

ABSTRACT

Title of Thesis: **EFFECTS OF PRE-EXISTING
SUBMERSED MACROPHYTES ON THE
INVASION SUCCESS OF *HYDRILLA
VERTICILLATA***

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I evaluated (1) the effects of a native submersed aquatic plant species, *Vallisneria americana*, on the colonization success of a non-native and highly invasive submersed aquatic species, *Hydrilla verticillata*, through field and greenhouse experiments; and (2) the effects of *H. verticillata* propagule density on its colonization success of patches dominated by the native species. Results of the field study, located in a tidal freshwater region of Chesapeake Bay, suggest that pre-existing vegetation did not have significant negative effects on *H. verticillata* colonization. However, pre-existing *H. verticillata* biomass and *H. verticillata* colonization success were strongly correlated. In contrast, results from the greenhouse study showed that *V. americana* had a strong inhibitory effect on *H. verticillata* colonization by fragments and increasing *H. verticillata* fragment density again increased colonization success. Reduced water column nutrient concentrations, resulting from *V. americana* growth, appeared to negatively affect successful rooting and subsequent colonization by *H. verticillata*.

**EFFECTS OF PRE-EXISTING SUBMERSED MACROPHYTES ON THE
INVASION SUCCESS OF *HYDRILLA VERTICILLATA***

By

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Chapter 1: Background Information

Introduction

The concept of priority effect predicts that the first species to establish will have a competitive advantage over later arriving species. Frequently, when one species establishes first it is capable of inhibiting growth, and reducing survival of subsequent arrivals (Keever 1950, Parenti and Rice 1969). For example, the initial density of plant propagules may greatly affect competitive outcomes (Grace 1987). Early arrivals may produce shade, which inhibits the growth of later arrivals, or root growth may inhibit germination of other species (Parenti and Rice 1969). Priority effects may also be dependent on plant size, for example juveniles of a given species may be competitively superior while the adults are competitively inferior (Grace 1985). However, it is also possible for the first arriving species to facilitate the establishment of other species (Connell and Slatyer 1977).

The idea that first arrivals have an advantage over later arrivals has important implications for the field of restoration ecology. Invasions of undesirable species may indeed be slowed or halted by the pre-establishment of native plant species (Madsen 2000). However, very little research has been conducted relating to the efficacy of such “biological control” methods in natural systems. Pre-existing vegetation may alter the outcome of competitive interaction or may decrease the chance that arriving propagules can colonize or establish in an area. I chose to research the latter mechanism, using submersed aquatic macrophyte communities as the model system. The term “aquatic

macrophyte” is a confusing one (Sculthorpe 1985). In this paper I refer to “macrophytes” strictly as vascular plants and do not consider algal species.

The introduction of non-indigenous species is a potential cause of native macrophyte displacement (Chambers et al. 1993). Chronic reductions and compositional changes in macrophyte communities in Chesapeake Bay have been documented since the time of European settlement, particularly in the last century (Orth and Moore 1983, Carter et al. 1985, Davis 1985). Exotic species have resulted in cumulative monetary losses in the United States of approximately \$97 billion over the last 75 years (OTA 1993). Hydrilla [*Hydrilla verticillata* (L.F.) Royle] is a submersed aquatic plant that causes substantial economic hardships, interferes with various water uses, displaces native aquatic plant communities, and adversely affects freshwater habitats (Langeland 1996).

In this study, I evaluated the effects of pre-existing native submersed macrophytes on the colonization success of *H. verticillata* in the field and in greenhouse mesocosms. The primary goal of this research was to determine whether pre-existing vegetation inhibits or facilitates the establishment of *H. verticillata*. The secondary goal of this research was to elucidate the mechanisms that regulate *H. verticillata* colonization success. If colonization success is reduced in vegetated areas, is the response due to a preemption of resources, such as nutrients and light, or is it due to a physical barrier created by native vegetation that does not allow roots from arriving propagules to reach the substrate?

The Problem of Invasive Species

The issue of invasive species has become one of global concern. Human alteration of the planet has resulted in biotic additions leading to the rearrangement of Earth's biotic systems (Vitousek et al. 1997). The introduction of non-native species can alter the patterns of many ecosystem processes (Chapin et al. 2002). Concerns about the spread of non-indigenous species and the effects of these species on their new environments dates back at least to the time of Charles Darwin (Ludsin and Wolfe 2001). Nearly 50% (1570 invading species) of the terrestrial flora of New Zealand is composed of introduced species (Heywood 1989). Out of 24 nature reserves distributed throughout the world, not one was "without at least one species of invasive vertebrate and at least several species of invasive vascular plants" (Usher et al. 1988). We can only assume that the situation has gotten worse in such areas in the last 15 years. In these terrestrial nature reserves Macdonald et al. (1989), report the following impacts of ecosystem disruption:

1. Acceleration of soil erosion rates (feral mammals)
2. Alteration of biogeochemical cycling (feral pigs, invasive nitrogen fixers, salt accumulators)
3. Alteration of geomorphological processes (dune and marsh grasses)
4. Alteration of hydrological cycles (phreatophytes, *Phytophthora*, invasive trees)
5. Alteration of fire regimes (invasive grasses and shrubs)
6. Prevention of recruitment of native species (alien plants, mammals, and ants)

Native submersed macrophytes are being displaced by introduced species at an alarming rate. Anthropogenic sources of these nonindigenous plant species include;

aquaculture, aquarium and pond trade, bait trade, and shipping (Mooney and Hobbs 2000). Successful introductions of exotic species may be intentional or unintentional. On the global scale, native freshwater macrophyte species have been displaced by *Myriophyllum spicatum* and *H. verticillata* in North America, *Elodea canadensis* in Europe, and *E. nuttallii*, *Egeria densa*, and *Cabomba caroliniana* in Japan (Chambers et al. 1993). Locally, *M. spicatum* displaced the three dominant native species in the Susquehanna Flats between 1958 and 1963 before its population crashed, putatively as a result of the Lake Venice disease (Bayley et al. 1978). The rapid dominance and displacement of native species by *H. verticillata* has been particularly dramatic (Langeland 1996, Madsen and Owens 2000).

Submersed macrophytes are important to regulating a broad range of ecosystem processes in aquatic ecosystems (Carpenter and Lodge 1986). Not only do macrophyte communities improve water quality (Carter et al. 1988), but they also provide important feeding and rearing habitats for waterfowl, fish, invertebrates and many other organisms (Kantrud 1990). Different species of submersed macrophytes contribute varying proportions of their primary production throughout the water column (Stevenson 1988) and play key roles in nutrient cycling (Kufel and Kufel 2002). Thus, when native species are displaced by nonindigenous species, regulation of these ecosystem processes may be altered.

In general, plant communities are subject to various degrees of community restructuring resulting from natural and anthropogenic disturbances. Temporal changes in species composition are more common in some habitats than others (Clements 1916). The aquatic habitat is one that is very prone to disturbance and thus may experience more

invasion pressure and compositional change. Flood events are an important source of disturbance to macrophyte communities. Floods influence the current velocity of streams, sediment deposition rates, and nutrient loading to aquatic systems (Bornette et al. 2001). Water flow can both negatively and positively affect macrophyte growth (Madsen et al. 2001). High stream velocity may directly affect macrophytes by causing mechanical damage to the tissues or scouring the benthic zone and removing vegetation. Increased stream velocity indirectly affects submersed vegetation negatively by increasing turbidity through the resuspension of sediments and altering sediment characteristics. Moderate increases in stream flow may facilitate gas exchange between macrophytes and the water (Madsen et al. 2001). Additionally, periodic flooding events function to increase species diversity by distributing propagules and creating disturbances for weaker competitors to colonize. Anthropogenic modifications of the landscape alter these disturbance regimes (Melillo et al. 1993, Vitousek et al. 1997, Riis and Sand-Jensen 2001, Van Breemen et al. 2002). Land-use change also alters the erosion, sediment transport, and deposition rates of watersheds. Agriculture, urban development, highway construction, silvicultural practices, and surface mining all increase the amount of erosion and the subsequent amounts of sediment delivered to aquatic ecosystems (Novotny and Olem 1994).

Invasion Ecology

An ecosystem's invasibility is a function of both environmental characteristics and species traits. Shea and Chesson (2002) state that "both effects and responses of resident species in a community determine whether that community provides opportunities for invasion." In order to successfully invade a new area the plant species

must first overcome geographic, environmental, reproductive, and dispersal barriers (Richardson et al. 2000). Many species traits have been proposed as being advantageous to invasion success. For a species to become established, it must first survive the transition phase. When comparing the relationships between characteristics of plant species (between invasive and noninvasive species) and completion of an invasion transition, positive correlations occur between successful invasion completion and number of seeds produced, history of invasion, if the family or genus is invasive, vegetative reproduction, dispersal mechanism, range area, and height. Negative correlations exist between invasion success and variability of seed crop, seed mass, and length of juvenile period (Kolar and Lodge 2001). Also, models predicting invasiveness are more accurate when considering the geographical range of the species (Goodwin et al. 1999). Species having larger native ranges are more invasive than species originating from smaller regions.

Characteristics of the environment are also important when considering the potential for invasion success. Successful invasion of natural areas is not only dependent on dispersal, establishment, and survival but also the formation of a patch suitable for colonization (Hobbs 1989). In one study, important predictors of the potential for a site to become invaded included number of native species present, whether the site was an island or mainland, and whether or not it was a nature reserve (Lonsdale 1999). However, other species (e.g. *Alliaria petiolata*) are capable of invading systems that have experienced no patch creation resulting from disturbances (Meekins and McCarthy 2001).

The creation of patches by the removal of alien species can benefit the recolonization of native species. Research on the invasive species *Delawarea odorata* (Cape ivy) has shown that its removal from a habitat can increase the abundance of native seedlings by 86%. But, in this same experiment, nonnative seedling abundance increased by 85% as a result of Cape ivy removal (Alvarez and Cushman 2002).

Several methods of controlling invasive plants exist, and each technique has advantages and disadvantages. Control methods include preventing the entry of the species, mechanical control, chemical control, and biological control (Groves 1989). Diverse assemblages of native plants have been shown to reduce invasion in some cases (Elton 1927, Tilman 1997, Kennedy et al. 2002). It is believed that greater diversity leads to greater community stability through higher productivity and competition (Lehman and Tilman 2000). Thus, it seems plausible that promoting native plant diversity could be a form of biological control of invasive species. However, other research has shown that more diverse communities are more likely to be invaded (Levine and D'Antonio 1999, Lonsdale 1999, Levine 2000). The relationship between community diversity and invasibility is one that needs further research.

