ABSTRACT

Title of Dissertation: COMPARATIVE ECOLOGY OF THE INVASIVE
                                      RUBUS PHOENICOLASIUS AND THE NATIVE
                                      RUBUS ARGUTUS.

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Invasive species are one of the most significant factors in human influenced
global change. Management actions that prevent the spread and impacts of invasive
species require knowledge of their ecological characteristics. The characteristics of the
invasive wine raspberry (*Rubus phoenicolasius* Maxim.) and the native sawtooth
blackberry (*Rubus argutus* Link) were examined in two forest habitats on the Maryland
Coastal Plain. The invasive had greater negative effects on a common herbaceous plant
(*Duchesnea indica* Andr. Focke) than the native. The invasive, *R. phoenicolasius* had
higher leaf nitrogen concentrations (N_{leaf}), greater specific leaf areas (SLA) and higher
maximal rates of photosynthesis (A_{max}) for a given dark respiration rate (R_d) than *R.
argutus*. *R. phoenicolasius* depended less upon pollinators for fruit development and had
higher fruiting rates with more seeds per fruit than the native species. In addition, seeds
of *R. phoenicolasius* had higher germination rates. Survival of invasive seedlings was

negatively affected by leaf litter additions, but seedling growth was not negatively influenced by shading. *R. phoenicolasius* seedlings grown in a greenhouse and inoculated with arbuscular mycorrhizal fungi produced less biomass than seedlings that were not inoculated. The distribution of *R. phoenicolasius* may be affected by leaf litter, but presence of AMF is probably not necessary for seedling success. A three year demographic study showed that both species were negatively impacted by drought, but the invasive recovered faster than the native species in the higher light forest.

Overall, results of these studies indicate that the invasive *R. phoenicolasius* was more likely to competitively exclude understory herbs which can coexist with the native *R. argutus*. The ability of *R. phoenicolasius* to adapt physiologically to different light levels helps explain its ability to form dense populations under varying environmental conditions. The combination of high fruit production, plasticity and lower mortality in high light habitats is in agreement with previous studies on invasive species. The combined characteristics demonstrated by *R. phoenicolasius* allow this invader to spread, expand and persist in mid-successional forests in the Coastal Plain of Maryland.

COMPARATIVE ECOLOGY OF THE INVASIVE *RUBUS PHOENICOLASIUS* AND
THE NATIVE *RUBUS ARGUTUS*

by

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For my husband William Innis
and my family
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TABLE OF CONTENTS

TABLE OF CONTENTS continued

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES continued

Chapter 1

Introduction

Comparative ecology of the invasive *Rubus phoenicolasius* and the native *Rubus argutus*

Invasive species are second only to habitat destruction as the cause of native species extinctions across the world. Extinction by habitat destruction is like death by automobile accident: easy to see and assess.

Extinction by the invasion of exotic species is like death by disease: gradual and insidious requiring scientific methods to diagnose.

E. O. Wilson 1997

The impacts of invasive species on global ecosystems have been of increasing interest since the publication of Elton's *The Ecology of Invasions by Animals and Plants* in 1958 (Kennedy *et al.* 2002, Simberloff 2004). While these impacts are particularly acute on island systems, the effects of invasives on continental habitats are also critical to native species diversity and community integrity (Vitousek *et al*. 1997). Theories of the competitive superiority of invasive species attempt to explain patterns of high invasive biomass and competitive effects in invaded habitats. Blossey and Notzold (1995) proposed the Evolution of Increased Competitive Ability (EICA) hypothesis, which states that since invasives are removed from co-evolved herbivores and pathogens, resources previously put towards defense are invested in growth and competitive abilities. Callaway and Ridenour (2004) suggested an addition to this theory in which invasives also possess "novel biochemical weapons", including allelopathic chemicals or favorable interactions with their new soil microbial communities.

1

Determining what characters make an exotic species a successful invader has proven difficult. The characteristics of weeds that Baker put forth in 1974 are still being examined to determine if they pertain to invasive species (Baker 1974, Parker 1997, Rambuda and Johnson 2004, Sutherland 2004). Rejmanek (1996) compiled characteristics of plant invaders from studies of more than 20 species of *Pinus.* Seedling relative growth rates with higher specific leaf areas, small seed masses and short generation times were the strongest predictors of invasiveness (Rejmanek 1996, Rejmanek and Richardson 1996, Grotkopp *et al*. 2002, Richardson and Rejmanek 2004).

The qualities leading to habitat invasibility are still being debated. Habitats where invasives experience positive feedback with the soil biota, while native or rare species have negative feedbacks, are often susceptible to invasion by exotic species (Klironomos 2002, Callaway *et al*. 2004b). The role of available resources and local species composition on the invasibility of habitats remains equivocal. At the forefront of the debate are two researchers working on long-term grassland studies, John Grime in England and David Tilman in Minnesota. Grime's group determined that species diversity does not influence habitat invasibility, instead the presence of bare ground and unutilized resources such as nutrients and light allow for invasion (Burke and Grime 1996, Thompson *et al*. 1996, Davis *et al*. 2000). Tilman's group has data supporting a role for higher species diversity leading to greater resistance to invasion regardless of resource availability and bare ground (Tilman 1999, Tilman 2000). However, the

characteristics of successful invasive species and susceptible habitats are still not well understood (Union of Concerned Scientists 2001, Mooney and Cleland 2001).

The history and impacts of invasives: The introduction of species beyond their natural ranges is not a new phenomenon. Before the era of European colonization, species were introduced into areas of Micronesia and Polynesia as early as 30,000 BC. What is alarming about the current introductions is the rate at which invasions are occurring. Since WWII there has been an increase in human trade and travel, which allows for intentional introductions through forestry, horticulture, and agriculture, as well as unintentional invasions through transport in crating materials, vehicles, and ship ballast (Cox 1999). The path to invasion begins with survival in transport, successful establishment, and a lag period followed by spread and eventual ecological impacts (Sakai *et al* 2001). By 2001 it was estimated that there were over 120,000 established invasive plant and animal species in the United States, United Kingdom, Australia, South Africa, India and Brazil (Pimentel *et al.* 2001). In the United States alone there are 50,000 invasive species, estimated to cost the economy $137 billion dollars a year (Simberloff 1996, Schmitz and Simberloff 1997, Pimentel *et al*. in 2000). This number remains speculative as it is difficult to estimate ecological costs.

Invasive species cause ecological harm through increasing the frequency and severity of fires, altering geochemical cycles and outcompeting native species. In the west, cheat grass (*Bromus tectorum*) was introduced from Eurasia in the late 1800's. *B. tectorum* produces high levels of litter which decomposes slowly, encouraging fires that destroy

local woody plants, allowing for more grasses to establish (Mooney and Cleland 2001). In Florida *Melaleuca quinquenervia* was introduced intentionally to aid in drying the Everglades, but it forms dense monocultures and leads to an increase in fires. It now occurs in over 600,000 hectares and easily resprouts from roots or germinates from seed following fires (Shrader-Frechette 2001). In Hawaii, volcanic flows are colonized by the invasive *Myrica faya* which is capable of fixing nitrogen at significantly greater levels than native species, increasing available nitrogen in the system (Vitousek *et al.* 1987). This has resulted in the elimination not only of low-nitrogen adapted native plant species, but also the insect herbivores and mutualists that depended upon these plants.

Characteristics of invasives and habitat invasibility: Successful invaders often demonstrate high levels of plasticity that allow them to succeed in a wide range of habitat conditions (Claridge and Franklin 2002). However, greater plasticity does not adequately explain the success of all invaders. Perhaps even more important are rates of biomass accumulation and higher reproductive output due to escape from native herbivores and pathogens. Invasives, released from their natural enemies, no longer need to invest in defense, instead directing energy toward growth (Blossey and Notzold 1995, Jakobs *et al.* 2004). In addition, the use of allelopathic chemicals may have a stronger effect on native species in invaded habitats than they do in the invasive's home range (Callaway and Aschehoug 2000, Callaway and Ridenour 2004). Long-term species associations allow co-evolution of tolerance to the biochemical effects of neighbors. This tolerance is absent in new associations in novel habitats. Increased physiological efficiency has also been explored as a reason for invasive success. This takes the form of lower tissue construction

costs, higher specific leaf areas, higher photosynthetic rates and greater transport capacities for water in invasive compared to native species (Forseth and Teramura 1987, Pattison *et al*. 1998, Nagel and Griffin 2001, Smith and Knapp 2001).

In investigating the characteristics that Baker (1974) proposed for successful weeds, Sutherland (2004) found that invasives were more likely to have an annual or biennial life history than a perennial lifespan. There has also been support for Baker's supposition that self-compatibility aids in invasion of novel habitats (Rambuda and Johnson 2004). Through studying the genus *Pinus* for characteristics of invasiveness, Rejmanek *et al*. (1996) determined that invasive woody species had small seed mass, short juvenile period and frequent seed production (Rejmanek 1996, Rejmanek and Richardson 1996, Grotkopp *et al*. 2002, Richardson and Rejmanek 2004).

Theories on habitat invasibility are linked with theories on ecosystem function and community assembly (Case 1990). Kennedy *et al*. (2002) summarized the influence that biodiversity has on invasion dynamics. At small scales, evidence has shown that as communities become more diverse they become less susceptible to invasion, however, at larger scales, the reverse has been shown (Levine 2000, 2001). Tilman found that communities become more stable, productive and resistant to invasion as diversity increased (Tilman 1999, 2000). However, Chapin *et al*. (2000) suggested that the likelihood of invasion both increased and decreased with species richness. In riparian habitats, an increase in diversity led to an increase in invasion. At a small scale, Chapin *et al*. agreed that diversity reduced invasion but at the level of communities there was an

increase in invasion. An examination of 40 years of data found that it may not only be

species richness but community-level influences that determine invasibility (Meiners *et*

al. 2004). In scrub and dune habitats, for example, disturbance did not influence invasion,

but it was a determining factor for invasives in grasslands (D'Antonio 1993, Burke and

Grime 1996, Thompson *et al*. 1996).

Another hypothesis for habitat invasibility involves resource availability. A habitat is not

static and the available resources change from year to year. This may cause

corresponding changes in susceptibility to invasion when there is an excess of resources.

Resources may be made available through disturbance, weather changes or a declining

native population (Davis *et al*. 2000).

The study described in this thesis focuses on two *Rubus* species (family Rosaceae)

growing in two forested habitats of the same age but with different levels of resources.

This approach was used in order to examine interactions between habitats for an invasive

species, *Rubus phoenicolasius* Maxim., compared to a native congener, *R. argutus* Link.

The two forested habitats, locally known as Fox Point and Corn Island, differ in the

amount of light and nitrogen available to the two species. Fox Point is a large undisturbed

mid-successional deciduous forest surrounded by both water and mature forest. Corn

Island is a narrow (50m x 1km) mid-successional deciduous forest bisected by a dirt road

and surrounded by cornfields. Corn Island has significantly higher light levels, higher soil

nitrate levels and more acidic soils than does Fox Point. I examined theories on the

characteristics of invasive species and their interaction with invaded habitats to determine

the bases for the aggressive spread of *R. phoenicolasius*. I measured photosynthetic gas exchange physiology for both *Rubus* species at both forests to determine if more efficient photosynthetic gas exchange responses would aid the success and survival of *R. phoenicolasius*. I compared the competitiveness of *R. phoenicolasius* and *R. argutus* on a common understory herb (*Duchesnea indica* Andr. Focke). I examined population demography, and quantified asexual as well as sexual reproduction in both species and forests to determine if the invasive had greater potential for population growth. The importance of fungal soil communities and microhabitat were investigated for their role in the establishment and growth of invasive seedlings. A description of each chapter in the dissertation follows.

Chapter 2

Comparative gas exchange physiology in two contrasting forest habitats for two *Rubus* species, an invasive and a native

Invasive species are often reported to produce greater biomass and higher net primary productivity than native species with similar growth forms (Blank and Young 2002, Ehrenfeld 2003). To test whether this observation holds in the *Rubus* system, I compared morphology and gas exchange physiology of *R. phoenicolasius* to *R. argutus* in two contrasting forest habitats. I hypothesized that the aggressive spread of *R. phoenicolasius* may be partially explained by greater rates of leaf-level photosynthesis. I further hypothesized that this photosynthetic advantage would be enhanced in the higher light, higher nitrogen Corn Island forest, indicating greater photosynthetic plasticity in the invasive species relative to the native species.

Chapter 3

The competitive impacts of native and invasive species of *Rubus* on a common understory plant in a deciduous forest

Invasive species may negatively impact local plant communities through exploitative competition for limiting resources. However, differential competitive abilities of invasive and native species are not always evident. In a recent review on the competitive abilities of invasive species, Vila and Weiner (2004) called for studies that compared the impacts of invasive and native species on a third "target" species. I adopted such an approach by comparing the size and number of individuals of *Duchesnea indica,* a common naturalized herb that occurs in both forest sites and is found growing with *R. phoenicolasius* or *R. argutus.* I asked: Does *R. phoenicolasius* have a greater impact on the abundance of *D. indica* than *R. argutus*? I hypothesized that *R. phoenicolasius* would have a greater impact on *D. indica*, than *R. argutus,* indicated by greater reductions in the size and number of individuals in plots. Data supporting this hypothesis would imply that *R. phoenicolasius* is more likely to competitively exclude species that coexist with *R. argutus*.

Chapter 4

Comparative population demography of an invasive and native *Rubus* in two contrasting deciduous forest habitats

To quantify subtle differences between species characteristics and interactions with habitat, a 2001 review by Sakai *et al*. recommended demographic studies of closely related invasive and native species across different habitats. Accordingly, I monitored

yearly changes in shoot (cane) density and fruit production in permanent plots in both

forests from 2002-2004. I hypothesized that individual and population growth of *R.*

phoenicolasius would exceed that of *R. argutus*. I also hypothesized that rapid individual

and population growth rates would be better supported in high resource environments for

both species. Predictions from these hypotheses are as follows: The invasive would have

higher densities, higher rates of cane production, lower rates of cane mortality, higher

rates of fruit and seed production, and higher rates of clonal propagation than the native

species; and that both species would increase density, cane production, fruit and seed

production, clonal propagation and decrease mortality in the high resource habitat.

Chapter 5

The relative roles of asexual and sexual reproduction in the success of the invasive

Rubus phoenicolasius

Traits of successful invasive plant species in novel habitats with limited opportunities for

outcrossing often include self-compatibility and vegetative spread. A key step in

successful sexual reproduction for forest understory species is seedling establishment. I

focused on both of these aspects of population spread in this chapter. I examined the

dependence of fruit set on pollinator visitation for both species through a series of floral

bagging manipulations. I hypothesized that *R. phoenicolasius* would have higher rates of

self-compatibility than *R. argutus*. I also quantified seedling survival for *R.*

phoenicolasius using manipulations of shade and litter depth. I hypothesized that seedling

survival would decrease with increased shade and increased litter depth. Decreased

survival under these conditions would imply that the invasive establishes best in disturbed sites relatively free of litter and under gaps in the forest canopy.

Mutualisms with arbuscular mycorrhizal fungi are important to the establishment and growth of most forest species. As a novel species in the eastern deciduous forest, I hypothesized that *R. phoenicolasius* would require successful inoculation by mycorrhizae in order to establish itself. I further hypothesized that mycorrhizae collected from roots of *R. phoenicolasius* would have greater positive effects on growth of *R. phoenicolasius* than would soil mycorrhizae associated with *R. argutus*. Accordingly, I conducted a greenhouse study on the comparative growth of *R. phoenicolasius* inoculated with arbuscular mycorrhizae from different soil and root sources.

Since partners for sexual reproduction may be limited in invasive species, I quantified the frequency of asexual reproduction in field populations of both *R. argutus* and *R. phoenicolasius*. I hypothesized that *R. phoenicolasius* would have greater levels of asexual reproduction than *R. argutus*. I also hypothesized that asexual reproduction would differ within patches of each species with greater asexual reproduction on the edges of patches.

Chapter 2

Comparative gas exchange physiology in two contrasting forest habitats for two *Rubus* species, an invasive and a native

Abstract

Invasive species are having extensive impacts on global ecosystems. Both the characteristics of an invasive species and those of the invaded habitat determine if an invasion will be successful. This study compares the photosynthetic gas exchange responses to light of two *Rubus* species in two contrasting forest habitats. My objective was to examine potential bases for the rapid growth and spread of the invasive species relative to a closely-related native congener. The invasive *R. phoenicolasius* had a significantly higher ratio of maximum photosynthetic rates (A_{max}) to dark respiration (R_d), higher leaf nitrogen concentrations (N_{leaf}) and specific leaf areas (SLA) than the native *R. argutus*. There were also significant differences in gas exchange with habitat as both species had higher A_{max} and photosynthetic nitrogen use efficiency (PNUE) and water use efficiency (WUE) in the forest with higher ambient light levels. The higher photosynthetic rates of *R. phoenicolasius* in higher light habitats, combined with lower tissue costs helps to explain its ability to be an aggressive invader in the eastern deciduous forest biome.

Introduction

As a general rule of thumb, there are 1000 non-native species introduced to novel habitats for every one that becomes a successful invader (Williamson and Fritter 1996). Scientists have had limited success in predicting which introduced species will become invasive and which habitats are more susceptible to invasion (Radosevich *et al.* 2003). The large ecological variation in invasive species as well as in the habitats they invade, has made it difficult to propose a unifying theory that appropriately describes invasive dynamics (Lambrinos 2002). Lacking a general theory, the construction of a library of case studies of habitat - invasive species interactions provides a mechanism that adds to our basic knowledge of species interactions and community structure, and will provide a foundation for advances in the ecological theory of invasive species (Meekins and McCarthy 2001).

Invasive plant species tend to have higher growth rates than native species, resulting in greater biomass production and net primary productivity (Blank and Young 2002, Morris *et al.* 2002, Ehrenfeld 2003). But what explains the faster growth rate of invasive species? In general, invasives have been shown to have higher photosynthetic rates, higher specific leaf areas (SLA, unit area per unit mass), higher leaf N (N_{leaf}), greater photosynthetic nitrogen use efficiency (PNUE), in addition to lower leaf construction costs (Baruch and Goldstein 1999). Thus, not only are they physiologically more efficient than native species, but also often have higher absolute rates of photosynthetic carbon gain. For example, *Lythrum salicaria* and *Alliaria petiolata,* two highly invasive species, produced greater biomass with lower tissue construction costs than species native to their

new habitats (Nagel and Griffin 2001, Smith and Knapp 2001). In Hawaii, 30 invasive

species were found to have higher photosynthetic rates, SLA, N_{leaf}, and PNUE than 34

native species (Baruch and Goldstein 1999). Previous studies on the invasives *Rubus*

discolor and *R. laciniatus* compared to the native species *R. ursinus* and *R. leucodermis*

in the Pacific Northwest forests of the United States found some of these patterns, but not

all (McDowell 2002). McDowell found that the invasive *Rubus* species had comparable

leaf construction costs and lower, rather than higher N_{leaf}. However, higher maximal rates

of photosynthesis for a given dark respiration rate, greater PNUE and higher water use

efficiencies (photosynthesis/transpiration) were major traits distinguishing the invasive

species from the natives.

With their rapid growth, competitive abilities and novel growth forms, invasive species

often have dramatic impacts on the native species within the habitats that they colonize

(Shrader-Frechette 2001, Mooney and Cleland 2001, Claridge and Franklin 2002, Jakobs

et al. 2004). Invasive species such as kudzu (*Pueraria montana*) can overtop trees and

sub-canopy dominants, out-competing natives for light (Forseth and Innis 2004). In South

Africa, the invasive *Acacia cyclops* reduced light availability to two native *Rhus* species,

suppressing their growth (Midgley *et al.* 1992). In New Zealand and Australian forests,

the presence of an invasive *Tradescantia fluminensis* resulted in shading and a reduction

in seedling establishment (Standish *et al.* 2001). *Bromus tectorum*, an invasive grass in

the western United States outcompetes native grasses for water by allocating more

biomass to root tissues and maintaining root elongation longer into the growing season

(Harris 1967).

Invasive species can have large impacts on hydrology and biogeochemical cycles in invaded habitats in addition to their effects on native species (Gordon 1998). Litter production by invasives may either increase or decrease rates of decomposition and nutrient cycling, depending on its refractory nature (Mooney and Cleland 2001, Ehrenfeld 2003). Higher decomposition rates result in additional nutrient influxes into colonized habitats. This may increase soil N levels, reducing the occurrence of low nitrogen adapted native species (Ehrenfeld 2003). Nitrogen fixing invasives can facilitate further invasions by species adapted to high soil N levels. *Chamaecrista nictitans* a nitrogen fixing invasive made it possible for the invasive *Pennisetum setaceum*, to establish in Hawaiian grassland (Carino and Daehler 2002).

Habitat qualities also influence the success of invasive species. Resource availability plays an important role, especially soil nitrogen and light availability. *Alliaria petiolata* is typical of invasives that perform well only under high light conditions, where maximum photosynthesis occurs (Dhillion and Anderson 1999). Hughes and Fahey (1991) found that experimental canopy removal facilitated colonization of a northern forest by *Rubus ideaus* (Ricard and Messier 1996). Fast-growing, resource-consuming invasives are also aided by high levels of soil nitrogen. The invasive *Phragmites australis* showed a greater response in biomass to increased nitrogen than the native *Spartina pectinata* (Rickey and Anderson 2004).

