containing approximately one plant and kept only if some fine and some coarse roots were still attached to the plant. Transplants were stored in garbage bags over-night in the shade until planting the next day (min air temp Belcher: ~6.0˚C, Converse:

~7.0˚C). At Belcher, transplants were planted using a trowel, without tilling the entire

plot. At Converse, the entire plot was tilled to plant into – this was only the case for this

treatment as a result of experimenter error. Plants were added to each plot (n ≈ 27 per

plot; Table A 1) at relatively constant species ratios (Table A 2).
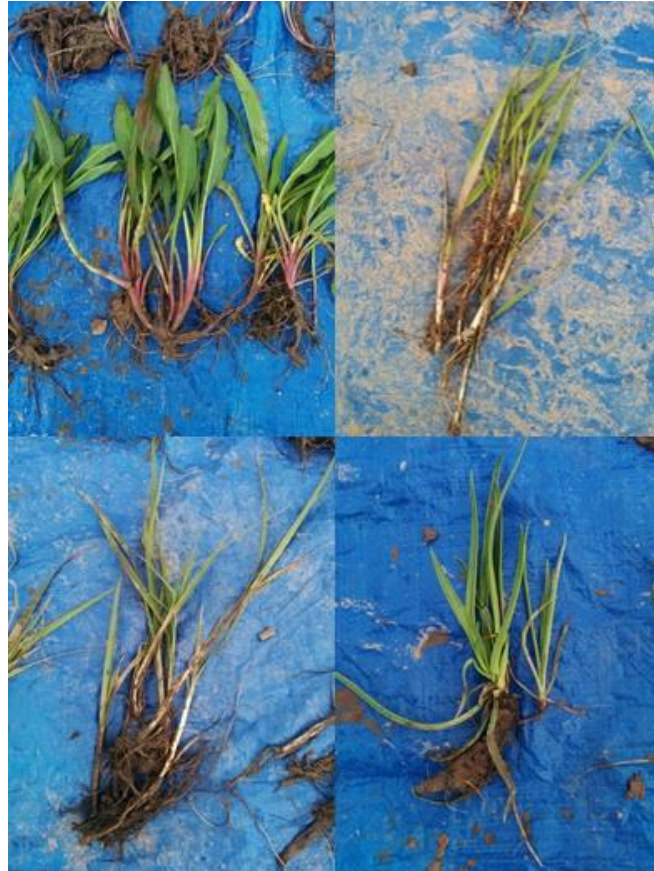
Figure 8. Photo of dug field transplants. Clockwise from top left: <u>Solidago sempervirens</u>, <u>Spartina alterniflora</u>, <u>Carex paleacea</u>, and <u>Plantago maritima</u>. Plants are ~ 5-15 cm wide.

<u>3.4.3 Seed</u>

    Seed mixtures were weighed and stored as above. Seeds were mixed in fixed

species ratios (≈ 320 seeds per species, except ≈ 40 seeds for *P. maritima* – see Table 2

for species included) and applied at a rate of approximately 2000 seeds per plot. In the field, each plot was cleared of existing live biomass and tilled. At Belcher seeds were planted approximately 10 cm deep. At Converse seeds were planted about 5 cm deep, this was due to a miscommunication during planting.

3.4.4 Wrack

Wrack was harvested from the high tide line at each site immediately prior to planting (June 2019). Wrack appeared to contain mostly *S. alterniflora* stems at Belcher, and a mixture of graminoid species at Converse. Plots were tilled and a single layer of wrack was buried 5-10 cm deep.

3.4.5 Manipulating Rugosity (Tilling)

Plots were cleared of existing biomass and tilled by digging with a shovel to a depth of ~ 20 cm. Where necessary, clumps were broken down by hand and at plots covered with dead grass, root mass was removed when it was in a solid layer. The size to which we were able to till depended heavily on the condition of the sediments, particularly the amount of moisture and the amount of root matter. No additional plant material was added to these treatments. This treatment acted as both a methodological control, and a potential treatment to facilitate seed trapping.

3.5.6 Passive Control

Passive plots were marked in configuration and no manipulation occurred in these plots.

3.5 Monitoring

Upon planting (June 2019), locations of planted individuals (potted seedlings and field transplants) were recorded and maximum height of plant (cm), maximum width of plant (cm) and health score (visual assessment of health from 0-4, see Table 3 for details) measurements were taken for each plant. Near the end of the growing season (mid- to late- August 2019, 3 months after planting), a second vegetation survey was completed where size and health (this health measurement is referred to as final health hereafter) measurements were taken at every treatment. In August 2019, plant community data were also collected for all treatments following the point-intercept method where a $1m^2$ quadrat (same size as planted plots) is divided into 25 squares (Figure 9) and a wooden dowel is dropped vertically at each intercept point (25 total points). Any species that is touching the dowel at each point is recorded as a hit (Bowron et al., 2011a). *Chenopodium* spp., *Atriplex* spp., and *Suaeda* spp. were identified only to genus level. Point-intercept surveys were also carried out in August 2020. Photographs were taken of every plot at each time of data collection.

Point-intercept surveys are a more objective alternative to visual plant cover estimates. They provide an estimate of relative cover of species in points which are related to the true percent cover. Any species that were present but were not hit were counted as a single hit in statistical analysis to represent their presence. This ensured that species richness numbers were correct but provided a slight overestimation of abundance. In July 2020 the over-winter survival of plantings was assessed (presence/absence of living above-ground biomass).

Table 3. Health index criteria. Modified from Anastasiou & Brooks, 2003.

Health Index	Category	Green stems	Growth	Wilting
0	Dead	0%	None	Brown and dry
1	Severely Stressed	<25%	No new growth or continued growth of existing stems	Mostly wilted
2	Moderately stressed	25-50%	Few new stems, little to no continued growth	Significant wilting
3	Slightly Stressed	50-75%	New stems present, some continued growth of existing stems	Some wilting
4	Healthy	>75%	New and continued stem growth	Little to no evidence of wilting

Figure 9. Photo of point-intercept procedure on a potted seedling plot (1m^2) at Belcher. Taken August 8, 2019.

3.6 Abiotic Variables

Once during the first growing season (2019), pore water salinity at each cluster (within 1 m of passive plot) was measured at 15 cm and 45 cm depths using a Spectrum 450 Series Conductivity/TDS/Salinity Handheld meter. Composite soil samples at each cluster were taken from the top 10-15 cm of soil in July 2019 for soil nutrient analysis (Total Nitrogen, pH, Organic Matter, P_2O_5, K_2O, Ca, Mg, Na, S, Al, B, Cu, Fe, Mn, Zn, CEC). Samples were analyzed at the Nova Scotia Analytical Lab in Truro, NS. Elevation was measured at each plot at the end of each season using a Leica GS14 Antenna RTK (Horizontal datum: NAD83 (CSRS) UTM Zone 20N, mean measurement accuracy = 7 mm; vertical datum: CGVD2013, mean measurement accuracy = 11 mm). Four hydrological variables were calculated in Excel using measured tidal elevations and surveyed plot elevations. Tidal elevations were measured using HOBO Level Loggers at both sites deployed in the river collecting data at five-minute intervals. At Belcher, data were collected from April 26, 2019 through August 12, 2019. At Converse, collected data from 2017 (September 7, 2017 – October 12, 2017) were used because loggers deployed in 2019 failed. Hydroperiod (%) was calculated as the total percentage of time that the tidal elevation was greater than or equal to the plot elevation. Inundation frequency (%) was calculated as the total number of high tides that flooded the plot. Inundation time (minutes) was calculated as the mean number of minutes the plot was flooded per high tide.

3.7 Statistical Analysis

All statistical analyses were conducted in R 3.6.1 (R Core Team, 2019) following a model selection procedure using Akaike Information Criteria (AIC) to select the most parsimonious models and to understand the importance of each predictor (Zuur et al., 2009). The AIC provides an estimate of out-of-sample model performance while penalizing models for adding parameters and can be used to compare the performance of models with different sets of predictor parameters on the same set of predicted data (Burnham & Anderson, 2002). This procedure can provide insight into which parameters are most important to explain trends in the data and which model is best suited for inference. Model selection was run using the dredge function in the "MuMIn" package, and the small-sample size adjusted AIC_c (Barton, 2019).

The American Statistical Association (ASA) advises cautious use of p-values and against the use of the words "statistically significant" due to problems with reproducibility, and widespread misinterpretation of these values (Halsey et al., 2015; Wasserstein & Lazar, 2016). A variety of alternatives have been suggested to quantify random variability in data and to present statistical results (Wasserstein et al., 2019): these range from not using p-values at all, to reporting all p-values from tests. In this thesis, I have mainly omitted p-values, save for the visualizations of statistical modelling outputs of post-hoc comparisons in the Appendix where they are helpful to visualize uncertainty of estimates and the magnitude of differences among groups. I have opted to make inference on "statistical importance" based upon a range of information including: consideration of various model specifications (the AIC selection procedure), p-values, estimates of effect size (least squares means) and magnitude (confidence intervals), and

in some cases confirmation of results through different statistical methods as suggested in Wasserstein et al. (2019). I have reported on or visualized all findings, including those that are statistically unclear or small. Note that figures throughout the main text of this thesis show raw data while displays of statistical model outputs can be found in Appendix A.

3.7.1 Abundance

To understand the differences in plant abundance between treatments and sites, a series of generalized linear models (GLM) (analogous to ANCOVAs) were run using the "stats" package (R Core Team, 2019) with treatment, site and their interaction as predictors, and either target species abundance per plot or total abundance per plot as the response. Each year of data was run separately. Target species abundance was calculated as the total hits of perennial halophyte species – planted or not – (*S. sempervirens*, *S. alterniflora*, *S. pectinata*, *S. patens*, *P. maritima*, *P. palustris*, *L. carolinianum*, *J. gerardii*, *Agrostis stolonifera*, *C. paleacea*, *Carex rostrata*, *Bolboschoenus maritimus*, and *Distichlis spicata*) per plot from the point-intercept survey, while total plant abundance was calculated as the sum of hits (all species) per plot. A negative binomial distribution was used for modelling as all response variables were count data and the distributions were right skewed. Normality of residuals and homogeneity of variance for each model were visually inspected using diagnostic plots to confirm model assumptions were met. Wrack abundance was omitted from the 2019 target species models to meet the assumption of homogeneity of variance since wrack plots at Converse had no germination. Post-hoc pairwise comparisons were made by plotting least squares means

with *p*-values (shown at α = 0.05 for reference) from a Tukey's post-hoc test for each group extracted with the "emmeans" package (Lenth, 2019).

3.7.2 Species Richness

A series of GLMs were performed using species richness (number of unique species) per plot as the response variable, and site, treatment and the interaction between them as the explanatory variables. Models were run for both target species (richness of perennial halophyte species as outlined above), or total species richness. These models were run using a Poisson distribution and model assumptions were assessed visually. Post-hoc pairwise comparisons were made as above. Since only potted seedling and field transplant treatments were successful at establishing a higher abundance of target species than the passive control and increasing species richness, further plant performance analysis was restricted to these treatments.

3.7.3 Plant Performance

Plant performance was evaluated using a series of models with plant survival (presence/absence of living above-ground biomass in August 2019), relative growth rate as defined below, and final health (health score at the end of 2019) as predicted variables and treatment, site, and species as fixed effects and cluster (i.e. location across the site) as a random effect. Mixed effects models were run using the "lme4" package (Bates et al., 2015), and fixed effects models were run using the "stats" package. Where necessary, diagnostic plots were visually inspected to confirm model assumptions were met. Post-hoc pairwise comparisons were made by plotting least squares means with *p*-values

(shown at α = 0.05 for reference) from a Tukey's post-hoc test for each group extracted with the "emmeans" package (Lenth, 2019). Missing initial size and health measurements (n = 6) were replaced with measurements taken on the same plants on July 3, 2019 where possible (n = 2) or omitted from further analysis.

Plant survival was regressed using a binomial distribution for the predicted data (logistic regression) and a logit link function. The "cluster" random term was included in the full model with all data (using treatment and site as predictors) because its variance was greater than zero; however, it was removed from subsequent models using subsets of the data due to convergence difficulties. Removing the random term from some models was necessary throughout the analysis. The cluster random term accounts for spatial autocorrelation in the data where results may be more similar when plots are closer together. Removing this term from the models increases the chances of a Type II error where statistical tests do not pick up a true difference between groups because variability in the data due to spatial autocorrelation is unaccounted for in the model. All further plant performance analysis was only evaluated for plants with surviving above-ground biomass at the end of the 2019 season (Table 4).

A proxy of plant size was calculated by multiplying the measured dimensions (max height of plant * max width of plant) for both initial measurements (June 2019) and final measurements (August 2019). These measurements were used to calculate relative growth rate (RGR) using the formula (Hunt, 1982):

$$\frac{\ln S_2 - \ln S_1}{\Delta t}$$

where S_2 = Final Size (cm^2), S_1 = Initial Size (cm^2) and Δt = difference in time (one growing season of ~ 3 months). RGR is useful to correct for the trend where larger plants

grow more (logarithmic growth) and to control for the initial size of the plant, allowing comparisons between plants of different sizes and with different growth forms. RGR is expressed as the rate of growth (cm^2) per unit of plant area (cm^2) over a period of time (in this case, 3 months). RGR was regressed using treatment, site, and species as fixed effects and cluster as a random effect. A normal distribution was used for the response variable. The variance of the "cluster" random term was greater than zero for all RGR models and was thus included in each model.

Table 4. Sample sizes for each group used in analysis: n planted June 2019 (n survived to August 2019) n survived over-winter to July 2020. Total n = 1804 (1068) 1076. Eight plants (2 P. palustris, 3 C. paleacea, 1 S. pectinata, 2 S. alterniflora) that survived over the winter had only living below-ground biomass at the end of 2019 and were not included in the survival data.

	Potted Seedlings		Field Transplants	
Species	BEL	CON	BEL	CON
Carex paleacea			52 (24) 23	100 (12) 2
Juncus gerardii	14 (13) 10	15 (3) 2		
Limonium carolinianum				
Plantago maritima	110 (95) 79	115 (90) 60		28 (16) 9
Poa palustris	141 (66) 51	150 (107) 73		
Solidago sempervirens	89 (83) 81	90 (69) 34	34 (31) 24	53 (33) 5
Spartina alterniflora			140 (11) 4	140 (83) 66
Spartina patens				
Spartina pectinata	134 (130) 122	134 (85) 28	157 (76) 76	108 (41) 20

Final health (health score in August 2019) data were analysed in a variety of ways. Ordinal data of this type are typically modelled using a proportional odds logistic regression model, which assumes that the effect of X is similar across each threshold θ, where θ represents the threshold separating $Y \leq j$ and $Y \geq j$ (j represents a health category in this case). I found that the data did not meet this assumption. This assumption is often violated but proportional odds models can still be useful in inference (Harrell, Jr.,

2015), so I chose to use this type of model and also model the data in a variety of other ways including: linear models assuming a continuous variable underlying the ordinal variable (Agresti, 2001), and partial proportional odds models. Results were confirmed by all models, and so I have chosen to present results from linear regressions since they are easiest to work with and interpret. Proportional odds and partial proportional odds models were run using the clm function in the "ordinal" package and a logit link (Christensen, 2019a, 2019b), while linear models were run using the "stats" package (R Core Team, 2019). Predictor variables were treatment, site, and species. Initial health (health score in June 2019) was found to have an important effect on final health score (lower categories had higher probabilities of staying in lower categories and vice versa), and so was included in all models of final health as a control. No random effects were included in these models.

3.7.4 Over-winter Survival

Over-winter survival was assessed using logistic regression with a logit link. This analysis excluded plants that died in the first growing season (Table 4). The "cluster" random term was included in the full model with all data (using treatment and site as predictors) because its variance was greater than zero; however, it was removed from subsequent models using subsets of the data due to convergence difficulties.

3.7.5 Abiotic Conditions

To understand the relationships between abiotic variables and how they differ spatially across sites, a Principal Components Analysis (PCA) was conducted. Where

more than one measurement was taken per cluster (elevation and inundation variables), data for the passive plot was used, as there was low variance within the clusters. The number of input variables was reduced to meet the assumption of sample adequacy using a Pearson's correlation matrix to remove variables that had correlation coefficients $\geq |0.7|$, while maintaining ecologically important variables. Variables included in the PCA were the primary (N, P, K) and secondary nutrients (Ca, Mg, S), along with the ecologically important elevation, salinity and mean inundation time. For the PCA and the following analyses I opted to use soil Na (kg/ha) as opposed to pore water salinity measurements as the salinity variable because pore water salinity measurements from the probe were highly unstable in the field with large fluctuations among replicates at a single point. The PCA was performed using the prcomp function in the "stats" package (R Core Team, 2019) and input variables were scaled and centered to unit variance. Outputs were visualized using the "factoextra" package (Kassambara & Mundt, 2019).

Further analysis was completed to understand the effects of abiotic variables on plant performance (RGR, survival, over winter survival, final health). Since only one measurement of each abiotic variable was taken per cluster, these values were repeated for each plant in the cluster for these analyses. Data from potted seedling and field transplants were pooled for analyses, except in the survival model where treatment was included as a predictor because it was previously found to be important to survival. Sites were modelled separately for each response variable. The same input variables as above were used as predictors in this modelling process except inundation time (N, P, K, Ca, Mg, S, elevation and salinity). Inundation time was highly inversely correlated with elevation at each site; however, in the pooled site data used above there was no

correlation. For this reason, it was removed from further analysis. Species was included

as a control variable in all models, and initial health was included in the final health

model. Input variables were mean-centered and scaled to unit variance (z-scores) to make

meaningful comparisons of regression coefficients (Schielzeth, 2010). Variance inflation

factors were calculated using the "car" package (Fox & Weisberg, 2019) using a

threshold of 5 to identify and remove collinear variables (Zuur et al., 2010). In the

Converse models, sodium (negatively correlated with elevation, Pearson's r = -0.69 and

positively correlated with K_2O, Pearson's r = 0.95) and magnesium (positively correlated

with K_2O, Pearson's r = 0.96) were removed. In Belcher models, magnesium (positively

correlated with Sodium, Pearson's r = 0.87) and sulfur (positively correlated with

Calcium, Pearson's r = 0.78) were removed. Subsequently, model selection was

performed and models were averaged using a threshold of Δ AIC$_c$ < 5 since there were no

clear 'best' models (Dormann et al., 2018; Grueber et al., 2011). This procedure provides

more stable estimates of effect sizes. Models were averaged using both the subset-

averaged (parameters are averaged over models only where they are present) and the full-

averaged (zeros are substituted into models where a parameter is absent) methods. This is

an ongoing area of research and there are conflicting viewpoints over which method is

more appropriate for different types of research questions (absolute vs. relative

importance of parameters) (Galipaud et al., 2017; Grueber et al., 2011), so both are

presented here.

Chapter 4: Results

4.1 Community Composition

4.1.1 Target Species Abundance

Potted seedling and field transplant treatments were the most successful at establishing a higher abundance of target species. Target species (perennial halophytes) abundance in potted seedling and field transplant treatments was higher than all other treatments at both sites after the first growing season (2019). Differences between the less successful treatments – passive, tilling, and seed – were statistically unclear (Figure 11, Figure A 1) and therefore unsuccessful over the first year. During the second growing season (2020), potted seedlings continued to have the highest abundance of target species at both sites (Figure 11, Figure A 2). At Belcher, the remaining treatments had relatively high abundance of target species due to natural colonization (where plants establish from an outside source) and, by the end of the season, had similar target species abundance to the field transplant plots. At Converse, where natural colonization was consistently lower than Belcher, the potted seedling and field transplant treatments continued to have the highest abundance of target species (Figure 10), followed by seed, then the rest of the treatments having similar abundance (Figure 11, Figure A 2). The model selection procedure revealed that the preferred model in all cases included both site and treatment as lower order terms, and an interaction between them (Table A 3), indicating that treatment performance did not follow the same trend at both sites. This interaction was mainly due to minor differences in the performance of the less successful treatments between sites.

Figure 10. Photograph taken at Converse on August 25, 2020 showing contrast in vegetation abundance between planted plot (potted seedling in foreground and field transplant at center-right) and the unplanted marsh surface. Quadrat is 1m².

*Figure 11. Perennial halophyte abundance (number of hits) per plot over two years in each treatment and site. Vegetation surveys were carried out in August of the respective year. The median is shown within the box, the boxes represent the range between the first and third quartile of the data, whiskers represent the min and max measurements no farther than 1.5 * Inter-Quartile Range, and outliers are represented by single points.*

4.1.2 Target Species Richness

Target species richness (number of perennial halophyte species) in potted seedling and field transplant treatments was higher than all other treatments at both sites in 2019. Differences between the less successful treatments – passive, tilling, and seed – were statistically unclear at Belcher, but at Converse seed had higher richness than passive and tilling (Figure 12, Figure A 3). The model selection procedure revealed that the preferred model included both site and treatment as lower order terms, and an interaction between them (Table A 3), indicating that treatment performance did not follow the same trend at

both sites. This interaction was mainly due to minor differences in the performance of seed and field transplant treatments between sites. Treatment alone was the next best predictor of these results.

In 2020, potted seedlings had higher species richness than all other treatments. At Belcher, the differences between the rest of the treatments were statistically unclear, where at Converse both seed and field transplants had higher species richness than all other treatments (Figure 12, Figure A 4). The model selection procedure indicated that both site and treatment were important indicators of species richness (Table A 3).
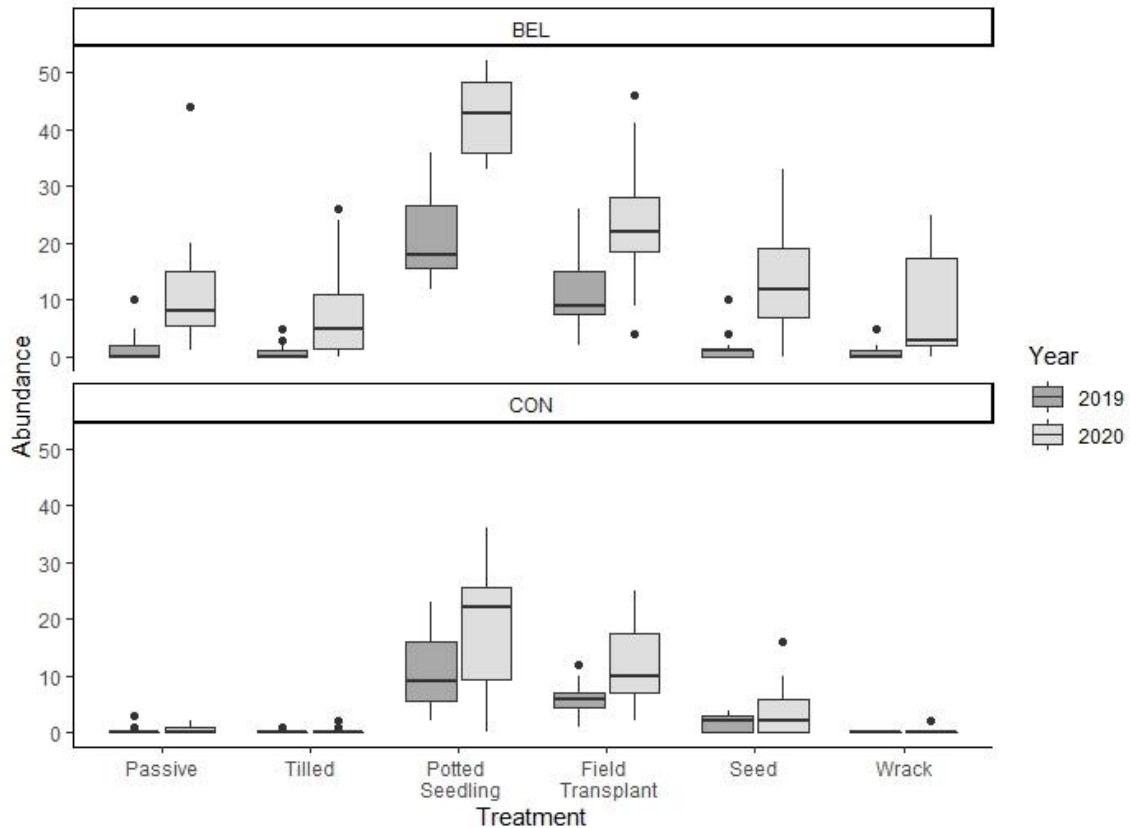

Figure 12. Perennial halophyte species richness per plot over both years in each treatment and site. Vegetation surveys were carried out in August of the respective year.

4.1.3 Total Abundance

At Belcher in 2019, total plant abundance was highest in potted seedling, field transplant and the passive control treatments while seed (no germination), wrack and tilling treatments had lower abundance (Figure 13, Figure A 5). The slight decrease in abundance in wrack, tilling and seed treatments from the passive treatment can be attributed to the tilling of these plots in the early spring which removed any would-be natural colonizers. In 2020, the total abundance of these less successful treatments had caught up to the total abundance in planted plots (Figure 13, Figure A 6). Much of the natural colonization at this site consisted of weedy annuals including *Chenopodium* spp. and *Atriplex* spp.. Total abundance in the transplant treatment was highest because these plots were not fully tilled (all other plots were) at the beginning of the season and so cover in the plots included both planted species and natural colonizers of *Chenopodium* spp. and *Atriplex* spp..