A great deal of research has been conducted in the area of competitive interactions in terrestrial plants (Schoener 1983, Goldberg and Landa 1991, Goldberg et al. 1999), and to a lesser extent in emergent plants (Brewer et al. 1998, Grace and Wetzel 1998), and macrophytes (McCreary 1991, James et al. 1999, Spencer and Ksander 2000). Unfortunately, very little research has been conducted relating to the effects of pre-existing aquatic vegetation on the colonization success of new arrivals. Research on terrestrial plants has shown that propagule availability is an important regulator of

colonization dynamics (Foster 2001). Aquatic plants with an “always ready” strategy, such as vegetative reproduction from fragments, colonize disturbed areas much more effectively than species with no such strategy (Barrat-Segretain and Bornette 2000). Many of these species traits associated with the “always ready” strategy (such as long distance dispersal capability, bare soil seedling “safe site”, and clonal reproduction) coincide with the characteristics of “persistence” species (Gross 1990).

Species Characteristics of Study Organisms

I evaluated the effect of pre-existing native vegetation (*Vallisneria americana* Michx. – wild celery) on the colonization success of an invasive species (*H. verticillata*) in field and greenhouse mesocosms. *Hydrilla verticillata* (Figure 1.1) is a highly invasive species of submersed macrophyte native to tropical Asia. This plant may be perennial or annual, monoecious or dioecious (Cook and Lüönd 1982). *Hydrilla verticillata* is a rooted vascular macrophyte that exhibits a canopy-forming growth structure. This plant typically branches infrequently until it reaches the surface of the water where it forms thick mats of vegetation. It may grow at depths of greater than 7 m in clear water. Occasionally, *H. verticillata* may become uprooted and survive in a free-floating form. *Hydrilla verticillata* is capable of growing in water with varying chemistries and nutrient concentrations (Cook and Lüönd 1982).

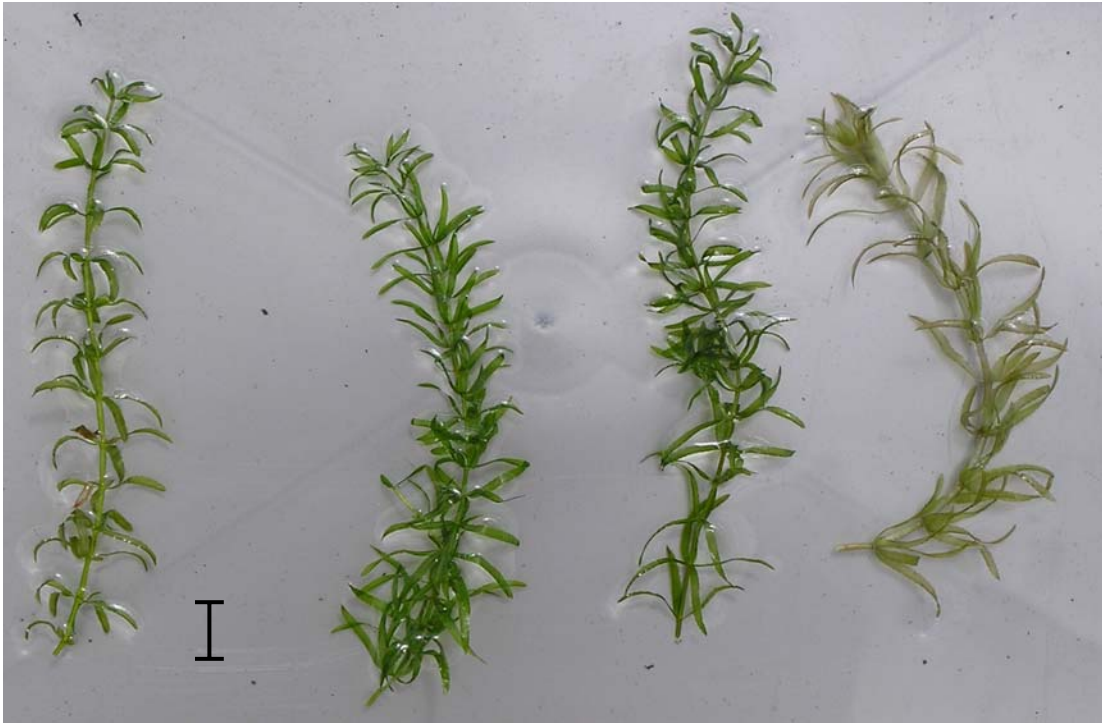


Figure 1.1. *Hydrilla verticillata* (scale bar = 1 cm).

The dioecious variety of *H. verticillata* was first discovered in the United States in 1960 in two locations in Florida, and by the early 1970s it was found in all major drainage areas in the state. The first U.S. record of the monoecious strain of *H. verticillata* was recorded in the Washington D.C. area in 1982 (Steward et al. 1984). This introduction most likely resulted from *H. verticillata*'s escape from transplanting and caging experiments conducted in 1980 using plants misidentified as the native *Elodea canadensis* (Steward et al. 1984). *Hydrilla verticillata* is now reported in 16 states, mostly in the South, but ranging up the West Coast as far as Washington and up the East Coast as far as Maine (Figure 1.2). The initial introductions of *H. verticillata* are suspected to be the result of ornamental plant importations and the aquarium trade.

Subsequent anthropogenic dispersal is most likely attributed to recreational boat use and the intentional introduction to lakes by fishermen.

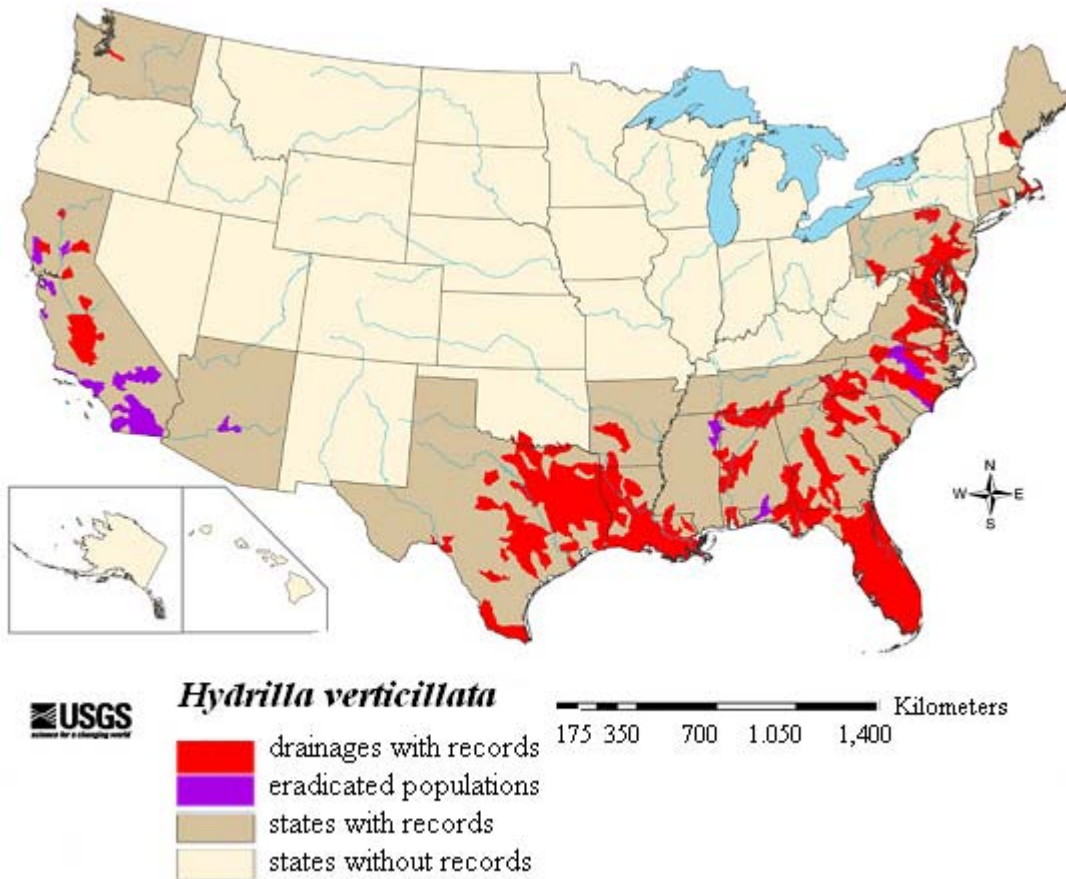


Figure 1.2. US distribution of *Hydrilla verticillata* (USGS 2003)

Hydrilla verticillata distribution is generally limited by its temperature tolerance. Growth of this species is regulated by temperature (Steward 2000, Best et al. 2001). The dioecious type commonly found in the southern states photosynthesizes optimally at temperatures greater than 32⁰ C (Barko and Smart 1981). *Hydrilla verticillata* germination from tubers and turions is also determined by temperature (Spencer et al.

2000, Spencer and Ksander 2001). In an experiment comparing monoecious *H. verticillata* and *V. americana*, 50% of the *V. americana* germinated at 13° C compared to 0% *H. verticillata* germination at this temperature (Rybicki and Carter 2002).

Hydrilla verticillata is an extremely productive plant capable of producing 4.2 g dry wt. m⁻² d⁻¹ in culture (Debusk et al. 1981). The ecosystem effects of this biomass production are both positive and negative. Increases in dissolved oxygen, pH, thermal stratification, and decreases in suspended particulate matter and chlorophyll-*a* concentrations are associated with vegetated sites in the Potomac River (Carter et al. 1988). These sites were dominated by *H. verticillata* at the time of the study. However, dense populations of *H. verticillata* can diminish the value of aquatic ecosystems for humans (Langeland 1996), and wildlife (Brown and Maceina 2002, Valley and Bremigan 2002).

Hydrilla verticillata has specialized growth, physiological, and reproductive characteristics that have permitted it to become a dominant species in a broad range of freshwater ecosystems (Langeland 1996). This exotic species typically demonstrates an exponential growth rate during its establishment phase. Environmental factors are considered to be important regulators to the expansion of this species, however to date no simple linear relationships have been found (Madsen and Owens 2000). These results failed to consider biotic factors such as competition and herbivory. It is likely that the distribution of *H. verticillata* is related to complex biotic and abiotic interactions.