Disturbed habitats generally have higher light and soil nutrient levels than adjacent, undisturbed areas, especially in forests. There is often a strong association between recent disturbance and invasive species colonization (Meekins and McCarthy 2001). Fewer invasions are reported in climax communities, notably old forest (Robertson *et al.* 1994).

In this study I examined the photosynthetic gas exchange characteristics of an invasive and native *Rubus* species in two forest habitats. Both forest sites are the same age, but differ in the amount of available light and soil nitrogen. By comparing two related species with similar growth forms in different habitats, I hoped to distinguish key characteristics of the invasive species that provide for its success. In examining two forest habitats, one of higher light, higher nitrogen and one of lower light, lower nitrogen I was able to evaluate the importance of differing abiotic conditions on the relative performance of the invasive and the native species.

I hypothesized that the aggressive spread of *R. phoenicolasius* may be partially explained by greater rates of leaf-level photosynthesis. This would be reflected in a greater maximum photosynthetic rate (A_{max}). I also hypothesized that the invasive would be more resource use efficient than the native species. Accordingly, I quantified light use efficiency by measuring quantum yield (A_{qe}) and light compensation point (LCP), photosynthetic nitrogen use efficiency (PNUE), leaf nitrogen concentrations (N_{leaf}) and specific leaf area (SLA) in both species.

I further hypothesized that the photosynthetic advantage for the invasive species would be enhanced in the forest with higher light and higher nitrogen conditions, indicating greater photosynthetic plasticity in the invasive species relative to the native species and a greater ability to utilize high resource levels for rapid growth.

Methods

Study species

The invasive species, *Rubus phoenicolasius* is originally from temperate Japan, Korea and China. *R. phoenicolasius* was introduced in the 1890's possibly through John Lewis Childs who ran a mail order seed company in Floral Park, New York (Hummer 1995). In the US, *R. phoenicolasius* can currently be found in fields and forests in the eastern coastal states. Co-occurring in this range is the native species, *Rubus argutus* (Alice and Small 1999). Both *Rubus* species produce biennial canes from a perennial root stalk. In the first year growth is entirely vegetative (primocane), with carbon allocation primarily into leaf production and elongation. Canes on average are 0.5 meters to 1.5 meters in length. In Maryland, both species are deciduous and lose their leaves in late November. In the following April, the second year canes (floricanes) produce new leaves with *R. phoenicolasius'* leaves appearing approximately 2 weeks prior to those of *R. argutus*. The 14 days that *R. phoenicolasius* has expanded leaves, in addition to the 210 day period that both species have leaves, translates to at least a 6% advantage for seasonal carbon gain in the invasive (Carter and Teramura 1988). This is a conservative estimate, as the light available for photosynthesis in April is higher than that in succeeding months due to the leafing out of canopy trees. In early May, new primocanes originate from the perennial

16

root stock that also supports primocanes that have transformed into floricanes. In late May second year canes may produce flowers and fruit production occurs in late June to July.

Study site

The Smithsonian Environmental Research Center (SERC), Edgewater, MD, USA (~10 km SSE of Annapolis, 38°53' N, 76°33' W) consists of 1,000 hectares of protected field and forest habitats that are typical of the region (Brush *et al.* 1980). Prior to the 1950's much of SERC property was farmland with fields for grazing cattle and cultivating alfalfa and corn. After the 1950's, the majority of the fields went fallow and forest succession began. In the 1970's the property was given to the Smithsonian Institution and the environmental research center was started. Today, the mid-successional forests on SERC are between 50-60 years of age (Dr. Geoffrey Parker, Research Scientist SERC, *pers. communication*). For this study, two separate forest sites were used, Fox Point and Corn Island. Fox Point is a large undisturbed mid-successional forest which is surrounded by mature forest. Corn Island is a narrow (50m x 1km) mid-successional forest that is divided into two approximately equal parts by a dirt road through the middle. Both sections of the Corn Island forest are bounded on the outer edge by active agricultural fields. Due to the fact that the Corn Island forest is primarily edge habitat, the Corn Island forest has higher light levels (Meiners *et al.* 2002b). Forests types were not replicated, with one higher light and one lower light habitat, so there is a limitation in the ability to generalize these results.

<u>Physiology and morphology</u>

Photosynthetic measurements were taken on seven randomly selected primocanes from each species, at each of two sites in Fox Point and Corn Island forests (total 28 primocanes per species). Measurements were made in July 2003, the middle of the growing season. Primocanes were chosen because it is during the first year that plant's resources are put into producing biomass, compared to the floricanes where resources are divided between producing fruits and biomass (Whitney 1982, McDowell and Turner 2002). I measured leaves that were fully expanded, which were about 4 leaves away from the apical meristem. Photosynthesis was measured using a Li-Cor 6400 open flow gas exchange system with a light source (Li-Cor, Lincoln Nebraska, USA). Net photosynthesis (A) was measured over a range of photosynthetic photon flux (PPF), 1800, 1400, 1000, 600, 100, 50, 25, 0 μmol m^{-2}s^{-1}, to generate a photosynthetic light response curve. Temperature (30°C), CO_2 concentration (370 ppm), and relative humidity (50%) were held constant inside the cuvette during these measurements (Durand and Goldstein 2001, Smith and Knapp 2001, McDowell 2002).

The leaves used for photosynthetic measurements were removed from the cane and combined with 30 other leaves collected from each species in each site to determine SLA and N_{leaf}. Leaves were immediately placed in wet paper towels and refrigerated for up to 48 hours prior to determination of leaf area with a LiCor leaf area meter (Li-Cor, Lincoln Nebraska, USA). Leaves were then dried at (60°C) to a constant weight. SLA was

calculated by leaf area/leaf dry mass. N_{leaf} was determined as percent dry mass using a PerkinElmer CHN 2400 tissue analyzer (PerkinElmer Wellesley, MA).

Abiotic measurements

Light levels and soil conditions were measured in Corn Island and Fox Point forests over a three year period. Each year measurements were taken at nine sites within each forest, for a total of eighteen sites (four of the eighteen sites were used in the physiology study). These sites were chosen for the presence of both *R. phoenicolasius* as well as *R. argutus*, and all sites were used for a separate demographic study (Chapter 4). Light levels were measured in August 2002, 2003 and 2004. In 2002, at each of the 18 sites a photo was taken with a fish-eye lens converter (Nikon FC E8) at a height of 1.5m using a Canon digital camera in the center of the patch of *R. phoenicolasius* and *R. argutus* (36 total photos). In 2003 and 2004 at each site photos were taken at a point between the patches of the two species (18 total photos). In 2003, five additional photos were taken at each site where physiology measurements were made (20 total photos). Photos were imported into HemiView 2.1 software and analyzed for visible sky which is described in three forms: global site factor (GSF), direct site factor (DSF) and indirect site factor (ISF) (Whitmore *et al.* 1993).

Soil samples were collected in August 2002, 2003 and 2004. In 2002 samples were taken from all nine sites in each forest. In 2003 and 2004 four sites were sampled from each forest. At each site, three 7 cm diameter soil cores were taken to a depth of 15cm, which is the depth of most of the roots of *R. phoenicolasius* and *R. argutus*. The cores from each

site were combined and sifted together to form a composite sample from which a 30 g

(dry weight) subsample was used for nutrient analyses. In 2002 the samples were

analyzed for pH and nitrate concentrations at the Maryland Cooperative Extension, Soil

Lab of the University of Maryland. In 2003 and 2004 samples were analyzed for pH and

nitrate concentrations at the Agricultural Analytical Service Laboratory at Pennsylvania

State University (Eckert and Sims 1995, Griffin 1995).

Analysis

To determine maximum photosynthetic rate (A_{max}), apparent quantum yield (A_{qe},

photosynthesis/incident light) and the light compensation point (LCP, light level where

net photosynthesis = 0) a nonlinear response curve (Mitscherlich model Eq. 1) was

combined with a mixed model in a SAS 8.1 analysis (Peek and Russek-Cohen 2002).

$A = A_{max} [1 - e^{-A_{qe}(PPF-LCP)}]$

In the Mitscherlich model A_{max} is the asymptote of photosynthesis in high light, A_{qe} is the

slope at low light, and LCP is the x intercept which occurs when net photosynthesis is

zero. The use of a mixed model analysis can more accurately determine error for the

repeated measures made on the same leaf to generate a photosynthetic light response

curve. Simple effects and main effects were compared between species and between

forests. Dark respiration (R_d) is the respiration at 0 PPF and the ratio of A_{max} to R_d was

calculated. Water use efficiency (WUE) is calculated as A_{max}/stomatal conductance (g), at

the highest light level (1800 μmol m^{-2} s^{-1}). Photosynthetic nitrogen use efficiency

(PNUE) was calculated by using A_{max}/ N_{leaf}. To determine SLA, 148 leaves per species

were measured for leaf area and dry weight. Twelve leaves from each site were analyzed

for N_{leaf}, seven from physiology measurements plus five additional leaves (a total of 48 leaves per species). A_{max}/Rd, WUE, PNUE, SLA and N_{leaf} were analyzed using a two-way ANOVA, with species and forest habitats as fixed effects. Global site factor and soil nitrogen were analyzed with a one-way ANOVA. Soil data were log transformed, original means are presented in graphs. All analyses were conducted in SAS 8.1 and a P value of .10 or smaller was considered significant (SAS 2004).

Results

Physiological measurements

There were no significant differences between species for light saturated photosynthetic rates ($F_{1,53}$=0.61, P>.05), although there was a trend for higher A_{max} in *R. phoenicolasius* (Fig. 1). There were significant differences between forests, with plants at Corn Island having higher A_{max} corresponding to the higher ambient light levels in this forest ($F_{1,53}$=15.27, P<.01). There were no significant differences in quantum yield (A_{qe}) between species ($F_{1,53}$=1.52, P>.05) or between forests ($F_{1,53}$=1.92, P>.05). There were no significant differences in light compensation point (LCP) between species or forest ($F_{1,53}$=0.47, P>.05) and ($F_{1,53}$=0.82, P>.05) respectively (Table 1). A_{max} divided by N_{leaf}, photosynthetic nitrogen use efficiency (PNUE) was higher for both species in Corn Island compared to Fox Point ($F_{1,52}$=9.06, P=.004) (Fig. 2), but there were no differences between species ($F_{1,52}$=0.18, P>.05).

The invasive *R. phoenicolasius* had significantly higher N_{leaf} than the native *R. argutus* ($F_{1,91}$=5.94, P=.02). There was no difference in N_{Leaf} between forests ($F_{1,91}$=1.43, P>.05)

(Fig. 3). There was also no significant interaction between species and forest ($F_{1,91}$=3.03, P>.05).

SLA was significantly larger for the invasive species ($F_{1,293}$=304.68, P<.01). A higher SLA indicates that per unit weight the invasive has more leaf surface area, which allows for greater photosynthesis per unit mass. Also there was a significant difference between forests with SLA being greater in Fox Point for both species ($F_{1,293}$= 49.96, P<.01) (Fig. 4). There was a significant interaction between forests ($F_{1,293}$= 4.89, P>.01). Due to the interaction, differences in simple means were examined to determine if main effect differences could be used. All SLA simple mean differences had P values <.0005. *R. phoenicolasius* had a higher ratio of A_{max} to dark respiration (A_{max}/Rd) than *R. argutus* ($F_{1,52}$= 2.74, P=.10). In addition both species had higher water use efficiency (WUE) in the Corn Island forest ($F_{1,52}$= 3.92, P=.05). ANOVA results for PNUE, $N_{leaf,}$ and SLA, A_{max}/Rd, WUE data are summarized in Table 2.

Light and soil measurements

Fish eye photos were analyzed for three characteristics of solar radiation: global site factor (GSF), direct site factor (DSF) and indirect site factor (ISF). In 2002, the sites in Corn Island had significantly higher GSF than the sites in Fox Point ($F_{1,34}$=4.72, P= .04) (Fig. 5). The same pattern can be seen with DSF ($F_{1,34}$=4.86 P=.03) however the indirect site factor did not differ between forests ($F_{1,34}$=2.98, P=.09) (Fig. 5). Both forests are the same age, yet Corn Island is effectively an edge habitat, so there are higher light levels.

Similar values were measured during the 2003 and 2004 growing seasons (data not presented).

In 2003, photos were also taken at each of the sites where physiological measurements were made on individual primocanes. The sites in Corn Island had consistently higher light levels than those in Fox Point, GSF ($F_{1,18}$=50.78, P<.01), DSF ($F_{1,18}$=43.95, P<.01), ISF ($F_{1,18}$=54.83, P<.01) (Fig. 6).

In 2002 and 2003, soil nitrate levels in the Corn Island forest were significantly higher than those at Fox Point, ($F_{1,23}$=27.13, P<.01) and ($F_{1,6}$=23.08, P<.01), respectively. In 2004, significant differences in soil nitrate between sites were not detected ($F_{1,4}$=.47, P>.05). In 2002 and 2004 soil pH in Fox Point was less acidic than Corn Island ($F_{1,23}$=19.27, P<.01) and ($F_{1,4}$=7.87, P<.05), respectively. Soil pH was not significantly different in 2003 ($F_{1,6}$=1.46, P>.05) (Table 3).

Discussion

Invasive species have been shown to grow larger and produce more biomass than their native counterparts (Blank and Young 2002, Ehrenfeld 2003). One explanation for this size difference is that invasive species are more physiologically efficient and capable of greater photosynthetic rates. In Hawaii, invasive trees were larger, had higher maximum photosynthetic rates and higher nitrogen use efficiency than did native species (Durand and Goldstein 2001). My results showed that the invasive *R. phoenicolasius* did not have significantly higher A_{max} compared to the native *R. argutus* (Fig. 1). Nor did *R.*

23

phoenicolasius have greater PNUE than *R. argutus* (Fig. 2). However, in agreement with McDowell (2002) and Pattison *et al.* (1998), *R. phoenicolasius* had higher A_{max}/R_d than *R. argutus*, indicating a greater photosynthetic return on carbon used for dark respiration. A higher ratio of A_{max} to R_d minimizes carbon costs and can lead to greater biomass production. I found higher leaf nitrogen concentration and greater SLA in *R. phoenicolasius* relative to *R. argutus*. Greater levels of leaf N may provide greater photosynthetic capacity in higher light environments than I measured, but this was not detected in the two sites that I measured photosynthesis in. Greater SLA, greater surface area per mass could provide a significant advantage for the invasive. It would allow the plant to develop more leaf area for a given amount of carbon investment compared to the native. This, combined with equal photosynthetic rates would allow for greater canopy development and vegetative growth (Fig. 4) (Nagel and Griffin 2001, Baruch and Goldstein 1999, Durand and Goldstein 2001).

Physiology on its own does not offer a complete explanation of a successful invasion. The presence of resources in a habitat determines whether a plant will be capable of reaching its photosynthetic potential. I predicted that in the higher light, higher nitrogen Corn Island forest both species would have greater A_{max} than the Fox Point forest. I measured significantly higher direct and indirect light factors in the Corn Island forest than the Fox Point forest (Fig. 6). This was expected as the Corn Island forest is comprised of two narrow strips, 50m wide on either side of a dirt road and surrounded by fields. Forest edges are subject to greater disturbance than forest interiors with forest edges receiving greater light levels (Gascon *et al*. 2000). In general, invasive species are

more successful in disturbed and edge habitats (Goldblum and Beatty 1999, Larson 2003). *Rubus* species have been shown to produce greater biomass and increase reproduction in forest canopy gaps (Whitney 1986, Hughes and Fahey 1991, Ricard and Messier 1996). The invasive *Alliaria petiolata* had higher A_{max} in higher light forests (Dhillion and Anderson 1999). In a greenhouse study in Hawaii, invasive species and native species were exposed to different light levels. Invasives had higher maximum photosynthetic rates and increased growth rates in higher light treatments (Pattison *et al.* 1998). While I did measure greater WUE, higher values of A_{max}, and higher PNUE in the higher light Corn Island forest (Figs. 1,2, Tables 1,2), these values were increased in both the native and invasive species, with no significant difference between them. Light limitation was eased in Corn Island leading to higher A_{max} which led to higher WUE and PNUE values. It is possible that the light differences in the forests were not large enough to detect any differences in photosynthetic capacity between the species. Photosynthetic capacity in C_3 plants is positively related to leaf nitrogen concentration, so the higher leaf nitrogen levels of *R. phoenicolasius* suggests that this species may be able to increase A_{max} to a greater extent than *R. argutus*, but I did not detect that response here.

The soil samples taken from both forests showed significant differences between soil nitrogen and pH, in two of the three years. The higher nitrate levels and lower pH in soils at Corn Island (Table 3) were most likely due to its proximity to an active agricultural field (Jordan and Weller 1996, Vitousek *et al.* 1997, Jordan *et al.* 1998). Soil nitrogen has been found to play a role in the success of invasive species. For example, in a Mojave Desert experiment, nitrogen addition led to increased density and biomass in invasives

25

such as *Bromus madritensis* and *Schimus arabicus, S. barbarus* and *Erodium circutarium* (Brooks 2003)*. Although soil N levels were higher in Corn Island*, there were no significant differences in N_{leaf} between forests. However, SLA was lower in the higher light, Corn Island forest (Fig. 4). This demonstrates plasticity in the ability of both species to efficiently capture light in lower light forests, and increase leaf thickness in higher light habitats (Tremblay and Larocque 2001). The ability of the invasive to efficiently utilize light in both high and low light conditions suggests that the invasive may be able to persist in older forests following gap closure.

In summary, the invasive *R. phoenicolasius* had significantly greater A_{max}/R_d, SLA and N_{leaf} than its native congener *R. argutus*. Although A_{max} and PNUE were not significantly different between species, greater SLA and N_{leaf} may allow the invasive to increase photosynthesis in higher light environments than were measured in this study. To fully investigate the ability of the invasive to survive in a range of light levels, physiological measurements should be taken across a wider range of light levels. Greater SLA for *R. phoenicolasius* translates to higher photosynthetic rates on a leaf mass basis than *R. argutus*. Thus, the invasive is able to build more light collecting leaf area for an equivalent carbon investment compared to the native. This less expensive leaf construction may provide the invasive with a competitive edge relative to the native species in forest interior and edge habitats. The physiology and ability of *R. phoenicolasius* to adapt to different light levels may help explain its size and density in its invaded habitats. Habitat also influenced the presence and success of *R. phoenicolasius.* Both species had higher WUE, A_{max} and PNUE in the higher light, higher

nitrogen Corn Island, which supports greater potential for growth and reproduction

(Chapters 4 & 5).

Figure 1. Photosaturated photosynthetic rates (A_{max})
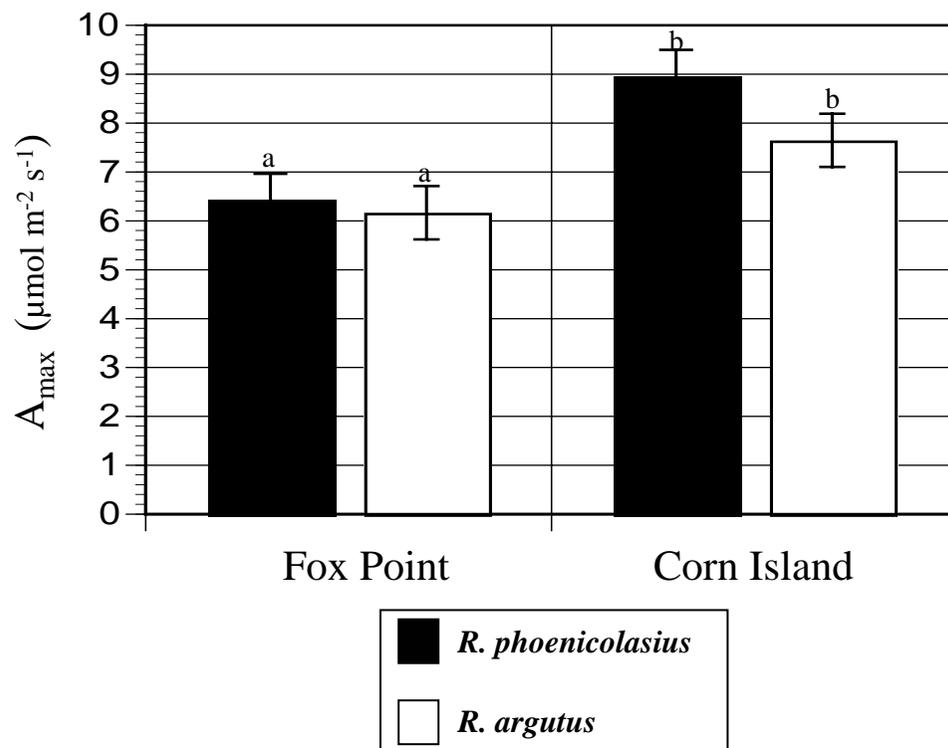
Figure 1. Maximum photosynthetic rate (A_{max}) measured on two species of *Rubus* in two forest habitats. *R. phoenicolasius* is an invasive species, *R. argutus* is native. There is a significant difference between forests but no difference between species. Data shown are mean ± SEM.