At Converse, potted seedling and field transplant treatments had higher abundance than all other treatments both years, with a larger gap between these treatments and the rest than at Belcher (Figure 13). Passive and seed plots had higher abundance than wrack and tilling treatments in 2019 because there was some germination from seeds (Figure 13, Figure A 5), these relationships were not as clear in 2020; however, there is an indication that seed plots had slightly higher abundance than the passive plot (Figure A 6). The preferred model for all the data included both site and treatment at main effects, as well as the interaction between them (Table A 3), indicating that the relative trend among treatments was different at each site.
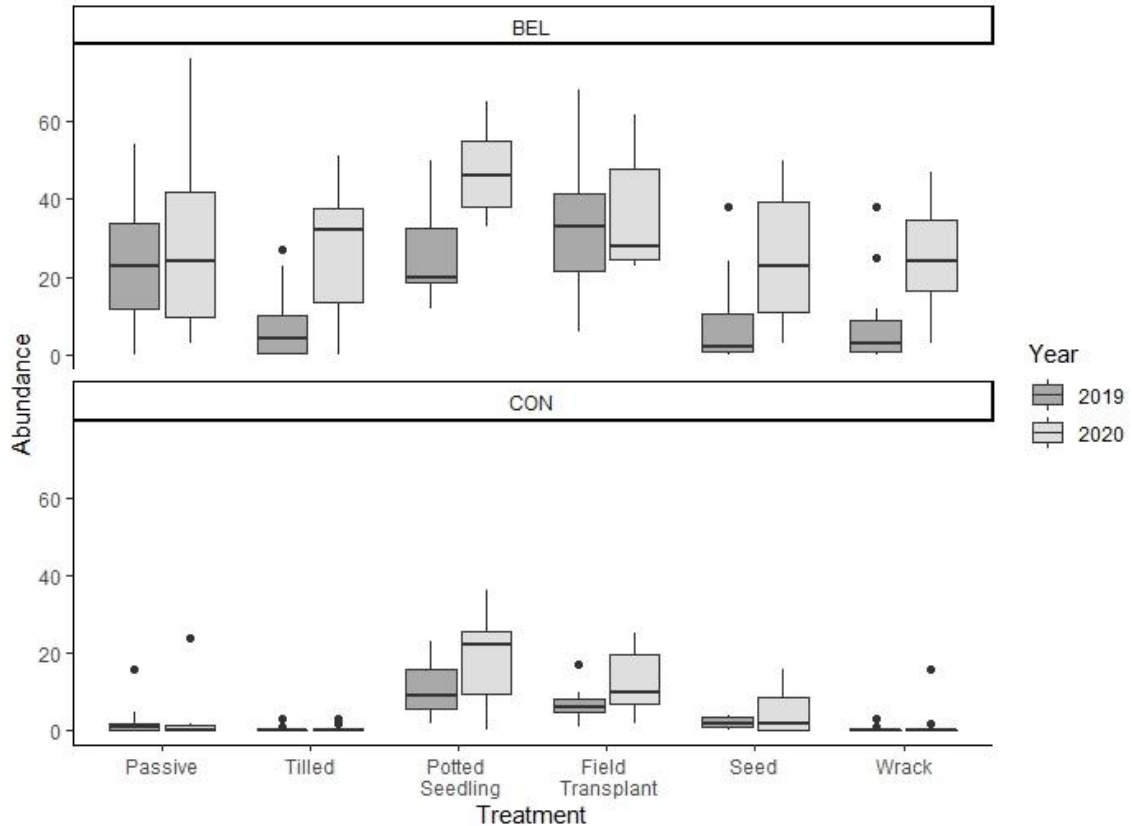
Figure 13. Total vegetative abundance (number of hits from all species) per plot over two years in each treatment and site. Vegetation surveys carried out in August of the respective year.

4.1.4 Total Species Richness

Total species richness in 2019 followed a similar trend to abundance, where potted seedling and field transplants had the highest richness (Figure 14, Figure A 7). At Belcher, this was followed by the passive plot (many natural colonizers), and the last three treatments not having clear differences. In 2020, the passive plot and the rest of the treatments had enough colonization that species richness was similar to potted seedling and field transplant plots (Figure A 8). At Converse over both years, the top two treatments were followed by seed with only a slightly higher richness than the last three

treatments. The preferred model for these analyses included treatment and site as

interactive predictors (Table A 3).

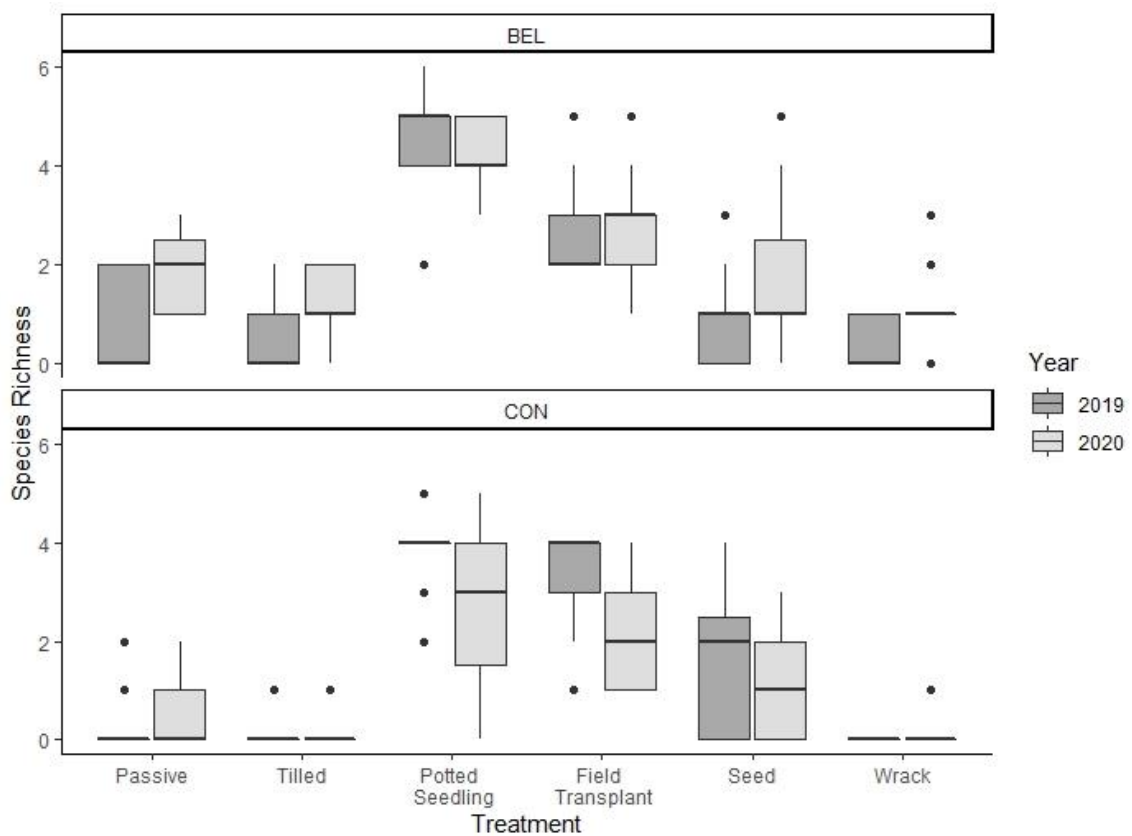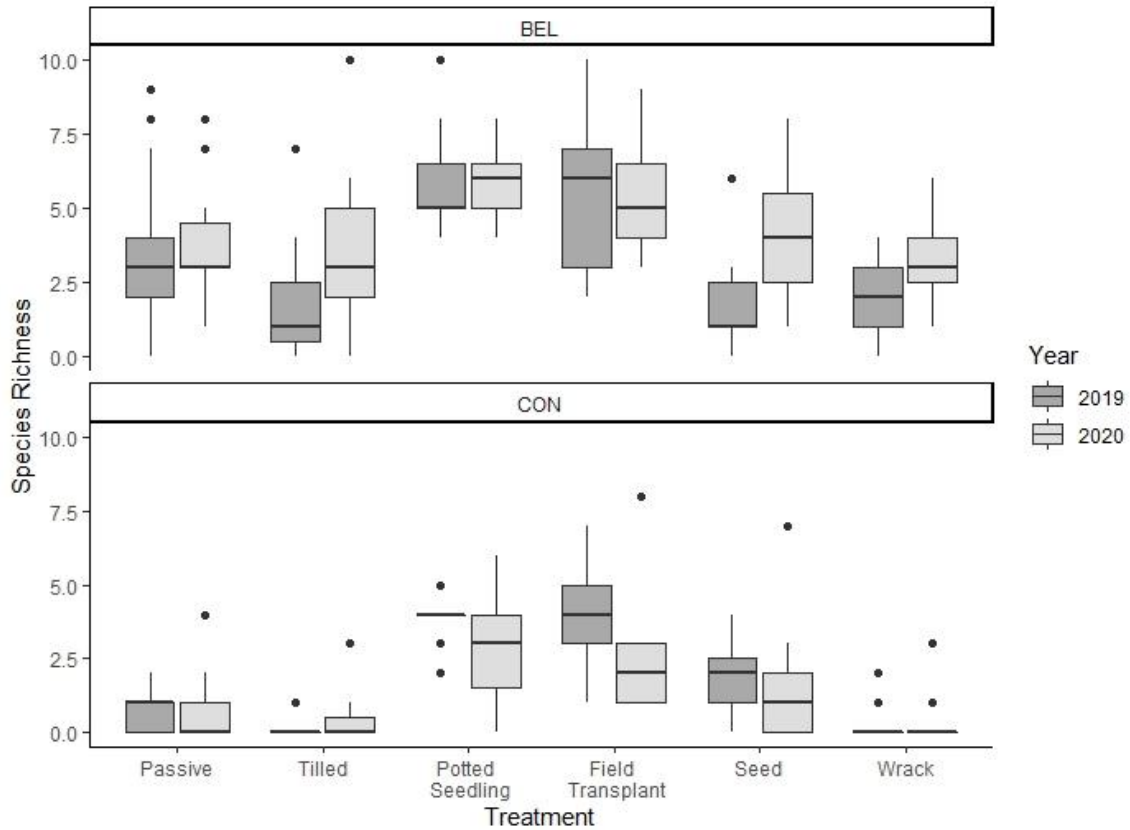*Figure 14. Total species richness per plot over both years in each treatment and site. Vegetation surveys carried out in August of the respective year.*

4.1.5 Seed Germination

There was minimal germination of seeds at Converse and none at Belcher and it

was not successful at producing higher plant abundance than the passive plots therefore

making it an unsuccessful treatment. Seeds were only sown in 2019 but seedlings were

seen germinating in these plots both years of this study in densities that were observed to

be higher than the surrounding areas. Of the species seeded, *L. carolinianum* had the highest number of germinated seedlings each year (Table 5). There was also some germination from *P. palustris* (both years) and *S. alterniflora* (only the first year) seeds (Table 5).

Table 5. Total number of seedlings in seed plots in 2019 and 2020 at each site.

	Belcher		Converse	
Species	2019	2020	2019	2020
Limonium carolinianum	0	0	40	11
Poa palustris	0	0	16	10
Solidago sempervirens	0	0	1	0
Spartina alterniflora	0	0	21	0
Spartina pectinata	0	0	5	3
Unknown grass	0	0	2	0

4.2 Plant Performance

4.2.1 Survival

Overall, potted seedlings had a higher likelihood of survival than field transplants at both sites (Figure 15, Figure A 9). Modelling was first conducted on all data using site and treatment as predictors. The preferred model included site and treatment along with an interaction term between the two and the cluster random term (Table A 3), indicating that both site and treatment were important variables to explain trends in survival. The interaction between site and treatment was a result of potted seedlings having higher survival at Belcher than Converse while field transplants had similar survival at the two sites.

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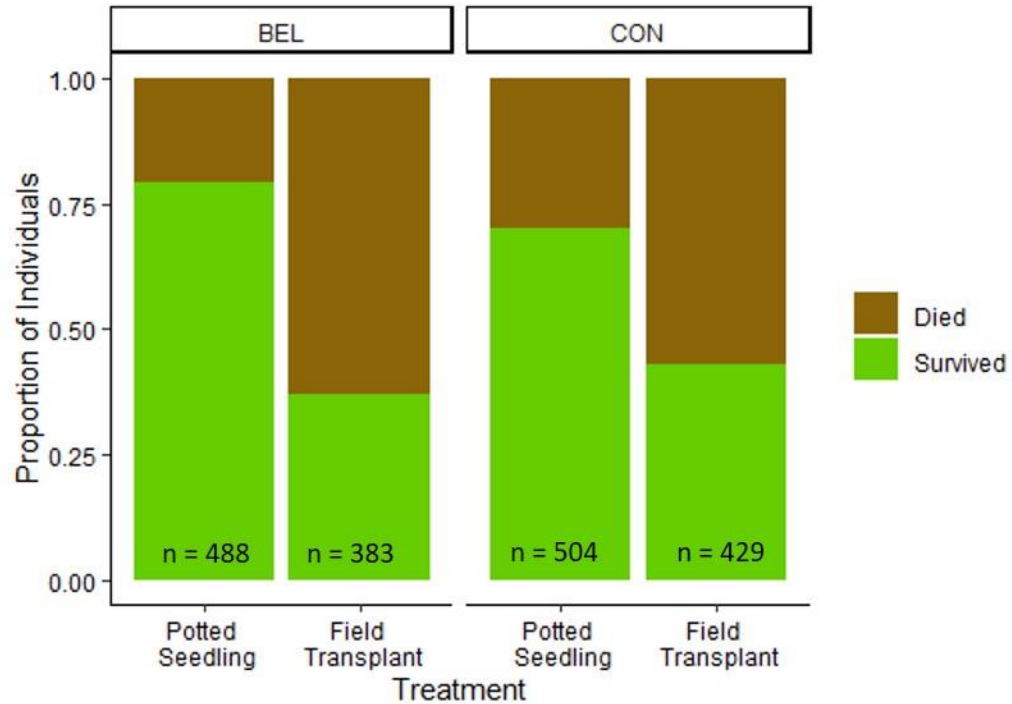
Figure 15. Proportion of individual plants surviving to the end of 2019 in each treatment and site (BEL is Belcher, CON is Converse) with associated total sample sizes for surviving and dead plants in each group. Data are pooled for all species.

Only *S. pectinata* and *S. sempervirens* were present in both treatments at both sites and *P. maritima* in both treatments at Converse, so the data for these species were used to examine species-specific differences in survival between the treatments. The model selection procedure provided strong evidence that all three predictor variables were important to predicting survival, and the preferred model included a three-way interaction term between them (Table A 3), indicating that there were differences in survival among species as well as among treatments and sites. Probability of survival of *S. pectinata* (at both sites) and *P. maritima* (at Converse) potted seedlings was higher than field transplants (Figure 16, Figure A 10), supporting the findings of the pooled species data above. Survival of *S. sempervirens* was similar between the treatments at

both sites. *S. sempervirens* had higher survival than *S. pectinata* in all group-wise comparisons except Potted Seedling*Belcher, indicating that survival success may differ among species.
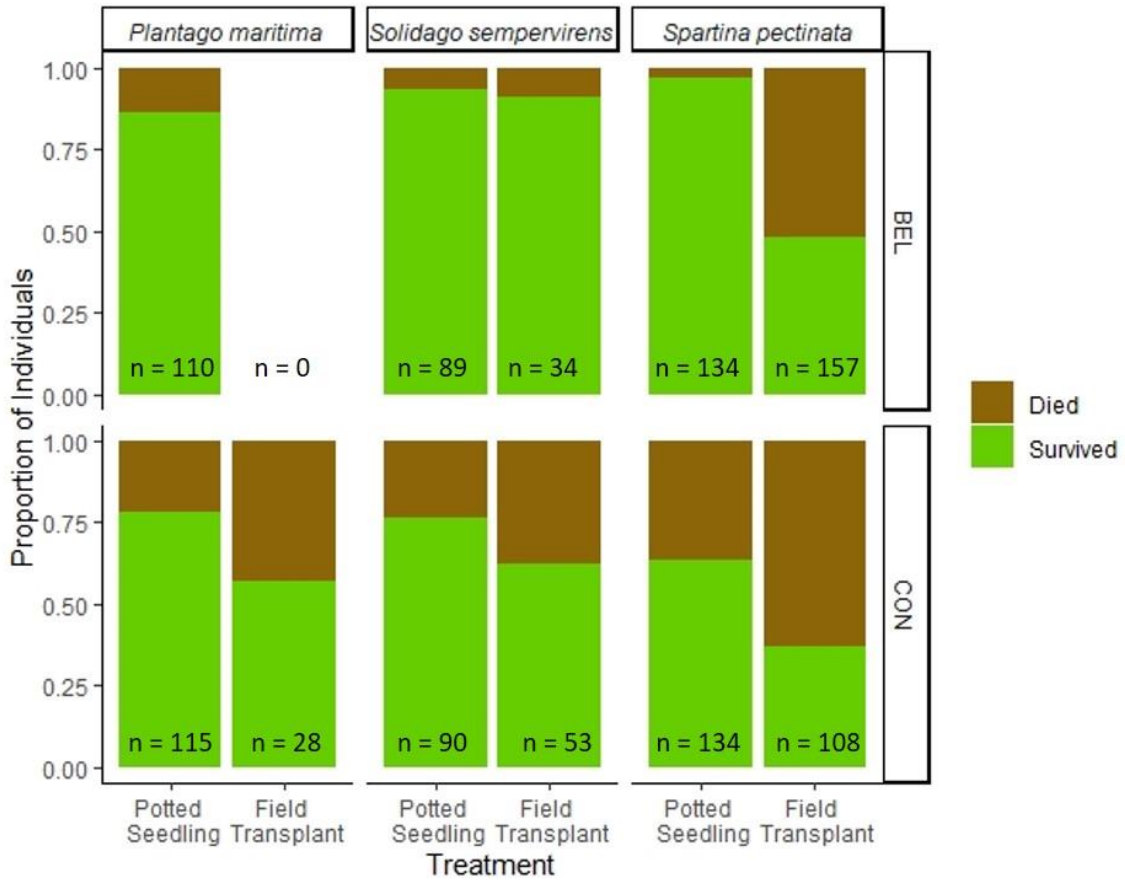
Figure 16. Proportion of individuals surviving to the end of 2019 for the two species that were present at both sites (BEL is Belcher, CON is Converse) in each treatment with associated total sample sizes for surviving and dead plants in each group. P. maritima was not present in the field transplant treatment at Belcher.

To compare survival among species, a model was run on treatments separately, using site and species as predictors. *P. maritima* was omitted from the field transplant model because it was only planted in this treatment at one site. The preferred model for both sets of data included both predictors, and an interaction term (Table A 3). Trends

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were different between sites with *C. paleacea*, *P. palustris*, and *S. alterniflora* having

survival lower than 50% at Belcher, and *C. paleacea* and *J. gerardii* having survival

lower than 50% at Converse. (Figure 17, Figure A 11, Figure A 12).
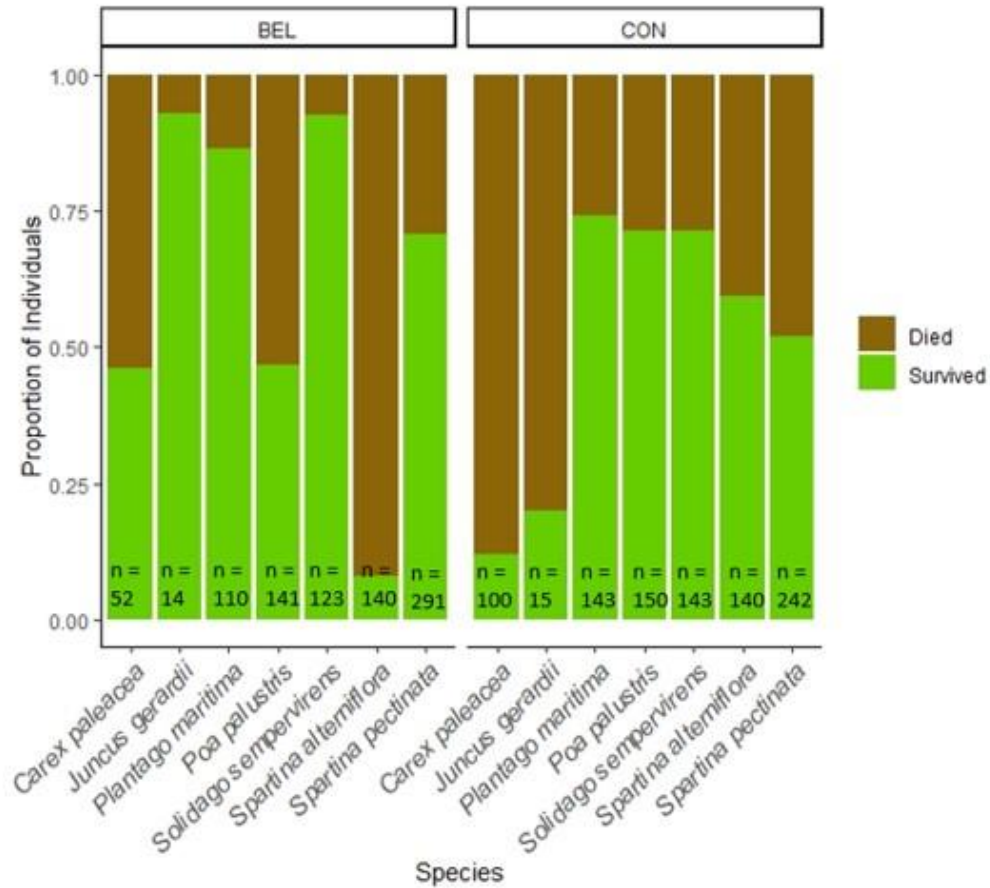
Figure 17. Proportion of individuals surviving to the end of 2019 for all species at each site (BEL is Belcher, CON is Converse) with associated total sample sizes for surviving and dead plants in each group. Data are pooled over treatments.

4.2.2 Relative Growth Rate

  Since not all species were found in all treatments, the data were first modelled

using only site and treatment as predictors. Site was found to be the strongest predictor of

RGR (Table A 3), which was 1.7x higher at Belcher than Converse (Figure 18, Figure A 13). To examine differences between treatments, a model using treatment and site as additive predictors was used. Treatments did not differ in RGR. Similar RGR between the two treatments may be a result of the pooled of species data, as discussed below.
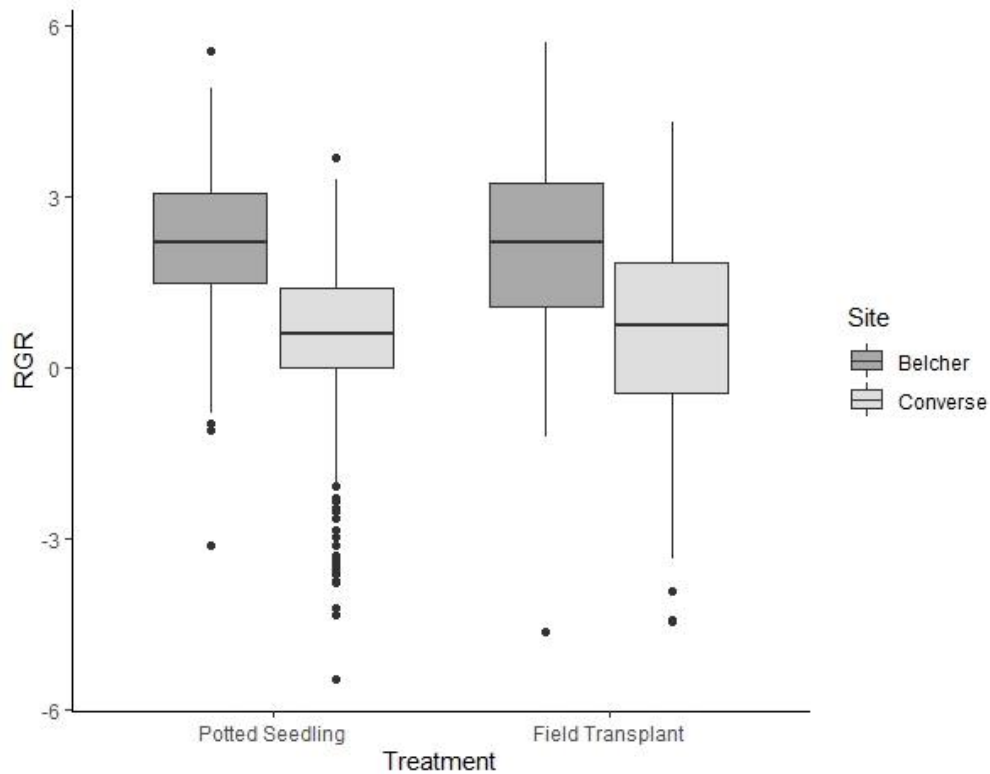
Figure 18. Relative growth rate (RGR) of all individuals in each treatment and site over summer 2019. RGR is presented as ln(cm²/cm²)·3 months⁻¹. An RGR of 0 indicates that a plant has not increased in size over the course of the growing season. Data are pooled over species.