It may be ascertained from the information above that *H. verticillata* has many of the species traits associated with other invasive species. *Hydrilla verticillata* has a history of invasion and covers a broad geographical range in its region of origin. *Elodea*

canadensis, also from the family Hydrocharitaceae, is native to North America. This macrophyte has become an invasive species in Europe and is now one of the most common macrophytes in Danish streams (Riis and Sand-Jensen 2001). *Hydrilla verticillata* produces large quantities of vegetative propagules in the form of fragments and turions. These fragments are capable of floating in the water column for periods of weeks before settling and rooting (personal observation) and thus serve as long distance dispersal mechanism. Finally, *H. verticillata* may be considered to have an “always ready” strategy associated with successful colonization of new areas.

Vallisneria americana is also a macrophyte of the family Hydrocharitaceae. This plant forms basal rosettes with leaves that may reach 2 m in length depending on water quality and depth (Korschgen and Green 1988). Unlike *H. verticillata* and *E. canadensis*, this species has no means of vegetative reproduction other than stolon formation.

Vallisneria americana does produce seeds, however seed masses settle close to the parent and may not disperse very far (Kaul 1978). Thus, this species does not exhibit an “always ready” strategy.

In general, quantitative data is lacking for biotic controls in macrophyte species declines and the mechanisms by which invasive macrophytes appear to out-compete native species (Chambers et al. 1993). Interactions between *H. verticillata* and *V. americana* frequently result in the exclusion of one of the two species. Research shows that *H. verticillata* is the superior competitor under high sediment nutrient availability (Van et al. 1999, Rybicki et al. 2001), however other research has shown *V. americana* to be the superior competitor when grown in sediments with elevated nutrient availability (Smart et al. 1994). There is also weak evidence based on shoot

elongation rates that *V. americana* out-competes monoecious *H. verticillata* under cooler conditions (Rybicki and Carter 2002).

In the next chapter, I present results of research that I conducted examining the effects of *V. americana* on the colonization success of *H. verticillata* in both field and greenhouse experiments. I also show the effects of *H. verticillata* propagule density indirectly in the field where experimental units were placed in different patch densities, and directly in the greenhouse where I controlled *H. verticillata* fragment input. In chapter 3, I frame the results of these experimental manipulations in the greater context of ecological theory and aquatic plant management.

Hypotheses

H₀₋₁ (Null Hypothesis): Pre-existing vegetation has no effect on *Hydrilla verticillata* colonization.

H₁: *Hydrilla verticillata* colonization success is inhibited by pre-existing vegetation.

H_{1A}: Native vegetation provides a physical barrier to colonization by *H. verticillata* only through the preemption of space and/or light.

H_{1B}: Native vegetation preempts resources (space and/or light and/or nutrients).

H₂: *Hydrilla verticillata* colonization is facilitated by pre-existing vegetation.

H_{2A}: Native vegetation serves as an anchor point for *H. verticillata* propagules.

H₀₋₂: (Null Hypothesis): *Hydrilla verticillata* colonization is independent of propagule density.

H₃: *Hydrilla verticillata* colonization success is dependent on propagule density.

To test these hypotheses, I conducted complementary field and greenhouse experiments that test for differences in *H. verticillata* colonization success among experimental units that were planted with live plants, planted with plastic plants, and left unplanted. I predicted that if H₁ was true, then colonization success would be lower in planted trays than in unplanted trays. If H_{1A} was true then colonization success would be reduced more in experimental units planted with plastic plants than in unplanted units. If H_{1B} was true, then colonization would be most reduced in experimental units planted with live plants. If H₂ was true, then experimental units planted with plants or plastic plants would experience more colonization by *H. verticillata*. If H₃ was true, then experimental units that received more propagules would experience different colonization success than those that received fewer propagules.

Chapter 2: Effects of *Vallisneria americana* on colonization success of *Hydrilla verticillata*

Introduction

An ecosystem's invasibility is a function of species traits and environmental characteristics. Species traits such as vegetative reproduction and high propagule output are often associated with a species' invasiveness (Kolar and Lodge 2001). A system's invasibility may be related to how well the existing species use available resources and the type and frequency of disturbance that the system receives (Connell and Slatyer 1977). Systems that are more disturbed typically experience more invasion pressure from exotic species (Meekins and McCarthy 2001), whereas a community with a low level of niche opportunity, is less likely to be successfully invaded by non-native species (Shea and Chesson 2002).

Pre-existing vegetation may inhibit the colonization of later arriving species through the preemption of resources such as light or nutrients (Grace 1987). When one species successfully establishes itself, it may lower these factors below the critical limit of other species (Tilman 1982). Conversely, early arrivals may facilitate the establishment of other species that manage to disperse propagules into the area (Levine 1999). Frequently, facilitation occurs by modifying environmental conditions such as pH, nutrients, or oxidation or water or sediments. These environmental alterations render the habitat more hospitable to other species. Pre-existing vegetation may also provide safe-sites by trapping propagules of other species and thereby creating local pockets of colonization.

Propagule pressure and disturbances to the environment relate both to the invasiveness of a particular species as well as to the invasibility of an environment (Williamson and Harrison 2002). Propagule pressure is defined here and elsewhere as the number of individuals introduced as well as the number of release events (Allendorf and Lundquist 2003). Increasing propagule pressure enhances the likelihood of successful colonization. Environmental disturbance may result in several outcomes. First, disturbances may remove potential competitors and thus facilitate colonization by competing species. Disturbances may also modify the environment, by altering sediment chemistry. Physical alterations to the environment can foster the colonization of invaders, but such disturbances may contribute to community stability (Barrat-Segretain and Bornette 2000).

Disturbances to a system may be either fine scale or coarse scale. In aquatic environments, local disturbances may result from boating events, or from wildlife activities such as grazing, nesting, digging, etc. Coarse scale disturbances are frequently caused by storm events, eutrophication, and water level changes. Disturbances on different spatial scales typically occur on different temporal scales as well, with finer scale disturbances generally more frequent than larger scale disturbances. Recovery from disturbance also occurs more rapidly when the disturbance is on the fine scale versus the coarse scale (Foster et al. 1998).

Hydrilla verticillata (L.F.) Royle (hydrilla), of the family Hydrocharitaceae, is a highly invasive species of submersed macrophyte native to tropical Asia. *Hydrilla verticillata* was first discovered in the United States in 1960 in two locations in Florida, and by the early 1970s it was found in all major drainage areas in the state. It is now

reported in 16 states, mostly in the South, but ranging up the West Coast as far as Washington and up the East Coast as far as Maine (*Public communication*, USGS website; Figure 1.3).¹ *Hydrilla verticillata* has many of the traits that are attributed to invasive species. This aquatic macrophyte has specialized growth, physiological, and reproductive characteristics that have permitted it to become a dominant species in a broad range of freshwater ecosystems (Langeland 1996). It also has a history of invasion and covers a broad geographical range in its region of origin, two additional traits of invasive species. *Hydrilla verticillata* produces large quantities of vegetative propagules in the form of fragments and turions. These fragments are capable of floating in the water column from days to weeks before settling and rooting (*personal observation*) and thus serve as a long distance dispersal mechanism. Finally, because this macrophyte reproduces primarily from fragments, it has an “always ready” strategy associated with successful colonization of new areas (Barrat-Segretain and Bornette 2000).

The aquatic vegetation in the tidal freshwater portion of Otter Point Creek, near Abingdon, Maryland has experienced substantial changes through time. *Hydrilla verticillata* was first observed at this site in the summer of 2002. Historical records show that the Susquehanna Flats, which are about 20 km northeast of Otter Point Creek, were dominated by the native macrophyte species *Vallisneria americana* Michx. (wild celery), *Najas sp.*, and *Elodea canadensis* before 1960. After this time, the community was dominated by the exotic macrophyte *Myriophyllum spicatum*. In 1972, all species drastically declined as a result of Hurricane Agnes (Bayley et al. 1978). During the summer of 2003, *H. verticillata* displaced *M. spicatum* as the dominant species at Otter Point Creek (J. Bortz, *unpublished data*). Recently, managers at the Otter Point Creek

¹ URL: http://nas.er.usgs.gov/plants/docs/hy_verti.html

National Estuarine Research Reserve have begun the daunting task of native plant restoration in this location dominated by invasive species.

I tested the alternative hypotheses that pre-existing native vegetation would (1) reduce the colonization success of invasive species through the preemption of resources (“preemption hypothesis”), or (2) facilitate the colonization of *H. verticillata* by trapping fragments floating through the water column (“facilitation hypothesis”); or (3) not have any effect on *H. verticillata* colonization (“null hypothesis”). I also tested the hypothesis that increasing propagule availability would increase the invasion success of *H. verticillata* (“propagule pressure hypothesis”). These hypotheses were tested using replicated greenhouse and field experiments that measured the colonization success of *H. verticillata* into created patches of *V. americana*. The study compared the colonization success of *H. verticillata* into experimental units previously populated with *V. americana* and experimental units with no existing vegetation. I considered the arrival, rooting, and tuber production of a *H. verticillata* fragment to be a successful colonization. To elucidate the mechanisms of any facilitation or inhibition of colonization success, I also used experimental units of plastic plants resembling *V. americana* in the experiments. The propagule pressure hypothesis was measured indirectly in the field by placing experimental units in areas of varying *H. verticillata* density and directly in the greenhouse by controlling the number of *H. verticillata* fragments introduced to each mesocosm.

Methods

Study Site

I conducted the field research at the Otter Point Creek National Estuarine Research Reserve, Abingdon, Maryland, USA (39° 27' N, 76° 16' W). This water body in the upper Chesapeake Bay (Figure 2.1) contains 106 Ha of tidal freshwater, and the maximum depth is 1.5 m. The Otter Point Creek Reserve is of particular interest because *H. verticillata* was first observed here in the summer of 2002 and had not yet reached full coverage by the time of my study (J. Bortz, *unpublished data*). In 2002 the submersed aquatic plant community at the study site consisted of the following species, listed from greatest abundance to least abundance; *Myriophyllum spicatum*, *Hydrilla verticillata*, *Ceratophyllum demersum*, *Elodea canadensis*, *Heteranthera dubia*, and *Potamogeton pusillus*.