Figure 2. Photosynthetic nitrogen use efficiency (PNUE)
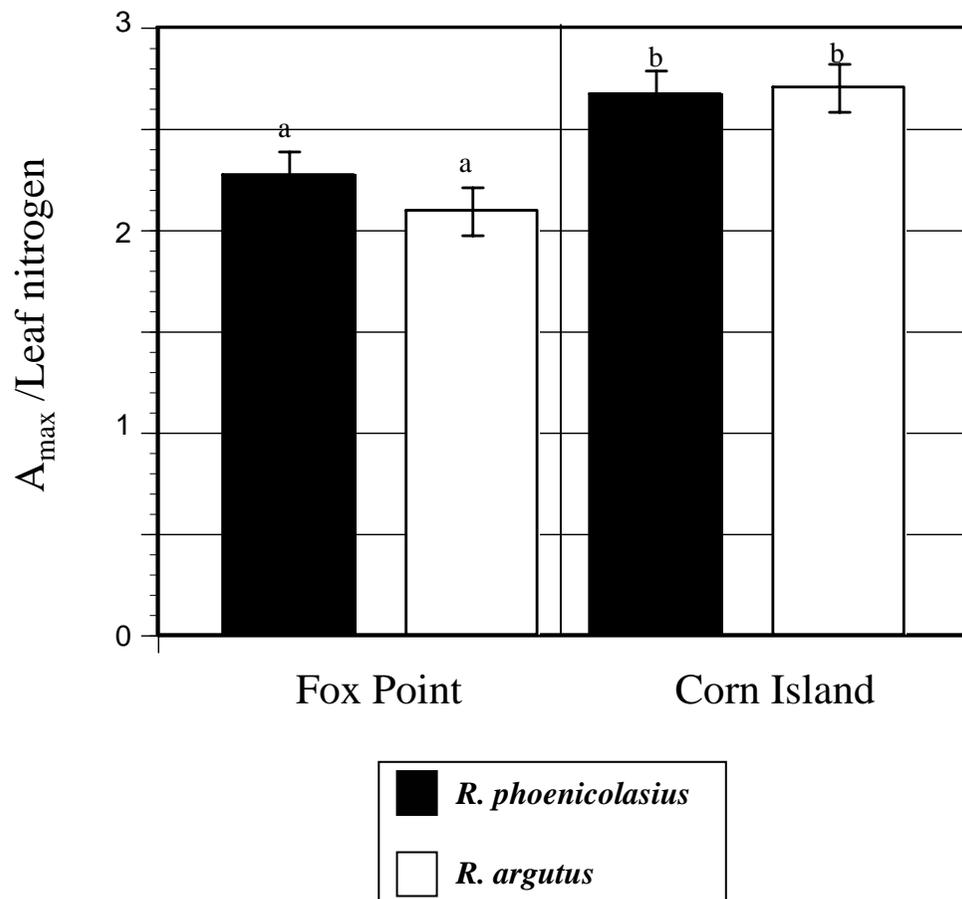
Figure 2. Photosynthetic nitrogen use efficiency measured on two *Rubus* species in two different forest habitats. There was a significant difference in nitrogen use efficiency between forests but no difference between species. Data shown are means ± SEM.

Figure 3. Leaf nitrogen (N_{leaf})
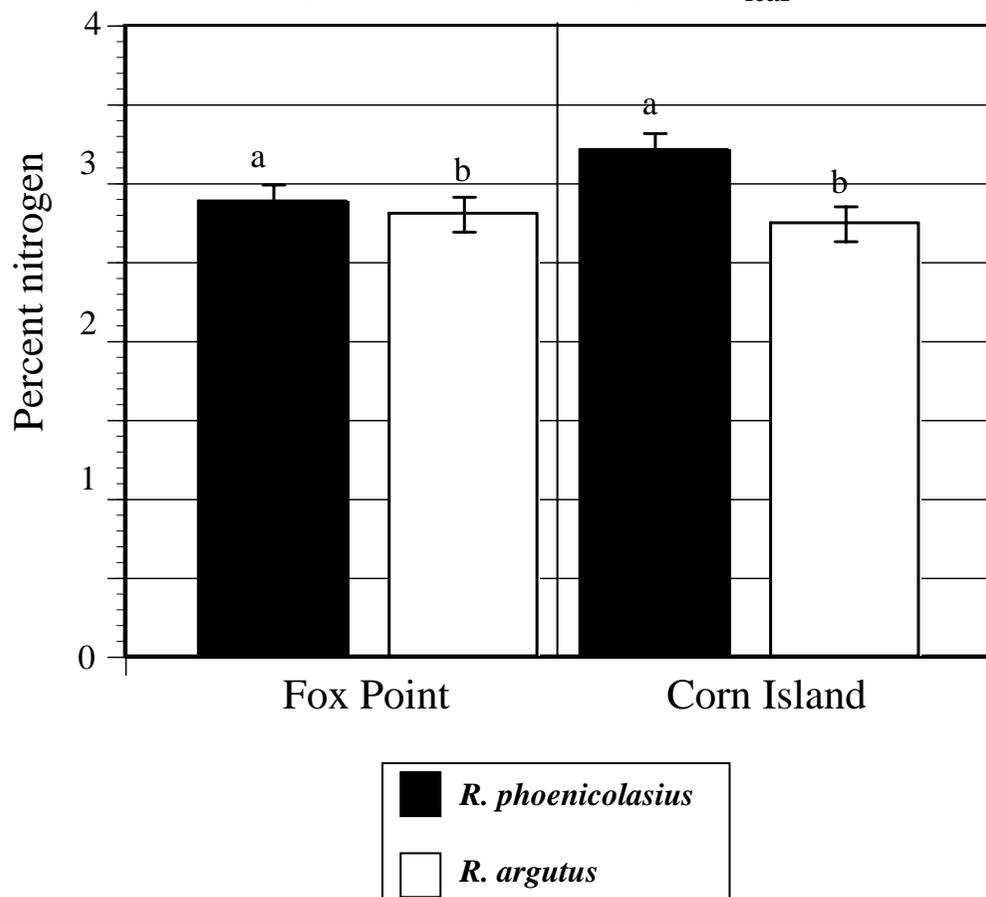
Figure 3. Leaf nitrogen contents measured on two *Rubus* species in two different forest habitats. The invasive, *R. phoenicolasius* had significantly higher leaf nitrogen levels per gram of leaf material. Data shown are means ± SEM.

Figure 4. Specific leaf area (SLA)
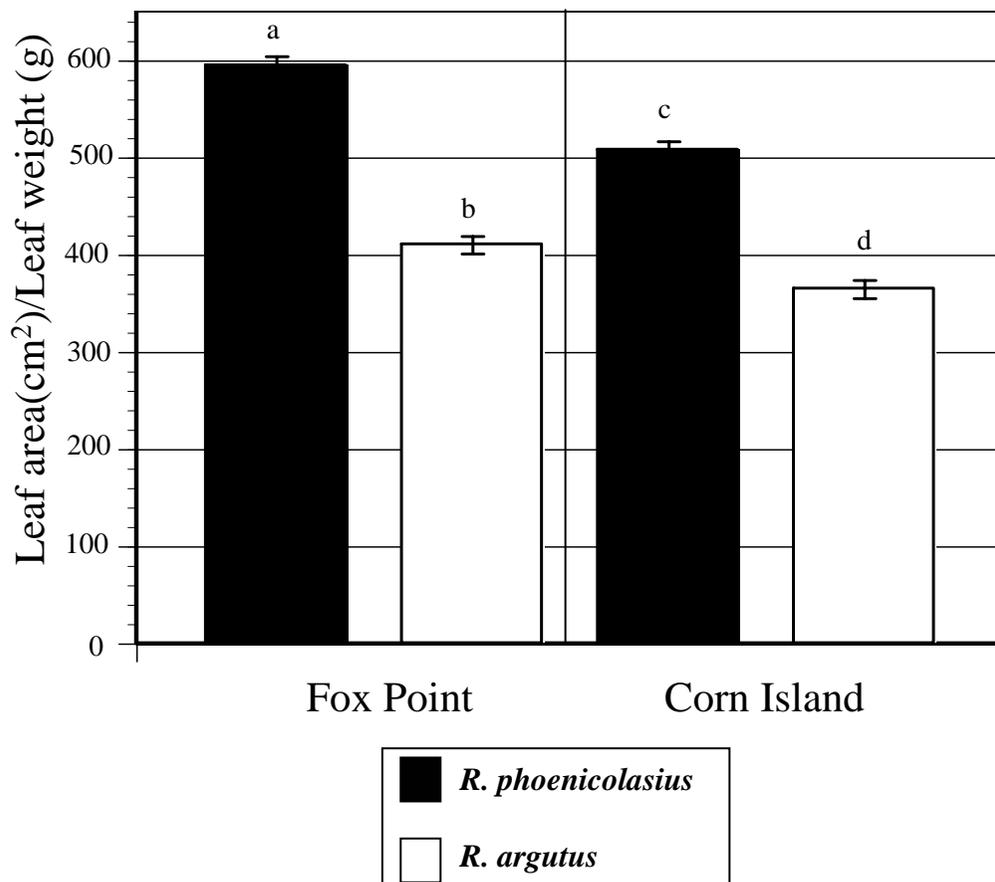
Figure 4. Specific leaf area measured on two *Rubus* species in two forest habitats. The invasive, *R. phoenicolasius* had significantly greater specific leaf area than the native in both forests. There were higher SLAs in both species in the Fox Point forest. Data shown are means ± SEM.

Table 1. Results of non-linear mixed model analysis of photosynthetic light curves

Source	Num df	Den df	F	P
A$_{max}$				
Species	1	53	0.61	.44
Forest	1	53	15.27	**.00**
A$_{qe}$				
Species	1	53	1.52	.22
Forest	1	53	1.92	.17
LCP				
Species	1	53	0.47	.50
Forest	1	53	49.96	.37

Table 1. Summary of non-linear mixed model analysis. There were significantly higher maximum photosynthetic rates (A$_{max}$) in the higher light forest. There were no significant differences between species or forests in quantum yield (A$_{qe}$) or light compensation point (LCP). Significant P values in bold.

Table 2. ANOVA for gas exchange physiology data

Source	Num df	Den df	F	P
PNUE				
Species	1	52	0.18	.67
Forest	1	52	9.06	**.00**
Species x Forest	1	52	0.39	.53
N_{leaf}				
Species	1	91	5.94	**.02**
Forest	1	91	1.43	.24
Species x Forest	1	91	3.03	**.09**
SLA				
Species	1	293	304.68	**.00**
Forest	1	293	49.96	**.00**
Species x Forest	1	293	4.89	**.03**
A_{max}/R_d				
Species	1	52	2.74	**.10**
Forest	1	52	0.13	.72
Species x Forest	1	52	0.09	.77
WUE				
Species	1	52	0.11	.74
Forest	1	52	3.92	**.05**
Species x Forest	1	52	0.37	.55

Table 2. Summary of ANOVA for photosynthetic gas exchange traits measured on two *Rubus* species in two forest habitats. Photosynthetic nitrogen use efficiency was greater in the Corn Island habitat than in Fox Point. *R. phoenicolasius* had higher N_{leaf} than *R. argutus*. *R. phoenicolasius* had higher SLA than *R. argutus* in both forests and there were higher SLAs in Fox Point for both species. *R. phoenicolasius* had greater (A_{max}/R_d) than *R. argutus.* Both species had higher WUE in the Corn Island forest. Significant P values in bold.

Figure 5. Solar radiation in each forest in 2002
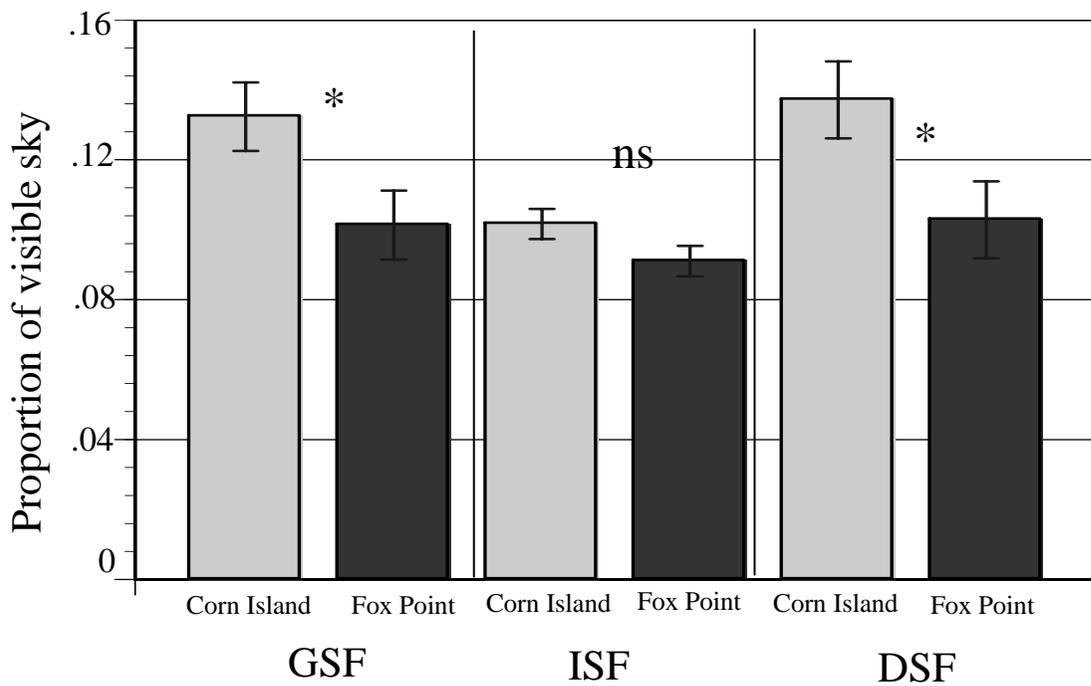
Figure 5. Proportion of visible sky at sites in both Fox Point and Corn Island in 2002, photos taken with a fish-eye lens and analyzed with HemiView 2.1. Data shown are means ± SEM. Asterisks indicate significant differences between means at the P<0.05 level.

Figure 6. Solar radiation in physiology sites in 2003
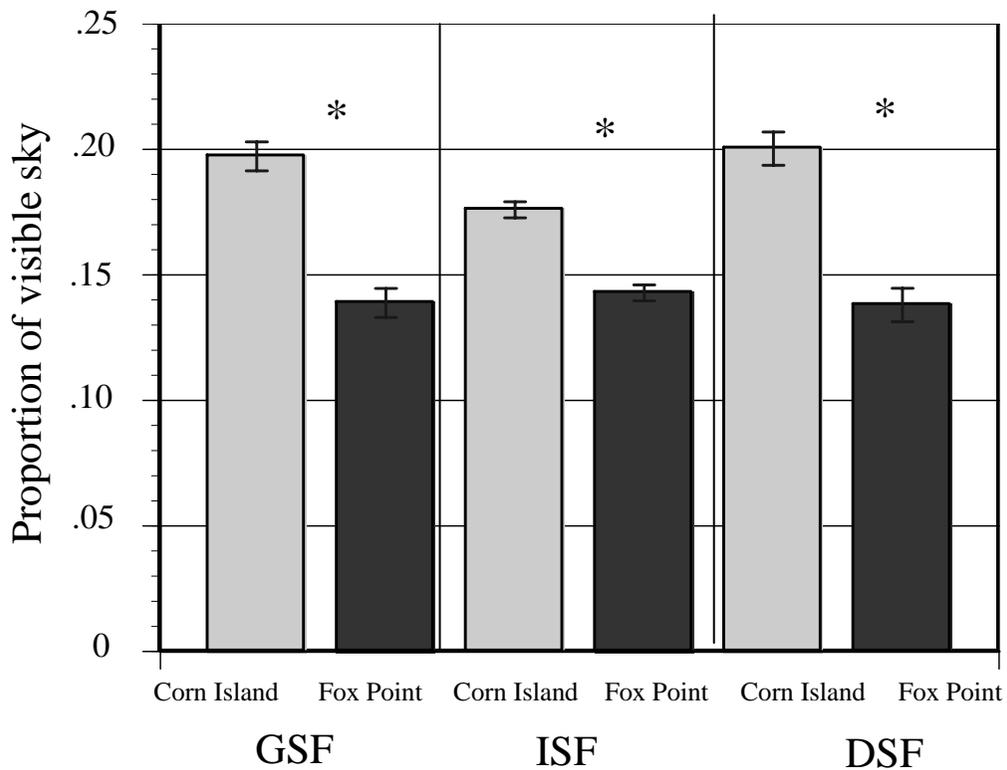
Figure 6. Proportion of visible sky at physiology sites in both Fox Point and Corn Island in 2003, photos taken with a fish eye lens and analyzed with HemiView 2.1. Data shown are means ± SEM. Asterisks indicate significant differences between means at the P<0.05 level.

Table 3. Soil nitrate and pH means for 2002 - 2004

	Fox Point	Corn Island
Soil nitrate (ppm)		
2002	1.82 ± .57	4.84 ± .57
2003	1.55 ± .15	2.55 ± .15
2004	6.77 ± 1.04	7.83 ± 1.04
Soil pH		
2002	5.38 ±.10	4.66 ± .10
2003	5.65 ± .35	5.10 ± .35
2004	5.93 ± .25	4.87 ± .25

Table 3. Nitrate levels at sites in Fox Point and Corn Island in 2002, 2003 and 2004. Levels given in parts per million (ppm). Soil pH at sites in Fox Point and Corn Island in 2002, 2003 and 2004. All data shown are means ± SEM.

Chapter 3

The competitive impacts of native and invasive species of *Rubus* on a common understory plant in a deciduous forest

Abstract

Invasive species are problematic in global ecosystems because they displace native species, threaten biodiversity and alter the function of ecosystems. Management actions to prevent the spread and impacts of invasive species require knowledge of their ecological characteristics. The most effective studies of invasive characteristics involve a comparison of closely related invasive and native species. In this study I examined the competitive impacts of two *Rubus* species, the invasive wine raspberry (*Rubus phoenicolasius*) and the native sawtooth blackberry (*Rubus argutus*) on Indian strawberry (*Duchesnea indica*), a naturalized clonal herb that is widespread and abundant in the understory of forests in the study area. In plots with the invasive *R. phoenicolasius* there were significantly fewer individuals and fewer ramets of *D. indica* compared to plots with the native *R argutus*. Although growth of *D. indica* over a single growing season did not differ in plots with the two *Rubus* species, lower densities of *D. indica* in plots with *R. phoenicolasius* indicate potential long term impacts of the invasive.

Introduction

Invasive plant species have been found to alter ecosystem disturbance regimes and biogeochemical cycles (Vitousek *et al*. 1987, Vitousek *et al*. 1997, Davis *et al.* 2000, Ehrenfeld 2001, Mack *et al.* 2001, Mooney and Cleland 2001). At the local level, competition between invasives and natives is often one-sided with natives generally suffering greater negative consequences from the interaction. Growth rates of natives may decrease or cease entirely, fecundity may decline and the establishment of new seedlings may be reduced by invasive species. In the mountains of New Mexico the growth of the native thistle *Cirsium vinaceaum* was significantly reduced in the presence of the invasive *Dipsacus sylvestris*, yet the growth of *Dipsacus* was not affected (Huenneke and Thompson 1995). In temperate forests, species richness has been shown to decrease in the close proximity of invasive species (Meekins and McCarthy 1999, Standish *et al.* 2001). In the presence of invasives, native species show reduced germination and decreased seedling growth and survival (Eliason and Allen 1997, Collier *et al.* 2002). The negative impacts of competition with invasive species on establishment and survival of native species can lead to changes in community structure (Meiners *et al.* 2002a, Sanders *et al.* 2003).

Why are invasives better competitors than native species? There are several hypotheses, including; invasives possess greater levels of plasticity, produce novel allelopathic chemicals, or have been released from inhibition by co-evolved predators, competitors, parasites and pathogens (Callaway and Aschehoug 2000, Claridge and Franklin 2002,

Callaway and Ridenour 2004, Jakobs *et al*. 2004). As invasives are removed from their

natural predators and pathogens, resources previously used for defense may be allocated

towards growth. This hypothesis has been called the Evolution of Increased Competitive

Ability (EICA) (Blossey and Notzold 1995, Rodger and Siemann 2004). This hypothesis

predicts greater competitive impacts of invasives on local species in the introduced

habitat than in the native range. For example, *Centaurea diffusa*, had greater impacts on

species of grasses in Montana habitats that it had invaded than it did on grasses in its

native range (Callaway and Aschehoug 2000). Plasticity may help invasive plants by

allowing them to exploit a wider range of environmental conditions than do native

species. For example, the invasive *Microstregium vimineum* was able to survive and

reproduce in a wide range of light and nutrient levels (Claridge and Franklin 2002).

Kudzu, *Pueraria montana*, is able to thrive in varied habitats from full sun to deep shade

(Forseth and Teramura 1987) while *Lonicera japonica* possesses greater plasticity than

native vines in its climbing and winter photosynthetic abilities (Carter and Teramura

1988, Schweitzer and Larson 1999). Some invasive species, for example *Centaurea*,

produce allelopathic chemicals that reduce the growth of local natives (Ridenour and

Callaway 2001, Callaway and Ridenour 2004). Invasives may also have novel allocation

patterns that allow them to be more successful in their invaded habitats than are native

species. In a greenhouse experiment, the invasive grass *Bromus madritensis* performed

better than two desert natives. The invasive had more efficient water use, better nitrogen

uptake, higher biomass, and produced seeds which were more likely to germinate

(DeFalco *et al.* 2003).