While the pooled data for all species showed no difference between RGR in each treatment, making species-specific comparisons revealed a different picture. Only three species (*S. sempervirens, P. maritima* and *S. pectinata*) were used in both treatments, two of which were used at both sites. Further models were run for these data to investigate

whether species, site, and treatment influenced the RGR of these species. This data were best described using a three-way interaction term between the predictor variables (Table A 3). Potted seedlings of *S. sempervirens* (at each site) and *P. maritima* (Converse only) had higher RGR than field transplants, indicating that potted seedlings may have higher growth potential than field transplants for some species. *S. pectinata* showed a different pattern where potted seedlings and field transplants performed similarly at Belcher, but potted seedlings performed worse than transplants at Converse (Figure 19, Figure A 14).
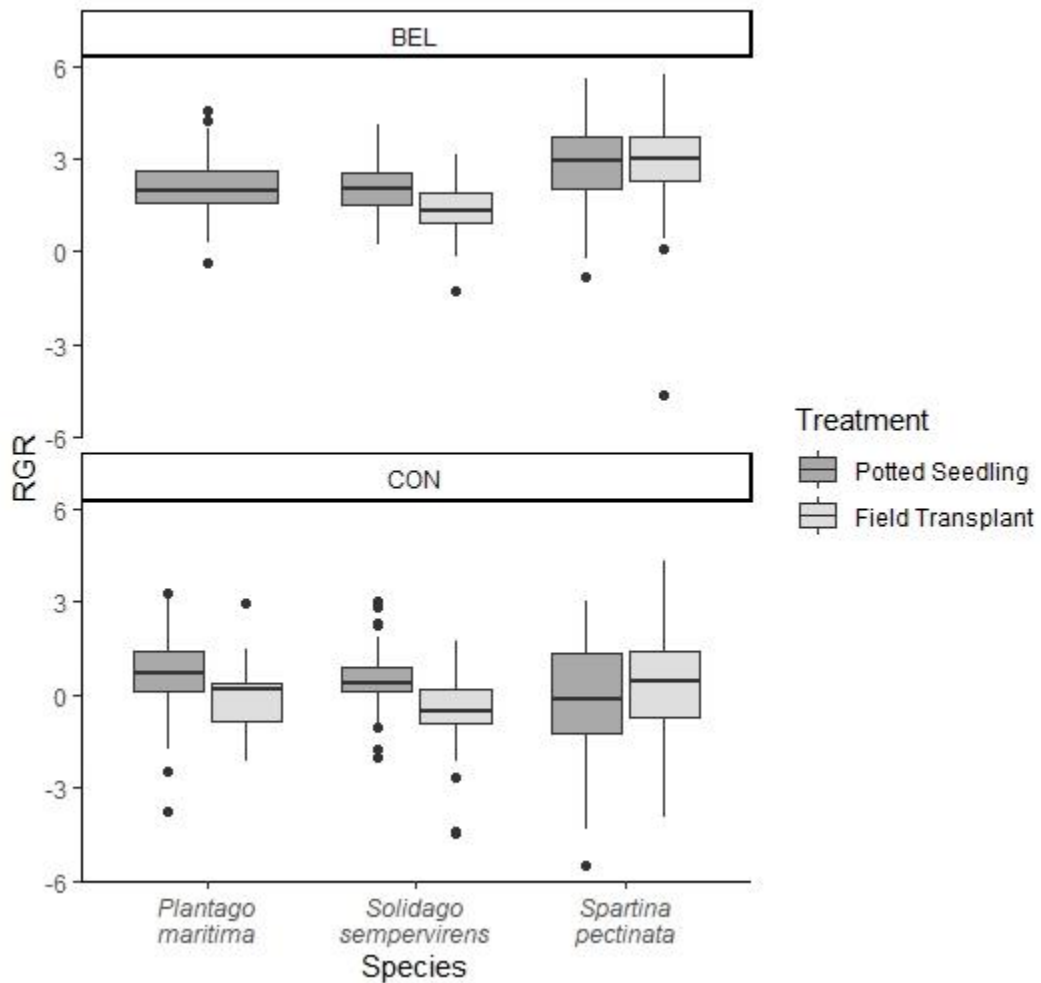
Figure 19. Relative growth rate (RGR) of species used in both treatments. RGR is presented as ln(cm²/cm²)·3 months⁻¹. An RGR of 0 indicates that a plant has not increased in size over the course of the growing season. P. maritima was not planted in the field transplant treatment in Belcher.

To identify high and low performing species, the data were modelled using site and species as predictors since the overall data showed no difference between treatments. The preferred model included an interaction term between site and species (Table A 3), indicating inconsistent trends among species growth between sites. All species had a higher RGR at Belcher, but there were no clear trends in species performance. *S. pectinata* was the top performer at Belcher however grew considerably worse at Converse because of poor plug performance as discussed above. Elsewise, *S. alterniflora* may have had a higher RGR than some of the other species, while *C. paleacea* seemed to grow poorly (Figure 20, Figure A 15). Most of the results were statistically unclear, which is likely due to low statistical power because of small sample sizes in many groups (particularly *J. gerardii*, *C. paleacea*, and *S. alterniflora*). While patterns in RGR (growth per unit biomass over time) were unclear among species, it is important to note that this means that in terms of absolute growth, larger plants grew more since RGR is relative to the size of the plant. As a result of differences in the RGR among species, pooled estimates of RGR may not reflect the true difference between treatments since the same species were not used in both treatments.
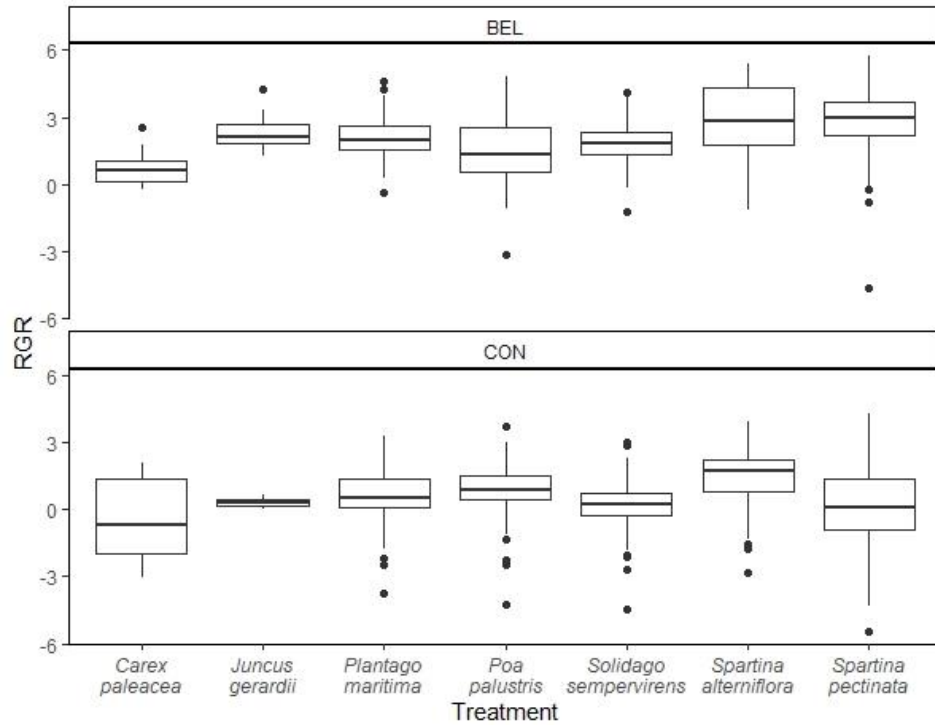
Figure 20. Relative growth rate (RGR) of species at each site (BEL = Belcher, CON = Converse). RGR is presented as $\ln(cm^2/cm^2)\cdot3$ months^{-1}. An RGR of 0 indicates that a plant has not increased in size over the course of the growing season. Data are pooled over treatments.

4.2.3 Final Health

Plants at Belcher were healthier than those at Converse at the end of the season in both treatments. At Belcher, plants were most likely to be in excellent health (category 4) while plants at Converse were most likely to be in good health (category 3) (Figure 21, Figure A 16). Field transplants at Becher had the highest final health score, possibly due to the high performance of *S. pectinata* field transplants which made up a large proportion of that group. There was little difference between the treatments at Converse. The preferred model for this analysis included site, treatment, and the interaction between them as predictors, and initial health as a control. Results of model selection indicated

that both site and treatment were important to explaining variation in final health scores,

with site being a better predictor overall (Table A 3).
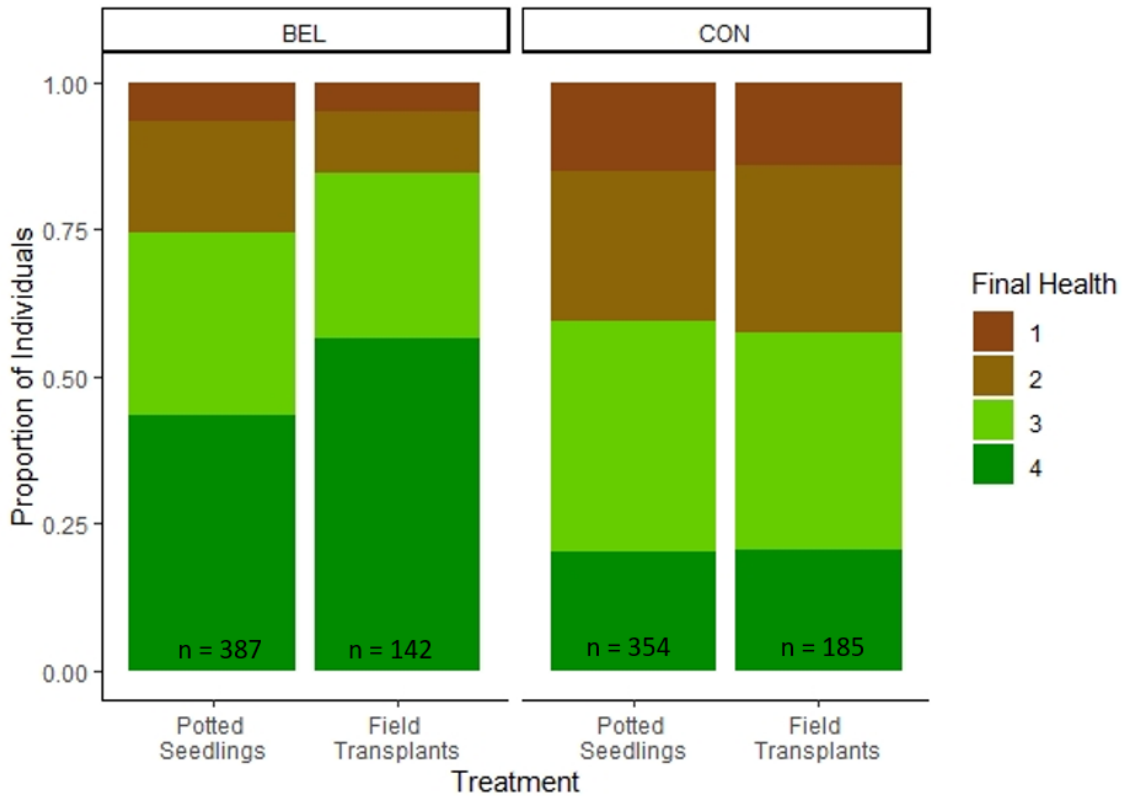
Figure 21. Proportion of individuals in each health category in August 2019 in each treatment at both sites (BEL is Belcher, CON is Converse). Total sample size for individuals in all health categories in each group is included. Health scores were assessed visually between 1 (worst health) and 4 (best health). Data are pooled over species.

Using species that were present in both treatments at both sites (*S. pectinata*, *S. sempervirens* and *P. maritima*), species-specific differences in final health between the treatments was examined. The preferred model included an interaction between site and species, with treatment and initial health as additive predictors (Table A 3). The findings from this model confirm that plants at Belcher were in better health than those at Converse for all three species, and that *S. pectinata* and *S. sempervirens* field transplants

were in better health than potted seedlings (Figure 22, Figure A 17). Average health score

was similar between treatments for *P. maritima*.
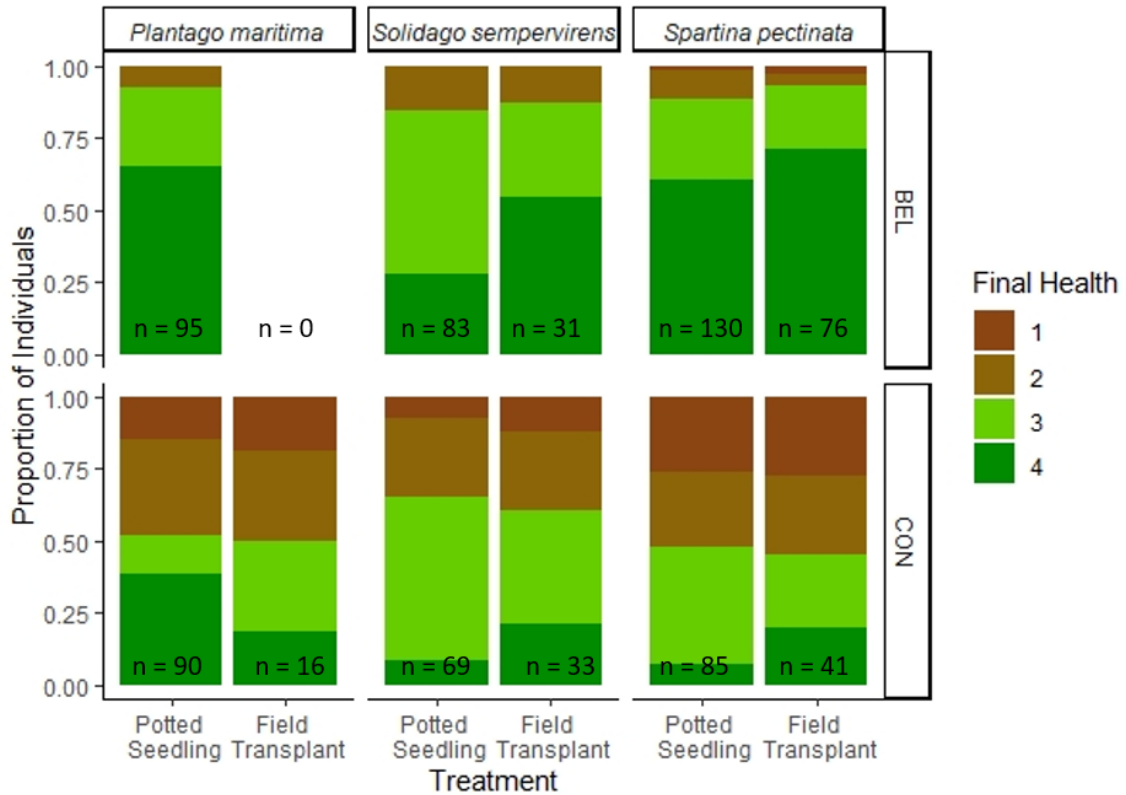
Figure 22. Proportion of individuals in each health category at the end of the season in each treatment at both sites (BEL is Belcher, CON is Converse). Total sample size for individuals in all health categories in each group is included. Health scores were assessed visually between 1 (worst health) and 4 (best health). P. maritima was not planted in the field transplant treatment in Belcher.
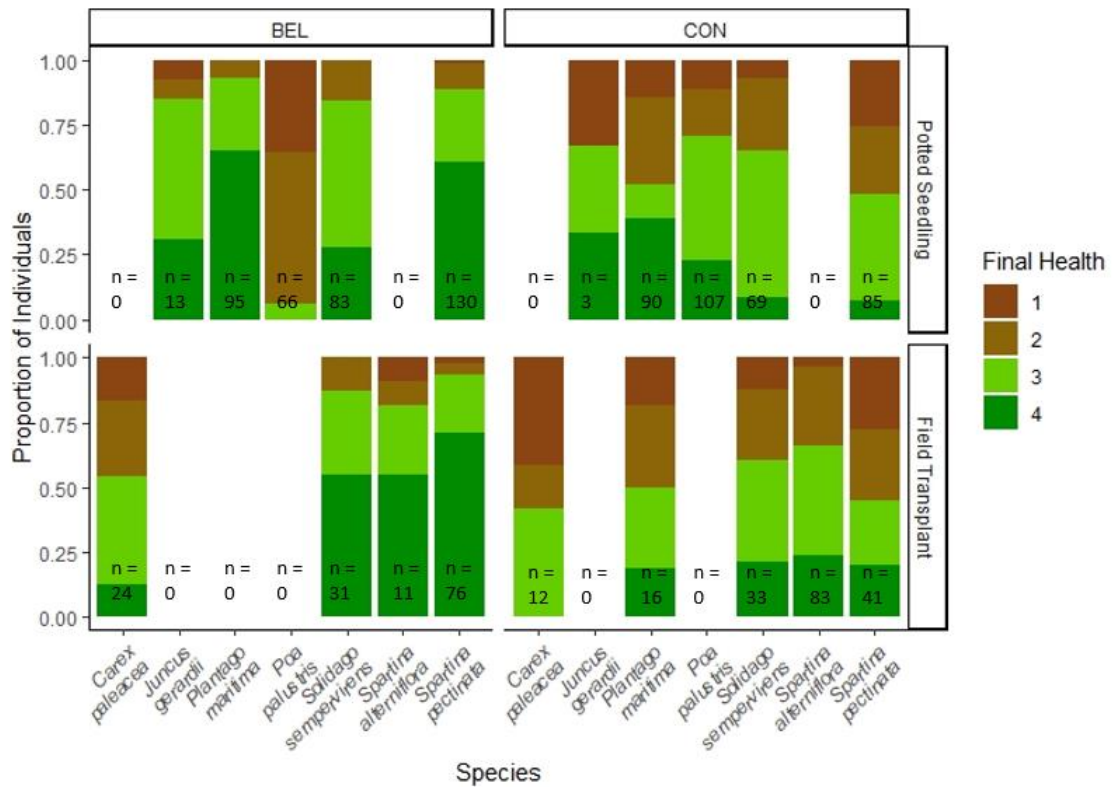
Figure 23. Proportion of individuals of a species in each health category at the end of the season in each treatment at both sites (BEL is Belcher, CON is Converse). Total sample size for individuals in all health categories in each group is included. Health scores were assessed visually between 1 (worst health) and 4 (best health). There were no plants in categories with no data.

To identify high and low performing species overall, data were then modelled using site and species as predictors. Since both treatment and site were found to be important predictors of final health score, data for each treatment was modelled separately. *P. maritima* was omitted from the field transplant model because it was only planted in this treatment at one site. The preferred model for potted seedlings included site, species and their interaction as predictors, as well as initial health as a control. The preferred model for field transplants included site and species as additive predictors, with initial health as a control (Table A 3). There were no consistent trends among potted

seedling species however health scores at Belcher were more variable than at Converse. At Belcher *P. maritima* and *S. pectinata* had the highest health scores followed by *S. sempervirens*, and *P. palustris* had particularly low health scores. At Converse, *S. pectinata* had the lowest health score, while *S. sempervirens, P. palustris*, and *P. maritima* had similar scores (Figure 23, Figure A 18). In the field transplant treatment at both sites, *S. pectinata, S. alterniflora, and S. sempervirens* all had similar average health score while *C. paleacea* had a lower score (Figure 23, Figure A 19). Estimates for *J. gerardii* were highly uncertain due to small sample sizes.

4.3 Over-Winter Survival

Site was the strongest predictor of over-winter survival (Table A 3), while treatments did not differ. Over-winter survival was higher at Belcher (88 %) than at Converse (55 %) (Figure 24, Figure A 20). Though treatment was not an important predictor of over-winter survival overall, a model comparing outcomes of species that were present in both treatments at both sites indicated that *S. sempervirens* potted seedlings had slightly higher survival than field transplants at both sites, while *S. pectinata* had slightly higher survival of field transplants than potted seedlings at both sites (Figure A 21). All species had higher survival at Belcher than Converse except *S. alterniflora*. *S. pectinata*, *S. sempervirens*, and *C. paleacea* had the highest over-winter survival at Belcher, and the lowest at Converse (Figure 25, Figure A 22), potentially explained by differences in site condition preferences of these species. All other species performed similarly.
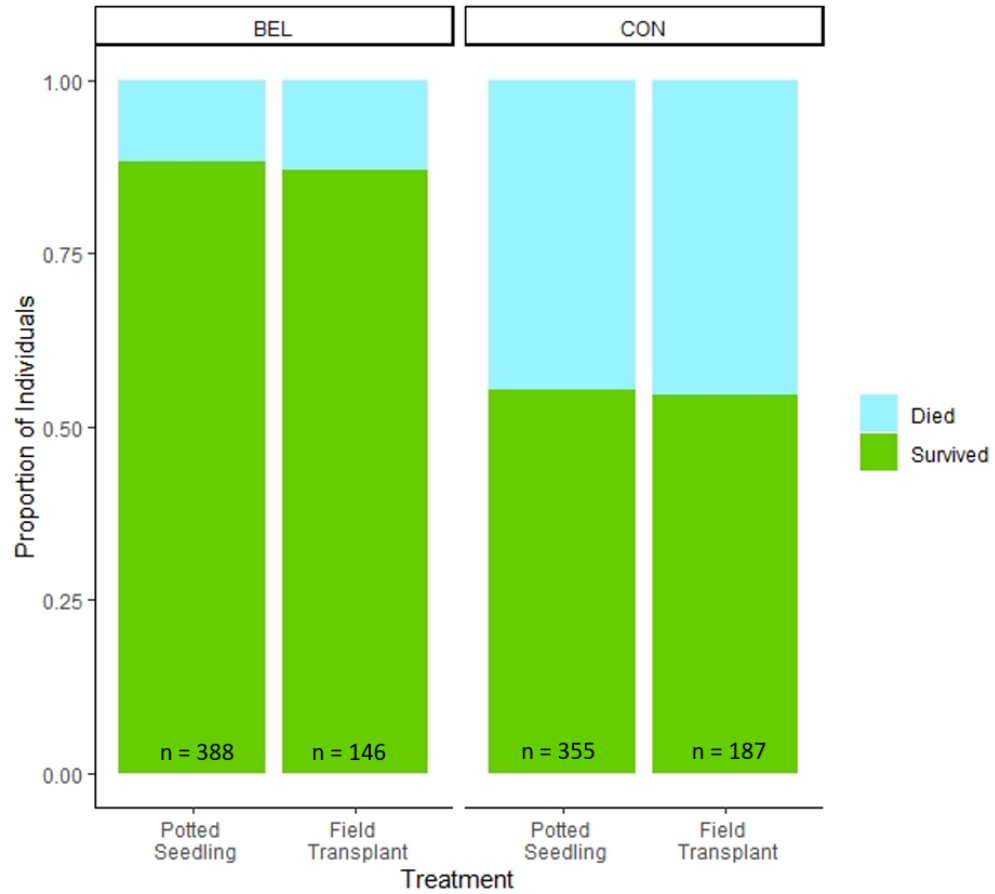
Figure 24. Proportion of surviving plants in 2019 that returned in July 2020 in each treatment and site (BEL is Belcher, CON is Converse). Total sample size for individuals that died and survived in each group is included. Data are pooled over species.
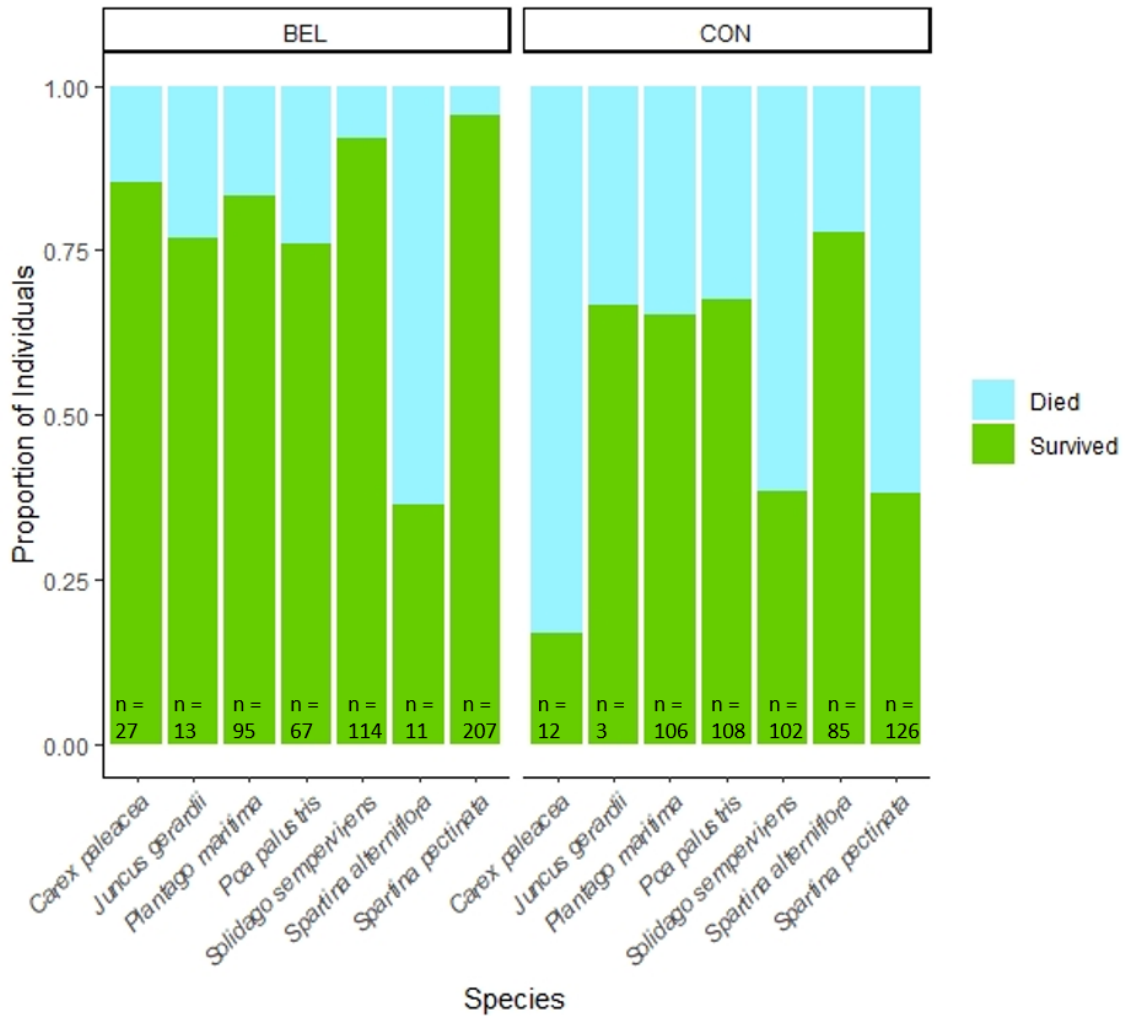
Figure 25. Proportion of surviving plants in 2019 that returned in July 2020 of each species at each site (BEL is Belcher, CON is Converse). Total sample size for individuals that died and survived in each group is included. Data are pooled over treatments.