Field Experiment

To compare the effects of pre-existing vegetation and to distinguish between potential mechanisms of competition, I created an unplanted control treatment (“Bare”), a treatment planted with *V. americana* (“Vallisneria”) and a treatment planted with plastic plants resembling *V. americana* (Plastic). I used polypropylene strapping to create artificial plants. This material is extremely strong, positively buoyant, relatively cheap, and is available in sizes that approximate *V. americana* leaves (1.3 cm wide by 0.04 cm thick). I cut the polypropylene strapping into 90 cm long pieces and stacked 4 pieces together, doubled at the center point, and then melted the strips together at the base with a

soldering iron. Each individual plastic plant measured 45 cm tall and had 8 leaves. I then fastened 17 of these plants into plastic trays measuring 34 x 24 x 9 cm.

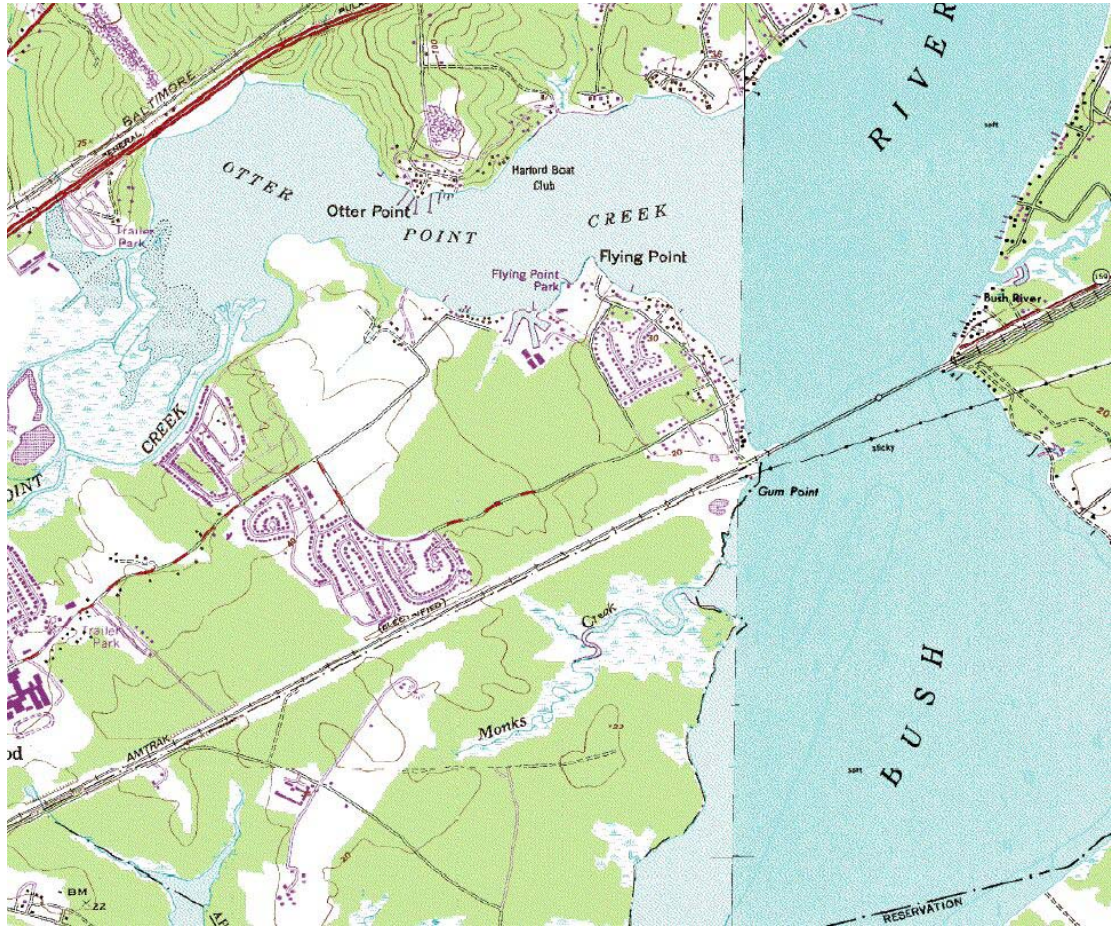


Figure 2.1. Map of Otter Point Creek study site.

I mixed equal parts of topsoil and sand to create the substrate for this experiment. Sixty empty trays and 30 trays with the plastic plants were filled to within 1 cm of the top of the tray with substrate. The final 1 cm was then filled with sand to reduce the loss of substrate to the water column. On April 14, 2003, 30 of the bare trays were seeded with *V. americana*. All trays were then placed in the greenhouse and submersed in 20 cm of freshwater. Because of poor germination, I planted 17 live *V. americana* plants in the

previously seeded trays on May 23, 2003. Resulting *V. americana* densities were 209 plants m⁻², which is similar to reported natural densities of this species (Korschgen and Green 1988). All trays (30 with live *V. americana*, 30 with plastic plants, and 30 unplanted) were then maintained in the greenhouse at the University of Maryland Center for Environmental Science's Appalachian Laboratory for 35 days to permit the *V. americana* to root sufficiently before placement in the field.

Experiment sites at the Otter Point Creek field location were chosen based on the *H. verticillata* density of the previous year (2002). I selected two sites that had high (>40 %) *H. verticillata* estimated percent cover in 2002 and two sites that had relatively low (<40%) *H. verticillata* percent cover in 2002. The final two sites were placed midway between the high and low-density sites. On June 28, 2003 all of the trays were transported to the field location and situated in the experiment sites on that day and the following day. Five replicates of each "Bare", "Plastic", and "Vallisneria" treatment were randomly placed in each site. Sediments at the site were soft enough to allow the trays to be pushed down until the top of the tray was flush with the natural sediment. Trays were placed approximately 2 m from one another and fastened in place with 3.05 m long 1.27 cm diameter PVC pipe run through the center of each tray.

I used a portable water current meter (Marsh-McBirney Model 201D) to measure current velocity at each of the 6 experimental sites over a 24-hour period between July 25 and 26, 2003 to test for equal current velocities between sites. Velocities were measured at 10 cm above the sediment surface and just below the water surface. I also recorded depths with a PVC depth rod at each of the sites on the hour during this period. Above ground biomass of each submersed macrophyte species was estimated on September 17,

2003 by collecting all above ground biomass in four 1 m² quadrats in each site. The biomass was not rinsed because I perceived the biomass of attached detritus and epiphytic growth to be negligible. I later dried all biomass at 60 ° C for 24 hours and weighed the material.

To identify any nutrient related mechanisms affecting the colonization success of *H. verticillata*, I analyzed soil pore water for total nitrogen and total phosphorus in a subset of the trays. I installed mini-tension lysimeters in 30 of the trays and collected approximately 15 ml of water for analysis during two sampling periods. The first soil pore water collection occurred on July 11, 2003. Due to time constraints imposed by Hurricane Isabel, the final soil pore water collection did not occur in the field. Instead, on September 17, 2003, 30 trays with their associated plants and substrate were collected, sealed in plastic bags, and transported to the laboratory to have the soil pore water extracted on September 18, 2003 using the lysimeters. I stored all water samples at -19 °C until analysis on January 24, 2004. Each water sample was digested, autoclaved, and analyzed for total nitrogen and total phosphorous on the Lachat QuikChem Automated Flow Injection Analysis System (APHA 1998).

The contents of each tray collected in the field were sifted to separate the substrate from the plant material. Biomass was separated into tubers, turions, and above ground biomass for *H. verticillata* and total biomass for *V. americana*. All vegetative material was dried for 24 hours at 60 ° C and then weighed.

I observed in the field that pumpkinseed sunfish (*Lepomis gibbosus*) were nesting in several of the trays and consequently removing some amount of substrate in these trays. When the trays were collected, there were marks left on the sides of the trays from

algal growth indicating how much substrate had been removed. Based on these marks, I quantified the disturbance in each tray as a percent of the substrate that was removed.

Greenhouse Experiment

To control environmental conditions and regulate propagule input, I replicated the field experiment in greenhouse mesocosms using 30 unplanted mesocosms as controls (“Bare”), 30 mesocosms planted with *V. americana* (“Vallisneria”) and 30 mesocosms planted with the plastic plants (“Plastic”). Plastic plants were created in the same manner as for the field experiment with the exception that the plants were 36 cm tall and placed in mesocosms measuring 26 cm diameter x 36 cm height. I began this experiment on May 23, 2003. On August 19, 2003, 10 cm long *H. verticillata* fragments, collected from Little Seneca Lake, Burdette, MD, were added to each of the treatments in densities of 1, 5, or 10 fragments per mesocosm. The mean dry mass of each fragment was 9.8 ± 0.1 mg (mean \pm SE). I collected soil pore water from 16 of the containers on August 26, 2003 and water on November 10, 2003 for the same nutrient analysis as was conducted for the field experiment. Biomass was sifted and separated into tubers, turions, and above ground biomass for *H. verticillata* and total biomass for *V. americana* on November 12, 2003.

Statistical Analysis

One-way ANOVA or a nonparametric equivalent tested for differences among treatments in the field and greenhouse experiments. Because data could often not be transformed to meet the assumptions of normality, I used Spearman correlation analysis to test for correlations among disturbance, *H. verticillata* tuber biomass, and total

V. americana biomass. I used an ANCOVA to assess the effects of site-treatment interactions on the dependent variable “*H. verticillata* tuber biomass” based on the categorical variable “treatment” and the continuous covariate “pre-existing *H. verticillata* biomass”.

Results

Field Experiment

Above ground *H. verticillata* biomass at the six sites ranged from 20.4 to 71.5 g m⁻². Sites 3 and 4 supported 70-72% more *H. verticillata* biomass than sites 5 and 6 (ANOVA; $F_{5,18} = 5.50$, $P = 0.003$; Figure 2.2). Biomass at sites 1 and 2 was not significantly different from other sites. The tidal range from July 25 to July 26, 2003 at the six sites averaged 58 cm. The mean depth at the sites was 45 cm at low tide and 103 cm at high tide. Average depth differed by 13 cm between the shallowest site (site 2) and the deepest site (site 6). Water current velocities at the six sites never exceeded 0.02 m s⁻¹.