To understand potential effects of introduced invasive species on native plant communities, it is important to quantify their competitive effects. To place these competitive effects in context, comparisons with the competitive effects of native counterparts are valuable. Closely related native species provide the most valuable comparisons. One approach for these comparative studies is to compare the impacts of a closely related invasive and a native on a third "target" plant species (Vila and Weiner 2004). In this chapter, I examined established populations to determine the impacts of an invasive compared to a native species of *Rubus* on a common understory species, *Duchesnea indica*. This study was conducted in two habitats, a forest edge habitat that had more light and soil nitrate than a forest interior habitat (Chapter 2). I had two hypotheses. First, the invasive *R. phoenicolasius* would have a greater impact on local species abundance than the native *R. argutus*. Second, the competitive interactions between the *Rubus* species and *D. indica* would be greater in the forest edge habitat. To address these hypotheses, I quantified two aspects of the spatial distribution of *D. indica* in the presence of both *Rubus* species: the density of *Duchesnea* individuals, and the seasonal growth of *Duchesnea* individuals.

Material and Methods

Study species

Rubus argutus is native to the United States ranging from Massachusetts to Florida and west to Missouri. *Rubus phoenicolasius* is native to Japan, Korea and China, and its U.S. introduced range is similar to *R. argutus*. *R. phoenicolasius* was introduced in the 1890's possibly through John Lewis Childs who ran a mail order seed company in Floral Park,

New York (Hummer 1995). *R. phoenicolasius* is listed by The United States Department of Agriculture, The National Park Service, National Biographical Information Infrastructure, The Nature Conservancy and The Maryland Department of Natural Resources as an invasive species. Both *Rubus* species are found in old fields and early to mid-successional forests.

Rubus phoenicolasius and *R argutus* have similar life histories, producing biennial above ground shoots, hereafter called canes, from a perennial rootstalk or from underground rhizomes. The first year cane, primocane, is vegetative while the second year cane, floricane, undergoes lateral branching and produces flowers and fruit. Both species produce aggregate fruits which ripen together (Ellis 1991). Both species are able to reproduce clonally through underground rhizomes, but only *R. phoenicolasius* is capable of tip rooting from parts of the cane that touch the ground.

Duchesnea indica is a non-native, low-growing, stoloniferous perennial that has become naturalized throughout the understory of successional deciduous forests in eastern North America (Greller 1979, Osborne *et al*. 1997, Ingram 2004). Stolons produce new leaves which are capable of rooting and forming new individuals.

Study site

The study was conducted at the Smithsonian Environmental Research Center (SERC), Edgewater, MD, USA (~10 km SSE of Annapolis, 38˚53' N, 76˚33' W). The Center includes agricultural fields, abandoned fields, and successional and mature forests that

are typical of the region (Brush *et al.* 1980). Two non-contiguous forests were used,

locally known as Fox Point and Corn Island. Fox Point is a large tract of undisturbed

mid-successional forest (60-70 years old). Corn Island is a narrow (50m x 1km) mid-

successional forest (50-60 years old) between an unpaved road and an agricultural field.

Due to the fact that the Corn Island forest is primarily edge habitat, the Corn Island forest

has higher light levels, 13% GSF as compared to 10% GSF in Fox Point (Chapter 2,

Meiners *et al.* 2002b). Corn Island also had higher soil nitrogen concentrations (Chapter

2) because the forest receives runoff from adjacent agricultural fields. Forest types were

not replicated and with one high light and one lower light habitat there is a limitation in

the ability to generalize the results.

Methods

In June 2002, 1m x 1m plots were established in three sites in each forest. At each site,

three sets of four plots were established: a) a plot with *R. argutus* and *D. indica*, b) a plot

with *D. indica* and no *R. argutus*, c) a plot with *R. phoenicolasius* and *D. indica*, d) a plot

with *D. indica* and no *R. phoenicolasius*. There were 12 plots per location, 36 plots per

forest and 72 plots total. Plots were paired such that plots with *R. argutus* absent were

physically distinct from plots with *R. phoenicolasius* absent (Fig. 1). In June 2002, the

total number of *D. indica* individuals and ramets were counted in each plot. An

individual was defined as one group of stems from one root stock; ramets were counted

as individual stems originating from the same root stock or stems along the stolen (i.e. a

root stock with 3 stems was considered one individual composed of three ramets). The

1m x 1m plots were divided into 5 equal areas of 20 cm x 100 cm to facilitate counting, but analyses were conducted on total individuals per plot.

In each plot, five individuals of *D. indica* were tagged in June 2002, one per 20 cm x 100 cm section. Height and number of ramets were recorded for these tagged plants. In September 2002, tagged individuals were re-measured. Individual growth was calculated as: number of September ramets/ number of June ramets.

Relative light levels were measured in August 2002 in each plot by taking two digital photos with a fish eye lens converter (Nikon FC E8) attached to a Nikon Cool Pix 990. Photographs were taken at a height of 1.5m. Photos were then imported into HemiView 2.1 software and analyzed for percent visible sky. Visible sky is described in three forms: global site factor (GSF), direct site factor (DSF) and indirect site factor (ISF) (Whitmore *et al.* 1993).

In August, 2002 soil samples were collected from each site as well as other randomly chosen sites throughout both forests. At each sampling location three soil cores (15cm depth by 7cm diameter) were collected. Fifteen cm represents the depth of most of the roots of *R. phoenicolasius* and *R. argutus*. The cores were combined prior to sieving through a 1.0 mm screen. Samples were dried for a week at (60°C) and 30 g sub-samples were sent to the Maryland Cooperative Extension, Soil Lab with the University of Maryland. Soils were analyzed for pH and nitrate levels in parts per million.

Temperature and precipitation data were obtained from a NOAA weather station at the

Baltimore Washington International Airport. Average temperatures and precipitation

were calculated for a 30-year period from 1970 to 2000 for comparison with data in 2002,

2003 and 2004.

Data Analysis

The numbers and growth of *D. indica* were analyzed using two-way mixed model

ANOVAs with forest and plot type in the model with random blocking for site using

SAS 8.1 (SAS 2004). For all analyses a P value of .05 or smaller was considered

significant. Soil data were log transformed prior to analysis to meet assumptions of

homogeneity of variances and analyzed with a one-way ANOVA. In the results section,

significance levels are reported for the transformed data but on the graphs, untransformed

data are shown for clarity of presentation.

Results

Comparisons of Rubus species and Duchesnea indica

There was a significant difference in the number of *D. indica* individuals per m^2 due to

plot type ($F_{3,60}$=4.38, P=.008) (Table 1), but not for forest or the interaction between

forest and plot type. Planned orthogonal comparisons between plot types showed there

was a significant difference between the plots with *R. phoenicolasius* and *R. argutus*

present compared to plots with *Rubus* absent ($T_{1,60}$= 2.56, P=.013). There was no

significant difference between the number of *D. indica* individuals in the plots with or

without *R. argutus* ($T_{1,60}$= 1.51, P=.135) but the difference was significant for plots with

44

and without *R. phoenicolasius* ($T_{1,60}$= 2.10, P=.040) (Fig. 2). There was also a significant difference in the numbers of *D. indica* ramets across the four plot types ($F_{3,60}$=4.93, P=.004) (Table 2). There was no significant effect of forest and no significant interaction between forest and treatment. Comparisons between plot types showed that there were significantly fewer *D indica* in plots with *R. phoenicolasius* compared to plots with or without *R. argutus* ($T_{1,60}$= 2.75, P=.008). There was no significant difference in number of *D. indica* ramets between the plots with *R. argutus* present and absent ($T_{1,60}$=1.72, P=.091), but there was a significant difference between the plots with *R. phoenicolasius* present and *R. phoenicolasius* absent ($T_{1,60}$= 2.16, P=.034) (Fig. 3).

There were no significant differences found for ramet growth for any of the tested variables (Table 3 and Fig. 4).

Light comparisons

Plots at Corn Island had significantly higher percent of available light, measured in GSF, than the plots at Fox Point ($F_{1,34}$=4.72, P=.037). The same pattern was found for DSF ($F_{1,34}$=4.86, P=.034) however for the indirect site factor there was no significant difference between the two forests ($F_{1,34}$=2.98, P=.093) (Fig. 5).

Comparisons of soil nutrients

Nitrate levels in soils at Corn Island were significantly higher ($F_{1,23}$=27.13, P<.001) (Fig. 6) and soil pH significantly lower than soils at Fox Point ($F_{1,23}$=19.27, P<.001) (Fig. 7).

Temperature and precipitation data from the Baltimore Washington International Airport were compiled for a 30-year period (1970 to 2000) for comparison with temperature and precipitation data for the study period. The summer of 2002 had drought conditions with May through September receiving precipitation which was 83% of the 30-year average for the same period (Fig. 8). Temperatures recorded in 2002 were 1.05° C higher than average for June through September (Fig. 9).

Discussion

In a review, Vila and Weiner (2004) found a general pattern in which invasive plant species have considerably stronger competitive abilities than their native congeners. My data is consistent with this pattern, as I found significantly lower densities of *D. indica* in plots with *R. phoenicolasius* than in plots with the native *R. argutus* (Fig. 2) and in plots without any *Rubus* species. Two invasive species, *Lonicera japonica* and *Lonicera maackii* have both been shown to negatively influence native species. *Lonicera japonica*, an invasive in successional deciduous forest in the Piedmont of New Jersey, was shown to lower local species richness and plant density by preventing establishment (Yurkonis and Meiners 2004). *Lonicera maackii* lowered species richness and decreased the number of seedlings and abundance of herbaceous plants (Collier *et al.* 2002). Removal of *Lonicera maackii* resulted in an increase in herbaceous herbs and vines in one study (Luken *et al.* 1997) and an increase in numbers of native species in a different Ohio forest (Hartman and McCarthy 2004). The invasive garlic mustard *Alliaria petiolata* has

also been shown to be a stronger competitor than local herbaceous plants and seedlings in forest habitats (Meekins and McCarthy 1999).

Forest plots with *R. phoenicolasius* had fewer *D. indica* ramets than plots with *R. argutus* (Fig. 3), suggesting that the invasive has a negative impact on clonal propagation. Consistent with my results, a five-year study demonstrated long term competitive impacts of an invasive shrub *Lonicera maackii* on the size of herbaceous species in a forest (Miller and Gorchov 2004). Another study compared the impacts of closely related native and invasive vines on *Liquidambar stryaciflua* saplings. There were negative impacts of an invasive vine *Lonicera japonica* on sweet gum morphology, physiology and biomass (Dillenburg *et al.* 1993a, 1993b, 1995). My results also agreed with previous studies that showed invasive species had greater competitive impacts on the biomass of local species than native species (Huenneke and Thompson 1995**,** Callaway and Aschehoug 2000, Vila and Weiner 2004).

Neither the native *R. argutus* nor the invasive *R. phoenicolasius* had a negative impact on the growth over the summer of 2002 of *D. indica*, as measured by comparing the number of ramets early and late in the growing season. Given the rapid clonal growth of *D. indica* I had expected to see a difference between treatments. However *D. indica* growth was very low during the time of the study. There are three possible explanations. First, there may not be an observable short term impact of *R. phoenicolasius* on *D. indica,* rather competitive effects are imposed over several years. A second possibility is that the growth of *D. indica* was suppressed by below average precipitation and above average

temperatures during the study period, obscuring any competitive inhibition (Figs. 8 and 9). I observed plant mortality and low growth across all plot types and the ratio of the number of ramets in September to the number of ramets in June was 1.2, even without *Rubus* present in the plots. Forest herbaceous species produce less leaf area and lower biomass when they are water stressed (Noda *et al.* 2004). Finally, since I chose established plots for these measurements, competitive inhibition may have already occurred, with an equilibrium density having been achieved prior to my observations.

The experiment was conducted in two forests of the same successional age but with differing resource levels. The forest at Corn Island receives more light because it is primarily an edge habitat, bounded by agricultural fields or roads. Global site factor and direct site factors were higher in Corn Island than Fox Point, indicating that understory plants received more direct light (Fig. 5). Light levels are positively related to photosynthetic rates and growth of woody and herbaceous species in forest habitats (Hall and Kuss 1989, Tremblay and Larocque 2001, Kikuzawa 2003). Soils at Corn Island also had higher nitrate levels (Fig. 6), most likely the result of the proximity of fertilized agricultural fields (Jordan and Weller 1996, Vitousek *et al.* 1997, Jordan *et al.* 1998). Nitrogen availability is an important factor in plant interaction (Witkowski 1991, Booth *et al*. 2003). The growth of *D. indica* and *Rubus* species has been shown to be greatest at higher soil nitrogen levels (Taylor 1982, Dong *et al.* 2000). I expected that competition between *R. phoenicolasius* and *D. indica* would be more intense at Corn Island because of the greater rates of growth associated with higher resource levels, and the growth advantage proposed for invasive species. This effect has been demonstrated in Ohio

where higher light conditions resulted in greater competitive effects for the invasive *Lonicera maackii* on annual species (Gould and Gorchov 2000) and in Maine where high light and nutrients increased the impacts of *Rubus idaeus* on *Picea glauca* (Lautenschlager 1999). I found, however, no significant differences between forests in the effects of the invasive species on *D. indica*. I also found no significant differences between the numbers of ramets per plot between forests nor was there a significant interaction between plot type and forest. In addition, there were no significant differences in growth between forests and no significant interactions between plot type and forest. My data suggests that *D. indica* performed the same regardless of habitat conditions.

In summary, my results showed a difference between plots containing the invasive *R. phoenicolasius* and the native *R. argutus* and the local species *D. indica*. I observed evidence of greater long term competitive effects of *R. phoenicolasius* on *D. indica*, in terms of reduced local densities and clonal size (number of ramets) of *D. indica*. I did not observe short-term competitive effects on the growth of *D. indica* nor did I detect different competitive impacts in different habitats. Further investigation of competitive effects should involve examining the responses of other species, especially seedlings of woody and herbaceous species of later successional stages, to the presence of the invasive *R. phoenicolasius*. Manipulative studies involving the removal of *R. phoenicolasius* and *R. argutus* may also demonstrate competitive release for local native species.

Figure 1. Experimental design
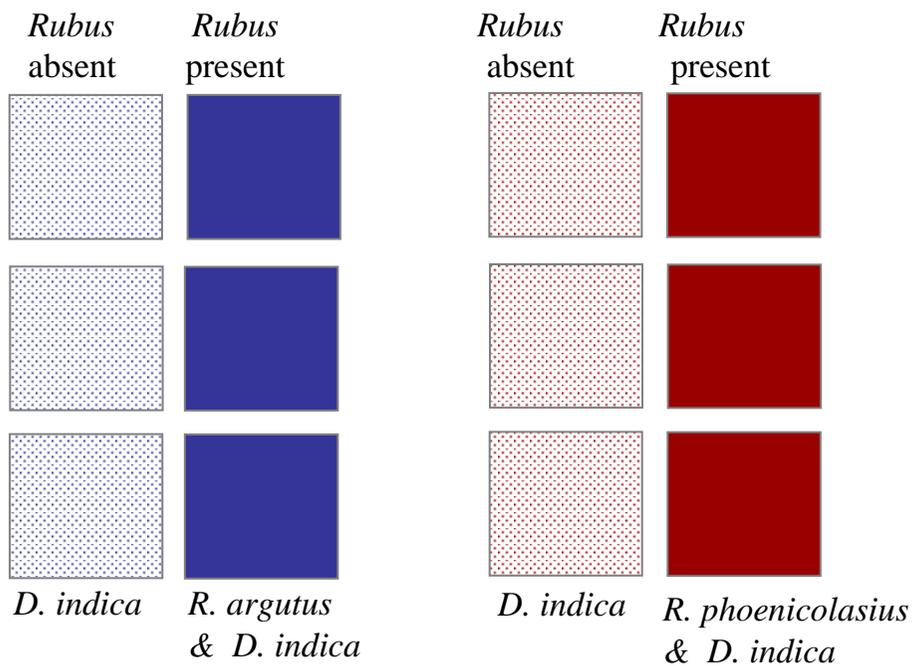
Figure 1. At each site 12 1m x 1m plots were established. Plots were paired with the *Rubus* absent plots for *R. argutus* being separate from the *Rubus* absent plots for *R. phoenicolasius*.

Table 1. ANOVA table for number of *D. indica* individuals

Effect	DF_{num}	DF_{den}	F	P
Plot type	3	60	4.38	**.008**
Forest	1	60	1.71	.195
Plot type x Forest	3	60	1.27	.292

Table 1. Summary of ANOVA table for the number of *D. indica* individuals. This examines the effect of plot type, forest and the interaction of forest and plot. There is a significant plot effect but no significant forest effect or significant interaction. Significant P values in bold.

Figure 2. Number of *D. indica* individuals
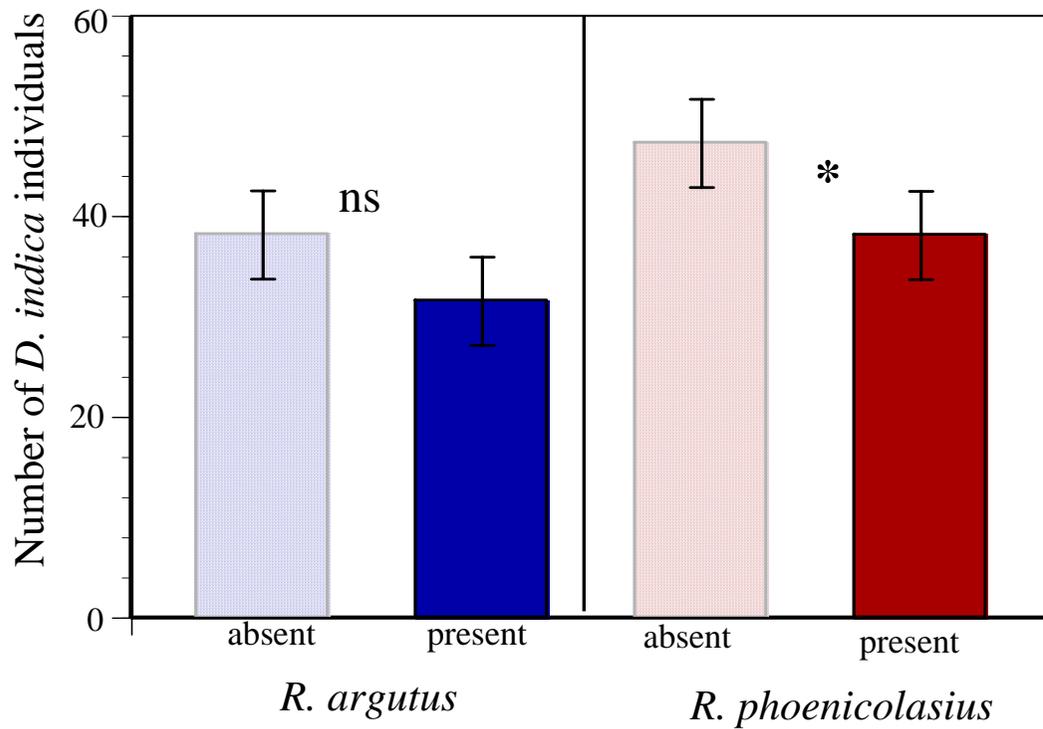
Figure 2. The plots with *R. argutus* present compared to plots without *R. argutus* showed no significant difference in the number of *Duchesnea indica* individuals, but there is a significant difference in number of *D. indica* individuals in plots with *R. phoenicolasius* present as compared to plots with *R. phoenicolasius* absent. Data are shown mean ± SEM. * P<.05.

Table 2. ANOVA table for number of *D. indica* ramets

Effect	DF_{num}	DF_{den}	F	P
Plot type	3	60	4.93	**.004**
Forest	1	60	.65	.422
Plot type x Forest	3	60	.24	.871

Table 2. Summary of ANOVA table for the number of *D. indica* ramets. This examines the effect of plot type, forest and the interaction of forest and plot. There is a significant plot effect but no significant forest effect or significant interaction. Significant P values in bold.