4.4 Abiotic Conditions

The first three principal components of the PCA had Eigenvalues greater than one, indicating that they explained more variance than any of the individual variables. The first two principal components of the PCA explain 67.3 % of the variance in the data, with the third explaining an additional 11.7 %. The first axis reveals a gradient from plots at a low elevation (and consequently more frequent flooding) with high salinity and rich

in potassium and magnesium, to plots at high elevations with low salinity, and low potassium and magnesium (Figure 26). The second axis shows a gradient from soils with high levels of calcium and phosphorus and long mean inundation times to plots with low levels of both nutrients and shorter inundation times. The third axis is characterized by a gradient in nitrogen concentration. Sulfur was a poor predictor of the variability across the sites. Interestingly, important soil nutrients did not follow consistent patterns across the sites.

Abiotic conditions at Converse covered a wider range than at Belcher, although Belcher was predominantly characterized by higher elevations, longer mean inundation times, lower salinity, nitrogen, potassium, magnesium and sulfur but higher calcium and phosphorus (see Table A 4 for summary statistics on all collected variables). There was an overall inverse relationship between elevation and soil salinity (Na kg/ha), and between elevation and inundation frequency. Inundation time was highly inversely correlated with elevation at each site, however in the pooled site data used above there was no correlation.
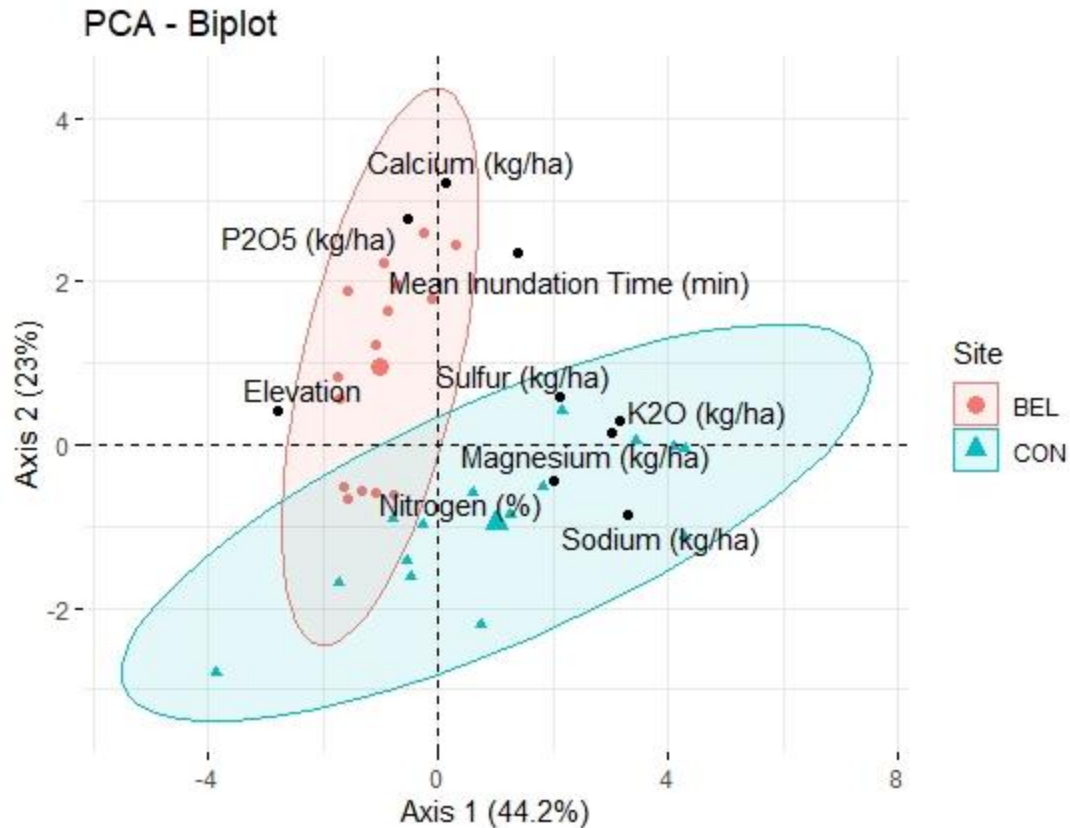
Figure 26. PCA Biplot displaying differences in abiotic conditions at each site (BEL = Belcher, CON = Converse) on the first two principal component axes. Each point represents a cluster, the large point represents the mean for each site.

Elevation had a moderately positive relationship with RGR and final health score at Converse, but had a moderate negative relationship on the same variables at Belcher (Figure 27, Figure 30). There was no relationship between elevation and survival or over-winter survival. Potassium had a consistently negative relationship with all response variables at Converse (RGR – moderate, final health – moderate, survival – strong, over-winter survival – strong), and the data suggested a positive relationship with RGR and final health at Belcher, although estimates were uncertain (Figures 27 - 30). Calcium had a strong positive relationship with RGR, survival and final health at Converse, but a slightly negative relationship with only survival and over-winter survival at Belcher

(Figures 27 - 30). Phosphorus showed a very slightly positive relationship with survival and a near-zero relationship with other all response variables at Converse. At Belcher, phosphorus had a positive relationship with survival and over-winter survival but a negative relationship with final health at Belcher (Figures 27 - 30). The data suggests positive relationships between nitrogen and RGR and survival and a negative relationship with final health at Belcher, although these estimates are unstable due to variability in the data (Figures 27 - 30). Nitrogen had no effect or extremely weak positive effects on all response variables at Converse (Figures 27 - 30). Sodium had a positive effect on final health and over-winter survival but a negative effect on other response variables (modelled at Belcher only), however there was a high degree of uncertainty in these estimates (Figures 27 - 30). Sulfur effects (modelled at Converse only) were relatively neutral (RGR, over-winter survival), slightly positive (survival), and slightly negative (final health) however there was some uncertainty around these effects as well. Each of these models performed better with species included as a fixed effect, indicating that the relationships with these variables may differ between species.
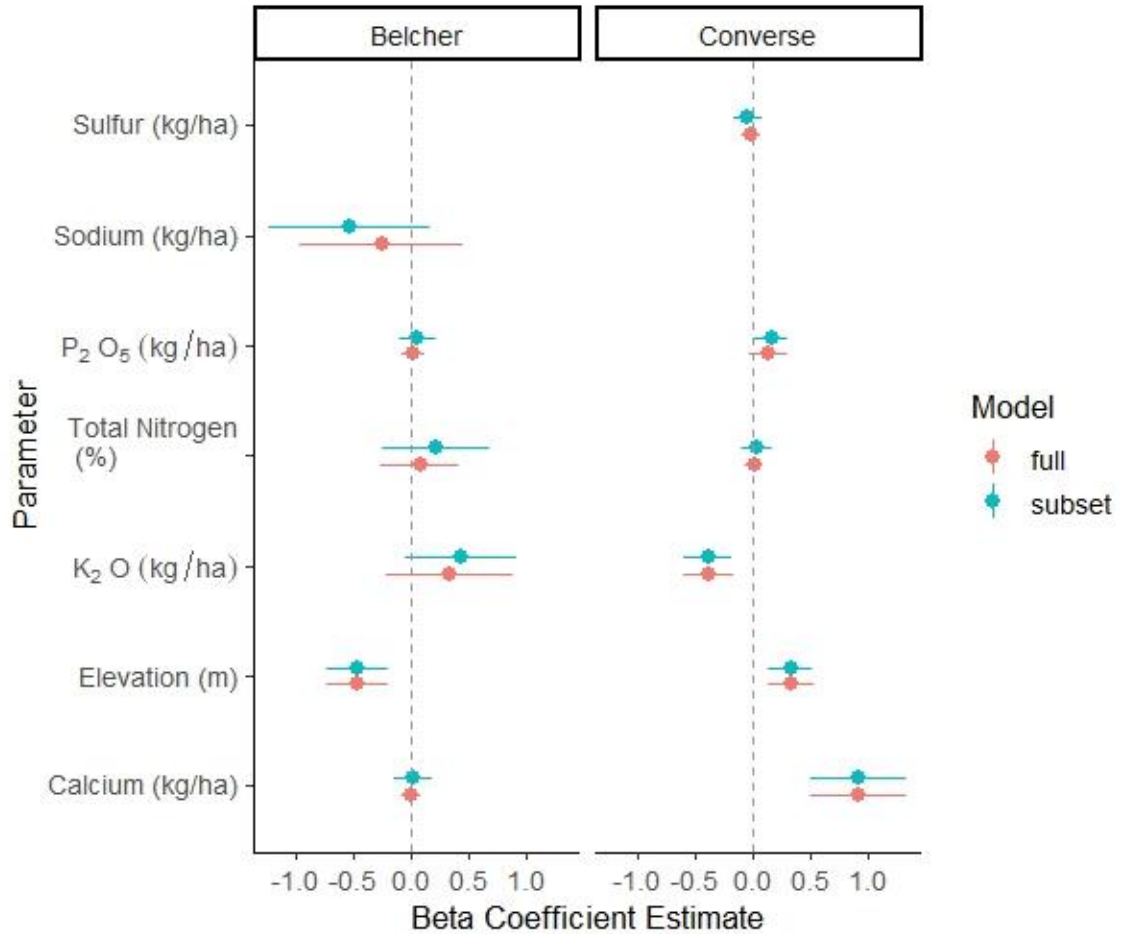
Figure 27. Standardized regression coefficient estimates from generalized linear model averaging procedure with relative growth rate (ln(cm²/cm²)·3 months⁻¹) from June - August 2019 as the predicted variable and 95% confidence intervals. Full coefficients (pink) are averaged over all possible models with Δ AICc < 5 (zeros are substituted if a parameter is not present in a model), subset coefficients (blue) are averaged over only models that include that parameter.
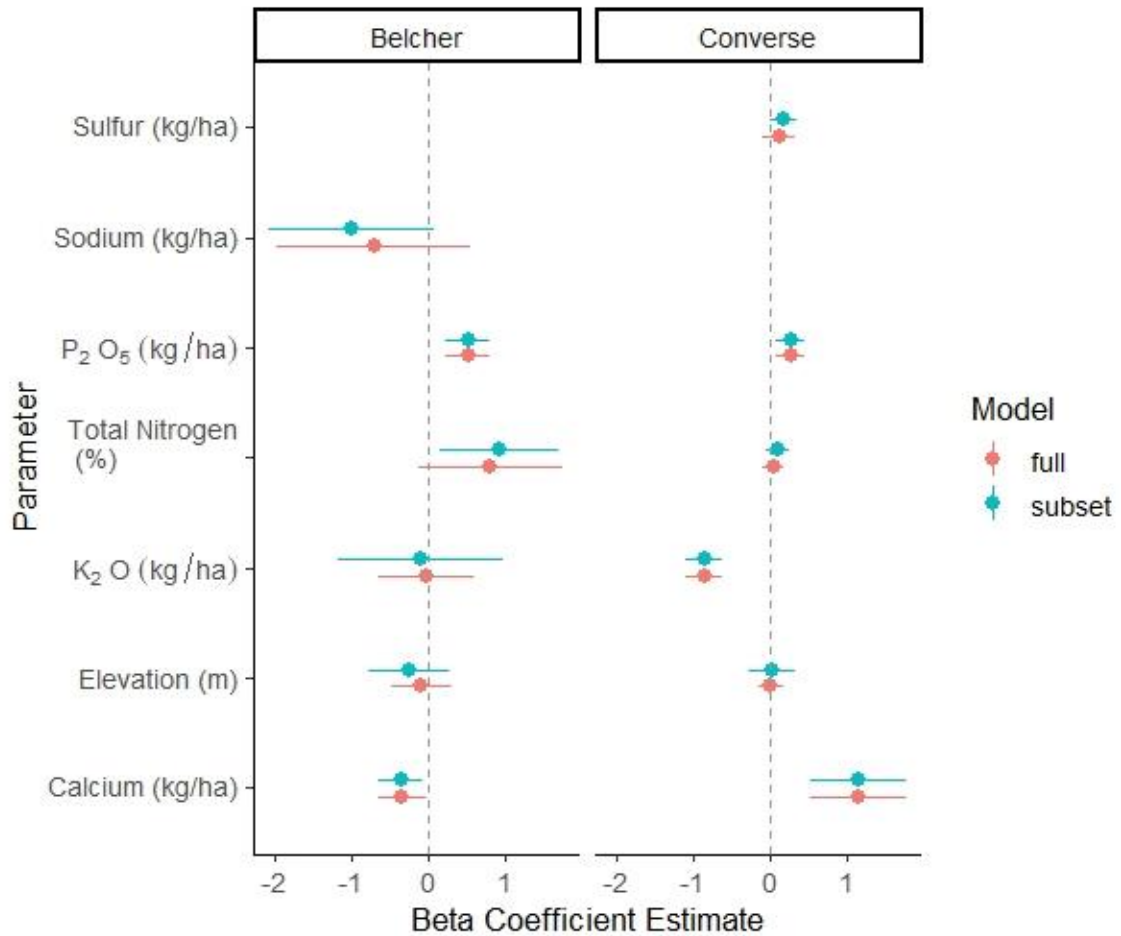
Figure 28. Standardized regression coefficient estimates from generalized linear model averaging procedure with survival to August 2019 as the predicted variable and 95% confidence intervals. Full coefficients (pink) are averaged over all possible models with Δ $AIC_c < 5$ (zeros are substituted if a parameter is not present in a model), subset coefficients (blue) are averaged over only models that include that parameter.
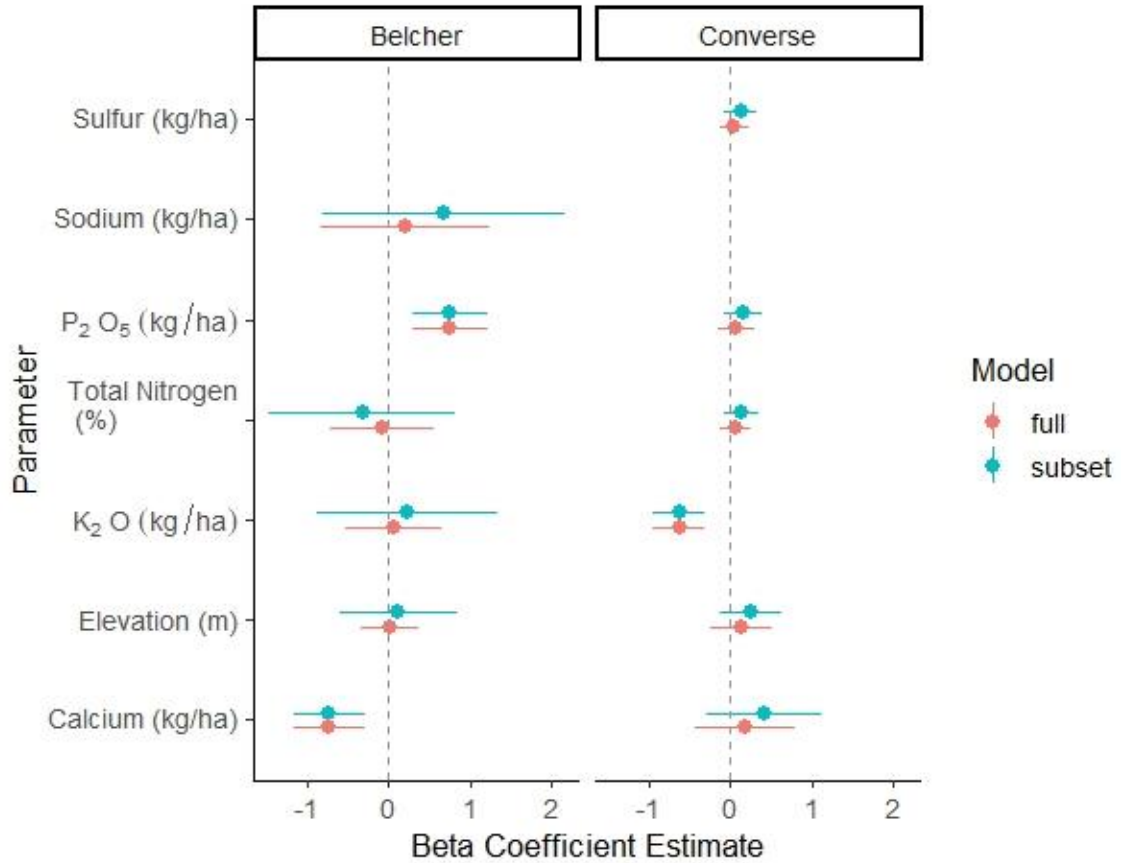
Figure 29. Standardized regression coefficient estimates from generalized linear model averaging procedure with over-winter survival (plants that came back in July 2020) as the predicted variable and 95% confidence intervals. Full coefficients (pink) are averaged over all possible models with Δ AIC$_c$ < 5 (zeros are substituted if a parameter is not present in a model), subset coefficients (blue) are averaged over only models that include that parameter.
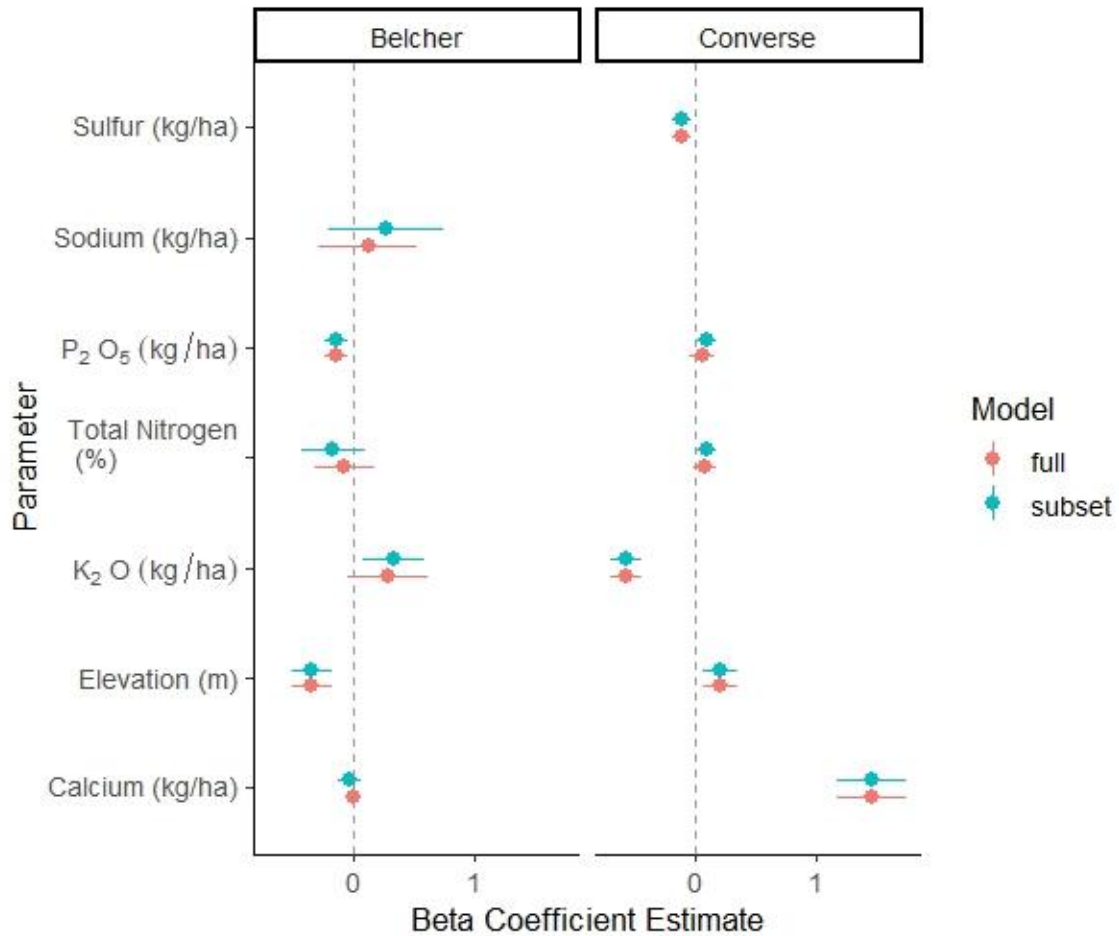
Figure 30. Standardized regression coefficient estimates from generalized linear model averaging procedure with health in August 2019 as the predicted variable and 95% confidence intervals. Full coefficients (pink) are averaged over all possible models with Δ AIC$_c$ < 5 (zeros are substituted if a parameter is not present in a model), subset coefficients (blue) are averaged over only models that include that parameter.

Chapter 5: Discussion

The main objective of this research was to determine whether active re-vegetation accelerated the recovery of plant communities at two new salt marsh restoration sites. I tested the efficacy of five methods of planting a range of species at two recently restored sites in the Bay of Fundy over two years. Of the tested methods, only planting potted seedlings and field transplants were successful methods of establishing higher abundance

and species richness of target (perennial halophyte) species compared with a passive control where no manipulation or addition of plant material occurred. Of these, potted seedlings had higher survival, while all other indices of plant performance were more affected by site differences in abiotic conditions.

5.1 Planting Live Plants Accelerated Re-Vegetation and Enhanced Species Richness

Planting a mixture of species as potted seedlings and field transplants increased the abundance and species richness of perennial halophytes over the course of two years as compared to the passive "do nothing" approach (Figure 11, Figure 12). Of these treatments, potted seedlings tended to have higher abundance than field transplants, especially after the second growing season, although the difference between the treatments was not statistically significant due to large variability across the sites. There was some survival of every species planted in the study, and many of the species were observed going to seed and spreading by rhizome over both growing seasons. The success of these treatments and species indicates that these are viable methods for quickly increasing the abundance of desired species at salt marsh restoration sites in the Bay of Fundy, providing immediate benefits to the restoration site.

Plant re-colonization on salt marsh restoration sites is correlated with species abundances in nearby vegetation (Rand, 2000; Wolters et al., 2005). On managed realignment sites, the nearest vegetation is typically in the fringe marsh outside the footprint of the old dyke. Halophytic vegetation present on a managed realignment site pre-breach, particularly *S. pectinata*, has been seen to survive salt water intrusion post-breach (Virgin et al., 2020) and these patches are another potential source of vegetative

spread. Generally, low diversity and large extents of bare ground at recently breached

sites may be a limitation to the rapid and long-term development of a healthy vegetation

community. Dense, species-rich "islands", like the ones established in my study act as a

source of vegetative spread beyond what is possible without planting. Establishing a

range of species early in the restoration trajectory increases the pool of potential

candidate species for establishment throughout the site, ultimately decreasing the chance

that sites will remain dominated by pioneer communities, as has been seen in passive

restoration and managed realignment projects in the past (Bowron et al., 2011b; Brooks

et al., 2014; Burdick et al., 1997; Byers & Chmura, 2007; Chang et al., 2016).