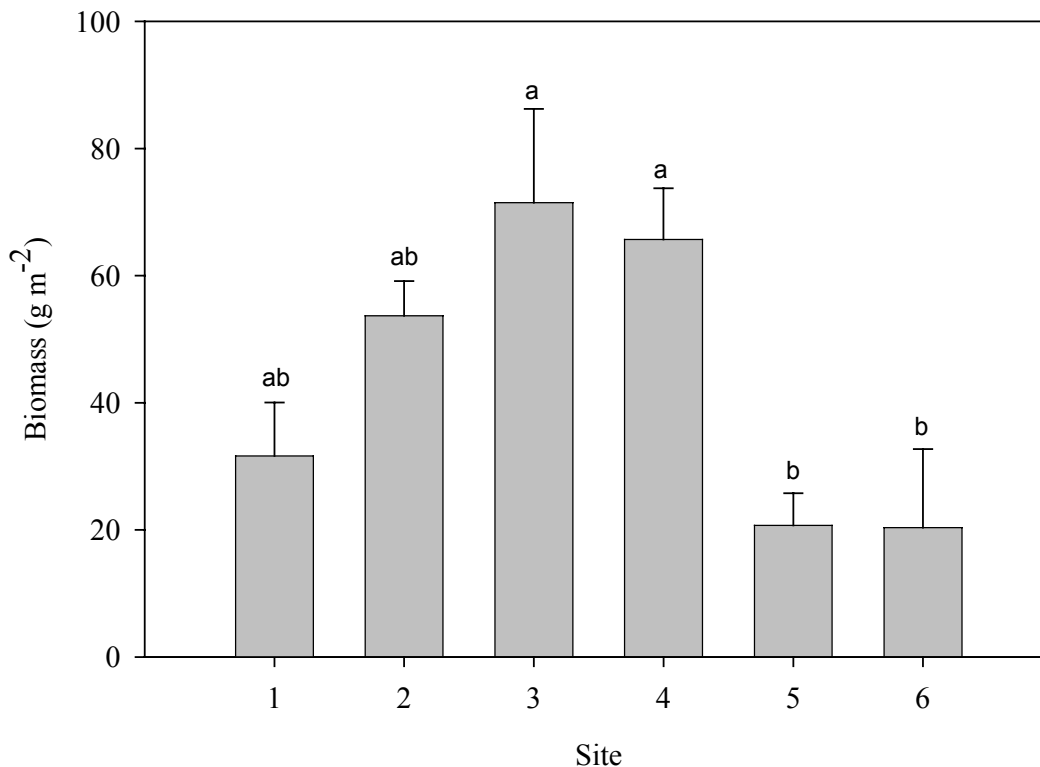


Figure 2.2. Existing *Hydrilla verticillata* biomass at each of six sites in Otter Point Creek (n=5/site; mean + 1 SE). Treatments sharing a lowercase letter are not significantly different (Tukey-Kramer hsd multiple pairwise comparisons, $\alpha = 0.05$).

Soil pore water nutrients in the experimental trays declined between July and September 2003 (Figure 2.3). Total phosphorous was significantly higher in the bare treatments than in other treatments on September 18, 2003 ($F_{2,27} = 6.41$, $P = 0.0053$), but not on July 11, 2003 (ANOVA; $F_{2,22} = 1.53$, $P = 0.2386$). Total nitrogen did not differ significantly between planted and unplanted trays on either sampling date (ANOVA; $F_{2,22} = 0.78$, $P = 0.4725$ and $F_{2,27} = 1.58$, $P = 0.2242$).

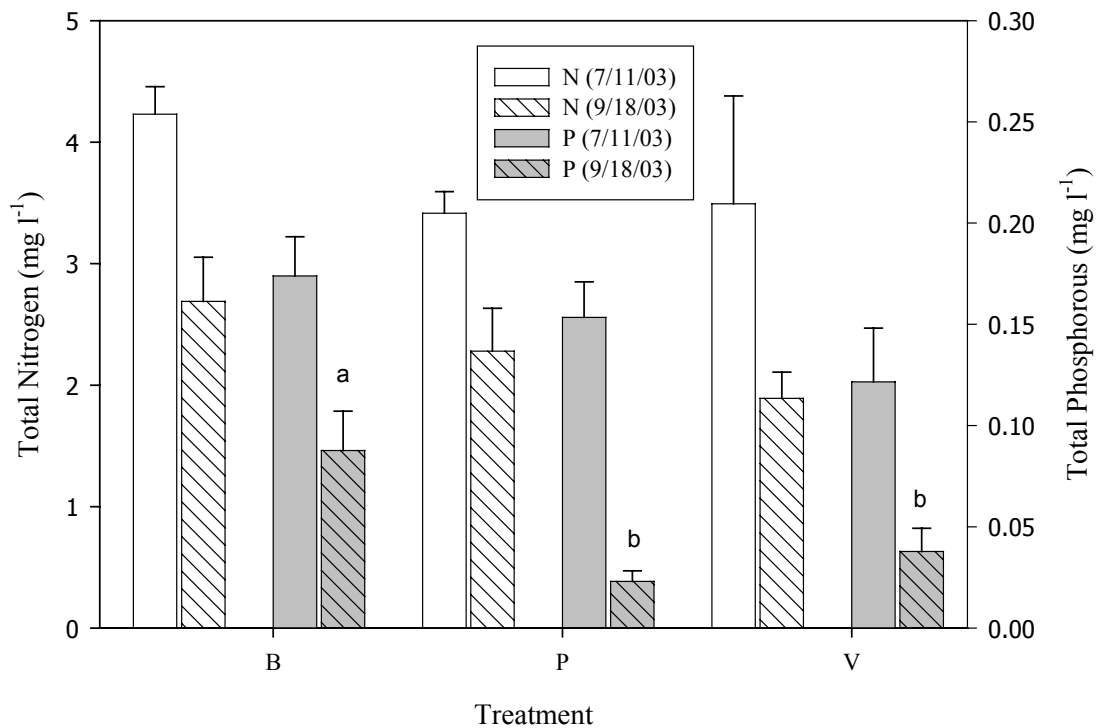


Figure 2.3. Soil pore water nutrient concentrations in samples extracted from the field experimental units (means + 1 SE). B = bare, P = plastic, V = *Vallisneria americana*. Total phosphorus and nitrogen declined from July to September 2003. Only September phosphorus concentrations differed significantly among treatments, where different lowercase letters denote significant differences (Tukey-Kramer hsd multiple pairwise comparisons, $\alpha = 0.05$).

All treatments accumulated the same amount of total *H. verticillata* biomass (ANOVA; $F_{2,86} = 0.82$, $P = 0.4424$; Figure 2.4A) and above ground *H. verticillata* biomass (ANOVA; $F_{2,86} = 0.62$, $P = 0.5421$). However, plastic treatments accumulated more tuber biomass than the bare or *V. americana* treatments (Kruskal-Wallis test statistic = 17.66, 2 df, $P = 0.0001$; Figure 2.4B). Significant interactions were also detected between existing *H. verticillata* biomass and treatment at the six sites (dependent variable = tuber biomass; independent variables = existing *H. verticillata* biomass and treatment; ANCOVA; $F_{5,83} = 13.59$, $P = <0.0001$; Figure 2.5).

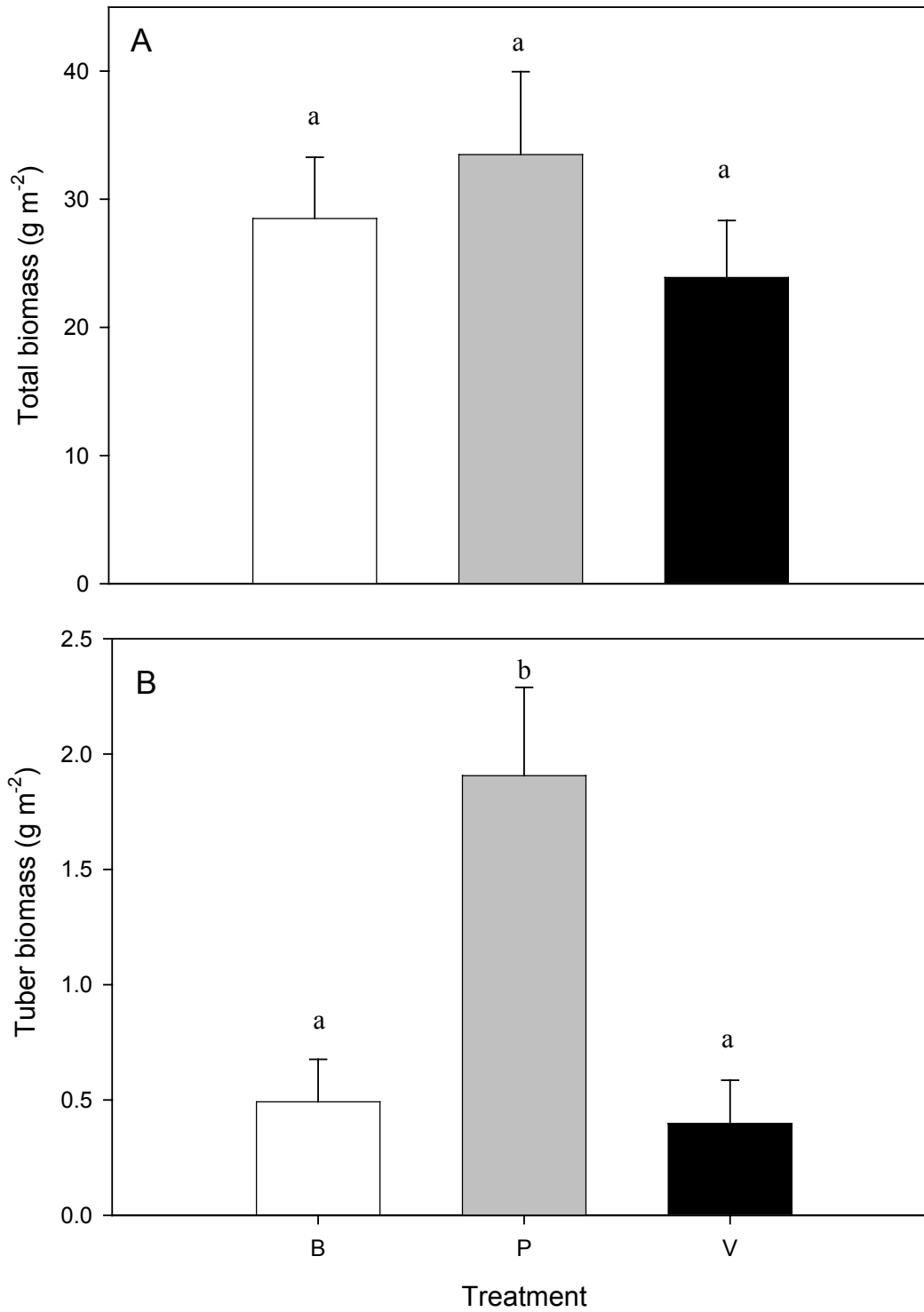


Figure 2.4. Effects of *Hydrilla verticillata* colonization on treatments (mean + 1 SE): (A) total *H. verticillata* biomass; (B) *H. verticillata* tuber biomass. Treatment abbreviations

are as in Figure 2.3 and different lowercase letters denote significant differences (Tukey-Kramer hsd multiple pairwise comparisons, $\alpha = 0.05$).