Figure 3. Number of *D. indica* ramets
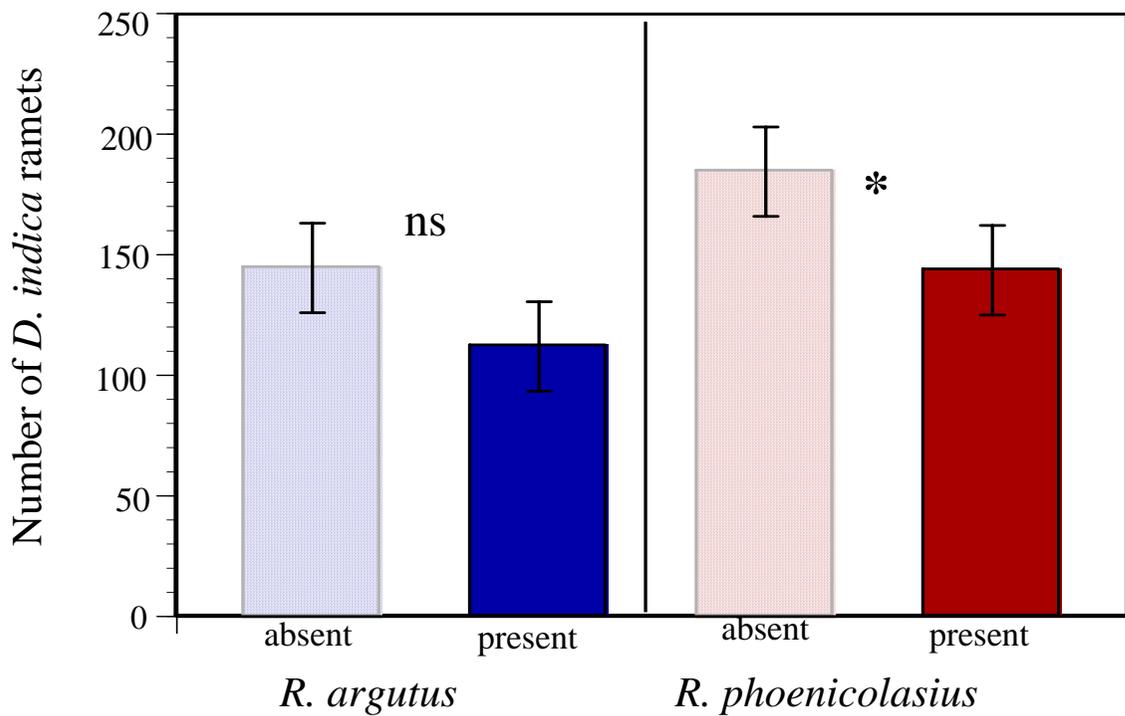
Figure 3. With planned comparisons, the plots with *R. argutus* present showed no significant difference in the number of *Duchesnea indica* ramets to plots with *R. argutus* absent, but there is a significant difference in number of *D. indica* ramets between the plots with *R. phoenicolasius* present and *R. phoenicolasius* absent. Data are shown mean ± SEM. * P<.05.

Table 3. ANOVA table for growth of *D. indica* individuals

Effect	DF_{num}	DF_{den}	F	P
Plot type	3	347	.31	.820
Forest	1	347	.01	.930
Plot type x Forest	3	347	.55	.646

Table 3. Summary of ANOVA table for the growth of *D. indica* individuals. This examines the effect of plot type, forest and the interaction of forest and plot. There are no significant plot, forest, or interaction effects.

Figure 4. Growth of *D. indica* individuals
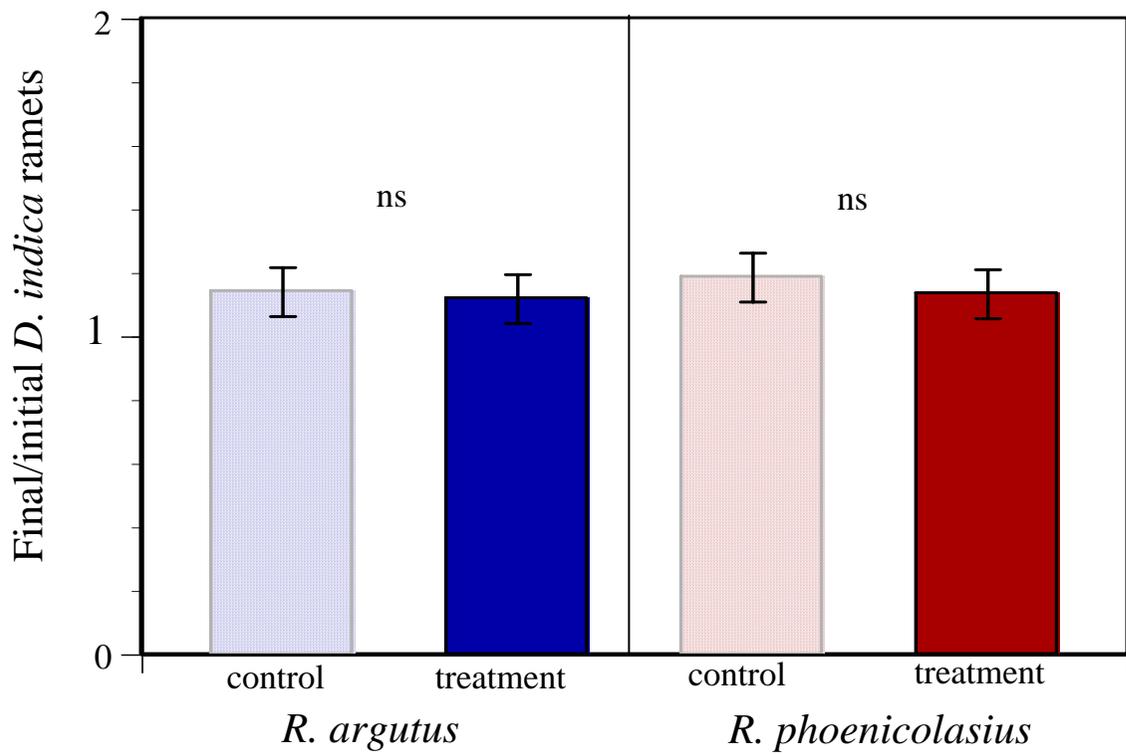
Figure 4.   The growth of *Duchesnea indica* from June 2002 to September 2002 showed no significant difference between control and *R. argutus* treatment or control and *R. phoenicolasius*. Data are shown mean ± SEM.

Figure 5. Solar radiation in each forest 2002
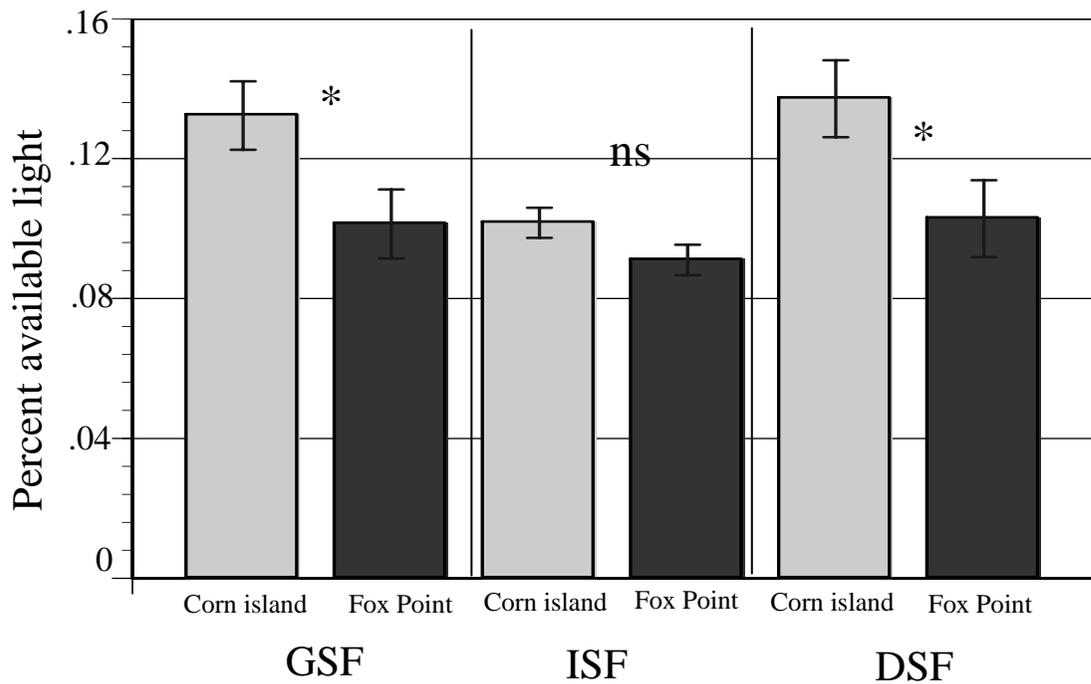
Figure 5. Percent of available light at sites in both Fox Point and Corn Island determined by photos taken with a fish eye lens and analyzed with HemiView 2.1. Data are shown mean ± SEM. * P<.05.

Figure 6. Nitrate levels (ppm) in the soil of each forest
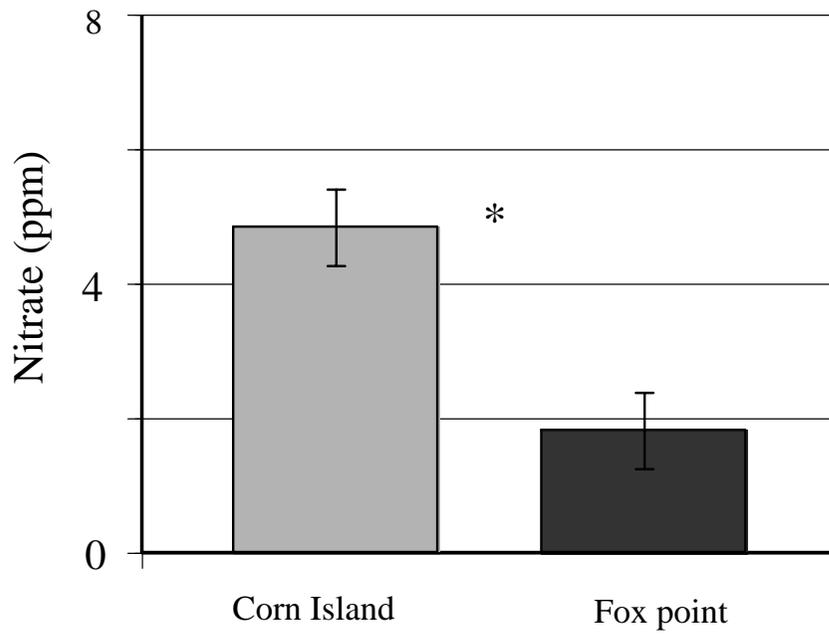
Figure 6. Nitrate levels at sites in Fox Point and Corn Island, levels given in parts per million (ppm). All data are shown mean ± SEM. * P<.05.

Figure 7. pH levels in the soil of each forest
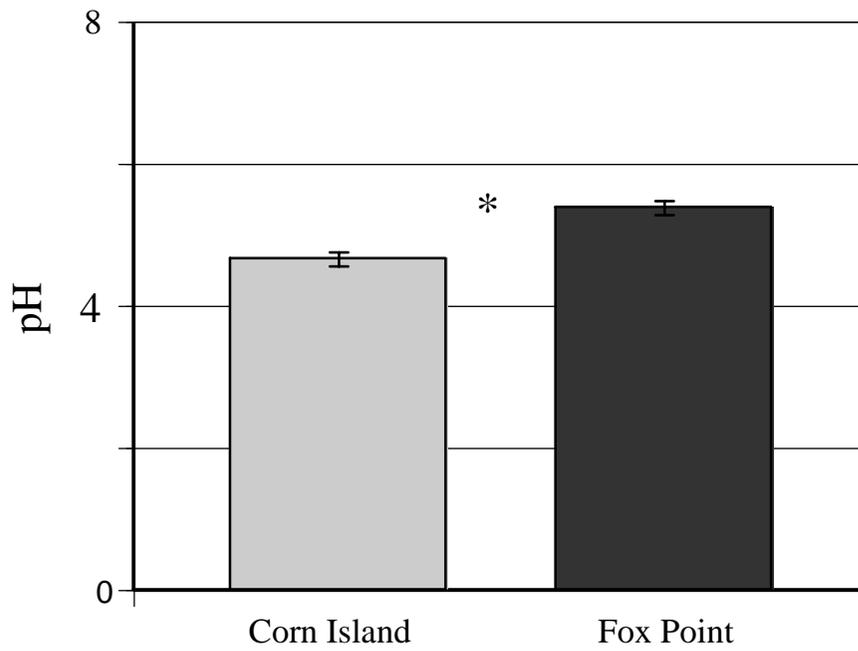
Figure 7. Soil pH at sites in Fox Point and Corn Island. All data are shown mean ± SEM. * P<.05.

Figure 8. Temperature in 2002 with the 30-year average
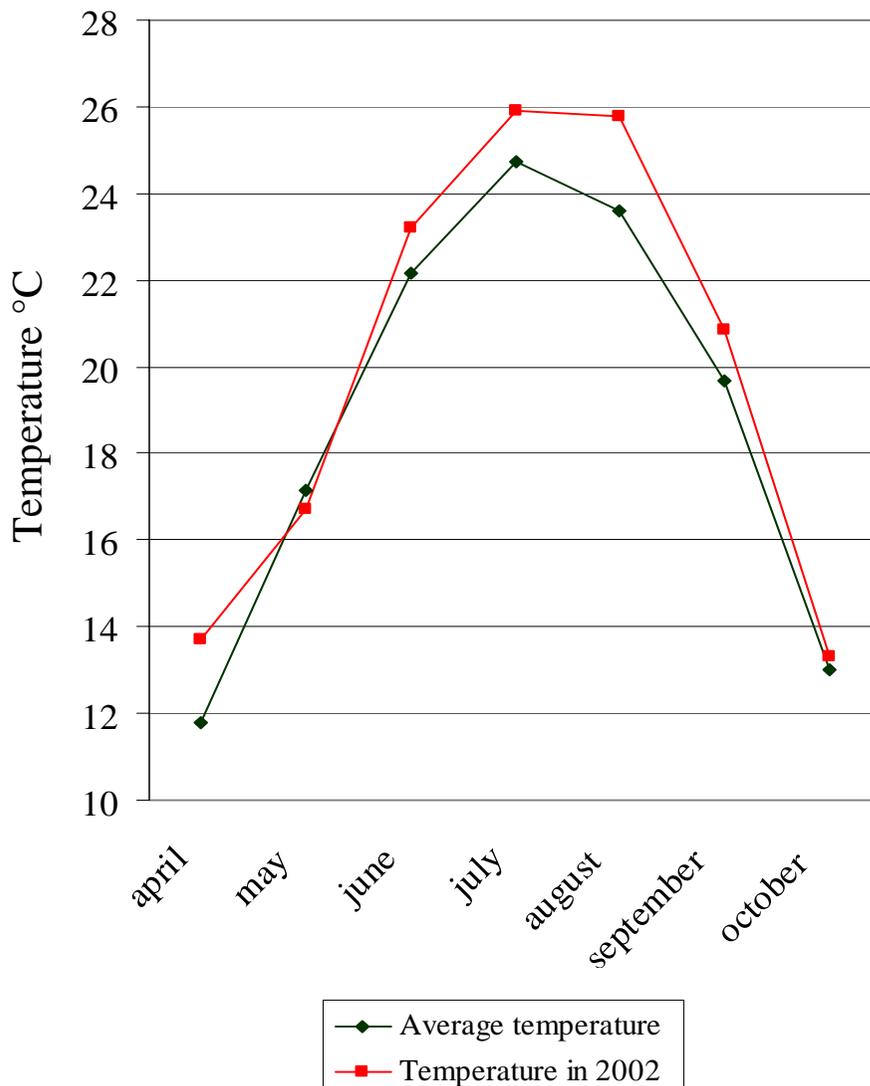
Figure 8. Average and observed monthly temperature in 2002 recorded by NOAA at Baltimore Washington International Airport. Average temperature based on 30-year period from 1970-2000. In 2002 the observed temperature was higher than the 30-year average during the growing season between April and October.

Figure 9. Precipitation in 2002 with the 30-year average
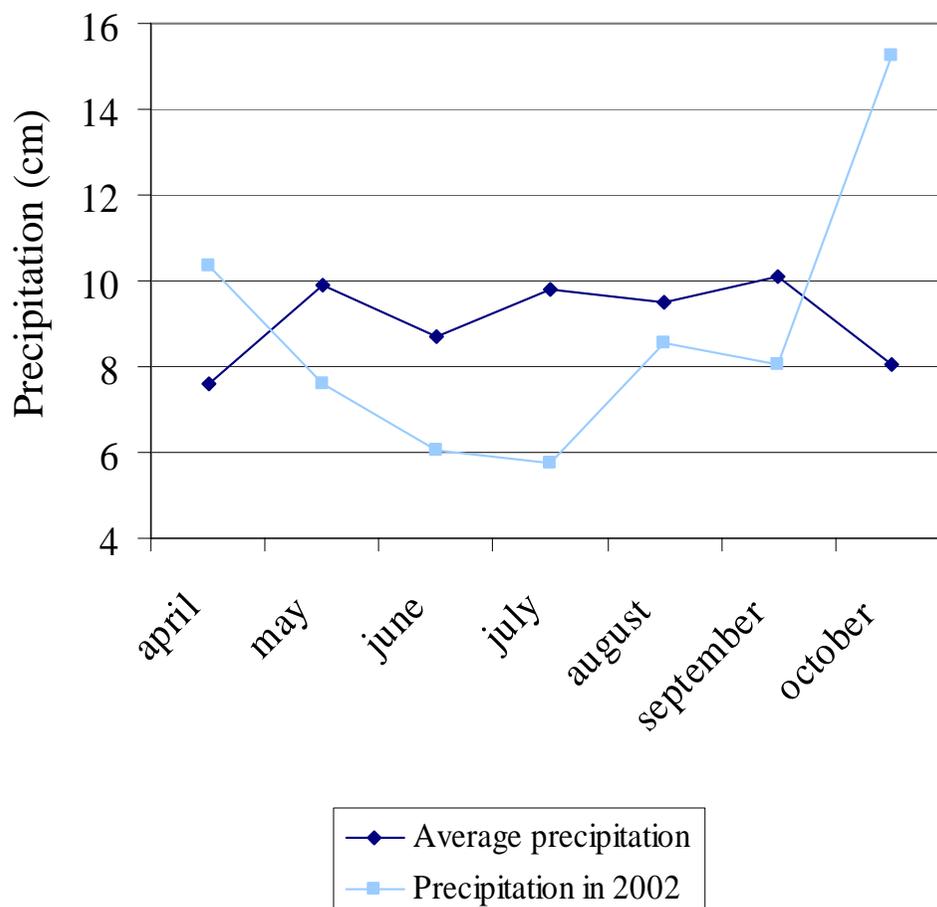
Figure 9. Average and observed monthly precipitation in 2002 recorded by NOAA at Baltimore Washington International Airport. Average precipitation based on 30-year period from 1970-2000. In 2002 the precipitation observed was lower than the 30-year average.

Chapter 4

Comparative population demography of an invasive and native *Rubus* in two contrasting deciduous forest habitats

Abstract

Invasive species threaten biodiversity by displacing native species and altering the availability of natural resources. Determining the traits that make invasive species successful and how these traits interact with their new habitats will enhance management and prevention of further invasions. This study examines the demography of two congeners, the invasive wine raspberry (*Rubus phoenicolasius*) and the native species, sawtooth blackberry (*Rubus argutus*), in two forest habitats, an edge forest (Corn Island) and an interior forest (Fox Point) on the Coastal Plain of Maryland. Yearly change in density and fruit production were monitored in permanent plots from 2002-2004. Density decreased in both forests in the second year of the study due to a severe drought. Even though the third year of the study had average precipitation, density had not returned to initial levels by the end of the study. Between 2002-2003, there was significantly less mortality of both species in the Fox Point populations. Conversely, Corn Island populations of *R. phoenicolasius* had significantly greater recovery in density in 2003-2004 than did *R. argutus*. The vertical shoots (canes) of both species are biennial and I quantified the survival of first year to second year canes in both forests. In both year transitions, survival was significantly higher for *R. phoenicolasius* in Corn Island than *R. argutus*. In two out of three years, the number of second year canes producing fruit and density of mature fruits produced per plot was significantly higher for *R. phoenicolasius* in both forests. In all three years *R. phoenicolasius* produced significantly more seeds per

fruit than *R. argutus* and seeds of *R. phoenicolasius* had significantly higher germination

rates. Overall mortality was lower for both species in the forest interior habitat that had

lower light and nitrate levels, suggesting the importance of habitat conditions for plant

performance. The combination of lower mortality and high fruit production in forest edge

habitats may help to explain the success of *R. phoenicolasius* as an invasive in eastern

deciduous forests.

Introduction

All habitats are potentially invasible (Meekins and McCarthy 1999, Thompson *et al.*

2001) and understanding the mechanisms that reduce invasibility of native communities

and/or decrease the success of invasive species is important for the conservation of native

biodiversity. Both characteristics of invasive species and characteristics of the habitat

determine whether an invasion will be successful (Davis *et al.* 2000, Larson *et al.* 2001).

One approach to studying the ecology of invasive species is to compare the relative

performance of invasive species with closely related congeners in different habitats

(Parker 2000, Radford and Cousens 2001). This approach has the advantage of

minimizing phylogenetic differences and allowing a closer examination of the basis of an

invasive species' success in a new habitat (Sakai *et al.* 2001).

A reason to focus on multiple habitats is that the demography of invasive species often

varies across habitats and their success is not uniform throughout their invaded ranges. In

some habitats invasives may be found at higher densities and with higher reproductive

rates than in other habitats (Byer and Quinn 1998, Yates *et al.* 2004). Habitats with

increased light and nutrients tend to be more productive for invasives which leads to higher growth rates and higher rates of spread. (Goldblum and Beatty 1999, Meekins and McCarthy 2001).

Demographic studies of plant populations can be used to identify the life history stages that are most responsive to the environment, those traits that allow population growth and persistence, and to compare performance between species and habitats (Radford and Cousens 2000). There is a need for more studies comparing the demography of a clonal native to an invasive species, as there have been few conducted previously (Erfmeier and Bruelheide 2004, McDowell and Radosevich 2005). Clonal species often go through a cycle of colonizing and building in population size followed by a maintenance period where there is less recruitment (Hartnett and Bazzaz 1985a, Whitney 1986, Ulanova 2000).