 While planting a range of species successfully increased the diversity and

abundance of target species, it is interesting to note that, at Belcher, total abundance was

similar between the passive treatment and both potted seedling and field transplants

during the first growing season, and during the second growing season most of the plots

had similar total abundance (Figure 13). This was the result of natural colonization by

opportunistic annuals (mainly *Chenopodium* spp. and *Atriplex* spp.). This type of

colonization after managed realignment has been seen at other sites in Nova Scotia

(Bowron et al., 2011a), and elsewhere in the world (Hughes et al., 2009; Mossman et al.,

2012); however, the function of these annuals in the restoration trajectory is largely

unknown. Salt marshes are thought to develop through facilitative succession, where

early colonizing plants facilitate further colonization through a variety of means

including facilitating accretion of marsh soils (Davy et al., 2000). It is possible that these

early colonizers provide some facilitative benefit by way of temperature changes,

shading, or modifications to the soil. However, at two managed realignment sites in

England these annual species did not provide any facilitative benefit by way of facilitating accretion for subsequent colonization and Hughes et al., (2009) hypothesized that these species are early colonizers solely as a result of their tolerance of early marsh conditions. It is also likely that these plants do not stabilize the marsh surface to any significant degree since annual roots are usually shallow. The characteristics of these plants indicate that, regardless of whether there is an initial influx of halophytic annuals at a site, the establishment of target species is important to promote facilitative succession and the return of ecosystem services.

Adding a propagule source (sowing seed and planting wrack) and encouraging seed deposition (tilling) did not increase the abundance or richness of target species (Figure 11, Figure 12). Unfortunately, in this study seeds were planted deeper than planned in the field due to miscommunication, which may have contributed to very low germination rates, particularly at Belcher where seeds were planted 10 cm deep. There are also problems with seeding at sites with strong tidal force, as is the case at Bay of Fundy marshes, or at sites with low elevation, where seeds may be scoured and washed away easily (Broome et al., 1988; Garbutt et al., 2005; Wrathall, 2016). Despite the low germination found in the study, previous studies have shown that sowing seed can successfully improve plant cover in salt marsh contexts (Broome et al., 1988). Seeding may still be an attractive method of re-vegetation since associated costs are very low and with some methodological development there may be some success of seed. There was some germination of seeds at Converse over both years, of which one species was *L. carolinianum*. This species was difficult to grow in the greenhouse, indicating that seeding may boost site diversity in similar situations. I suggest that seeding may be most

beneficial in conjunction with some other method of planting. Adding plants and sowing seed together, for example, may prevent seed scouring through slowing of wave energy through stems or provide some other facilitative benefit to seeds in the rooting zone (i.e. increased oxygen (Renzi et al., 2019) or decreased soil salinities (Bertness et al., 1992). This option may offset some of the unpredictability associated with seed germination and be a good strategy to "hedge-bets" for diversity and for quickly establishing cover.

Wrack and tilling treatments were both wholly unsuccessful in this study for establishing vegetation. Planting wrack has been unsuccessful in the past (Wrathall, 2016) and I suggest that wrack may not be useful for establishing vegetation. The high variability of wrack composition makes it an inconsistent seed source for this application. However, wrack may be useful when partnered with another method of planting or seeding to act as a readily available mulch, to secure seeds in place and to protecting plantings. Similarly, adding microtopographic features was unsuccessful for establishing vegetation though it has been shown to increase seed trapping in other studies (Wang et al., 2018). In some cases, particularly at Converse, any increased rugosity was negated by ongoing sedimentation and repeated tidal flooding. This method would need considerable reimagining if used again and it is likely that introducing larger topographic features such as creeks or concave and convex features on a larger scale (e.g., 1 m^2 mounds) may be more effective than these small-scale features.

5.2 Potted Seedlings Twice as Likely to Survive

Potted seedlings and field transplants, the two successful treatments at establishing higher target species abundance than that of the passive approach, performed

similarly in most plant performance measures, with the marked difference of survival through the first growing season. Potted seedlings on average were approximately twice as likely to survive through the first season (survival ≈ 75%) as field transplants (survival ≈ 40%) at both sites (Figure 15). These results were supported by data directly comparing species planted in both treatments, though differences between treatments was not as pronounced (Figure 16). This is unsurprising since field transplants underwent considerably more trauma to their roots through the transplant process. Since many of the transplanted species grow in dense clonal mats with deep, interconnected root systems, it was difficult to dig up and separate plants. As a result, potted seedlings were planted with more intact root systems.

Damage to the roots of field transplants varied among species, with gramminoids being most difficult to dig, particularly *C. paleacea*. This is reflected in low survival at both sites for this species (~47 % at Belcher and ~15 % at Converse). *S. alterniflora* transplants also had very low survival at Belcher (~10 %) but considerably higher at Converse (~60 %). Past research has found that transplanted *S. alterniflora* can have survival rates anywhere between 0 and 100 % (Bergen et al., 2000; Stalter & Batson, 1969). Variability in this species' hardiness to transplanting may be due to its tolerance to abiotic conditions at the particular location of planting (Stalter & Batson, 1969), or to differences between planting techniques. One potential area for improvement of this technique would be to plant transplants immediately upon digging. As transplants were stored in bags for at least one day before planting in my study, it is possible that this caused unnecessary stress to the plants. While there may be some room for improvement of techniques, transplants were generally treated with greater care before planting at

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Converse than Belcher (as a result of the order that sites were planted in and resultant experience handling the plants) and there was no indication that their treatment increased survival on a species-by-species basis.

Another potential strategy for increasing survival of field transplants may be to plant in larger clumps which, by decreasing the ratio of damaged edge roots to inner roots, may decrease the trauma to roots and provide a better chance of survival for the inner portions of the plant. These clumps may be particularly beneficial in higher stress areas where larger root systems and more stems can facilitate shared oxygen, among other benefits (Renzi et al., 2019). Despite the field transplants having lower survival, no species-groups at either site died out completely, and the plants that did survive still grew well, were healthy, and survived the winter. For this reason, using field transplants may still be useful in restoration schemes, for example if specific species are difficult to grow in the greenhouse, or due to time or budget constraints. In a restoration project if there is a desired amount of cover it may be necessary to combine field transplants with some other method, or to increase the number of transplants in expectation that survival will be low.

5.3 Abiotic Conditions Trump Planting Treatment for Survival

In all other measures of plant performance examined here, site was a more important determinant of performance than treatment. RGR (Figure 18), health scores (Figure 21), over-winter survival (Figure 24), and plant abundances overall (Figure 13) were higher at Belcher. This agrees with past research which found that planting outcomes were driven primarily by site, as opposed to method of establishment (Greet et

al., 2020). Analysis of collected data on abiotic conditions at each site revealed that Belcher was predominantly characterized by higher elevations (and consequently less frequent flooding), longer mean inundation times, lower salinity, nitrogen, potassium, magnesium and sulfur but higher calcium and phosphorus (Figure 26) therefore making it a less stressful site overall. These, among other site differences may be accounting for the differences in plant performance observed in my study.

The differing conditions between sites were associated with very different relationships between plant performance variables and each of the abiotic variables. In some cases, an abiotic variable had the opposite relationship with plant performance at each site. Overall, growth rates and survival were associated with similar abiotic properties, while final health scores and over-winter survival were associated with similar abiotic properties.

Elevation mediates salinity and flooding (both inversely related to elevation) on salt marshes. Together, these are frequently cited as the main abiotic stresses that govern plant community organization in coastal marshes (Broome, 1989; Broome et al., 1988). Higher elevations on the marsh surface typically have less saline, less frequently flooded soils and are therefore more hospitable environments for plants. I found that elevation was positively related to RGR and final health scores at Converse (Figure 27, Figure 30), supported by past modelling showing elevation to be positively correlated with primary production in salt marshes (Miller et al., 2019). At Belcher however, I found a negative relationship between the same response variables and elevation (Figure 27, Figure 30). These results may be indicative of drought effects since elevations at Belcher were on

average 54 cm higher than Converse and many of the planting locations flooded with less than 25 % of high tides, particularly in the eastern portion of the site.

Saline soils at low elevations can cause a decrease in water availability to plants through increased osmotic potential, can cause nutrient imbalances and can have a toxic effect directly on plants (Schulze et al., 2019). At Belcher, estimates of the effect of soil Na concentrations on plant performance were unstable; however, models suggested negative relationships with RGR and survival (Figure 27, Figure 28). These results are in line with the hypothesis that more saline soils have a negative impact on plant performance. At Converse, K_2O was highly positively correlated with Na (Na was not included in the model at this site) and I found a negative effect of K_2O for all response variables (Figures 27 - 30). It is likely that the relationship between K_2O and Na was the underlying reason for this relationship, supporting the hypothesis that higher soil salinities are a considerable stress on plants through all stages of growth.

Analysis of survival data indicated that phosphorus concentrations had a weak positive relationship with probability of survival across both sites, and a weak positive relationship with probability of over-winter survival at Belcher only (Figure 28, Figure 29). Phosphorus is a primary nutrient that is important for root development and growth of new tissue in plants (Schulze et al., 2019) and it is possible that root development may be a critical factor contributing to plant survival in the marsh. Plants with healthier root systems are able to respond more effectively to stressful events (such as prolonged flooding or drought), and having well-established roots is critical over-winter when plants die back and regrow from the roots in the spring. Phosphorus is a limiting nutrient in salt marsh systems (Broome et al., 1983; Delaune & Pezeshki, 1988), and although I did not

find a relationship between phosphorus and plant growth, the positive relationship between summer- and winter-survival and phosphorus concentrations indicate that phosphorus may limit plant survival in Fundy systems.

The positive relationship between calcium concentration and plant performance variables at Converse is an interesting result as calcium is not typically a limiting nutrient in salt marshes (Broome et al., 2019). Calcium was positively correlated with survival, RGR, and over-winter survival at Converse (Figures 27 - 30), but slightly negatively related to survival and over-winter survival at Belcher (Figure 28, Figure 29). Converse had lower concentrations of calcium than Belcher overall (Figure 26), so this result may indicate that plants at Converse were limited by calcium. However, this result may also be because of an underlying relationship between calcium and other soil parameters. Typically, frequently flooded soils present a high stress environment because they have low redox potentials, which causes the creation of compounds that are toxic to plants including H_2S (Schulze et al., 2019), particularly in areas with poor drainage (Skinner, 2016). Fe and Mn can act as a buffer in low redox conditions (Reddy et al., 2000; Schoepfer et al., 2014), reducing the production of toxic compounds. At Converse, calcium concentrations were positively correlated with Fe (Pearson's r = 0.74) and Mn (Pearson's r = 0.93) and it is possible that this buffering capacity provided an important benefit for plantings since plots were flooded more frequently than at Belcher.

A notable characteristic not measured here but observed as starkly different between the two sites was the condition of the soil upon planting. Belcher had a strong influx of fresh sediment over the first year post-breach and we planted into a deep, fresh layer of sediment. In contrast, Converse had considerably less sedimentation and plants

were planted into dry, compacted agricultural soils with a mat of dead vegetation on top. Fundy restoration sites with high sedimentation rates have been seen to be rapidly colonized by halophytic vegetation in the past (Lemieux, 2012; Virgin et al., 2020), indicating that the fresh sedimentation may provide a sort of "clean slate" for plant growth. Typically, fresh sediments are associated with an influx of nutrients which can promote higher plant performance (Broome et al., 2019); however, the present study did not find strong evidence to suggest nutrient limitations at either of these marshes. Fresh Fundy sediments may trap and hold seed more effectively due to increased "stickiness" as compared to older, dry agricultural soils. The compacted soils at Converse may have also presented issues with decreased oxygenation in the rooting zone or poor site drainage. Artificially aerated salt marsh soils have been shown in the past to increase stem density, height and above- and below-ground biomass of *S. alterniflora* (Linthurst & Seneca, 1981). The compacted soils at Converse may limit the oxygen entering the root-zone in already oxygen-depleted soils, and these effects may have been compounded by the layer of decomposing vegetation depleting oxygen, contributing to high reducing conditions thereby limiting plant growth.

5.4 Conclusions and Future Research

The research in the present thesis has shown that there is merit to active planting in Bay of Fundy restoration projects. Planting live plants grown in the greenhouse and directly from the field both yielded healthy plants that may kick-start plant colonization on site. Potted seedlings had the highest survival and there was some indication that potted seedlings may have had slightly higher growth rates in species-by-species

comparisons. Growing these plants required considerable time and effort and is a costly option for restoration projects. The potted seedlings used in my study were approximately 5 months old upon planting, and over the growing period they required regular care approximately 3 times per week. Seedlings of most species became rootbound in 3-inch pots quickly and needed repotting within 2 months. Growth-time could be cut down; however, planting younger plants may result in decreased performance. Total costs for this method included labour (seed collection, potting, watering, planting), greenhouse space, materials (including soil, pots and trays) and transport costs. I was unsuccessful at growing all desired species, some of which (including *S. alterniflora*) required more specific environmental requirements and consistent care than I could provide. Growing potted seedlings would take one dedicated grower over the course of at least 3 months, and at a similar site size and planting density as this project would require approximately 6 people for 1 day to plant. When comparing methods of planting for vegetation restoration, these costs are an important consideration.

Field transplants are also a viable option for planting; however, planting high numbers of field transplants may be required to achieve the same vegetation density goals as potted seedlings due to decreased survival. Planting field transplants at a similar density and site size as this project would take around 6 people over 2 days to plant. Field transplants have the additional consideration of environmental damage, and it may be prudent not to dig from small patches of plants.

All species used in these treatments showed some survival and growth, indicating that species from all zones can be planted across the marsh in early-succession restoration projects. This provides ample opportunities for a diverse range of species to colonize the

site and for competitive forces and stress-tolerance levels of each individual species to inform its survival and role in the successional trajectory. Long-term monitoring of high diversity plantings may provide insight into whether planting these species does indeed benefit salt marsh diversity over time, and monitoring spread may provide insight into ideal planting densities across sites.

Site conditions are also a critical component to understanding how to design planting schemes. My results indicate that relationships between plant performance and abiotic conditions can be highly site specific, suggesting that baseline monitoring and modelling of restoration outcomes may greatly improve the ability to forecast planting outcomes. A range of abiotic factors, including the classic elevation, inundation frequency and salinity, but extending to soil nutrients such as phosphorus, potassium and calcium were all found to impact plantings at different stages of their development. Complex interactions of these abiotic variables with the physical characteristics of a site may cause plants to respond differently to the same abiotic conditions at different sites, as appeared to be the case with flooding frequency. By gaining an understanding of abiotic conditions at prospective sites it may be possible to improve planting success through manipulation of site conditions, for example, through fertilization or soil aeration.

This research raised some interesting questions about the relationships between abiotic variables and planting success. Both physical and edaphic factors seem to play an important role in plant success but there is not one clear answer as to which factors are most important, particularly considering differences in site conditions. An interesting avenue for future research would be to investigate the relationships between sedimentation rates, sediment characteristics (such as compaction and bulk density) and

vegetation colonization and growth in Bay of Fundy marshes. Fresh sediment seems to provide a "fresh start" for plantings and being able to mimic or promote these conditions would be beneficial. Another area for more research is to investigate soil redox potentials at early restoration sites and do in depth chemical analysis of proportions of toxic chemical forms to non-harmful forms and measure soil oxygen levels, in relation to site characteristics. This analysis would help to understand whether reducing conditions are a limitation to planting at Bay of Fundy sites and whether further measures need to be taken to abate these conditions in early restoration.

The results of my study are key to informing future planting projects in Bay of Fundy salt marsh restoration sites, and to identifying factors that influence planting success in these systems. Along with future research, this study can provide a strong base for ensuring future planting projects are successful.

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Appendix A. Visualization of Statistical Outputs and Raw Data

Table A 1. Summary statistics for the number of plants added per plot.

Treatment	Site	Median	Min	Max
Potted Seedlings	Belcher	32	31	34
Potted Seedlings	Converse	34	32	34
Field Transplants	Belcher	25	24	29
Field Transplants	Converse	28	22	33

Table A 2. Summary statistics for the number of each species planted per plot. Data are pooled across sites as numbers were similar.

	Potted Seedlings			Field Transplants		
Species	Median	Min	Max	Median	Min	Max
Carex paleacea				5	2	9
Juncus gerardii	1	1	1			
Plantago maritima	8	6	8	2	1	3
Poa palustris	10	7	11			
Solidago sempervirens	6	5	6	3	2	4
Spartina alterniflora				9	5	12
Spartina patens						
Spartina pectinata	9	8	10	10	3	13

Table A 3. Model selection statistics. AIC_c is the computed small-sample size adjusted AIC for a given model, ΔAIC_c is the deviance of a model from the preferred model, and weight is a value that ranges from 0 to 1 indicating the amount of support for the model. Note that all models that include interactions also include all lower order terms. Terms in brackets indicate a random intercept term.

Model	AIC_c	Δ AIC	Weight	Random Term Var	STDEV
Target Species Abundance - 2019					
Site x Treatment	660.2	0	0.804		
Site + Treatment	663.0	2.8	0.195		
Treatment	674.4	14.3	0.001		
Site	828.6	168.4	0.000		
Intercept	840.5	180.4	0.000		

Target Species Abundance - 2020

Site x Treatment	1058.3	0.0	1.000
Site + Treatment	1092.2	33.9	0.000
Treatment	1188.9	130.6	0.000
Site	1216.3	157.9	0.000
Intercept	1267.0	208.7	0.000

Target Species Richness - 2019

Site x Treatment	397.8	0.0	0.931
Treatment	403.6	5.8	0.051
Site + Treatment	405.6	7.9	0.018
Intercept	591.4	193.7	0.000
Site	593.3	195.6	0.000

Target Species Richness - 2020

Site x Treatment	435.5	0.0	0.936
Site + Treatment	440.8	5.4	0.064
Treatment	460.7	25.2	0.000
Site	511.6	76.1	0.000
Intercept	531.5	96.1	0.000

Total Abundance - 2019

Site x Treatment	1038.5	0	0.994
Site + Treatment	1048.8	10.2	0.006
Site	1138.7	100.1	0.000
Treatment	1155.4	116.9	0.000
Intercept	1223.9	185.3	0.000

Total Abundance - 2020

Site x Treatment	1257.5	0.0	1.000
Site + Treatment	1283.5	26.0	0.000
Site	1334.4	76.9	0.000
Treatment	1418.0	160.6	0.000
Intercept	1429.5	172.0	0.000

Total Species Richness - 2019

Site x Treatment	615.1	0.0	1.000
Site + Treatment	640.1	25.0	0.000
Treatment	684.2	69.2	0.000
Site	803.7	188.6	0.000
Intercept	848.0	232.9	0.000

Total Species Richness - 2020

Site x Treatment	643.5	0.0	1.000
Site + Treatment	666.4	22.9	0.000
Site	710.8	67.3	0.000
Treatment	814.5	171.0	0.000
Intercept	859.0	215.5	0.000

Survival: All plants

Site x Treatment + (Cluster)	2139.0	0	0.944	0.35	0.59
Treatment + (Cluster)	2145.4	6.3	0.040		
Site + Treatment + (Cluster)	2147.2	8.2	0.016		
Intercept + (Cluster)	2377.6	238.6	0.000		
Site + (Cluster)	2379.3	240.3	0.000		

Survival: Comparable Species (Note: Only models weighted above 0 included)

Site x Species x Treatment	820.3	0	0.866
Site x Treatment + Species x Treatment	824.8	4.5	0.091
Site x Species + Site x Treatment + Species x Treatment	826.8	6.5	0.034
Site x Treatment + Species	830.1	9.8	0.006
Site x Species + Site x Treatment	831.2	10.9	0.004

Survival: Potted Seedling Species

Site x Species	980.3	0	1.000
Site + Species	1064.4	84.1	0.000
Species	1073.4	93.1	0.000
Site	1119.8	139.5	0.000
Intercept	1128.5	148.2	0.000

Survival: Field Transplant Species

Site x Species	878.1	0	1.000
Site + Species	994.7	116.6	0.000
Species	995.6	117.5	0.000
Intercept	1054.3	176.2	0.000
Site	1054.4	176.3	0.000

RGR: All plants

Site + (Cluster)	3712.4	0	0.595	0.10	0.32
Site + Treatment + (Cluster)	3714.4	2.0	0.217	0.12	0.34
Site x Treatment + (Cluster)	3714.7	2.3	0.188		
Intercept + (Cluster)	3763.0	50.6	0.000		
Treatment + (Cluster)	3765.0	52.6	0.000		

RGR: Comparable Species (Note: Only models weighted above 0 included)

Site x Species x Treatment + (Cluster)	1856.4	0	0.875	0.29	0.53
Site x Species + Species x Treatment + (Cluster)	1861.3	4.8	0.078		
Site x Species + Site x Treatment + Species x Treatment + (Cluster)	1862.2	5.8	0.048		

RGR: Species

Site x Species + (Cluster)	3550.4	0	1.000	0.12	0.35
Site + Species + (Cluster)	3629.8	79.3	0.000		
Species + (Cluster)	3684.4	134.0	0.000		
Site + (Cluster)	3712.4	162.0	0.000		
Intercept + (Cluster)	3763.0	212.6	0.000		

Final Health: All plants

Site x Treatment + Initial Health	2884.8	0	0.905
Site + Treatment + Initial Health	2889.3	4.5	0.094
Site + Initial Health	2899.8	15.0	0.000
Site x Treatment	2904.4	19.7	0.000
Site + Treatment	2906.4	21.7	0.000
Site	2907.4	22.7	0.000
Treatment + Initial Health	2965.8	81.1	0.000
Initial Health	2973.5	88.8	0.000
Intercept	2987.2	102.4	0.000
Treatment	2988.3	103.5	0.000

Final Health: Comparable Species (Note: only models weighted above 0 included)

Site x Species + Treatment + Initial Health	1285.8	0	0.439

Site x Species + Site x Treatment + Initial Health	1287.2	1.4	0.214		
Site x Species + Species x Treatment + Initial Health	1287.8	2.0	0.159		
Site x Species x Treatment + Initial Health	1288.6	2.8	0.109		
Site x Species + Site x Treatment + Species x Treatment + Initial Health	1289.2	3.4	0.079		

Final Health: Potted Seedling Species

Site x Species + Initial Health	1809.4	0	0.862		
Site x Species	1813.0	3.7	0.138		
Site + Species + Initial Health	1975.2	165.8	0.000		
Site + Species	1981.3	172.0	0.000		
Species + Initial Health	2001.8	192.5	0.000		
Species	2012.9	203.5	0.000		
Site + Initial Health	2021.7	212.3	0.000		
Site	2030.2	220.8	0.000		
Initial Health	2056.8	247.4	0.000		
Intercept	2070.9	261.6	0.000		

Final Health: Field Transplant Species

Site + Species + Initial Health	780.0	0	0.872		
Site x Species + Initial Health	783.8	3.8	0.128		
Site x Species	797.0	17.0	0.000		
Site + Species	800.5	20.5	0.000		
Site + Initial Health	817.4	37.4	0.000		
Site	829.7	49.7	0.000		
Species + Initial Health	839.3	59.4	0.000		
Species	853.9	74.0	0.000		
Initial Health	868.3	88.3	0.000		
Intercept	870.3	90.4	0.000		

Over-Winter Survival: All Plants

Site + (Cluster)	1114.5	0.0	0.652	0.36	0.60
Site + Treatment + (Cluster)	1116.4	1.9	0.254		
Site x Treatment + (Cluster)	1118.4	3.9	0.094		

Intercept + (Cluster)	1144.4	29.9	0.000
Treatment + (Cluster)	1146.2	31.7	0.000

Over-Winter Survival: Species

Site x Species	1057.6	0.0	1.000
Site + Species	1131.7	74.0	0.000
Site	1141.1	83.5	0.000
Intercept	1288.7	231.0	0.000
Species	1295.8	238.1	0.000

**Over-Winter Survival:
Comparable Species**

Site + Species x Treatment	422.8	0.0	0.497
Site x Species + Species x Treatment	424.6	1.8	0.200
Site x Treatment + Species x Treatment	424.8	2.0	0.179
Site x Treatment + Species x Treatment + Site x Species	426.7	3.9	0.072
Site x Treatment x Species	427.3	4.5	0.053

Table A 4. Mean and standard deviation for each measured abiotic variable (n=30).