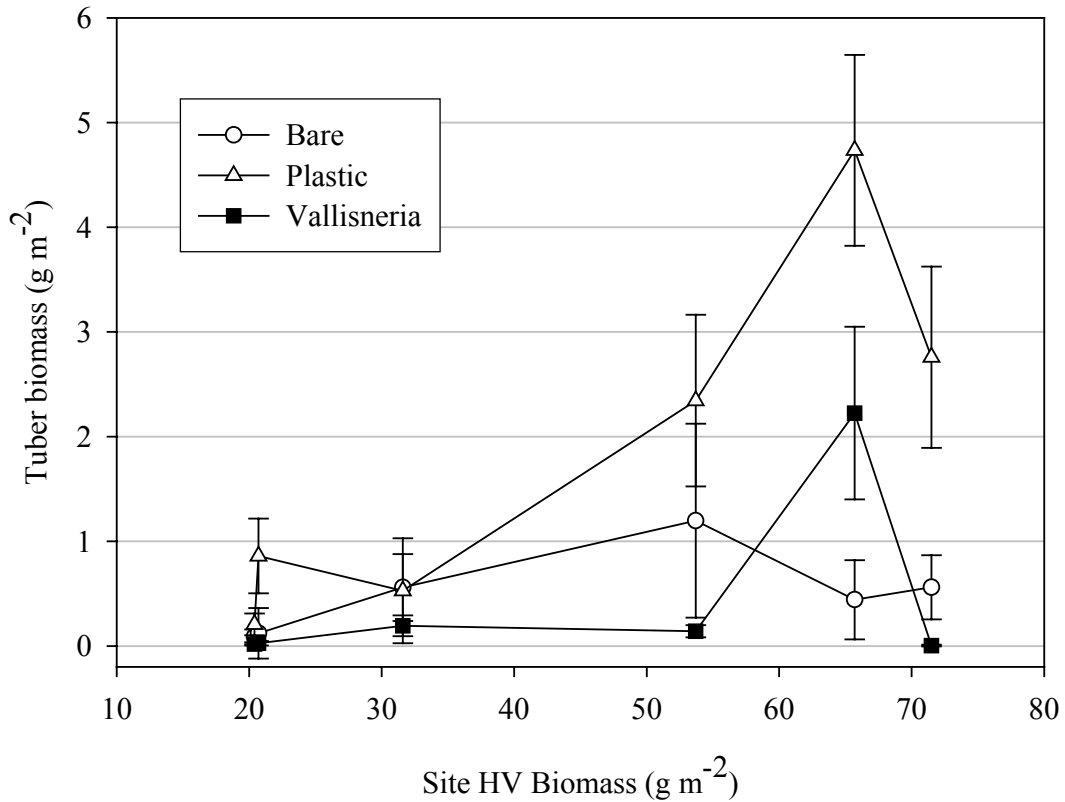


Figure 2.5. Covariance of site *Hydrilla verticillata* biomass and treatment (means \pm 1 SE).

Hydrilla verticillata colonization generally increased with increasing pre-existing *H. verticillata* biomass. Based on accumulated tuber biomass, significant differences of *H. verticillata* colonization existed between sites (ANOVA; $F_{5,83} = 5.74$, $P = 0.0001$). Trays in site 4, the site supporting 66 g m^{-2} *H. verticillata* biomass, received significantly more *H. verticillata* tuber biomass than all other sites except for site 2 (Tukey-Kramer hsd multiple pairwise comparisons, $\alpha = 0.05$).

Vallisneria americana biomass and *H. verticillata* tuber biomass were negatively correlated (Spearman correlation; $r_s = -0.306$, $n = 89$, $P = 0.0036$). A strong relationship between pre-existing *H. verticillata* biomass at the six sites and *H. verticillata* tuber mass in the experimental trays (Spearman correlation; $r_s = 0.376$, $n = 89$, $P = 0.0003$) was also detected. Disturbance and total *V. americana* biomass were generally positively correlated at the six sites, but only significantly so at site 3 (Table 2.1). Disturbance and *H. verticillata* tuber biomass as well as *V. americana* biomass and *H. verticillata* tuber biomass were generally negatively correlated at the individual sites, but only significantly so in some cases (Table 2.1).

Table 2.1. Spearman correlations among variables (Dist = percent disturbance, VAtotal = total *Vallisneria americana* biomass, Hvtuber = *Hydrilla verticillata* tuber biomass) at each site.

Site	Coefficient	n	Variables		
			Dist * Vatotal	Dist*Hvtuber	Hvtuber*VAtotal
1	r_s	1	-0.221	-0.018	-0.181
	P	5	0.4294	0.9480	0.5185
2	r_s	1	0.488	-0.301	-0.331
	P	5	0.0648	0.2759	0.2275
3	r_s	1	0.626	-0.627	-0.535
	P	5	0.0125	0.0123	0.0400
4	r_s	1	0.055	-0.490	-0.115
	P	4	0.8523	0.0753	0.6945
5	r_s	1	0.251	-0.334	-0.527
	P	5	0.3661	0.2240	0.0437
6	r_s	1	0.053	0.164	-0.164
	P	5	0.8504	0.5589	0.5599

Note: bold text indicates significance at $\alpha = 0.05$ level.

Disturbance in the trays in sites 1, 2, and 3 was about three times that of the trays in the other sites (Figure 2.6). Additionally, bare and *V. americana* treatments experienced 50% less disturbance than trays with plastic plants ($F_{2,86} = 3.65$, $P = 0.0302$). Because disturbance was a significant factor in the field experiment, sites were classified as low disturbance or high disturbance (Table 2.2). *Hydrilla verticillata* tuber biomass in bare and *V. americana* treatments did not differ significantly between the two disturbance categories. However, opposing trends were seen in these groups; (1) bare treatments accumulated more *H. verticillata* tuber biomass than *V. americana* treatments in the high disturbance sites, but (2) trays with *V. americana* accumulated more *H. verticillata* tuber biomass than bare trays in the low disturbance sites. Trays with plastic plants accumulated the same amount of *H. verticillata* tuber biomass in both high and low disturbance sites.

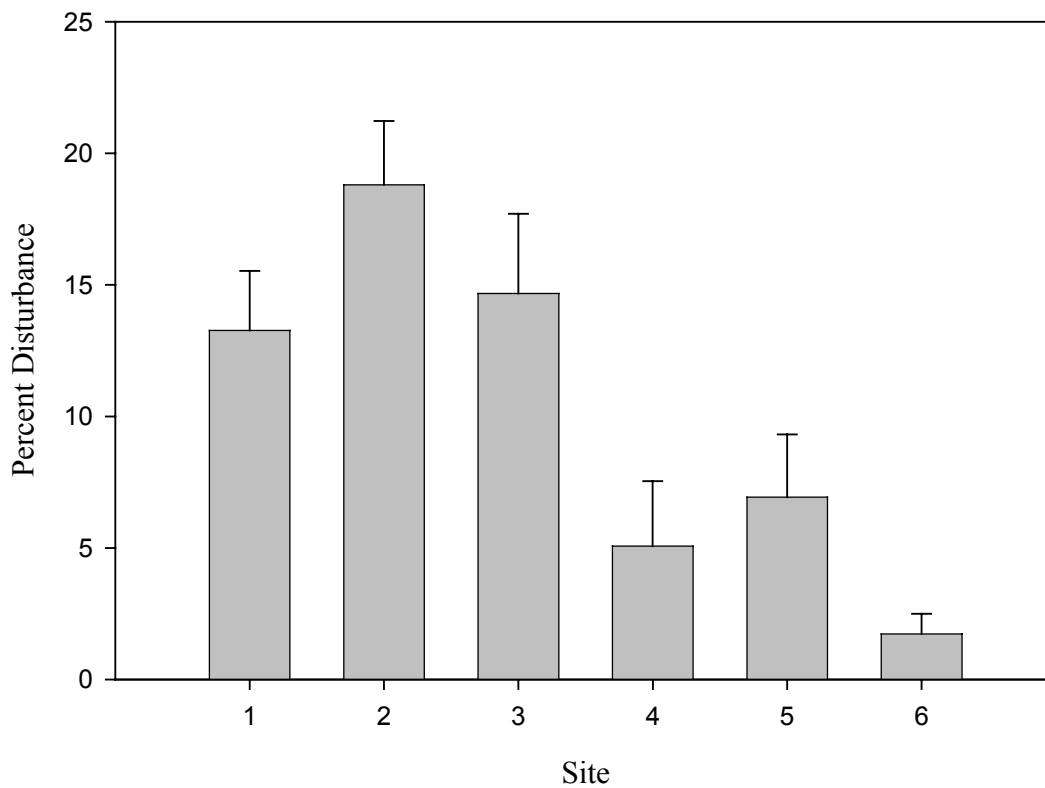


Figure 2.6. Percent disturbance by site (mean + 1 SE).

Table 2.2. Results from one-way ANOVA of *Hydrilla verticillata* tuber biomass recovered from sites subject to high disturbance and low disturbance.

Treatment	Mean <i>H. verticillata</i> tuber biomass (g m ⁻²)	
	High disturbance sites	Low disturbance sites
B	0.70 a	0.27 a
P	1.90 b	1.91 b
V	0.10 a	0.70 ab

Notes: Treatment abbreviations: B = bare, P = Plastic, V = *Vallisneria americana*. Different letters after the values indicate significant differences [for high disturbance sites (1, 2, and 3) $F_{2,42} = 8.04$, $P = 0.0011$; for low disturbance sites (4, 5, and 6) $F_{2,41} = 3.77$, $P = 0.0315$].

Greenhouse Experiment

Total nitrogen (ANOVA; $F_{2,12} = 0.48$, $P = 0.6314$) and total phosphorous (ANOVA; $F_{2,12} = 2.34$, $P = 0.1384$) in the soil pore water did not differ significantly among treatments 12 weeks after planting *V. americana* in the experimental units. Because few *H. verticillata* fragments were observed rooting in the *V. americana* treatments, water column nutrients were analyzed instead of soil pore water at the end of the experiment to more appropriately reflect the nutrient environment that *H. verticillata* fragments were encountering. Water column nutrient analyses showed significantly more total nitrogen ($F_{2,12} = 5.12$, $P = 0.0226$) in the bare treatments than in the *V. americana* planted treatments, but not the plastic treatments. No significant differences in total phosphorous concentration were observed among treatments (ANOVA; $F_{2,12} = 0.48$, $P = 0.6281$).