In this study, I examine the demographic characteristics of established populations of two *Rubus* species in two distinct forest habitats. Fox Point is a low light, low nitrate forest interior habitat while Corn Island, an edge habitat adjacent to agricultural fields has more light and higher soil nitrate levels (Chapter 2). Both forests have established populations of the native species *R. argutus*, sawtooth blackberry, and the introduced species *R. phoenicolasius,* wine raspberry.

To explain the establishment and spread of *R. phoenicolasius* in these forest habitats, I hypothesized that population growth would exceed that of the native *R. argutus*. In

addition, I hypothesized that rapid individual and population growth rates would be better

supported in environments with greater resource levels. From these hypotheses, I

predicted that the invasive would have higher densities, higher rates of cane production,

lower rates of mortality, higher rates of fruit and seed production, and higher rates of

clonal propagation. I further predicted that both species would perform better in the forest

edge habitat with higher light and higher soil nitrogen.

Methods

Study species

The invasive species, *Rubus phoenicolasius* is originally from temperate Japan, Korea

and China. *R. phoenicolasius* was introduced in the 1890's possibly through John Lewis

Childs who ran a mail order seed company in Floral Park, New York (Hummer 1995). In

the U.S., *R. phoenicolasius* can currently be found in fields and successional forests from

Massachusetts to Florida and west to Missouri. Co-occurring in this range is the native

species, *Rubus argutus* (Alice and Small 1999). *R. phoenicolasius* and *R. argutus* have

similar life history characteristics, with aboveground biennial shoots (referred to as

canes) and a perennial rootstalk, and both are capable of sexual and asexual reproduction.

In the first year growth is entirely vegetative (primocane), with carbon allocation

primarily into leaf production and elongation. Canes on average are 0.5 meters to 1.5

meters in length. In Maryland, both species are deciduous and lose their leaves in late

November. In the following April, the second year canes (floricanes) produce new leaves

with *R. phoenicolasius'* leaves appearing approximately 2 weeks prior to those of *R.

argutus*. In early May, new primocanes originate from the perennial root stock that also

supports primocanes that have transformed into floricanes. The majority of primocanes

observed originated from rootstocks with existing floricanes (Anne Innis *pers. obs.*). Both

species are also capable of underground propagation through rhizomes and *R.*

phoenicolasius is able to produce new primocanes by tip rooting. During the spring,

floricanes produce branches and additional leaves. In late May they also produce flowers,

with *R. argutus* flowering 1-2 weeks before *R. phoenicolasius. R. phoenicolasius* matures

fruit before *R. argutus*. For both species, flowers and fruit mature acropetally on the

floricane, thus there is an overlap of both flowering and fruiting. For simplicity,

individual primocanes and floricanes will hereafter be referred to as first year canes and

second year canes.

Study site

The study was conducted at the Smithsonian Environmental Research Center (SERC),

Edgewater, MD, USA (~10 km SSE of Annapolis, 38˚53' N, 76˚33' W). The 1,000

hectares that are part of the SERC property include agricultural fields, abandoned fields,

and successional and mature forests that are typical of the region (Brush *et al.* 1980).

Two separate mid-successional forest habitats were used for this study. Fox Point is a

mid-successional forest, between 50-60 years old, that is surrounded by mature forests on

one side and brackish tidal wetland on the other (Dr. Geoffrey Parker, Research Scientist

SERC, *pers. communication*). The second forest, Corn Island, is the same age but is a

narrow (50m x 1km) stand that lies between two active corn fields. The stand is also

divided in half along the long axis by an unpaved road. The Corn Island understory has

higher light levels and the soils have higher nitrogen levels (Chapter 2) compared to Fox

Point. Forests types were not replicated and with one high light and one lower light habitat there is a limit to generalization of these results to other locations.

Measurements

In April 2002, nine sites with both species were located in each forest. At each site four 1m x 1m plots were established (N = 36 per species per forest). In the summer of 2002, all canes (N = 797 *R. argutus* and N = 613 *R. phoenicolasius*) in the 72 plots (per species) were tagged and monitored during the growing season. The following data were determined for each tagged cane: cane age (primocane or floricane), number of fruits produced on floricanes, number of *R. phoenicolasius* canes that propagated by tip rooting, origin of each cane (seedling, clonal offspring from an elongated underground rhizome, clonal offspring from the rootstock). Plots were resampled in the summers of 2003 and 2004 and the same data were collected from previously tagged canes and new canes, which were also tagged.

In 2002 fruits of *R. phoenicolasius* and *R. argutus* were collected from canes at both forests. In 2003 and 2004 fruits of *R. phoenicolasius* were sampled from both forests, but *R. argutus* fruits were only collected in Corn Island. The fruits were sampled from canes outside the 72 plots. Thirty fruits from each species and each forest were dissected and the number of seeds per fruit determined.

In 2002, additional fruits of both species were collected from both forests and the seeds were mixed into composite samples for each species. The seeds were used in field and

67

greenhouse germination experiments. In the fall of 2002, 18 sites in each forest received

ten seed packets (five per species). Each seed packet contained 10 seeds. At each site the

seed packets were distributed in a 15 x 15cm square grid and they were placed on the soil

surface after the surface litter was removed. Seed packets were made from plastic slide

mounts (Gepe slide mounts) that held 50 x 30 mm nylon mesh Shandon tissue specimen

bags. Eighteen seed packets of each species were also placed in full sun in a common

garden at SERC. In the spring of 2003, the seed packs from the field and garden were

retrieved and scored for percent germination. No seeds germinated in any seed packet so

the seeds in each seed packet were scarified. Dry seeds were placed in a glass scintillation

jar on ice. Ice-cold concentrated 96%+ sulfuric acid was poured over the seeds and they

were kept on ice. The amount of time that seeds remained in the sulfuric acid was based

on seed size. The smaller seeds of *R. phoenicolasius* were scarified for 30 minutes and

the larger *R. argutus* seeds were scarified for 60 minutes. Seeds were then placed into a

sieve and washed. They were then immersed in a 1% sodium bicarbonate solution for 10

minutes. Seeds were then rinsed with water and placed into containers that contained 3g/l

calcium hypochlorite along with 12g/l of calcium hydroxide. Seeds were refrigerated in

this solution for 6 days, rinsed in water and placed onto trays that contained a 75:25

mixture of Promix (peat bark based growing medium) and sand. The seeds were then

stratified for 10 weeks at 4°C (*sensu* Swartz 2002). Following stratification, seeds from

each field site were combined with seeds from the garden experiment. Fifty seeds of each

species, chosen from the composite samples, were put into individual cells in seedling

trays to germinate in the greenhouse at SERC. The 36 trays were placed in the

greenhouse in 90% sun and watered every other day and germination was recorded once a week for 6 weeks.

In 2003 the seed germination experiment was repeated but with only 30 seeds per site because of low rates of fruit production. Based on results from 2002, I scarified and stratified seeds (see procedures above) before I placed them into seed packets and then into the field sites. Seed packs were observed for germination in the field during the spring and summer and in late summer they were retrieved and placed in the greenhouse in trays that contained a 75:25 mixture of Promix and sand. Again seeds were grouped by site. Trays of seeds were placed in the greenhouse in 90% sun and watered every other day and germination was recorded once a week for 6 weeks.

Temperature and precipitation data were obtained from a NOAA weather station at the Baltimore Washington International Airport. Average temperature and precipitation were calculated for a 30-year period from 1970 to 2000 for comparison with data in 2002, 2003 and 2004.

Analysis

All demographic data were analyzed with a mixed model (PROC MIXED) analysis of variance (ANOVA) with random blocking for site within a forest (nine sites per forest). The fixed effects were species (*R. argutus* or *R. phoenicolasius*) and forest (Corn Island or Fox Point) and the interaction effects were between species and forest. In cases where the interaction was significant, simple effects were investigated using simple mean

differences analyzed with T-tests and sequential Bonferroni adjusted P-values. The simple effects that were tested when the interaction term was significant were: *R. argutus* at Corn Island (RACI), *R. argutus* at Fox Point (RAFP), *R. phoenicolasius* at Corn Island (RPCI), *R. phoenicolasius* at Fox Point (RPFP). Germination data were analyzed on a site basis. The number of seeds per fruit was compared between species and between forests in 2002 using a two-way ANOVA. Seed counts per fruit were based on data from 30 fruits per species per site. In 2003 and 2004 *R. argutus* did not produce any seeds at Fox Point. Interactions between forest and species were not examined in 2003 and 2004. Instead, comparisons were made between species with a one-way ANOVA. All analyses were conducted using SAS 8.2 (SAS 2004).

Results

In 2002, *R. argutus* had a significantly higher cane density ($F_{1,124}=13.21$, P=.004) in both forest habitats (Table 1, Fig. 1) for first year canes ($F_{1,124}=13.54$, P=.0003) and second year canes ($F_{1,124}=10.52$, P=.0015) (Table 2). In 2003, there were no significant differences in cane densities between species and total cane and first year cane density were significantly higher at Fox Point for both species ($F_{1,124}=9.93$, P=.002, $F_{1,124}=4.81$, P<.030) (Table 1, Fig. 1). Due to a significant interaction between species and forest for second year canes, simple mean differences were examined. In 2003, the difference between *R. argutus* at Corn Island (RACI)=0.72 ± 0.338 and *R. argutus* at Fox Point (RAFP)=2.75 ± 0.338, was significant ($T_{1,124}=4.24$, P<.0001). The difference between *R. phoenicolasius* at Corn Island (RPCI=0.97 ± 0.338) and *R. phoenicolasius* at Fox Point (RPFP=2.03 ± 0.338) was also significant ($T_{1,124}=2.21$, P=.01). In addition, the difference

between *R. argutus* at Fox Point (RAFP=2.75 ± 0.338) and *R. phoenicolasius* at Fox

Point (RPFP=2.21± 0.338) was significant ($T_{1,124}$= 2.2, P=.015) (Table 2). In 2004, there

was no significant difference between species, but cane density was significantly higher

in the Fox Point forest (Table 1, Fig. 1). There was a significant interaction, so the simple

mean differences were examined, the difference between RACI=3.14 ± 0.770 and

RAFP=8.03 ± 0.770 was significant ($T_{1,124}$=4.49, P<.0001) and the difference between

RPCI = 4.44 ± 0.770 and RPFP=6.86 ± 0.338 was significant ($T_{1,124}$=2.22, P=.009)

(Table 1, Fig. 1). For both species there were greater numbers of canes at Fox Point.

When examining the first and second year canes in 2004 there was no significant

interaction and there were more canes at Fox Point for *R. argutus* ($F_{1,124}$=11.76, P=.0008)

and *R. phoenicolasius* ($F_{1,124}$=20.27, P<.0001) (Table 2).

The ratio of the total number of canes per plot from one year to the next (i.e., 2003/2002

and 2004/2003) can be used to estimate inter-annual population changes. A ratio greater

than 1 would indicate a net increase in density and a ratio less than 1 would indicate a net

decline. Between 2002 and 2003 both species declined in the two forests and the ratio

was not significantly different between species. The ratio, however, was significantly

higher at Fox Point ($F_{1,124}$= 4.60, P<.0339), indicating lower cane mortality (Table 3, Fig.

3). Between 2003 and 2004 there was an interaction between forest and species, so

simple effects were examined. The difference between RACI=0.62 ± 0.101 and

RAFP=1.19± 0.101 was significant ($T_{1,124}$=4.01, P<.0001) and the difference between

RPCI=1.24 ± 0.101 and RACI=1.03 ± 0.101 was significant ($T_{1,124}$=4.43, P<.0001)

(Table 3, Fig. 2).

The ratio of second year canes to first year canes from one year to the next can be used to estimate survival. A ratio of 1 would indicate 100% survival and a ratio less than 1 would indicate mortality. In both year transitions there were significant species and forest interactions, so simple means were examined. At Corn Island, *R. phoenicolasius* had significantly lower mortality than *R. argutus*, in both year comparisons 2002-2003: RPCI=0.29 ± 0.067, RACI=0.16 ±.067 ($T_{1,124}$= 2.07, P=.0134) and 2003-2004: RPCI=0.60 ± 0.068, RACI=0.19± 0.068 ($T_{1,124}$=5.14, P<.0001). (Table 3, Fig 3).

The density of fruiting canes of the invasive species was significantly higher in both forests in 2002 and 2004. In 2003 there was a significant difference between *R. phoenicolasius* and *R. argutus* at Fox Point but not Corn Island. In 2002 and 2003 there was a significant interaction, therefore simple mean differences were examined. In 2002 there were significant differences between species in each forest. The difference between RACI=0.86± 0.235 and RPCI=2.56± 0.235 was significant ($T_{1,124}$=3.95, P<.0001), the difference between RAFP=0.06 ± 0.235 and RPFP=2.06± 0.235 was also significant ($T_{1,124}$=8.28, P<.0001). In 2003 *R. phoenicolasius* only had significantly more fruiting canes at Fox Point (RAFP=0.00 ± 0.155 and RPFP=1.08 ± 0.155; $T_{1,124}$=7.45, P<.0001). There were also significantly more canes fruiting at Fox Point than Corn Island for *R. phoenicolasius*, RPFP=1.08 ± 0.155 vs. RPCI=0.22 ± 0.155 ($T_{1,124}$=3.95, P<.0001). In 2004 there were significantly more fruiting individuals of *R. phoenicolasius* than *R. argutus* ($F_{1,124}$= 52.58, P<.0001) (Table 1, Fig. 4).

The number of fruits per plot followed the same pattern as the number of fruiting canes where, in 2002 and 2004, there were significantly more fruits per plot for *R. phoenicolasius* than for *R. argutus* at both forests ($F_{1,124}=53.01$, $P<.0001$ and $F_{1,124}=21.15$, $P<.0001$ respectively). In 2003 there was a significant difference between *R. phoenicolasius* and *R. argutus* at Fox Point, RPFP=6.19 ± 1.035 and RAFP<0.00 ± 1.035 ($T_{1,124}=6.11$, $P<.0001$). There were also significantly more fruits produced by *R. phoenicolasius* at Corn Island compared to Fox Point RPCI=6.19 ± 1.035 and RPFP=0.89 ± 1.035 ($T_{1,124}=3.63$, $P=.0001$).

Comparisons in the number of seeds per fruit were made across four treatment types 1. *R. argutus* at Corn Island, 2. *R. argutus* at Fox Point, 3. *R. phoenicolasius* at Corn Island, 4. *R. phoenicolasius* at Fox Point. In 2002 there was a significant difference ($F_{3,156}=201.87$, $P<.001$) in the four treatments and a significant difference between *R. argutus* and *R. phoenicolasius* ($T_{1,156}=32.19$, $P<.001$) with *R. phoenicolasius* having greater number of seeds per fruit. In 2003 and 2004 there was significant difference between the three treatments 1. *R. argutus* in Corn Island, 2. *R. phoenicolasius* in Corn Island 3. *R. phoenicolasius* in Fox Point (2003 - $F_{2,87}=63.21$, $P<.001$, 2004 - $F_{2,87}=54.84$, $P<.001$). The number of seeds per fruit again differed significantly between species with *R. phoenicolasius* having significantly more seeds per fruit (2003 -$T_{1,87}=9.43$, $P<.001$, 2004 - $T_{1,87}=10.40$, $P<.001$). In addition, in both years seeds of *R. phoenicolasius* germinated at a significantly higher rate (2003 - $F_{1,68}=66.37$, $P=.0001$; 2004 - $F_{1,32}=19.89$, $P=.0001$).

There were few seedlings or canes arising from clonal propagation or tip rooting during the course of the study. In 2002 out of 797 canes there were 6 seedlings of *R. argutus* and 3 canes which had arisen from clonal propagation. For *R. phoenicolasius*, out of 613 canes surveyed there were only 3 seedlings, no canes had arisen from clonal propagation and only 6 canes produced new shoots by tip rooting. In 2003 there were 441 canes of *R. argutus* of which 2 were seedlings and 2 had arisen from clonal propagation. There were 357 canes of *R. phoenicolasius* in 2003 and only 2 were seedlings. Seven canes were produced by clonal propagation in 2003 and none were produced by tip rooting. In 2004 there were 403 canes of *R. argutus* and there were only 3 seedlings and two canes that were produced by clonal propagation. There were 409 canes of *R. phoenicolasius* in 2004, including no seedlings, 7 clonally produced canes and 28 canes by tip rooting.

The summer of 2002 had drought conditions with May through September receiving rainfall 83% of the 30-year average and the total precipitation for the year, January to December, was 94% of the 30-year average (Fig. 5). The summer of 2003 had higher precipitation than average. Over the year of 2003 recorded precipitation was 50% above the 30 year average (Fig. 6). The summer of 2004 had normal rainfall with a yearly total within 10% of the average (Fig. 7). Temperatures in 2002 for April through October were 1.05° C higher than the 30-year average for the same period (Fig. 8). Temperatures in 2003 and 2004 were within 1% of the 30-year average (Fig. 9, 10).

Discussion

Following introduction or initial colonization, invasive species can often be found at higher densities than in their native habitats (Grigulis *et al* 2001, Paynter *et al* 2003). Although it is difficult to identify habitats that are more invasible, habitats that have higher levels of disturbance are often more susceptible to invasion. Disturbed habitats have more exposed ground for invasion and often have increased or under-utilized resources, such as light and nutrients (Burke and Grime 1996). When invasives and natives are able to exist in the same habitats, particularly disturbed sites, it is important to examine their behavior in those habitats in order to distinguish those traits that underlie the invasives successful establishment (Call and Nilsen 2003). I predicted that the invasive, *R. phoenicolasius*, would occur in higher densities than the native species at both forests. I expected that cane density and fruit production would be greater in the invasive. I also predicted that at the Corn Island forest, which had higher light and nutrient availability, both species would occur in higher densities. In a related study (Chapter 2), I found that both species had higher rates of photosynthesis and leaf nitrogen levels at Corn Island, thus supporting higher growth rates. Similar results were measured for the invasive *Alliaria petiolata* when plants were grown in garden conditions with higher light and nutrient levels (Meekins and McCarthy 2002). Many clonal plants respond positively to increased light level through increased growth (Marino *et al.* 1997). However in the first year of the study when I surveyed existing populations of both species in both forests, I found no differences between forests and that the native had higher cane densities than the invasive.

Differences between habitats became apparent after all populations were stressed in the first year of the study. The first summer of the study there was a drought, with lower rainfall and higher temperatures than the 30-year average (Fig. 5 and 8). Counter to my predictions, there was greater mortality of canes in the Corn Island forest from 2002-2003 for both species (Fig 2). Individuals in the Fox Point forest may have been sheltered from drought conditions, whereas individuals in the Corn Island habitat, which is effectively an edge habitat, may have been subjected to higher transpirational demand for water (Gascon *et al.* 2000, Cadenasso and Pickett. 2001). Drier habitats were shown to be less favorable to the growth and survival of *Alliaria petiolata* an invasive which is also found in deciduous forests (Byer and Quinn 1998). Davis *et al.* in (2000) discussed a theory on habitat invasibility where invasibility varies temporally as resources become more and less available. As water levels decreased, invasibility of both habitats may have also diminished, but more so in the warmer, higher light edge forest habitat of Corn Island.

Following the drought was a season with precipitation above the 30-year mean (Fig. 6). Both species increased cane density in Fox Point but the population of *R. argutus* at Corn Island continued to decrease in 2003 and 2004. As populations of *R. argutus* decreased in Corn Island, *R. phoenicolasius* increased in cane density in 2004 (Fig. 1-3). In addition, the recovery of *R. phoenicolasius* in Corn Island was similar to the recovery in Fox Point, even though populations in Corn Island were more affected by the drought.

The ability of *R. phoenicolasius* to recover similarly in both habitats and survive environmental impacts better than *R. argutus* in the edge habitat may indicate greater

plasticity in the invasive (Jurjavcic *et al.* 2002). In addition, the survival and recovery of established patches may indicate long-term survival of populations of *R. phoenicolasius* in edge habitats (Luken and Goessling 1995, Damman and Cain 1998). This would be in agreement with studies which have found greater number and higher densities of invasive species in forest edges than forest interior habitats (Goldblum and Beatty 1999, Meekins and McCarthy 2001, Yates *et al.* 2004).

One of the more important characteristics of invasive species is their ability to spread into new habitats. I predicted that the invasive would produce higher numbers of seeds than the native, as Grotkopp *et al.* (1996) and Richardson and Rejmanek (2004) found for the genus *Pinus*. I found high levels of fruit and seed production in the invasive, which followed predictions. In all three years and at both forests *R. phoenicolasius* produced a higher density of fruiting canes and fruits per plot. The exception was in 2003 at Corn Island where, due to high levels of mortality of developing fruits, there were no differences between the number of fruiting canes and density of fruits per plot. In addition to higher numbers of fruits, the fruits produced by *R. phoenicolasius* had higher numbers of seeds. Clonal species often establish populations with seeds then reproduce clonally (Meyer and Schmid 1999). The combination of a greater number of seeds produced by *R. phoenicolasius* with a higher germination rate would allow *R. phoenicolasius* to spread at greater rates than the native *R. argutus*. High germination rates allowed a clonal herb, *Silene dioca*, to spread into many habitats (Matlack 1987). The production of copious amounts of seeds has also been observed in other invasives (Morris *et al.* 2002, Ellsworth *et al.* 2004). Over the three year period, there were few

seedlings in plots and rarely were seedlings observed in areas in the two forests, except in

2004 when *R. phoenicolasius* seedlings were found in abundance on trails. In another

study (Chapter 5) I found seedling survival was significantly reduced under leaf litter,

which may be more prevalent in forest interiors than on trails. Few seedlings were

observed in a study on *Rubus saxitalis* (Eriksson and Bremer 1993). In a study on *Rubus*

ideaus, a species which is morphologically similar to *R. phoenicolasius* and *R. argutus*,

seedlings were only observed in patches during the first few years of colonization

(Whitney 1986, Ulanova 2000) and it was during the same time period that a large

number of canes were produced by clonal propagation (Whitney 1986). In this study, few

new canes were produced by propagation via stolons or by root tipping. This suggests

that the populations of the invasive and native were not spreading nor increasing in

density rapidly in either habitat. I focused on established populations, which may explain

the lack of colonization behavior or high rates of clonal growth. Colonization of new

patches may be episodic, occurring only in disturbances of an appropriate size and in

years of appropriate weather conditions. Hartnett and Bazzaz (1985a) observed time-

limited recruitment restricted to a 3 year window in an old field *Solidago*. In addition, the

density of the established patches may have been suppressing population growth, a

phenomenon reported in *Rubus* in northwestern forests (McDowell and Radosevich

2005). It is quite possible that the variable precipitation and limited extent of this three

year study was not long enough to observe habitat patch recruitment in either species.