	Nitrogen (%)		pH		Organic Matter (%)		P_2O_5 (kg/ha)		K_2O (kg/ha)	
Site	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Belcher	0.13	0.02	7.19	0.57	2.18	0.21	167.00	33.45	972.67	138.94
Converse	0.18	0.07	6.65	1.09	3.17	1.12	128.80	33.37	1,236.73	553.17

	Calcium (kg/ha)		Magnesium (kg/ha)		Sodium (kg/ha)		Sulfur (kg/ha)		Aluminum (ppm)	
Site	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Belcher	3,916.60	1,906.10	1,804.93	326.57	3,716.60	1,362.04	647.73	362.84	522.87	77.49
Converse	1,733.00	1,010.31	2,152.80	932.78	11,261.47	6,349.94	987.13	592.89	528.80	204.84

	Boron (ppm)		Copper (ppm)		Iron (ppm)		Manganese (ppm)		Zinc (ppm)	
Site	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Belcher	4.41	1.55	1.68	0.64	537.87	75.17	190.13	93.00	2.47	0.26
Converse	6.12	3.03	0.83	0.54	642.33	345.48	131.20	116.56	2.58	0.69

|	Elevation (m)		Hydroperiod (min)		Hydroperiod (%)		Inundation Frequency (%)		Mean Inundation time (min)	
Site	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Belcher	6.57	0.21	1,719.61	1,224.70	1.13	0.81	14.13	7.48	56.25	10.95
Converse	6.03	0.33	888.94	703.28	1.69	1.34	22.12	14.77	46.33	15.74
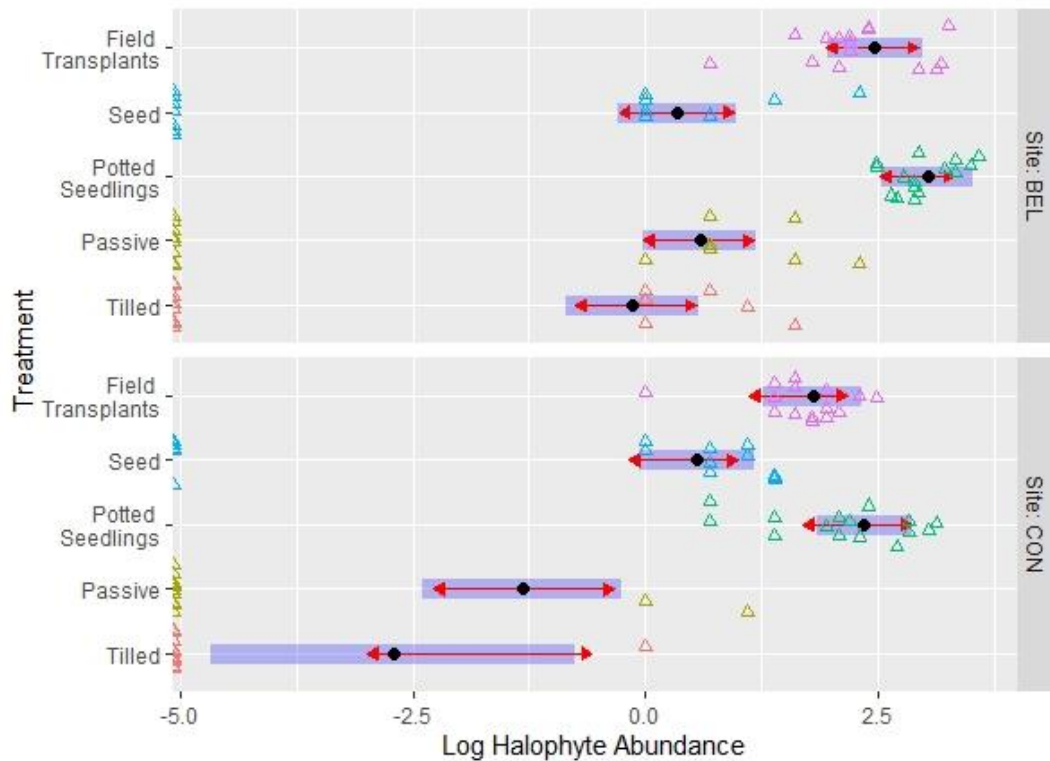
Figure A 1. Results from GLM on target species abundance (number of hits from perennial halophyte species) per plot in August 2019 among treatments and site (BEL = Belcher, CON = Converse) with raw data overlaid from 15 replicates. Data are shown as natural logarithms. Points are predicted least squares means (predicted estimate of response in a group), blue boxes are 95% confidence intervals, and red arrows are Tukey's p-values. Overlapping red arrows indicate statistically unclear differences among groups at the α=0.05 level. Wrack was removed from the 2019 model as there was no germination in these plots.
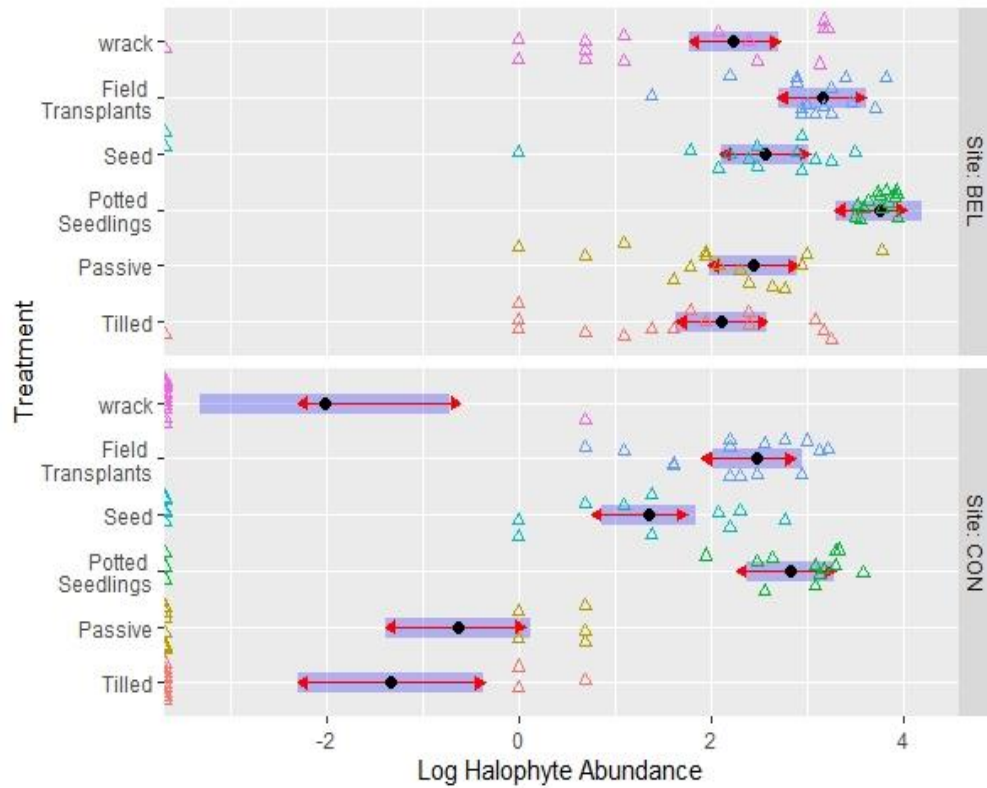
Figure A 2. Results from GLM on target species abundance per plot in August 2020 among treatments and site (BEL = Belcher, CON = Converse) with raw data overlaid from 15 replicates. Data are shown as natural logarithms. Points are predicted least squares means (predicted estimate of response in a group), blue boxes are 95% confidence intervals, and red arrows are Tukey's adjusted p-values. Overlapping red arrows indicate statistically unclear differences among groups at the α=0.05 level.
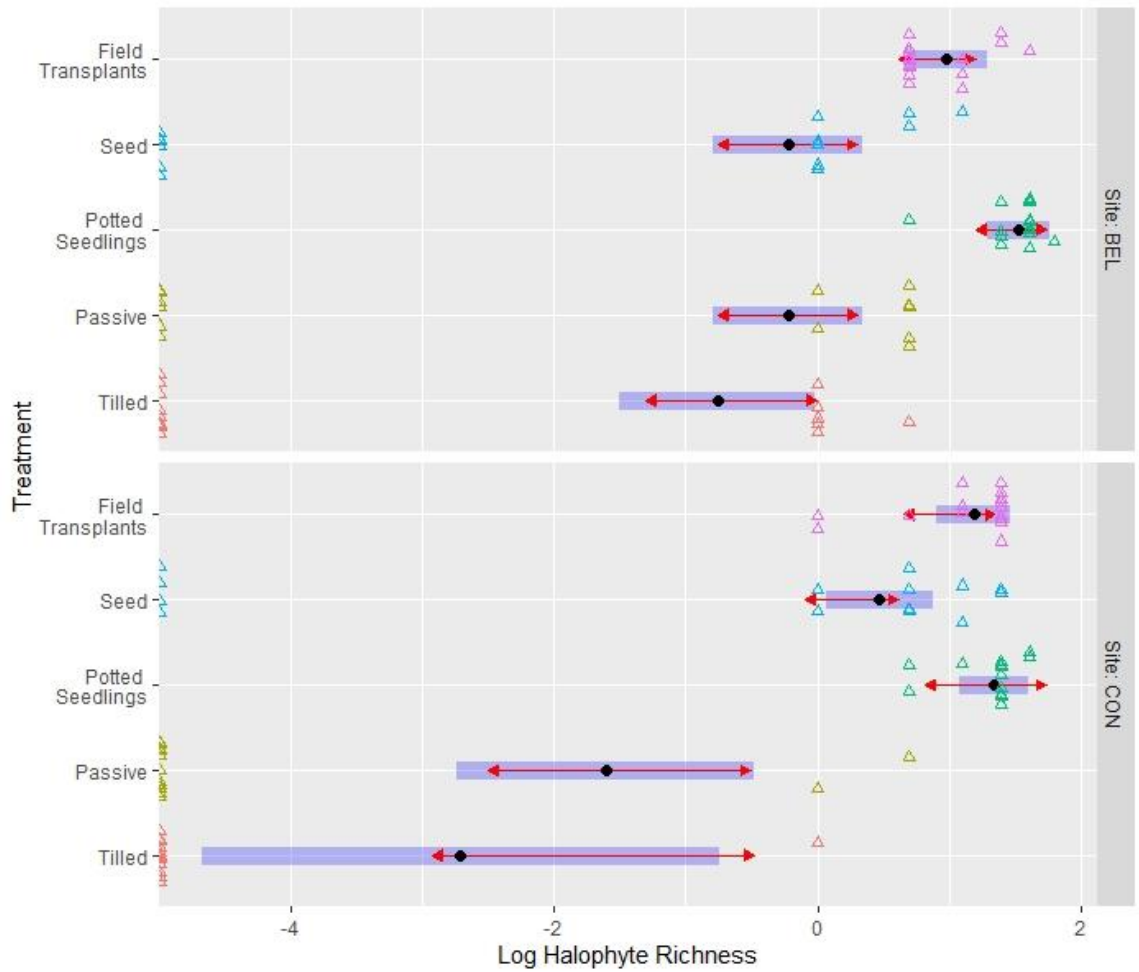
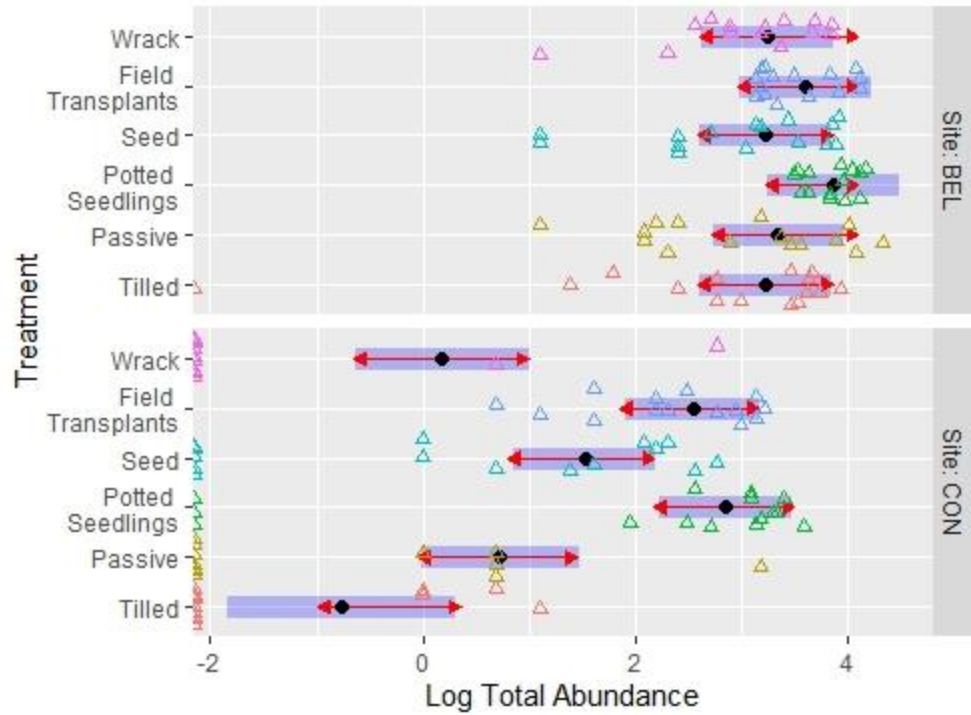*Figure A 3. Results from GLM on target species richness (number of perennial halophyte species) per plot in August 2019 among treatments and site (BEL = Belcher, CON = Converse) with raw data overlaid from 15 replicates. Data are shown as natural logarithms. Points are predicted least squares means (predicted estimate of response in a group), blue boxes are 95% confidence intervals, and red arrows are Tukey's adjusted p-values. Overlapping red arrows indicate statistically unclear differences among groups at the α=0.05 level.*
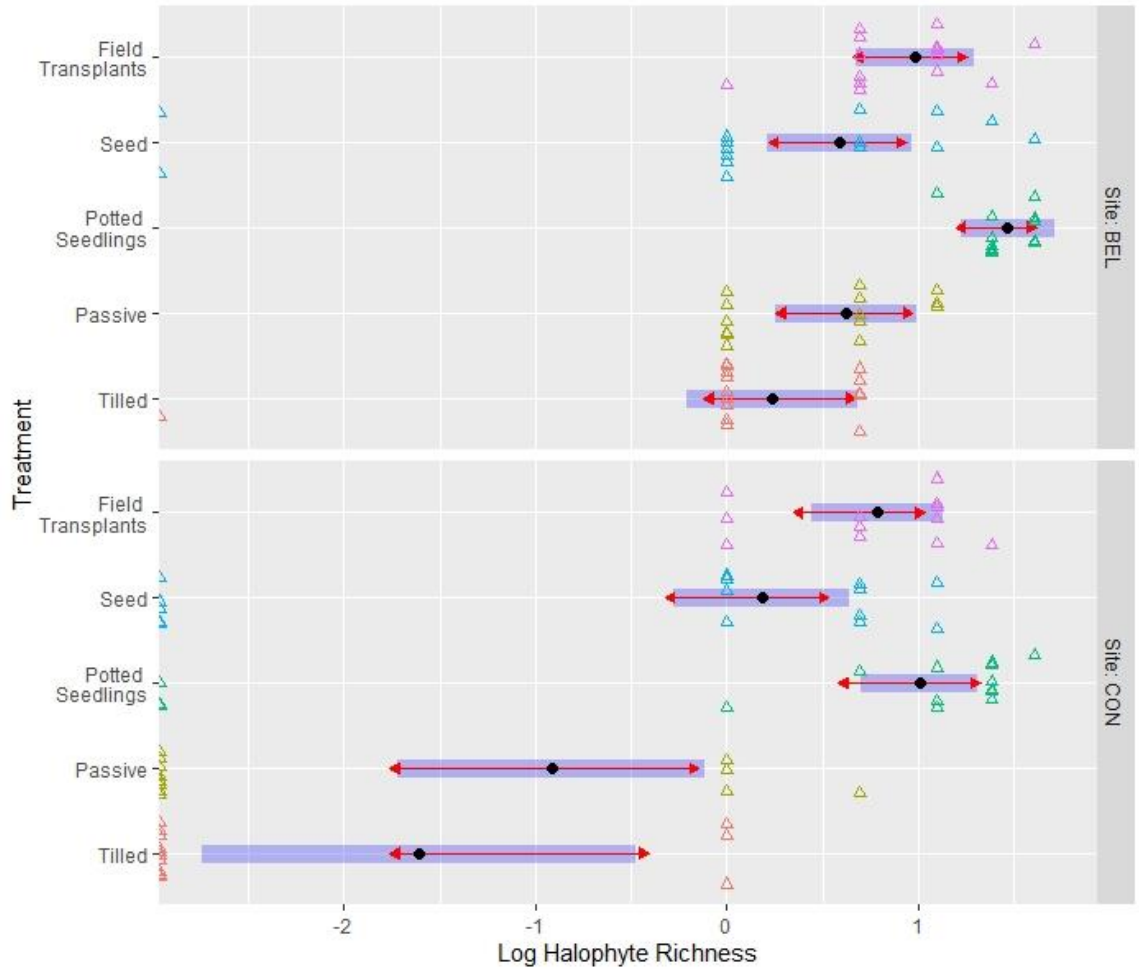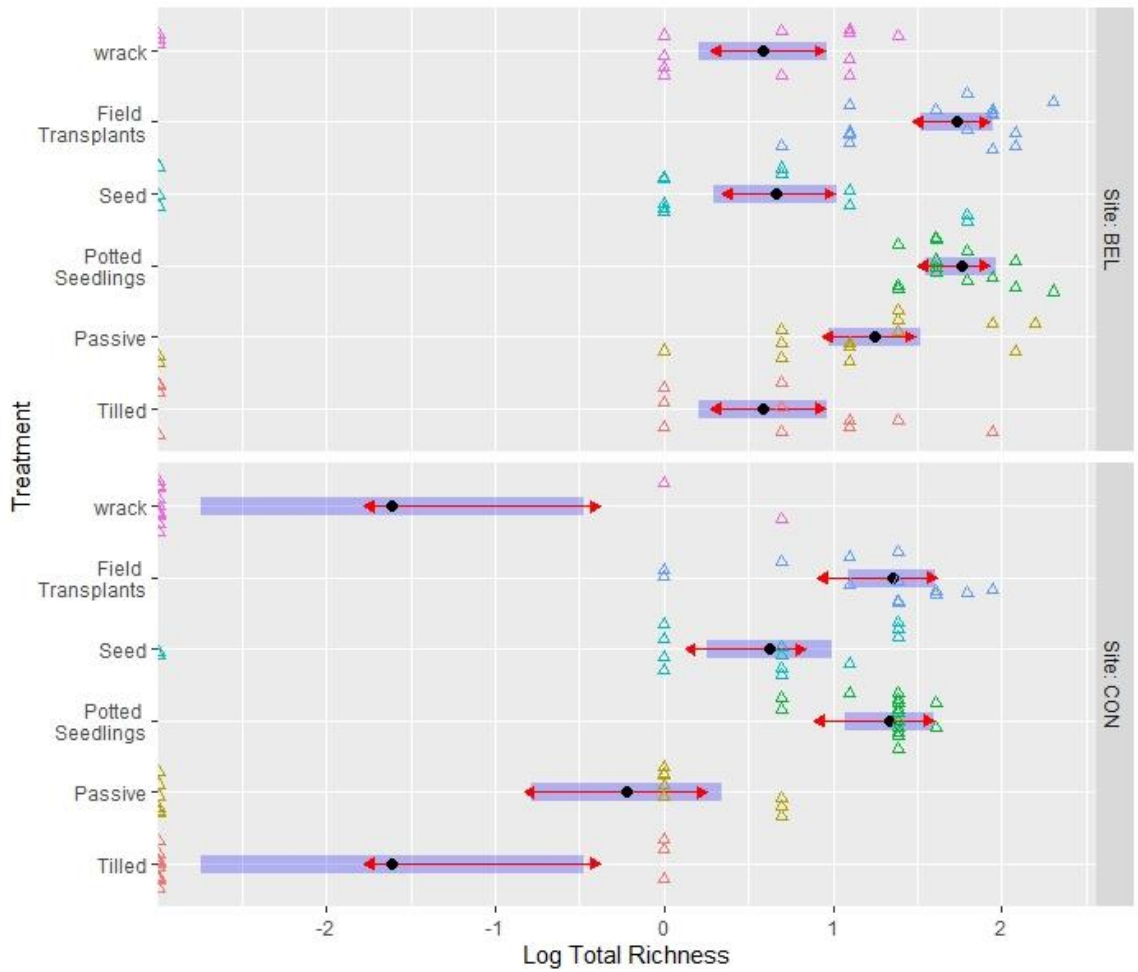
Figure A 4. Results from GLM on target species richness per plot in August 2020 among treatments and site (BEL = Belcher, CON = Converse) with raw data overlaid from 15 replicates. Data are shown as natural logarithms. Points are predicted least squares means (predicted estimate of response in a group), blue boxes are 95% confidence intervals, and red arrows are Tukey's adjusted p-values. Overlapping red arrows indicate statistically unclear differences among groups at the α=0.05 level.
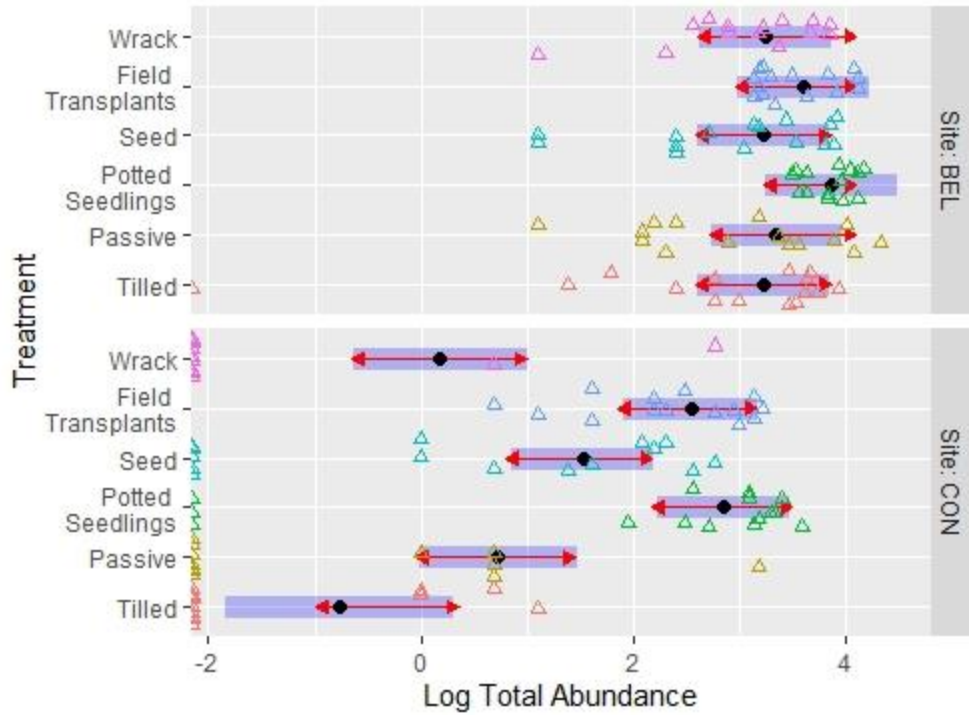
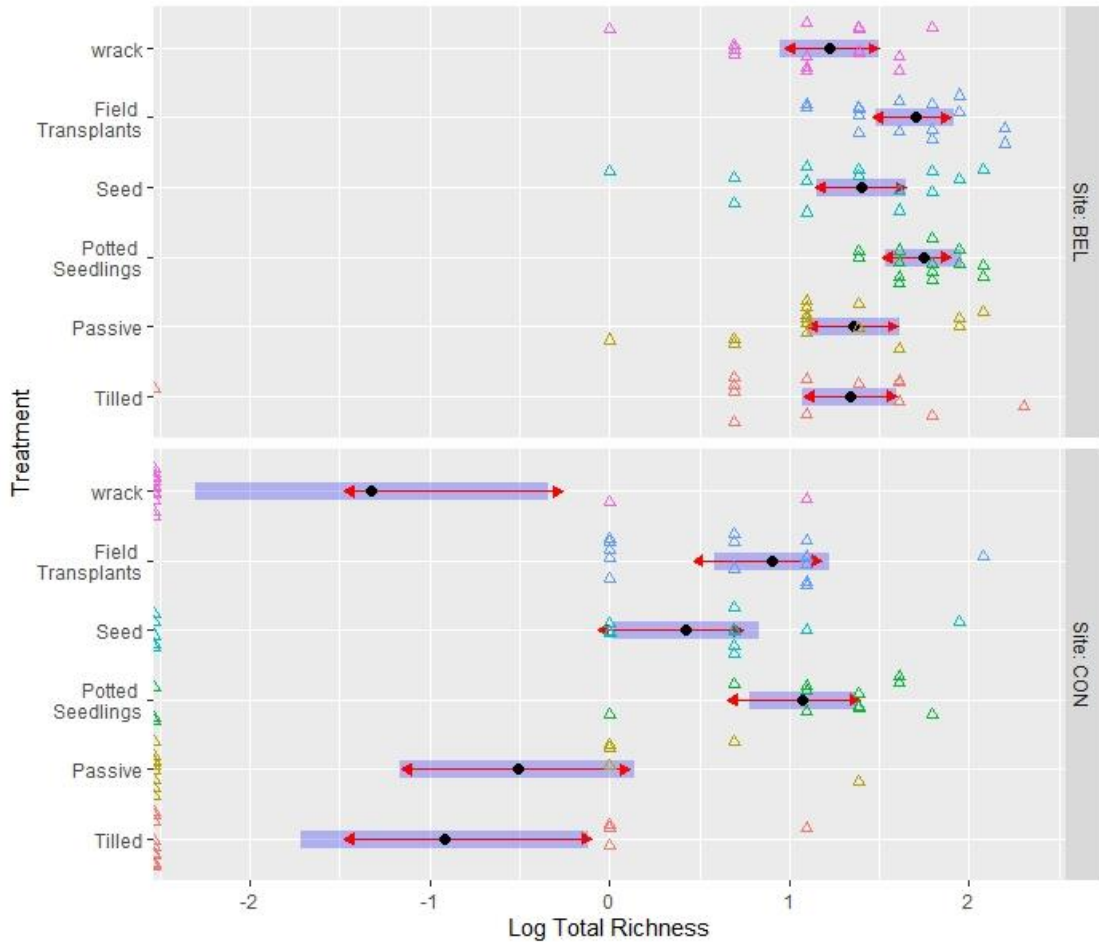*Figure A 5. Results from GLM on total abundance (number of hits from all species) per plot in August 2019 among treatments and site (BEL = Belcher, CON = Converse) with raw data overlaid from 15 replicates. Data are shown as natural logarithms. Points are predicted least squares means (predicted estimate of response in a group), blue boxes are 95% confidence intervals, and red arrows are Tukey's adjusted p-values. Overlapping red arrows indicate statistically unclear differences among groups at the α=0.05 level.*

*Figure A 6. Results from GLM on total abundance per plot in August 2020 among treatments and site (BEL = Belcher, CON = Converse) with raw data overlaid from 15 replicates. Data are shown as natural logarithms. Points are predicted least squares means (predicted estimate of response in a group), blue boxes are 95% confidence intervals, and red arrows are Tukey's adjusted p-values. Overlapping red arrows indicate statistically unclear differences among groups at the α=0.05 level.*

Figure A 7. Results from GLM on total species richness (total number of all species) per plot in August 2019 among treatments and site (BEL = Belcher, CON = Converse) with raw data overlaid from 15 replicates. Data are shown as natural logarithms. Points are predicted least squares means (predicted estimate of response in a group), blue boxes are 95% confidence intervals, and red arrows are Tukey's adjusted p-values. Overlapping red arrows indicate statistically unclear differences among groups at the α=0.05 level.