Total biomass of *H. verticillata* increased during the study period in all experimental units that had *H. verticillata* fragments introduced to them. Analyses on the length and biomass of individual *H. verticillata* fragments could not be performed because fragments unavoidably fragmented during the experiment and at harvesting. Fragments trapped at the surface of containers were able to send roots more than 20 cm through the water column before penetrating the substrate. Based on total accumulated *H. verticillata* biomass, *H. verticillata* colonization success was poorest in the *V. americana* treatments (ANOVA; $F_{2,33} = 6.27$, $P = 0.0049$). Only one *H. verticillata* fragment successfully rooted in any of the *V. americana* experimental units, and *H. verticillata* fragments appeared very chlorotic in these units. No significant difference was detected in *H. verticillata* tuber biomass between plastic and bare treatments; but no

H. verticillata tubers were formed in *V. americana* treatments. Fragments that were able to take root were observed to grow more vigorously than non-rooted fragments. Spearman correlations revealed positive correlations between rooted *H. verticillata* biomass and total *H. verticillata* biomass ($r = 0.83$, $n = 36$, $P < 0.0001$) as well as between rooted *H. verticillata* biomass and *H. verticillata* tuber biomass ($r = 0.86$, $n = 36$, $P < 0.0001$).

One-way ANOVA tested the hypothesis that propagule number influences colonization success of *H. verticillata* fragments. Increasing propagule numbers greatly enhanced the success of *H. verticillata* colonization (ANOVA; $F_{2,41} = 4.32$, $P = 0.0198$; Figure 2.7). Mean tuber biomass for 1-fragment introductions was $0.34 \pm 0.19 \text{ g m}^{-2}$, $0.68 \pm 0.35 \text{ g m}^{-2}$ for 5-fragment introductions, and $2.33 \pm 0.94 \text{ g m}^{-2}$ for 10-fragment introductions.

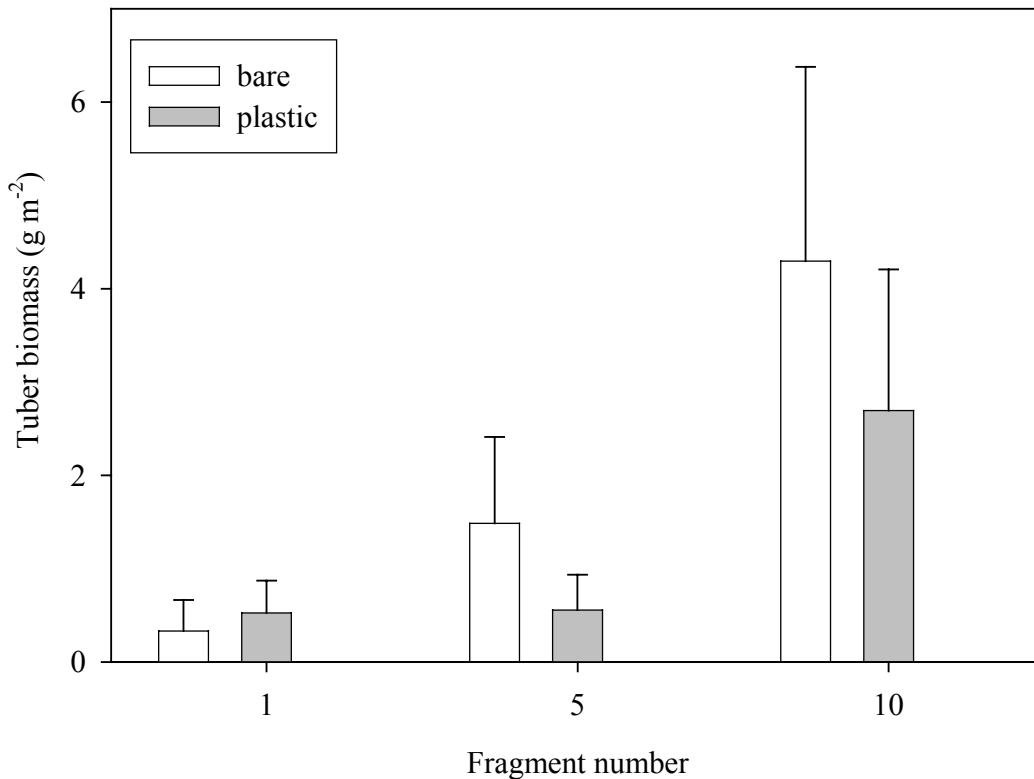


Figure 2.7. Effects of increasing *Hydrilla verticillata* propagule (plant fragments) load to mesocosms (means + 1 SE). No tubers were produced in the *Vallisneria americana* treatment.

Discussion

Results of the concurrent field and greenhouse experiments were somewhat contradictory. If a successful colonization is defined as the establishment of the invading species, then pre-existing vegetation did not affect *H. verticillata* colonization in the experimental units at Otter Point Creek (Figure 2.4A). Even when considering *H. verticillata* tuber biomass production, a more robust measure of colonization success, no differences were detected between bare and *V. americana* treatments in the field

(Figure 2.4B). However, five out of six sites at Otter Point Creek showed greater tuber production in bare treatments than in *Vallisneria americana* treatments (Figure 2.5). In the greenhouse experiment *H. verticillata* colonization by fragments was severely inhibited by pre-existing populations of *V. americana*. Discrepancies between the field and greenhouse experiments are most likely a result of nutrient availability, propagule flux, scale, and disturbance.

Nutrient Availability

Sediment nutrients are considered key determinants to the outcome of direct competition between mature *H. verticillata* and *V. americana* plants (Smart et al. 1994, Van et al. 1999). Although Smart et al. (1994) reported that *V. americana* is the superior competitor in high nutrient substrates, experiments by Van et al. (1999) showed that *H. verticillata* dominates the competition under elevated nutrient conditions. Soil pore water analyses were remarkably similar in my results. I originally predicted that substrate nutrients would be reduced in treatments with *V. americana*; however, total nitrogen and total phosphorus did not differ among treatments even after *V. americana* had been growing in the trays in the field for seven weeks and in the greenhouse for 12 weeks. However, soil pore water samples from the field collected sixteen weeks after planting *V. americana* showed slightly reduced phosphorus levels in the *Vallisneria* and plastic treatments. Although nutrient reduction in substrates was most likely a result of uptake by plants (*V. americana* and invading *H. verticillata*), some reduction may have resulted from leaching to the water column.

Nutrient assimilation by the shoots and leaves of submersed plants has been researched less thoroughly than uptake by roots. Madsen and Cedergreen (2002)

concluded that submersed vegetation in Danish streams acquires adequate amounts of nitrogen and phosphorus from the water column. Results from my study show that water column nutrients were lowest in the greenhouse *V. americana* treatments, although these values are not significantly different than the nutrient values for the plastic treatments. Because very little epiphytic algal growth was observed in any of the mesocosms, I attributed reductions in nutrient concentrations in the water in bare and plastic treatments to assimilation by *H. verticillata*. Water analyses at the beginning of the experiments would have allowed testing whether the *V. americana* treatments reached this oligotrophic state sooner than the other treatments. I observed that it took many weeks before *H. verticillata* fragments were able to root into the substrate, if they were able to at all, suggesting that mineral nutrients in the water column must have been the only nutrients available to the fragments during this period. If nutrients were not obtainable to sustain the fragments while they produced roots, then colonization was most likely inhibited. Small mesocosms likely allowed the plants to reduce nutrients in the water column, in contrast to the field experiment, which was in an open system.

Propagule Pressure and Timing

Proximity to a propagule source proved to be strongly related to *H. verticillata* colonization success in the field. Measurement of propagule flux at the different sites was attempted with little success; thus, existing site *H. verticillata* biomass was used as a surrogate for propagule density. Although it is logical to assume that propagules were more abundant near the source, and the data presented here strongly support this assumption, it is possible that some colonization resulted from stolon production and not from fragments. Results of the propagule density greenhouse experiment support the

field results in that increasing the number of fragments introduced to greenhouse mesocosms enhanced the chances of a successful colonization through increased tuber production.

Timing of the propagule introduction may have been a confounding factor in my experiment. I introduced *H. verticillata* fragments to greenhouse mesocosms in August because this is when *H. verticillata* in the field was experiencing maximum production and producing large numbers of fragments. However, I have observed small numbers of *H. verticillata* fragments floating in the water at Otter Point Creek as early as May. Because trays were placed in the field 7 weeks before *H. verticillata* fragments were introduced to the greenhouse mesocosms, colonization likely began in the field before the greenhouse. Competitive interactions between plants are often related to the timing of the establishment. If the first species to arrive has more time to establish it has a better chance of resisting invasion (Grace 1987). Because *V. americana* in greenhouse mesocosms was 7 weeks older than *V. americana* in the field when *H. verticillata* fragments may have begun arriving, the *V. americana* in the greenhouse may have inhibited invasion more successfully.

Disturbance

Disturbance played a strong role in the field component of this experiment. Because water velocities were negligible at the study site, and I frequently experienced defensive behavior by male sunfish nesting in the trays, I am willing to attribute most of this disturbance to sunfish nesting. Sunfish behavior was primarily observed in the first month of the experiment. Table 1.2 demonstrates some interesting trends in colonization pressure in the field. In both high and low disturbance sites, trays with plastic plants

accumulated the same amount of *H. verticillata* tuber biomass. In the high disturbance sites, less *H. verticillata* colonized the *V. americana* treatments than the bare treatments. This trend was reversed in the low disturbance sites. If sunfish were the cause of the disturbance and kept trays cleared of *H. verticillata* fragments in the first few weeks of the experiment, *V. americana* may have had a temporal advantage over *H. verticillata* in high disturbance sites. Again, temporal advantages are the basis of the theory of priority effect and strongly influence competitive displacement (Grace 1987).

The plastic treatments did not qualify as a valid test of the mechanisms affecting colonization inhibition or facilitation in the field because they experienced disproportionately less disturbance than the other treatments. While the exact disturbance mechanism is unknown, the polypropylene plants were anchored firmly to the trays and offered more resistance to substrate removal by sunfish. In contrast, mesocosms in the greenhouse were not disturbed and plastic treatments did not inhibit or facilitate the colonization of *H. verticillata* there.