Differences between habitats were most pronounced during a drought year. There was

significantly lower cane density in the higher light Corn Island forest following the

drought. In Fox Point the effects of the drought were muted, perhaps due to lower light levels and transpiration. Both species decreased in number in the second year but recovered in the third year in this habitat. In the Corn Island habitat *R. phoenicolasius* was able to recover more quickly than *R. argutus*, which continued on a trend of decreasing density for the entire study. My results support the theory that habitat invasibility is not constant. Following the drought both habitats became less invasible with high levels of mortality leading to density decreases until two years following the drought (Davis *et al*. 2000). By comparing the two species I was able to highlight that the recovery of *R. phoenicolasius* was significantly greater than its native congener. This species difference was evident in both forest habitats, indicating greater plasticity in the environmental responses of *R. phoenicolasius*.

I quantified expected differences in terms of higher fruit and seed production with higher germination rates for the invasive. These traits are associated with greater potential for dispersal. The combination of high fruit production, plasticity and less mortality in edge habitats is in agreement with previous studies on invasive species (Grotkopp *et al*. 2002, Jurjavcic *et al.* 2002, Yates *et al.* 2004). All of these characteristics allow for the survival of stressful events and maintenance of fitness levels leading to the persistence of an invasive.

Confirmation of the results from this study should be evaluated further. Experiments should be conducted in a broader range of habitats in which the invasive occurs and studies should be conducted for longer periods of time. The differences observed between

years, with differing amounts of rainfall, clearly demonstrate that variations in environmental conditions can have dramatic and long-lasting influences on the demography of *R. phoenicolasius*. As we compile more and more information on invasive species, it is also necessary to observe the colonization dynamics in different habitats in addition to observing the maintenance of established populations.

Table 1. ANOVA table for the number of canes and fruiting canes per plot

	Canes per plot				Fruiting canes per plot				
Source	Num df	Den df	F	P	Source	Num df	Den df	F	P
2002					**2002**				
Species	1	124	13.21	**.0004**	Species	1	124	74.78	**<.0001**
Forest	1	124	0.64	.4261	Forest	1	124	0.36	.5492
Species x Forest	1	124	0.13	.7198	Species x Forest	1	124	9.34	**.0027**
2003					**2003**				
Species	1	124	2.87	.0926	Species	1	124	36.90	**<.0001**
Forest	1	124	9.93	**.0020**	Forest	1	124	4.32	**.0396**
Species x Forest	1	124	.13	.7198	Species x Forest	1	124	19.85	**<.0001**
2004					**2004**				
Species	1	124	.01	.9114	Species	1	124	52.58	**<.0001**
Forest	1	124	16.75	**<.0001**	Forest	1	124	0.78	.3783
Species x Forest	1	124	3.94	**.0494**	Species x Forest	1	124	1.71	.1934

Table 1. ANOVA for the total number of canes per plot and number of fruiting canes per plot. This examines the differences between the density of *R. phoenicolasius* and *R. argutus* in two forest habitat types. Significant P values in bold.

Figure 1. Number of canes per 1m² plots
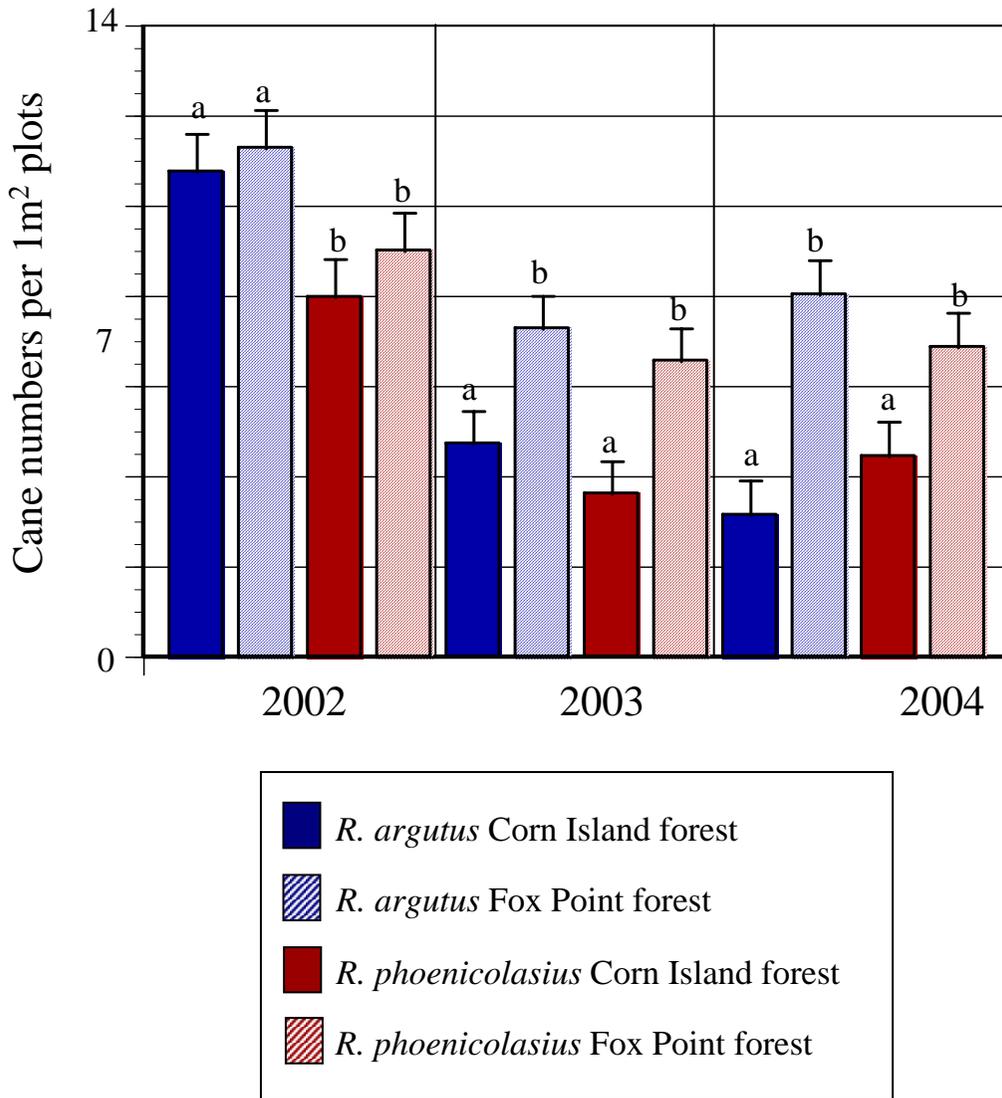
Figure 1. In 2002 there was a significant difference between species with a higher density in *R. argutus*. In 2003 there was no significant difference between species, but there were significantly greater numbers of both species in the Fox Point forest. In 2004 due to the interaction we looked at difference between simple effects using a sequential bonferroni adjusted T-tests and P-values. In both species there were greater cane numbers in Fox Point. Data shown are mean + SEM.

Table 2. ANOVA table for density of first and second year canes

Source	Numbers age 1				Numbers age 2			
	Num df	Den df	F	P	Num df	Den df	F	P
2002								
Species	1	124	13.54	**.0003**	1	124	10.52	**.0015**
Forest	1	124	1.04	.3097	1	124	0.22	.6372
Species x Forest	1	124	.75	.3882	1	124	0.06	.8082
2003								
Species	1	124	3.03	.0840	1	124	1.03	.3116
Forest	1	124	4.81	**.0301**	1	124	13.58	**.0003**
Species x Forest	1	124	3.03	.0840	1	124	4.38	**.0385**
2004								
Species	1	124	1.88	.1725	1	124	3.39	.0680
Forest	1	124	11.76	**.0008**	1	124	20.27	**<.0001**
Species x Forest	1	124	3.40	.0678	1	124	3.74	.0555

Table 2. ANOVA for the total number of first year and second year canes per plot. In 2002 there was a significantly higher density for first and second year canes for *R. argutus* than *R. phoenicolasius*. In 2003 there was a significantly higher density for first and second year canes in Fox Point forest than in Corn Island. Due to an interaction in the second year, simple effect means were compared. In 2004, again there were significantly higher densities for first and second year canes in Fox Point forest than in Corn Island. Significant P values in bold.

Table 3. ANOVA table for change in canes between years and change in first year cane density to second year cane density

Source	2002-2003				2003 - 2004			
	Num df	Den df	F	P	Num df	Den df	F	P
Δ canes								
Species	1	124	0.89	.3473	1	124	5.35	**.0223**
Forest	1	124	4.60	**.0339**	1	124	3.10	.0809
Species x Forest	1	124	0.00	.9480	1	124	15.60	**.0001**
Δ first year to second year canes								
Species	1	124	0.62	.4332	1	124	14.49	**.0002**
Forest	1	124	5.75	**.0180**	1	124	12.55	**.0006**
Species x Forest	1	124	4.61	**.0338**	1	124	11.97	**.0007**

Table 3. ANOVA for the change in the number of canes per plot between years 2002-2003 and 2003-2004. and for the change in the number first year canes per plot to number of second year canes per plot between years 2002-2003 and 2003-2004. This is a measure of survival. The difference in number of canes between years was examined between species, forests and their interaction. Significant P values in bold.

Figure 2. Change in number of canes between years
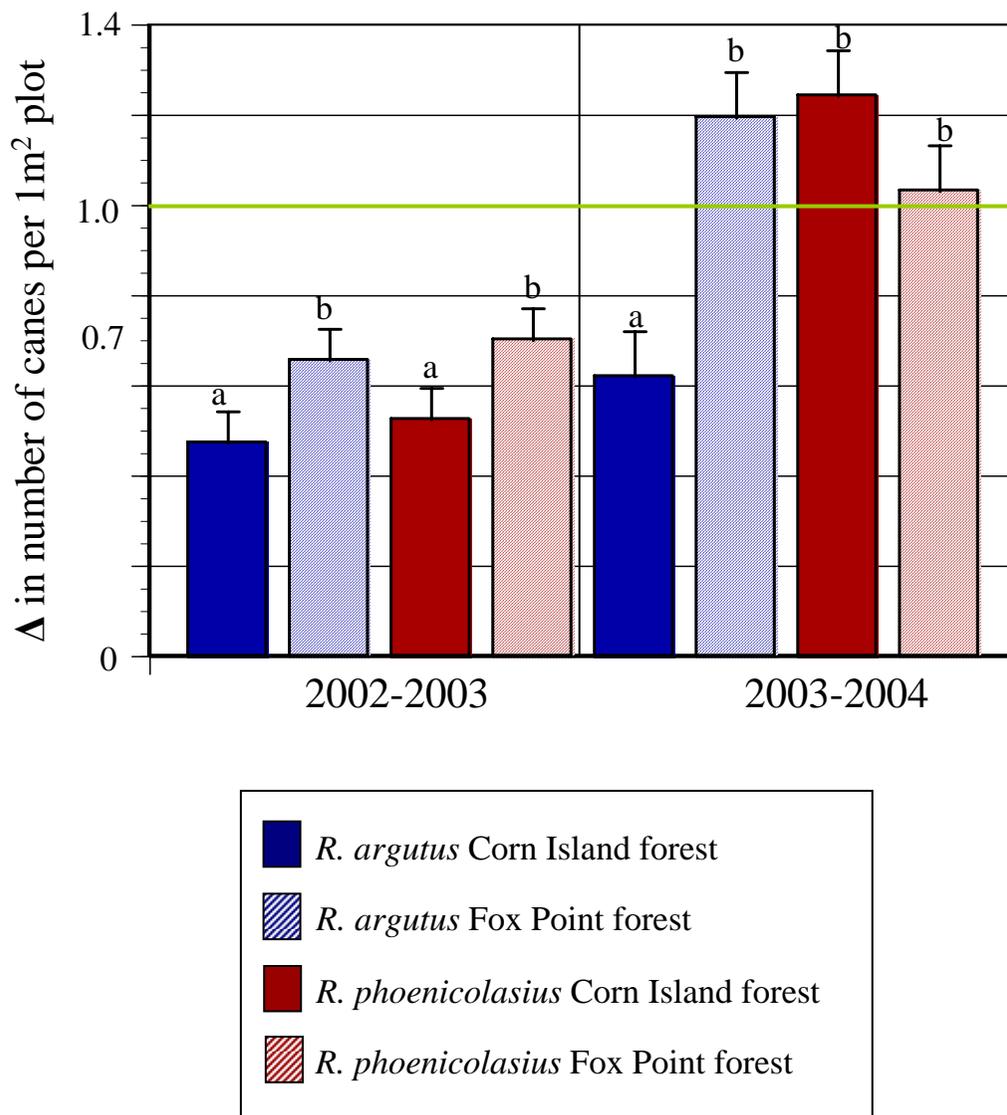
Figure 2. The green line on the graph indicates no change in cane number from year to year, below the green line indicates a decrease in number of canes from year to year, above the green line indicates an increase in cane numbers. Between 2002-2003 there was a significant difference between forests with a higher rate of increase in the Fox Point forest. Between 2003-2004 *R. argutus* had a greater increase in Fox Point and there was a greater increase in *R. phoenicolasius* in Corn Island forest as compared to *R. argutus*. There were no significant differences in species comparisons. Data shown are mean + SEM.

Figure 3. Survival of first year canes
to second year canes

Δ numbers first years per 1m² plot to numbers of second years per 1m² (y-axis, ranging 0 to 1.0)

Legend:
- ■ *R. argutus* Corn Island forest
- ▨ *R. argutus* Fox Point forest
- ■ *R. phoenicolasius* Corn Island forest
- ▨ *R. phoenicolasius* Fox Point forest
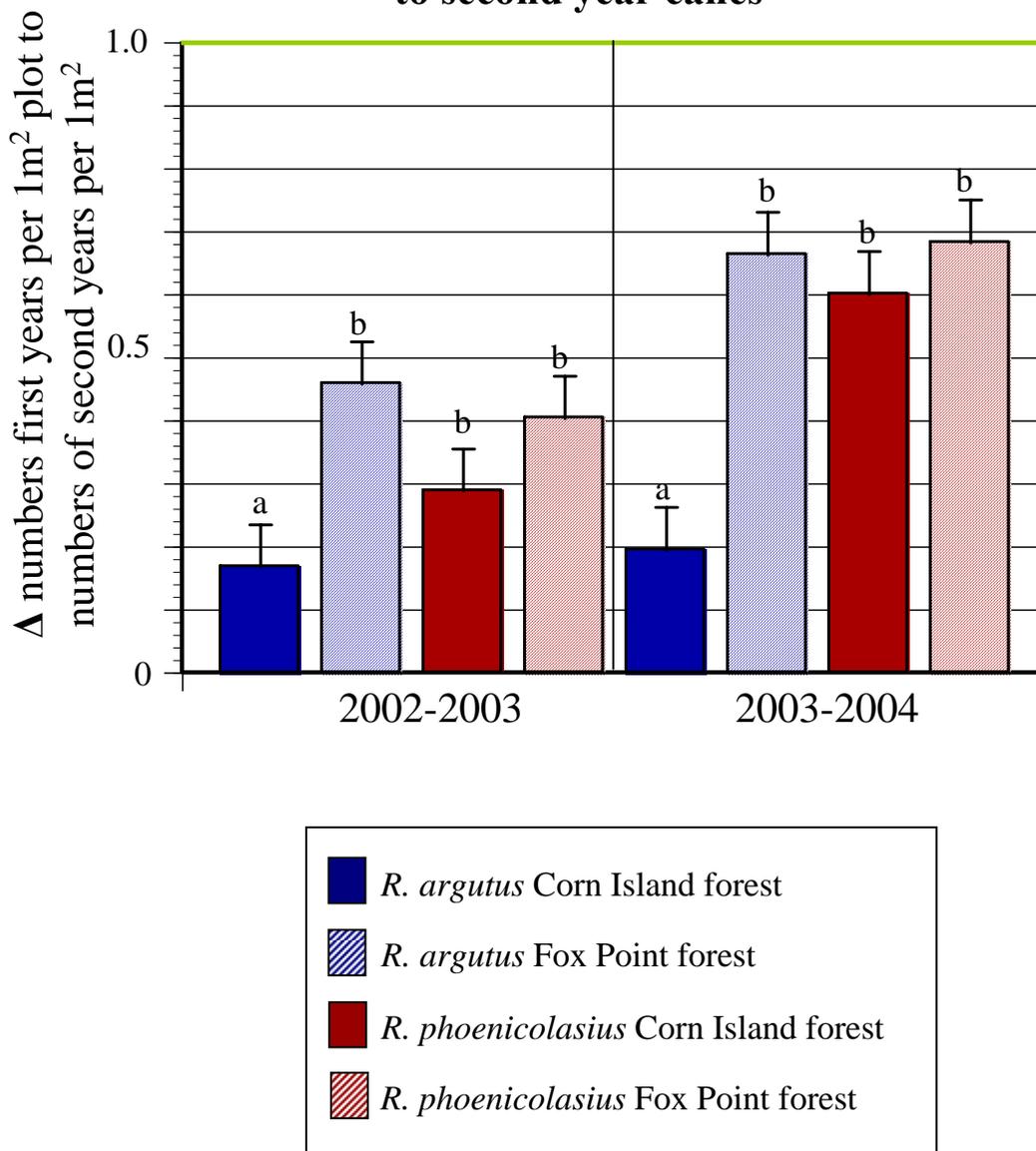
Figure 3. The green line on the graph indicates 100% survival from year to year, below the green line indicates a decrease in number of canes from year to year. In both 2002-2003 and 2003-2004 there was an interaction between species and forest. There were significant differences between forests for *R. argutus*, and *R. argutus* and *R. phoenicolasius* in the Corn Island forest. Data shown are mean + SEM.

# Figure 4. Number of fruiting canes per 1m² plot in each year
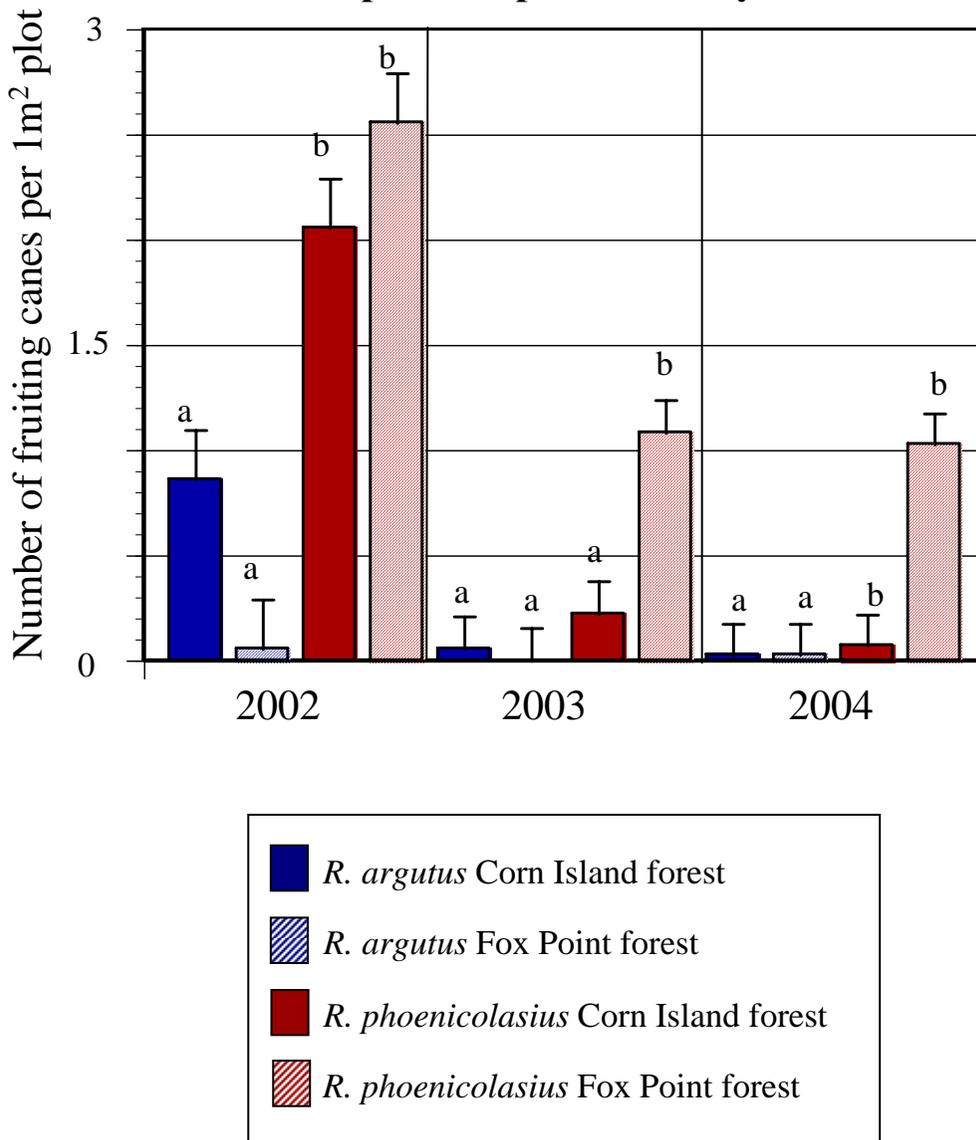
Figure 4. In 2002 in the Corn Island forest, *R. phoenicolasius* had greater numbers of fruiting canes per plot than *R. argutus*, this was also observed in Fox Point forest. In 2003, in the Corn Island forest *R. phoenicolasius* did not have significantly greater fruiting canes than *R. argutus*, but in Fox Point *R. phoenicolasius* had a greater number of fruiting canes than *R. argutus*. When fruiting canes were compared for *R. phoenicolasius*, there were significantly greater numbers in Fox Point than Corn Island. In 2004 there was no interaction and *R. phoenicolasius* produced greater numbers of fruiting canes than *R. argutus*. Data shown are mean + SEM.