*Figure A 8. Results from GLM on total species richness per plot in August 2020 among treatments and site (BEL = Belcher, CON = Converse) with raw data overlaid from 15 replicates. Data are shown as natural logarithms. Points are predicted least squares means (predicted estimate of response in a group), blue boxes are 95% confidence intervals, and red arrows are Tukey's adjusted p-values. Overlapping red arrows indicate statistically unclear differences among groups at the α=0.05 level.*
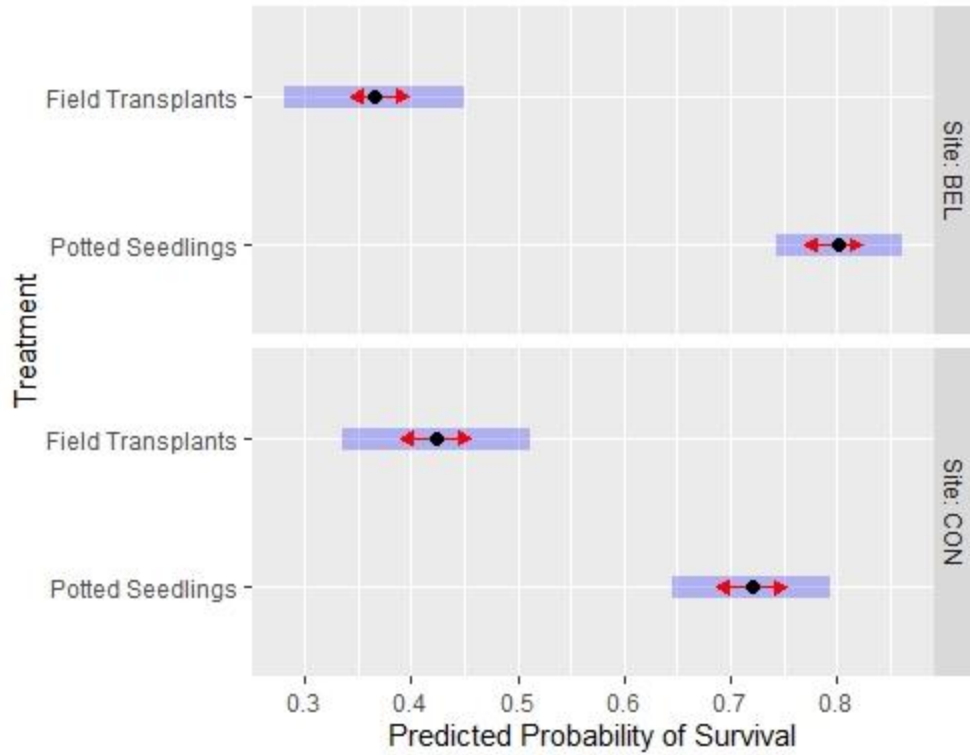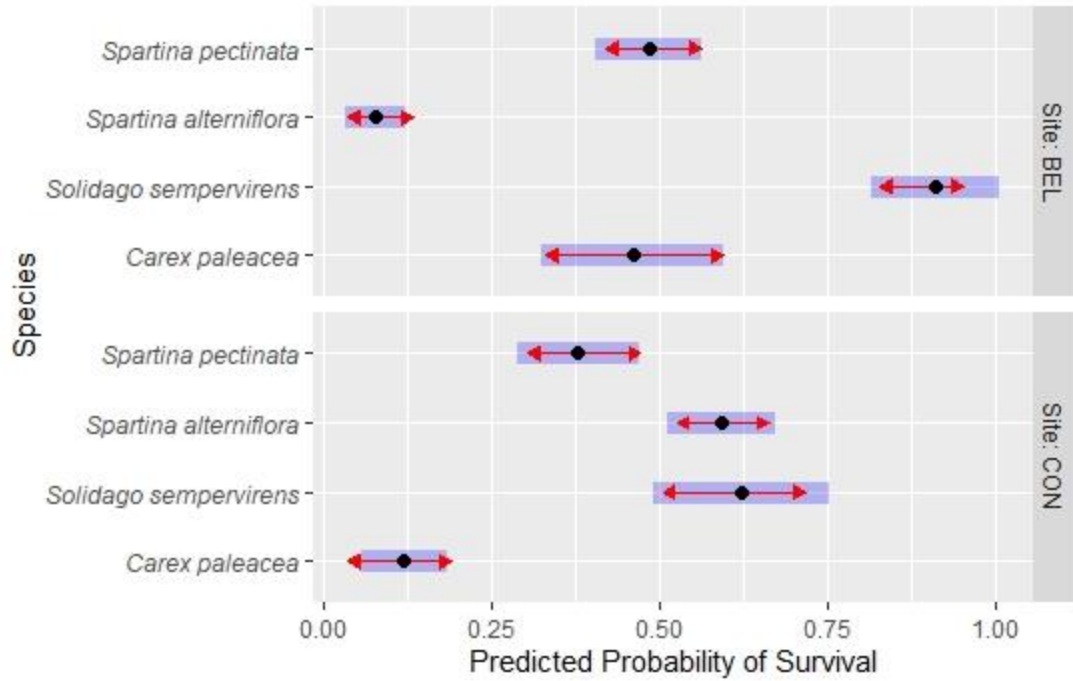
Figure A 9. Results of logistic regression on survival to August 2019 among treatments and sites (BEL = Belcher, CON = Converse). Data are pooled over species. Points are predicted least squares means (predicted estimate of response in a group), blue boxes are 95% confidence intervals, and red arrows are Tukey's adjusted p-values. Overlapping red arrows indicate statistically unclear differences among groups at the α=0.05 level.
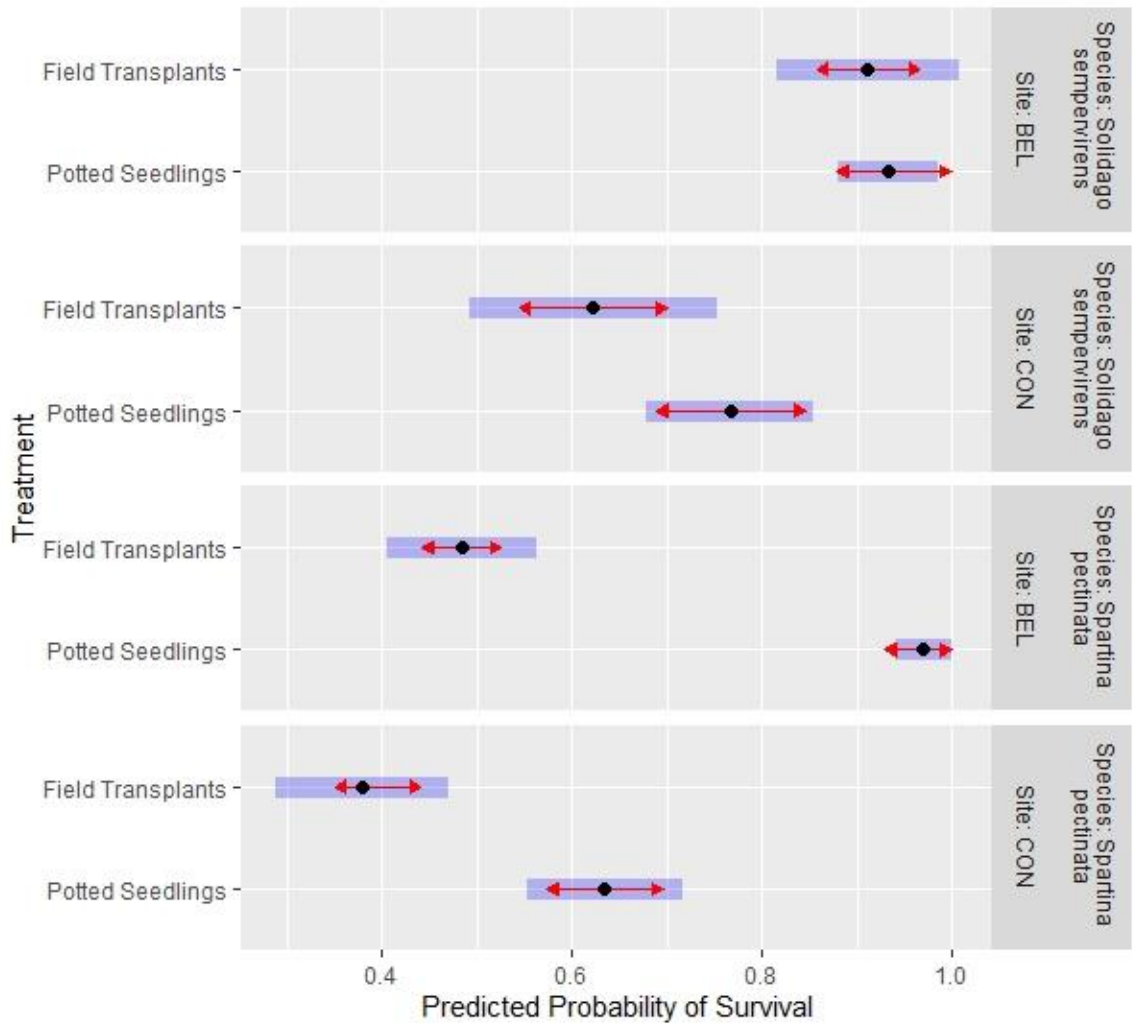
Figure A 10. Results of logistic regression on survival to August 2019 of species present in both treatments at both sites (BEL = Belcher, CON = Converse). Points are predicted least squares means (predicted estimate of response in a group), blue boxes are 95% confidence intervals, and red arrows are Tukey's adjusted p-values. Overlapping red arrows indicate statistically unclear differences among groups at the α=0.05 level.
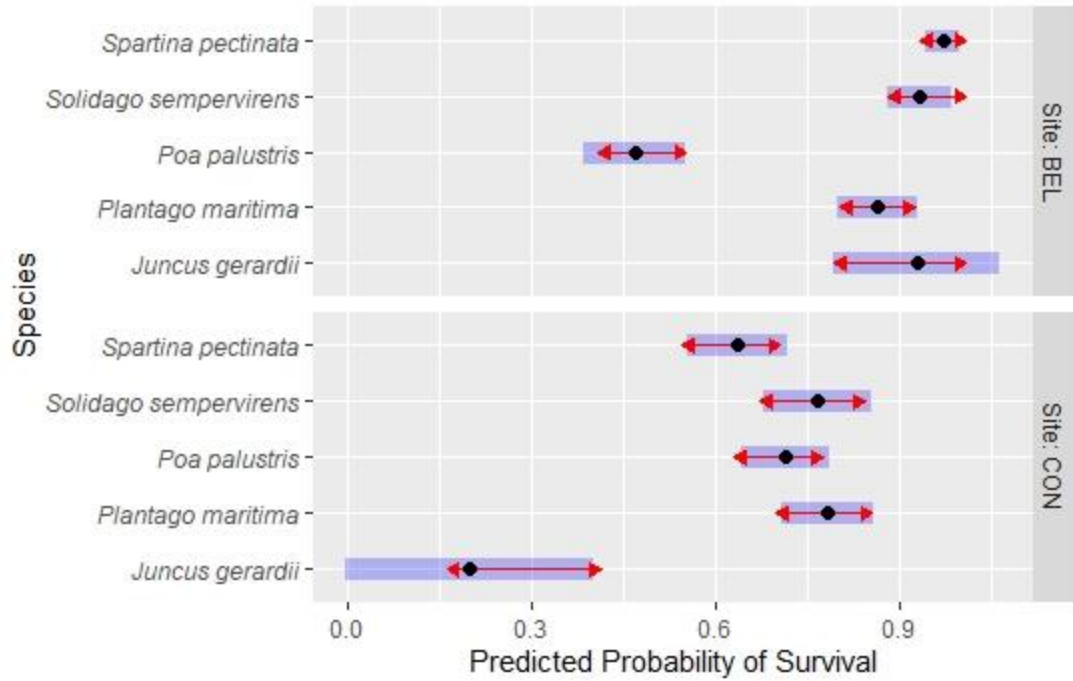
Figure A 11. Results of logistic regression on survival to August 2019 of species in potted seedlings among sites (BEL = Belcher, CON = Converse). Points are predicted least squares means (predicted estimate of response in a group), blue boxes are 95% confidence intervals, and red arrows are Tukey's adjusted p-values. Overlapping red arrows indicate statistically unclear differences among groups at the α=0.05 level.

Figure A 12. Results of logistic regression on survival to August 2019 of species in field transplants among sites (BEL = Belcher, CON = Converse). Points are predicted least squares means (predicted estimate of response in a group), blue boxes are 95% confidence intervals, and red arrows are Tukey's adjusted p-values. Overlapping red arrows indicate statistically unclear differences among groups at the α=0.05 level. <u>P. maritima</u> was removed as there was only data at one site for this species.
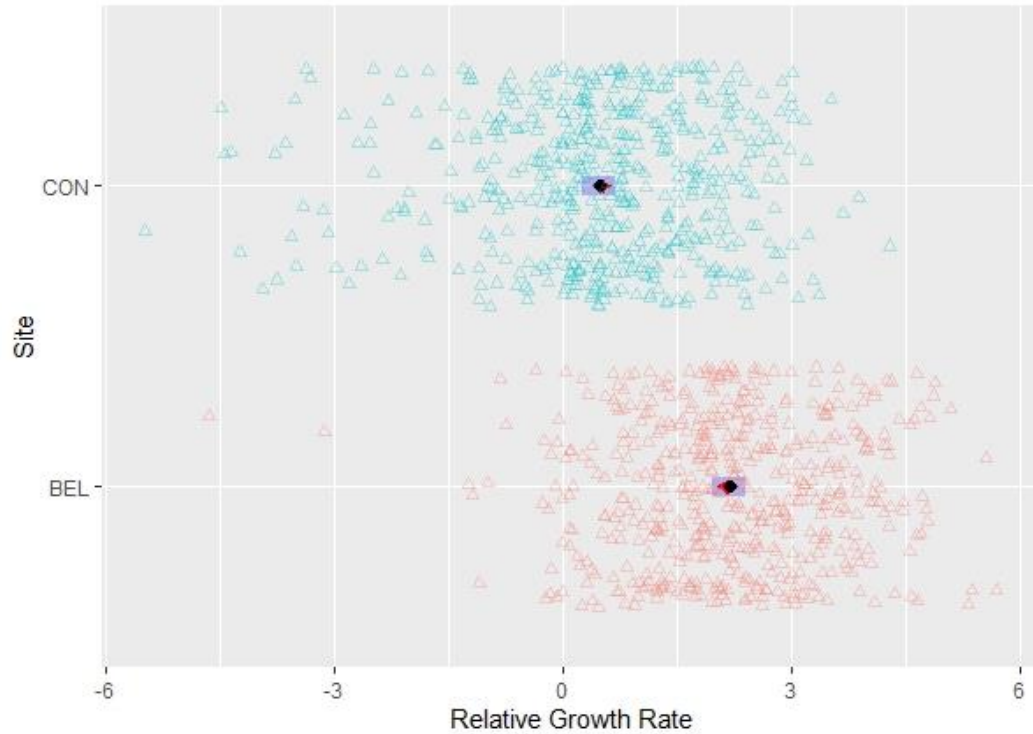
Figure A 13. Results of regression on relative growth rate (RGR – a measure of growth per unit of size over a period of time) between sites (BEL = Belcher, CON = Converse) with raw data from individual plants overlaid. RGR is presented as $ln(cm^2/cm^2)\cdot 3$ months^{-1}. Data are pooled over species and treatments. Points are predicted least squares means (predicted estimate of response in a group), blue boxes are 95% confidence intervals, and red arrows are Tukey's adjusted p-values. Overlapping red arrows indicate statistically unclear differences among groups at the α=0.05 level.
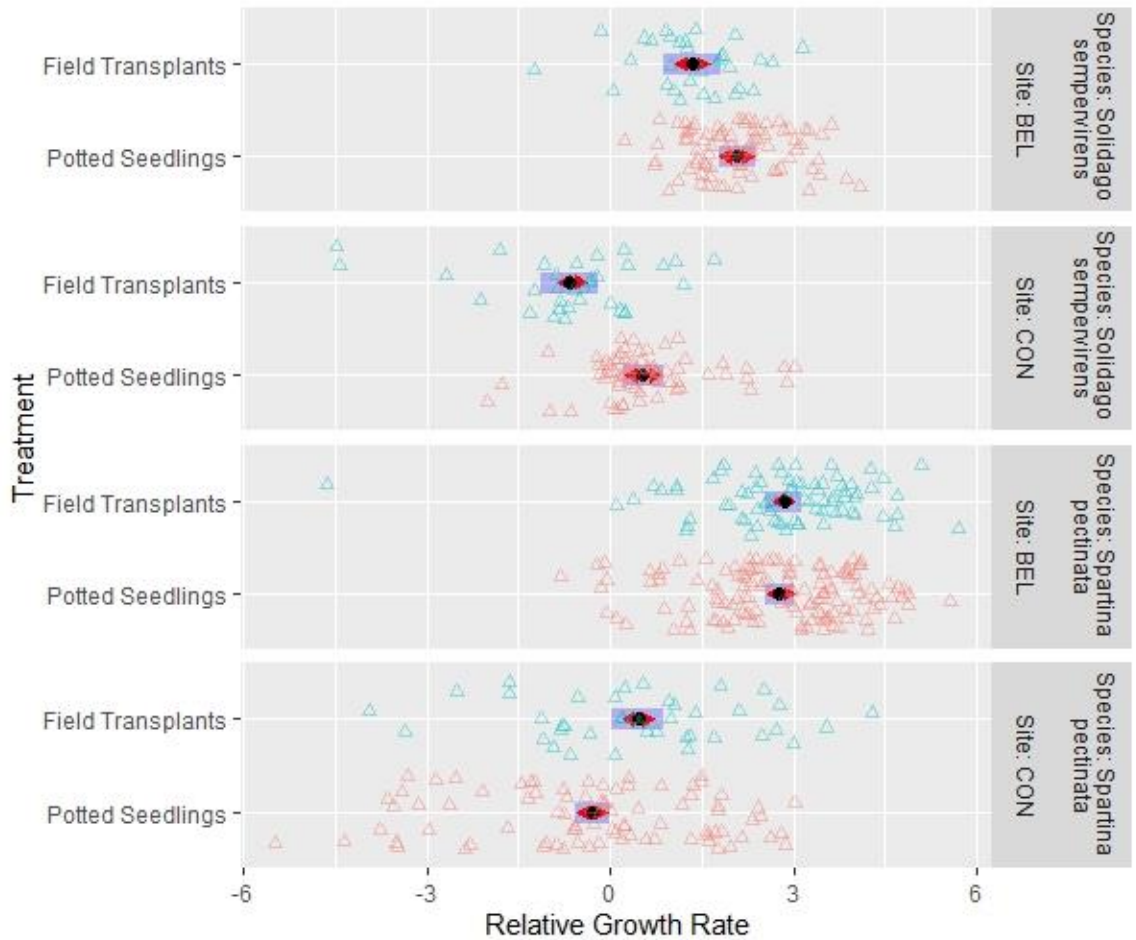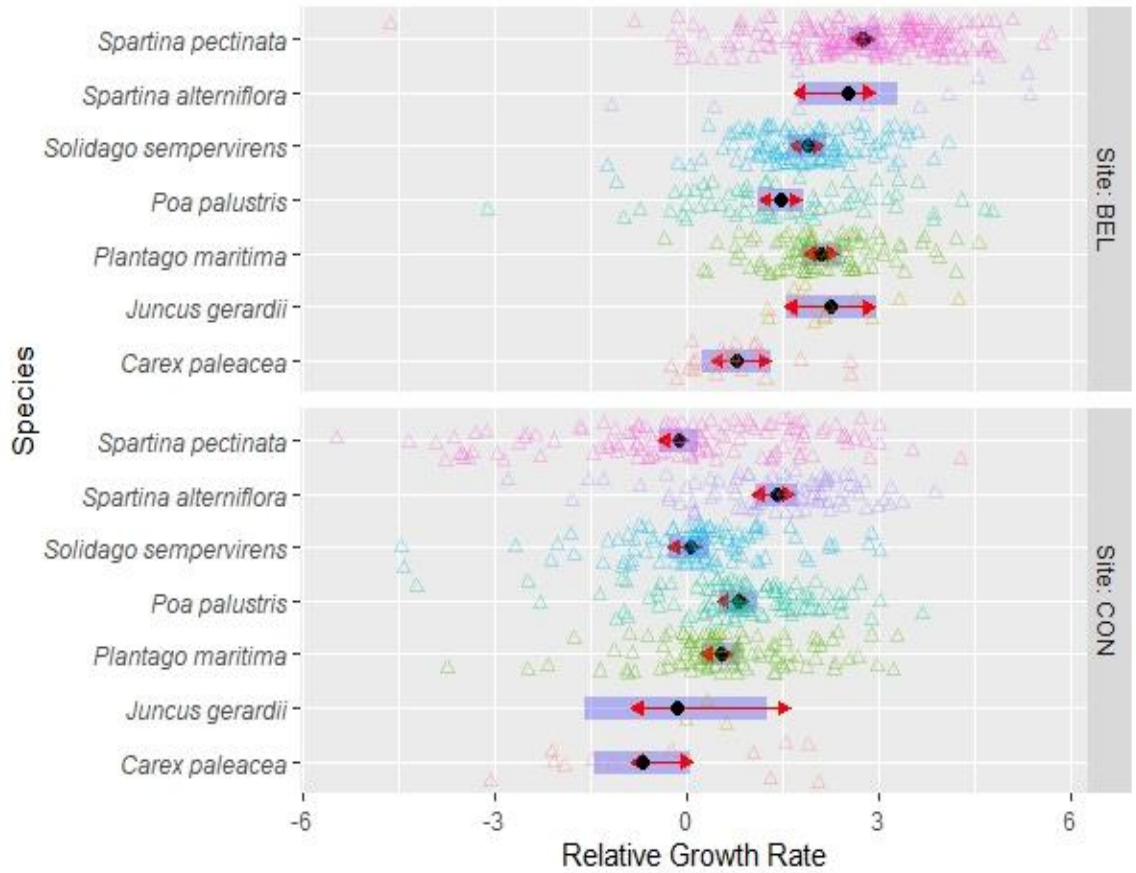
Figure A 14. Results of regression on relative growth rate (RGR– a measure of growth per unit of size over a period of time) among species present in both treatments and sites (BEL = Belcher, CON = Converse) with raw data for individual plants overlaid. RGR is presented as $ln(cm^2/cm^2)\cdot3$ $months^{-1}$. Points are predicted least squares means (predicted estimate of response in a group), blue boxes are 95% confidence intervals, and red arrows are Tukey's adjusted p-values. Overlapping red arrows indicate statistically unclear differences among groups at the α=0.05 level.