Scale

Submersed aquatic vegetation is capable of modifying its local environment (Carter et al. 1988). The outcome of competition is influenced by a plant's abilities to lower nutrients below the tolerance level of a competitor (Tilman 1982). Resource variation within a habitat is scale dependent (Anderson et al. 2004). Because the mesocosms in the greenhouse were small (19 L) and closed to outside nutrient inputs, the effect of nutrient reduction by *V. americana* on *H. verticillata* was probably significant. Thus, one small tray (34 x 24 x 9 cm) of *V. americana* in a closed 19 L mesocosm

probably had a greater effect on the nutrient levels in the water column than the same tray in the open system at Otter Point Creek.

Management Implications

Methods for the control of invasive aquatic macrophytes such as *H. verticillata* currently include: herbicides, mechanical harvesters, and biotic controls such as grass carp (*Ctenopharyngodon idella*) and released insects. Grass carp are indiscriminate and illegal in many states, including Maryland. Control of *H. verticillata* by introduced insects has experienced very little success thus far (Langeland 1996). Herbicides have limited efficacy in moving water and are prohibited in many bodies of water. Finally, mechanical harvesters cause invasions in new areas by releasing large numbers of fragments (Owens et al. 2001).

Native plant restorations have little chance of success if initiated in patches of already existing *H. verticillata*. Although the conflicting results of the experiments do not allow me to conclude that *V. americana* would inhibit colonization by *H. verticillata* fragments, the results do suggest that pre-existing beds of native *V. americana* will not facilitate the colonization of *H. verticillata*. Indeed, a negative relationship between *V. americana* biomass and *H. verticillata* biomass was evident in the field although comparison between bare and *V. americana* treatments showed no effect on *H. verticillata* success. Additionally, experiments in the greenhouse mesocosms demonstrated that *H. verticillata* tuber production was eliminated in the presence of established *V. americana* plantings. If *H. verticillata* colonization was indeed inhibited by reduced nutrients in the water column, then reduction of nitrogen and phosphorus inputs to waterways may be a viable management option for controlling further

H. verticillata invasions. Further research in planting larger patch sizes to reduce water column nutrients locally is warranted. Finally, if water column nutrients can be decreased, mechanical harvesters may be a viable option under some circumstances.

Chapter 3: Broader Theoretical Context and Management

Implications

Non-indigenous species exhibit their effects at the individual, population, community, and ecosystem levels (Byers et al. 2002). Byers, Reichard et al. (2002) propose several guidelines to reduce the impacts of invasive species. Efforts to control invasive species should be prioritized based on the impacts of the non-indigenous species, how likely the species is to spread, system invasibility, and impact thresholds (the acceptable abundance of an invasive species before its control or the recovery of native species is unfeasible). Two of the research questions suggested by Byers, Reichard et al. (2002) to better address invasive species management are: 1.) Why do invasions fail (the need to look at numbers of propagules introduced)? and 2.) What limits the spread of non-indigenous species (climate, soils, geology, competition, etc.)?

My research has addressed some of these points by investigating the invasion success of *Hydrilla verticillata* based on propagule density and species interactions. My results did not show any strong inhibition of *H. verticillata* by *Vallisneria americana* in field experiments, but strong colonization inhibition by *V. americana* in greenhouse mesocosms. Additionally, existing *H. verticillata* patch density was strongly correlated with colonization success in the field and releasing more *H. verticillata* fragments into greenhouse mesocosms enhanced the colonization success of this species. In the following discussion I frame the results of my research into the broader context of ecological theory and aquatic plant management.

Issues of scale are a fundamental problem of ecology (Levin 1992). Conflicting results of my research were most likely a result of spatial and temporal differences in scale. The fact that colonization was inhibited by *Vallisneria americana* in the greenhouse most likely resulted from the fact that mesocosms were small and nutrients were depleted more rapidly in planted mesocosms. Alternatively, *V. americana* may have lost its temporal advantage in the field because *H. verticillata* propagules were introduced to greenhouse mesocosms 7 weeks after they probably began colonizing field mesocosms. Spencer and Ksander (2000) studied competition between *H. verticillata* and *Potamogeton nodosus*. They found that *P. nodosus* was the superior competitor when propagules of both species were pre-sprouted, but when tubers of each species were permitted to emerge on their own, *H. verticillata* experienced more initial growth and coexisted with the former species.

The scaling issue of planting size warrants further investigation. Mesocosms in this experiment were small (88 L) and closed (no nutrient and propagule inputs from the outside). *Vallisneria americana* is capable of reducing phosphate in soil pore water lower than *H. verticillata* (Wigand et al. 1997), suggesting that in mesocosm situations it has a lower R^* (Tilman 1982) and may therefore have a competitive advantage. It has also been shown that submersed macrophytes can uptake all of their mineral nutrients through their leaves (Madsen and Cedergreen 2002). In addition, water quality (dissolved oxygen, secchi depth transparency, and chlorophyll- α concentrations) is improved in dense macrophyte beds (Carter et al. 1988). Thus, because submersed macrophytes alter their environment and because *V. americana* is particularly good at reducing nutrients, it seems plausible that larger plantings of *V. americana* may limit

resources available to invading species more than smaller plantings. In addition, if *V. americana* is capable of trapping *H. verticillata* fragments, larger plantings will reduce “edge effect” (perimeter to interior ratio). In water less than 1 m, *H. verticillata* fragments might be confined to the edge. In deeper water, larger plantings would not be advantageous because *H. verticillata* fragments could drop in from above as occurs in seagrass beds colonized by macroalgae (Bell et al. 1995).

The topic of how biodiversity relates to an ecosystem’s susceptibility to invasion has received a great deal of attention recently. This relationship appears to be controlled by scale. Frequently, small areas with high diversity offer some resistance to invasion (Tilman 1997, Kennedy et al. 2002), but at the regional scale native species diversity is positively correlated with exotic species presence (Lonsdale 1999, Levine 2000). Submersed macrophyte communities in temperate zones are composed of relatively few species. Seed stratigraphy of a tidal freshwater area in Chesapeake Bay showed only six species between 340 and 1980 B.C. (Davis 1985). If the theory that increased biodiversity reduces invasion is true, then native submersed macrophyte communities in temperate zones are at severe risk of being invaded. Peterson, Allen et al. (1998) claim that functional diversity is important for recovering ecosystems after disturbance. Perhaps this is why the macrophyte community was so slow in recovering after Hurricane Agnes in 1972 (Orth and Moore 1983).

Disturbance (substrate removal by sunfish) played an important role in my experiment. Maintaining a natural disturbance regime is important to an ecosystem’s functioning and community structure (Hobbs and Huenneke 1992). However, disturbance may also increase the invasibility of a system (Hobbs 1989). For example,

physical disturbances (removal of matrix vegetation) and higher nutrients in wetland soils increase the spread of *Phragmites australis* (Minchinton and Bertness 2003). Similarly, large-scale disturbances that remove native vegetation will likely promote *H. verticillata* invasion because this is a highly opportunistic species. However, the small-scale disturbances that occurred in this experiment appeared to inhibit *H. verticillata* colonization in field experiments.

Propagule pressure and source-sink dynamics may interact in invasion ecology. Classic source-sink theory maintains that export of excess production in source habitats can maintain populations in sink habitats that would not otherwise support a population (Pulliam 1988). Environments with a high invasion resistance (Shea and Chesson 2002) could potentially be overcome by increased propagule pressure. For example, competition for resources by one species may inhibit the successful invasion of another species thus making this a sink habitat for the latter species because mortality of the invading species would exceed production. However, if the source population of the invading species produces enough propagules, the invasion resistance of the native population would potentially be reduced and permit a successful invasion. A theoretical example of this phenomenon would be a reservoir where the photic zone is dominated by a species that resists invasion by *H. verticillata*. When the occasional *H. verticillata* fragment lands in this zone, colonization is inhibited by existing vegetation. However, *H. verticillata* fragments may colonize deeper waters because its light requirements are more plastic than most species. This deepwater population could then grow and produce enough propagules (fragments) to overwhelm the competitive abilities of plants in shallow waters, thus transforming the sink population into a source population.

Finally, the use of plant harvesters to control submersed macrophytes is frequently discouraged because the process creates large numbers of fragments that can re-colonize an area or spread the invasion. If the source of the *H. verticillata* inhibition in the greenhouse mesocosms was indeed a nutrient deficiency, then harvesters might be a potential control method where water column nutrients are sufficiently low. A logical time to use a harvester would be in June or July when carbohydrate stores in *H. verticillata* are at their lowest (Madsen and Owens 1998, Owens and Madsen 1998). However, if the results of *H. verticillata* inhibition were a result of a temporal advantage given to *V. americana*, then early season cutting may actually increase the spread of *H. verticillata*. Thus, plant harvesting where native vegetation exists should be conducted later in the season.

In summary, pre-existing *V. americana* strongly inhibited tuber formation of *H. verticillata* in greenhouse experiments. In the field, although *H. verticillata* colonization was no more successful in bare treatments than *V. americana* treatments, five out of six sites showed greater *H. verticillata* tuber production in bare treatments than in *V. americana* treatments. Although I cannot explain why site 4 experienced more colonization success in *V. americana* treatments I can speculate that it may be because this site was the only one that had a relatively high biomass of existing *H. verticillata* while experiencing a low disturbance regime. I conclude that, in situations of high *H. verticillata* biomass and high disturbance, or low *H. verticillata* biomass and low disturbance, planting *V. americana* may function to reduce colonization by *H. verticillata*. *Hydrilla verticillata* tuber formation was strongly influenced by patch density in the field and the number of fragments introduced to the greenhouse

mesocosms. This would suggest that reducing fragment availability would reduce *H. verticillata* colonization success.

Future research should consider the production of axillary turion production by *H. verticillata* and how this affects the colonization success of this species in pre-existing beds of native vegetation. Because *H. verticillata* fragments were able to rest on top of plants and send roots down to the substrate, competition for light did not appear to be a factor in these experiments. Axillary turions that fall below the canopy of pre-existing vegetation may experience more competition for light. Nutrient reduction in the water column appeared to negatively affect the viability of *H. verticillata* fragments because they are dependent on these nutrients until the fragments successfully root. Although axillary turions that fall below the canopy of pre-existing vegetation may experience more competition for light, their proximity to the substrate surface may allow their roots to access nutrients more rapidly than *H. verticillata* fragments. Thus, turions may be superior to fragments in their colonization ability under low-nutrient situations.

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