*Figure A 15. Results of regression on relative growth rate (RGR – a measure of growth per unit of size over a period of time) among species and sites (BEL = Belcher, CON = Converse) with raw data for individual plants overlaid. Data are pooled over treatments. RGR is presented as ln(cm²/cm²)·3 months⁻¹. Points are predicted least squares means (predicted estimate of response in a group), blue boxes are 95% confidence intervals, and red arrows are Tukey's adjusted p-values. Overlapping red arrows indicate statistically unclear differences among groups at the α=0.05 level.*
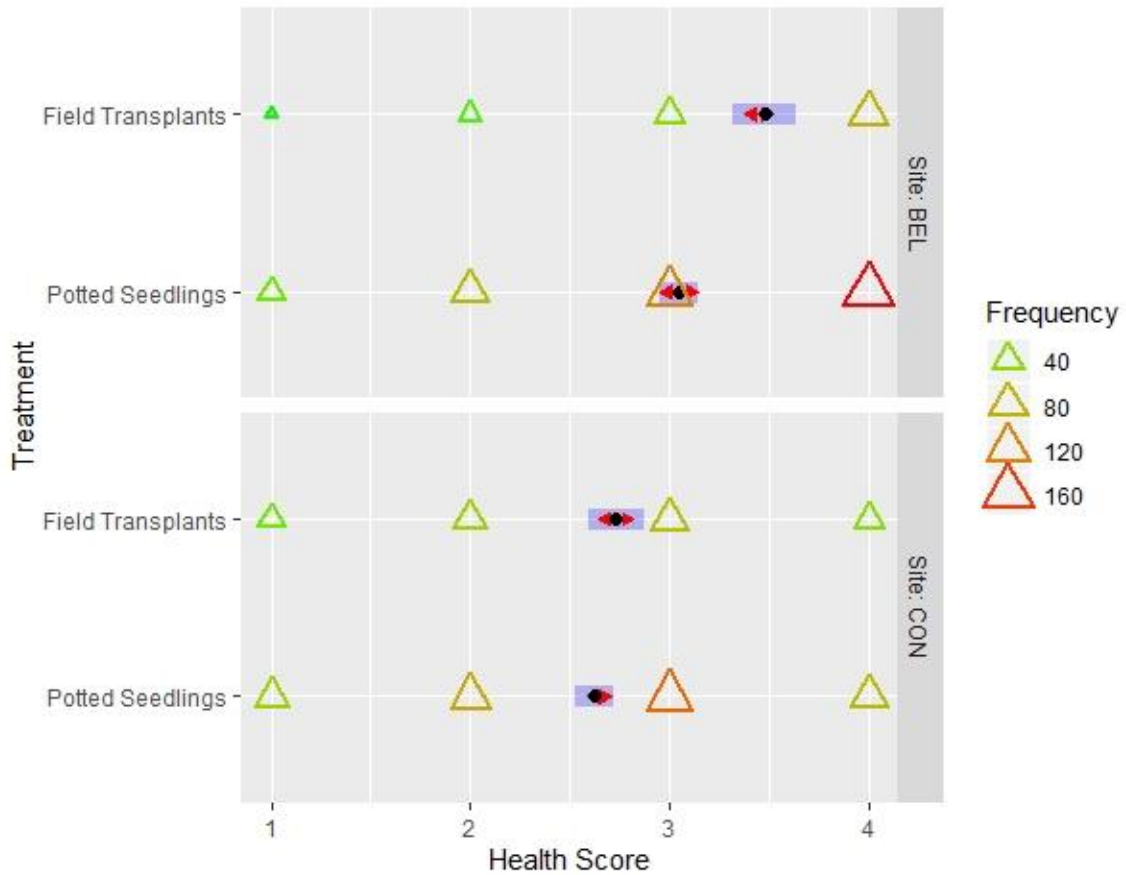
Figure A 16. Results of linear regression on health score in August 2019 (final health) data of potted seedlings and field transplants at both sites (BEL = Belcher, CON = Converse). Data are pooled over species. Raw data are overlaid (triangles) as the frequency of occurrences of a health score for an individual plant in a group. Health scores were assessed visually between 1 (worst health) and 4 (best health). Points are predicted least squares means (predicted estimate of response in a group), blue boxes are 95% confidence intervals, and red arrows are Tukey's adjusted p-values. Overlapping red arrows indicate statistically unclear differences among groups at the α=0.05 level.
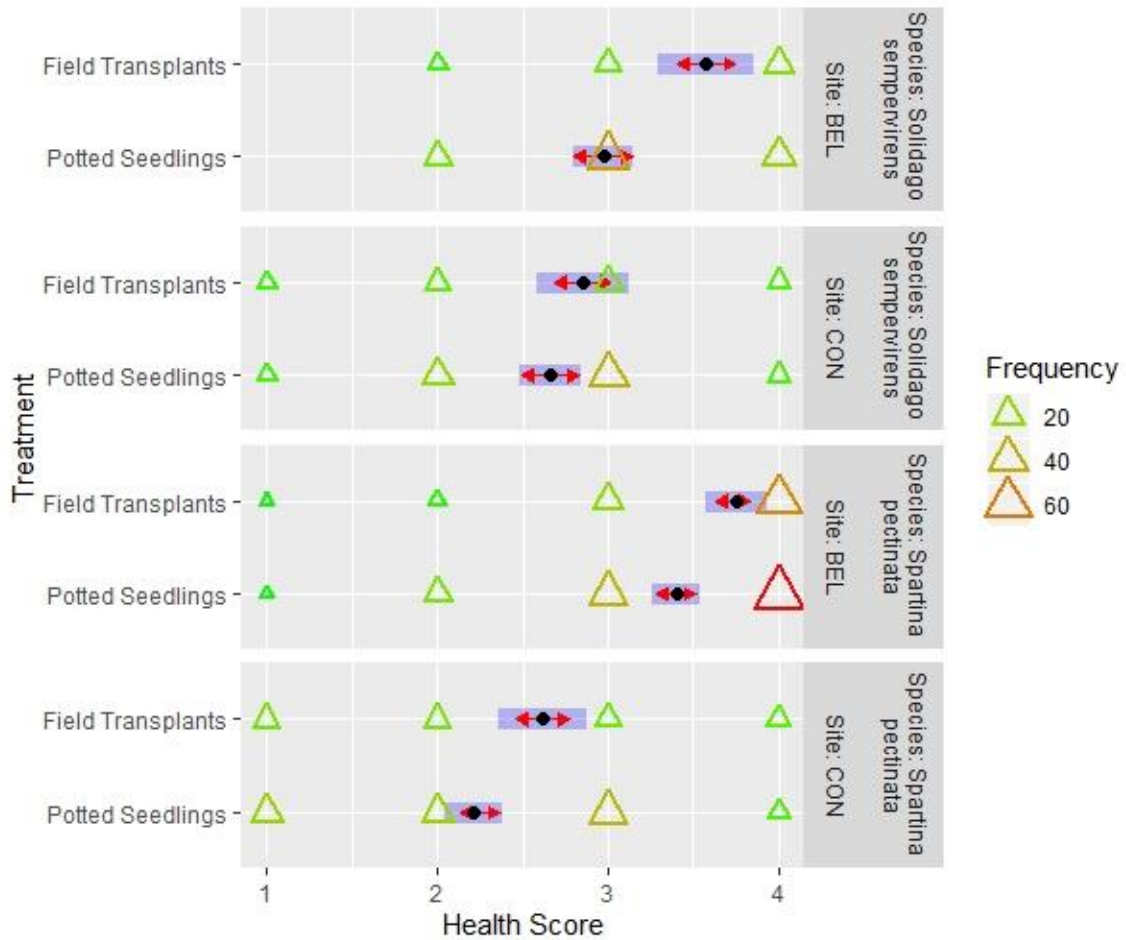
Figure A 17. Results of linear regression on health score in August 2019 (final health) data of species found in both treatments at both sites (BEL = Belcher, CON = Converse). Raw data are overlaid (triangles) as the frequency of occurrences of a health score for an individual plant in a group. Health scores were assessed visually between 1 (worst health) and 4 (best health). Points are predicted least squares means (predicted estimate of response in a group), blue boxes are 95% confidence intervals, and red arrows are Tukey's adjusted p-values. Overlapping red arrows indicate statistically unclear differences among groups at the α=0.05 level.
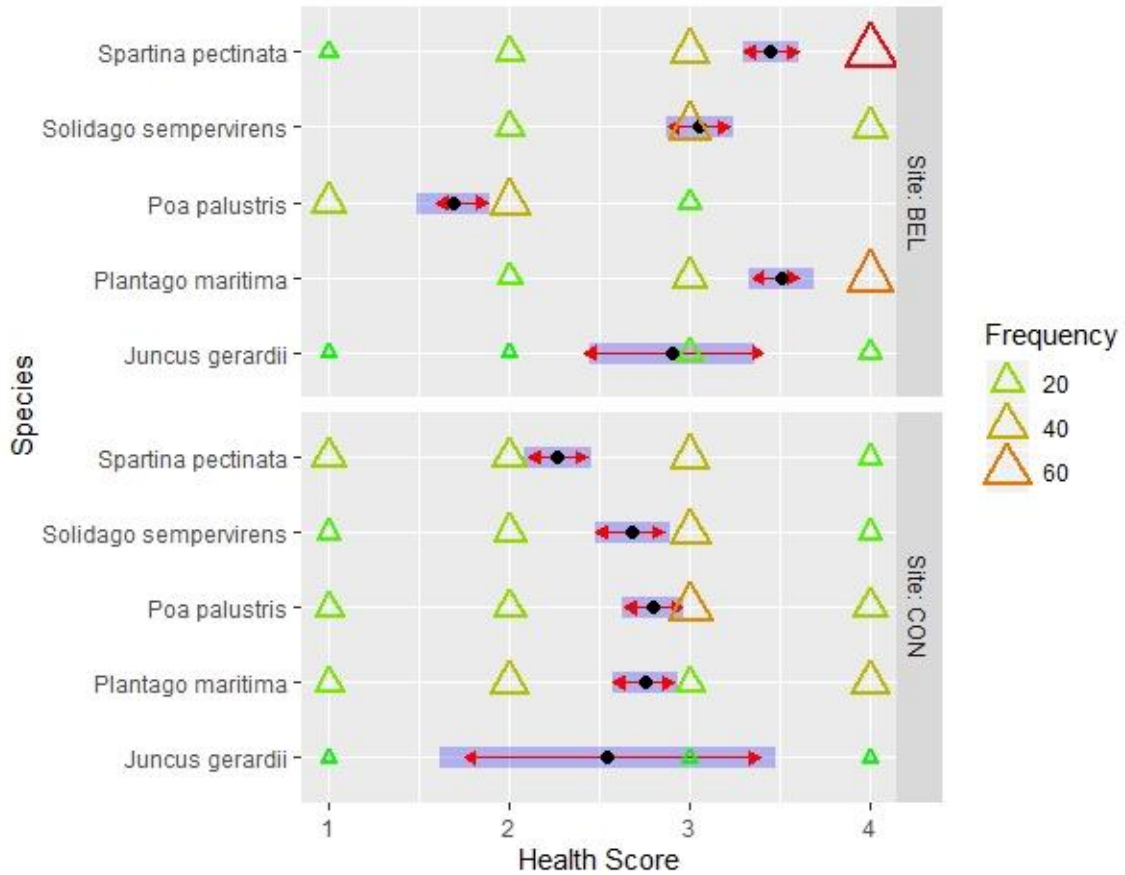
Figure A 18. Results of linear regression on health score in August 2019 (final health) data of species in potted seedling treatment among sites (BEL = Belcher, CON = Converse). Raw data are overlaid (triangles) as the frequency of occurrences of a health score for an individual plant in a group. Health scores were assessed visually between 1 (worst health) and 4 (best health). Points are predicted least squares means (predicted estimate of response in a group), blue boxes are 95% confidence intervals, and red arrows are Tukey's adjusted p-values. Overlapping red arrows indicate statistically unclear differences among groups at the α=0.05 level.
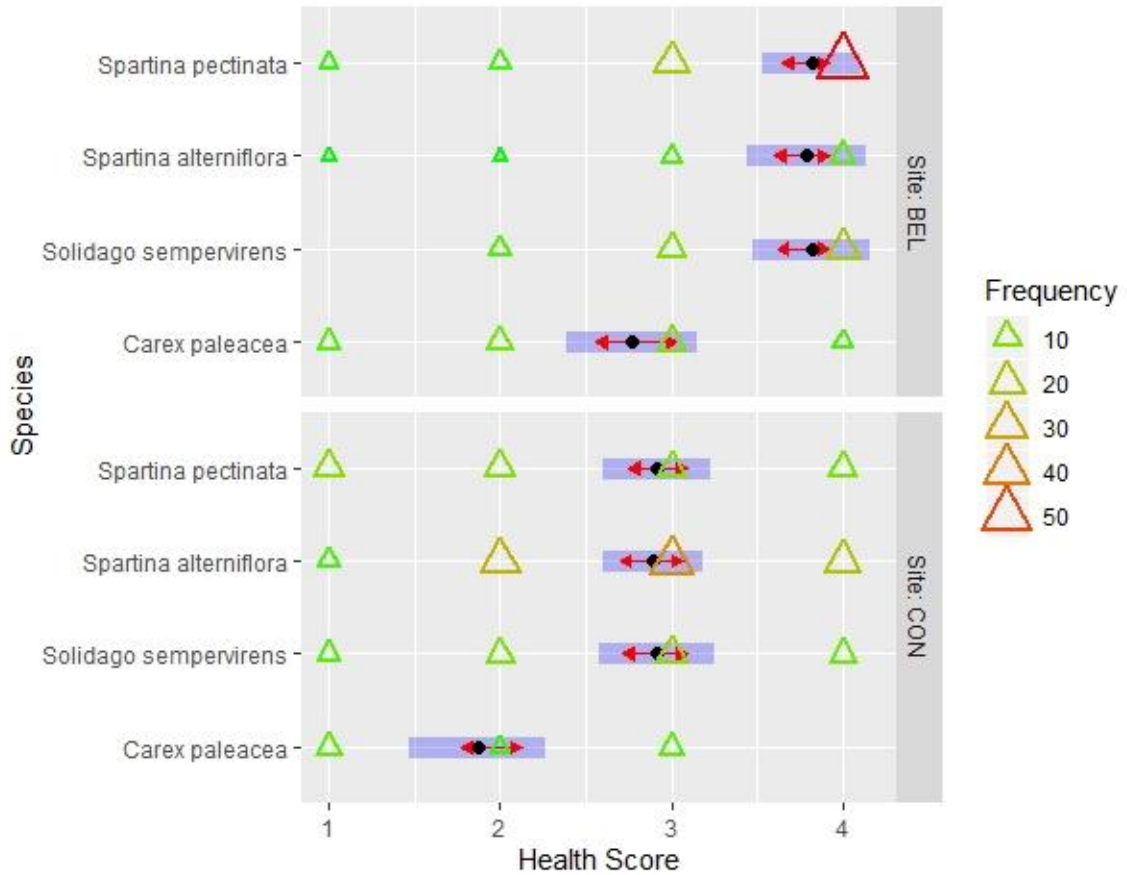
Figure A 19. Results of linear regression on health score in August 2019 (final health) data of species in field transplant treatment among sites (BEL = Belcher, CON = Converse). Raw data are overlaid (triangles) as the frequency of occurrences of a health score for an individual plant in a group. Health scores were assessed visually between 1 (worst health) and 4 (best health). Points are predicted least squares means (predicted estimate of response in a group), blue boxes are 95% confidence intervals, and red arrows are Tukey's adjusted p-values. Overlapping red arrows indicate statistically unclear differences among groups at the α=0.05 level.
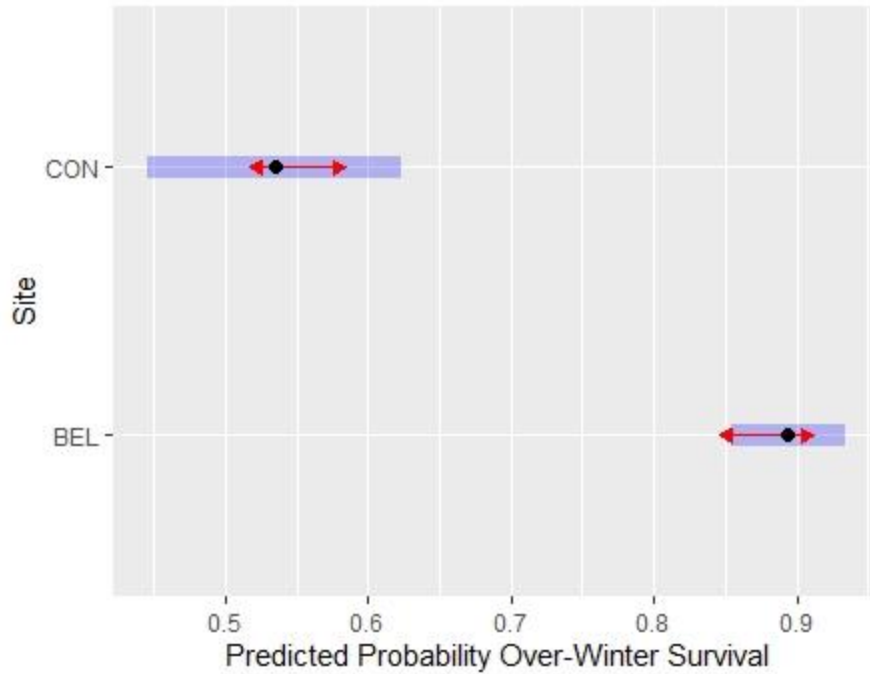
Figure A 20. Results of logistic regression on over-winter survival to July 2020 of species in both treatments among sites (BEL = Belcher, CON = Converse). Data are pooled over species and treatments. Points are predicted least squares means (predicted estimate of response in a group), blue boxes are 95% confidence intervals, and red arrows are Tukey's adjusted p-values. Overlapping red arrows indicate statistically unclear differences among groups at the α=0.05 level.
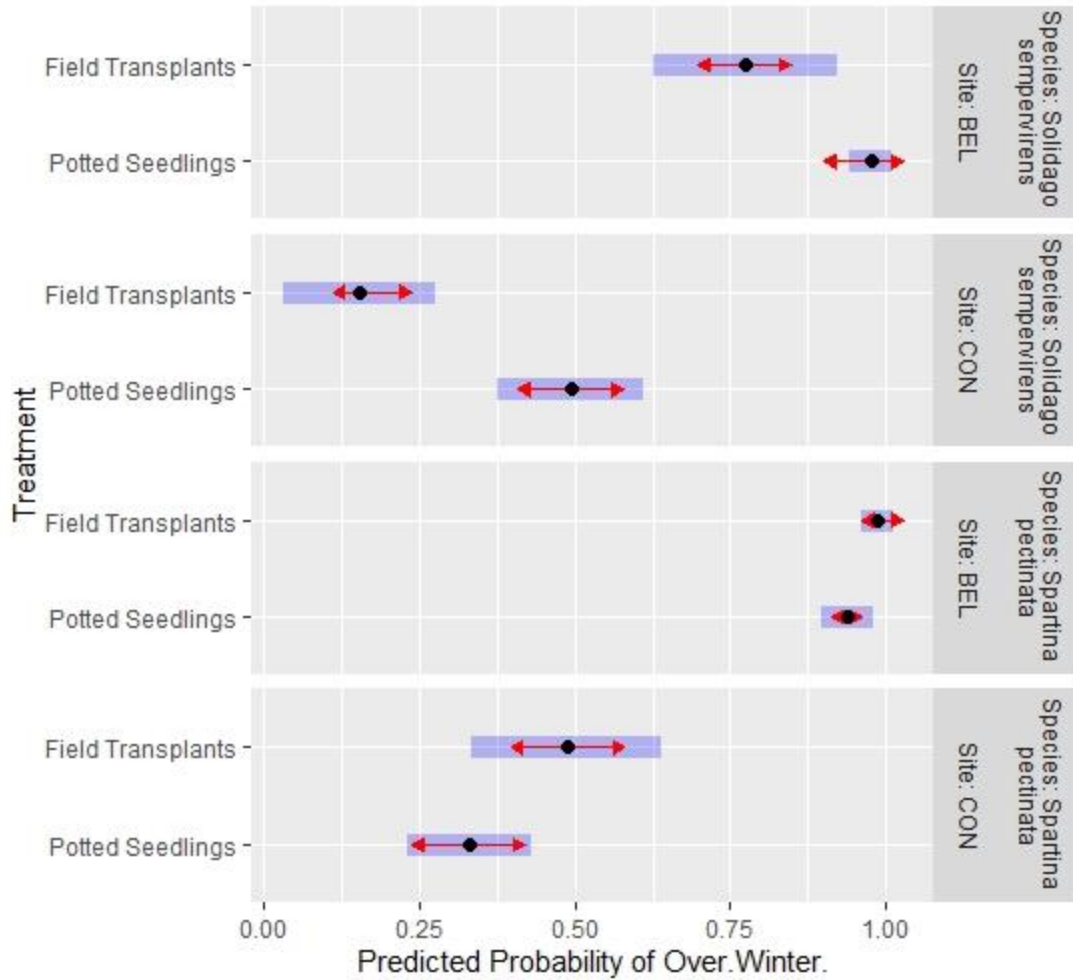
Figure A 21. Results of logistic regression on over-winter survival to July 2020 of species found in both treatments at both sites (BEL = Belcher, CON = Converse). Points are predicted least squares means (predicted estimate of response in a group), blue boxes are 95% confidence intervals, and red arrows are Tukey's adjusted p-values. Overlapping red arrows indicate statistically unclear differences among groups at the α=0.05 level.
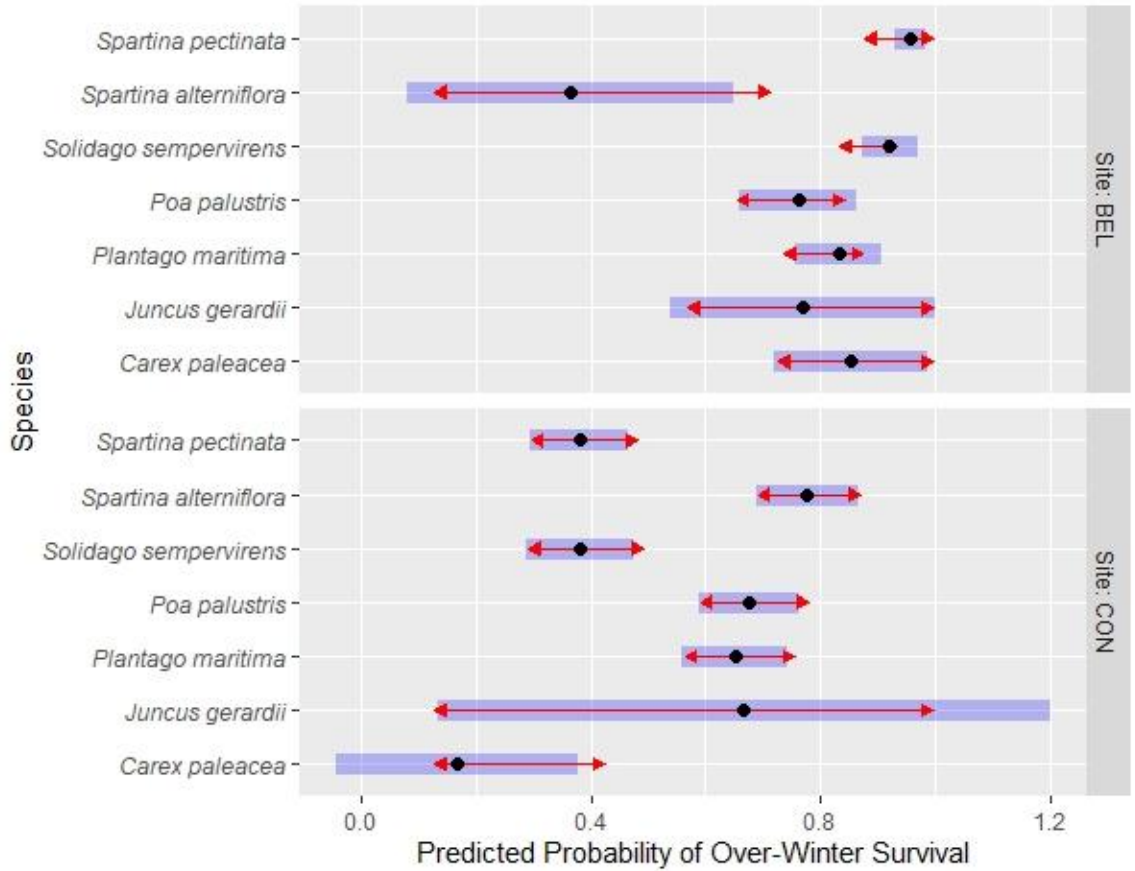
Figure A 22. Results of logistic regression on over-winter survival to July 2020 of all species at each site (BEL = Belcher, CON = Converse). Data are pooled over treatments. Points are predicted least squares means (predicted estimate of response in a group), blue boxes are 95% confidence intervals, and red arrows are Tukey's adjusted p-values. Overlapping red arrows indicate statistically unclear differences among groups at the α=0.05 level.