Figure 5. Precipitation in 2002 with the 30-year average
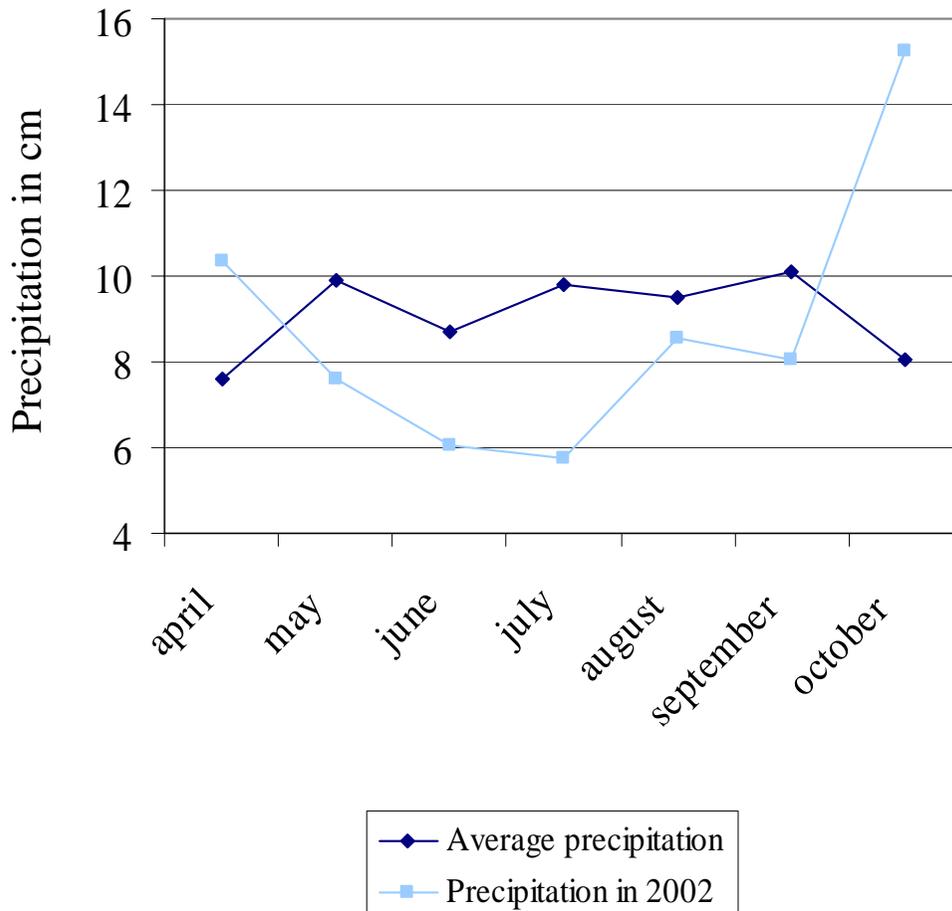
Figure 5. Average and observed monthly precipitation in 2002 measured in cm. Recorded by NOAA at Baltimore Washington International Airport weather station. Average over 30-year period from 1970-2000. In 2002 the precipitation observed was lower than the 30-year average.

Figure 6. Precipitation in 2003 with the 30-year average
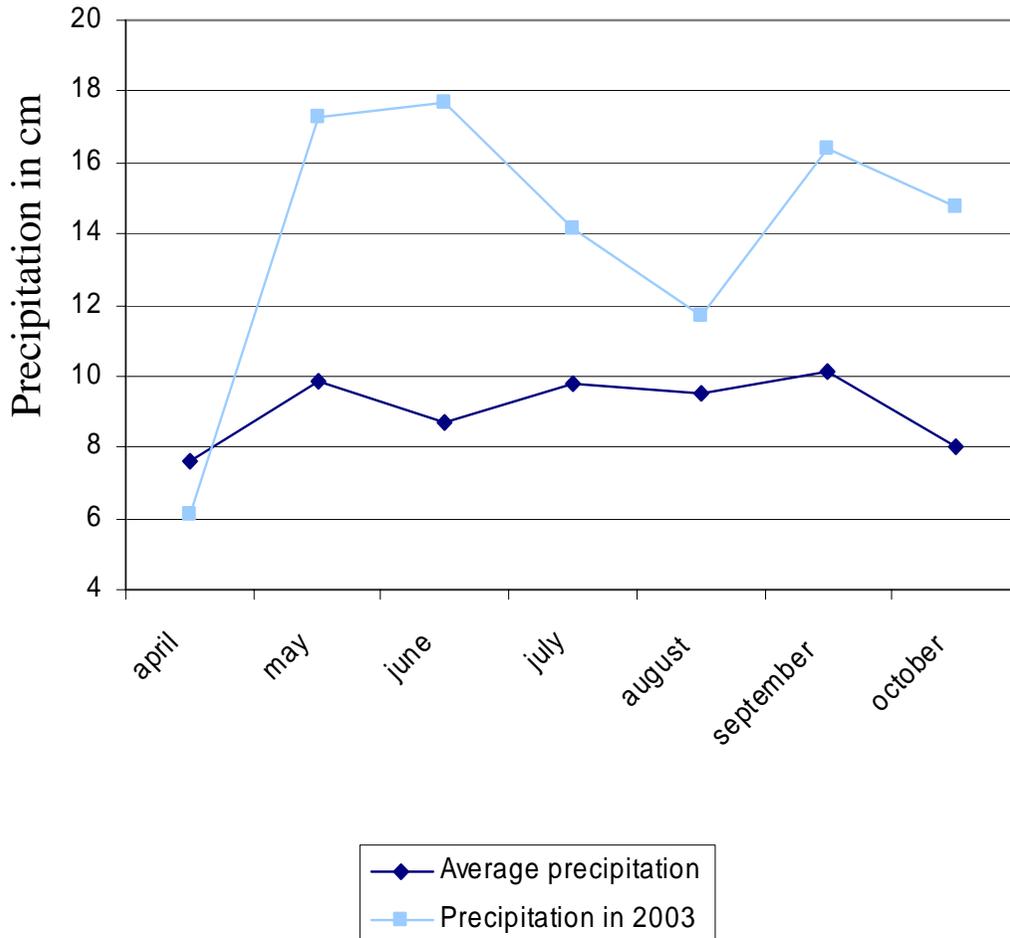
Figure 6. Average and observed monthly precipitation in 2003 measured in cm. Recorded by NOAA at Baltimore Washington International Airport weather station. Average over 30-year period from 1970-2000. In 2003 the precipitation observed was higher than the 30-year average.

**Figure 7. Precipitation in 2004 with the 30-year average**
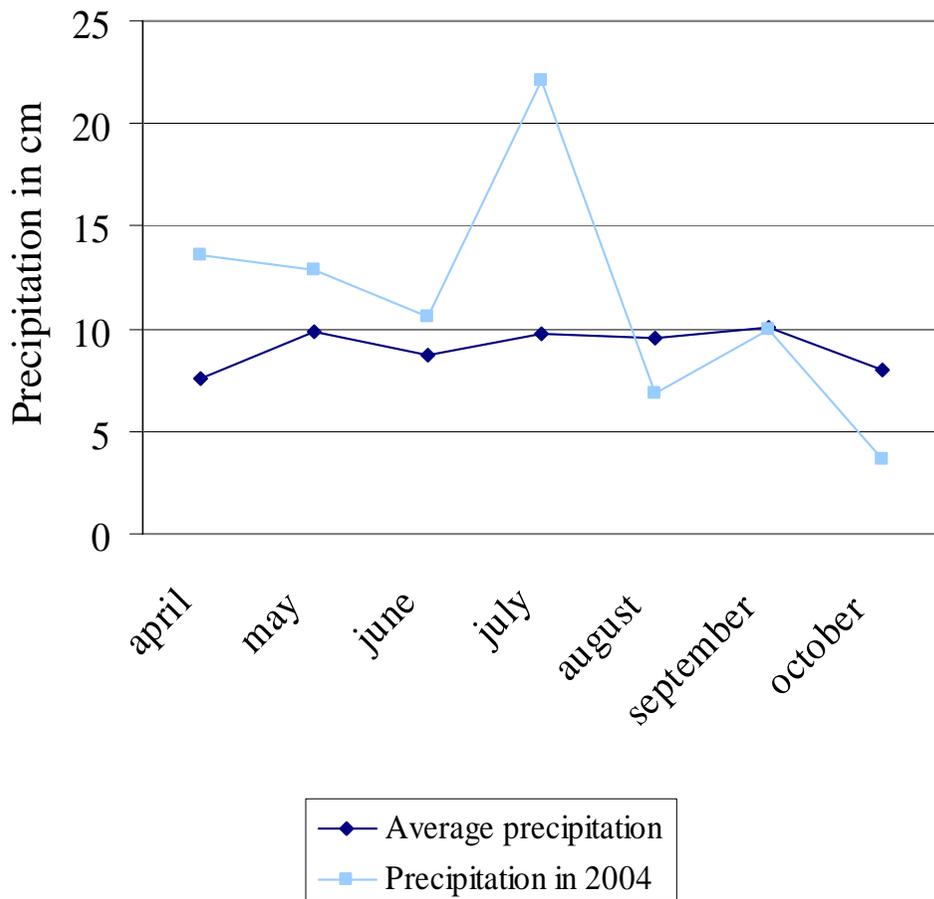
Figure 7. Average and observed monthly precipitation in 2004 measured in cm. Recorded by NOAA at Baltimore Washington International Airport weather station. Average over 30-year period from 1970-2000.

Figure 8. Temperature in 2002 with the 30-year average
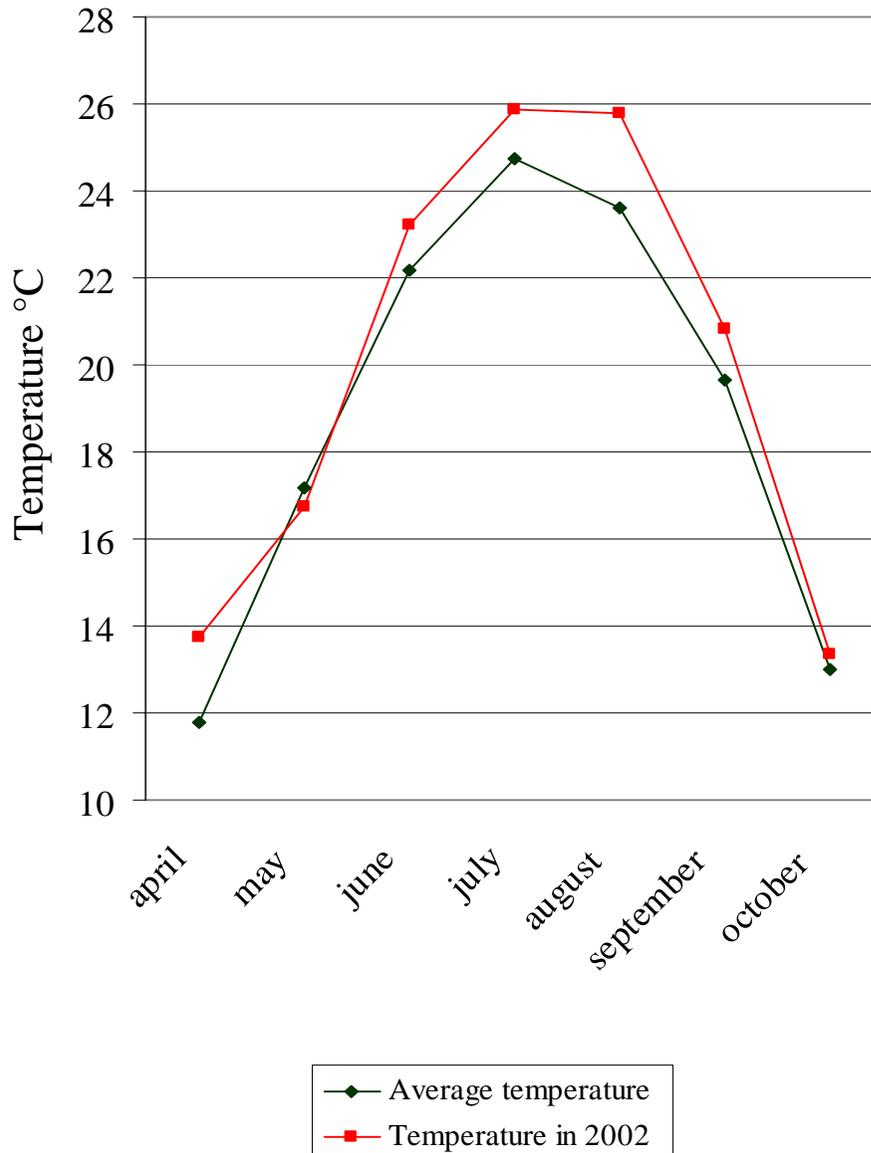
Figure 8. Average and observed monthly temperature in 2002 measured in Celsius. Recorded by NOAA at Baltimore Washington International Airport weather station. Average over 30-year period from 1970-2000. In 2002 there was higher observed temperature than the 30-year average during the growing season of April until October.

Figure 9. Temperature in 2003 with the 30-year average
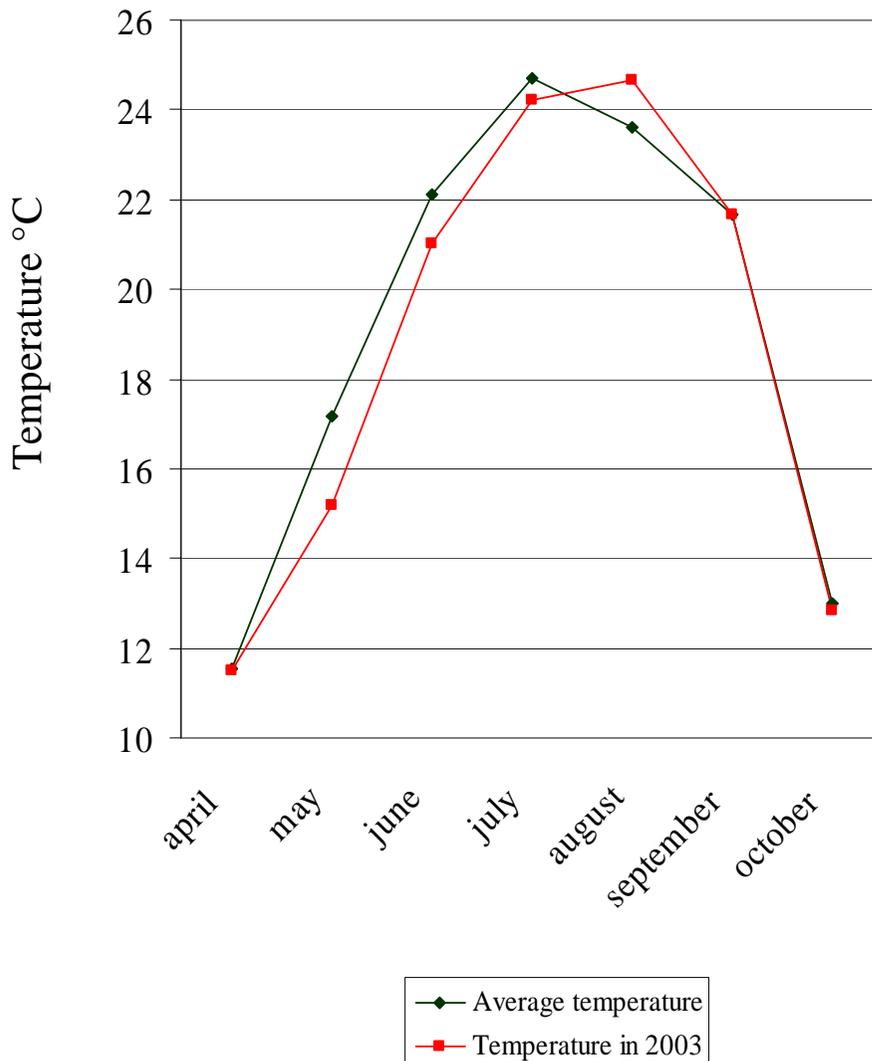
Figure 9. Average and observed monthly temperature in 2003 measured in Celsius. Recorded by NOAA at Baltimore Washington International Airport weather station. Average over 30-year period from 1970-2000.

**Figure 10. Temperature in 2004 with the 30-year average**
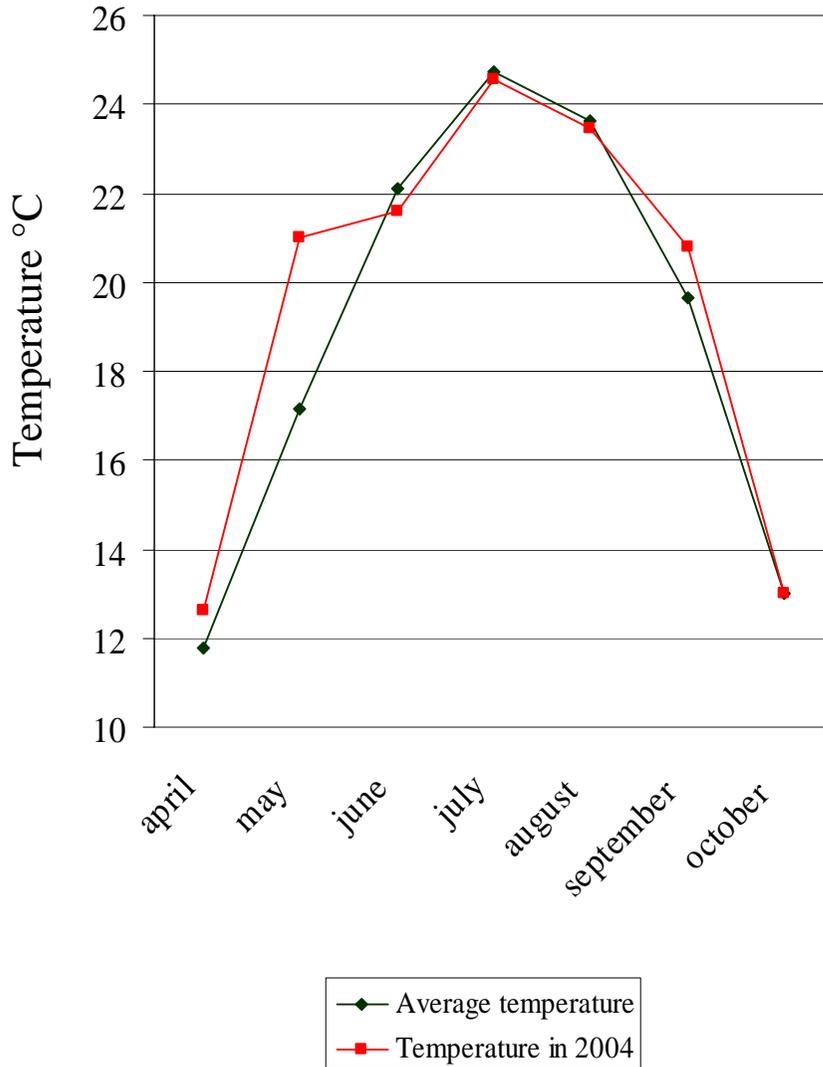
Figure 10. Average and observed monthly temperature in 2004 measured in Celsius. Recorded by NOAA at Baltimore Washington International Airport weather station. Average over 30- year period from 1970-2000.

Chapter 5

The relative roles of asexual and sexual reproduction in the success of the invasive *Rubus phoenicolasius*

Abstract

Invasive species negatively impact the environment and create financial costs through eliminating native species and altering ecosystem services. *Rubus phoenicolasius*, an invasive species in North America, occurs at high population densities within its new range. Studies were conducted at Smithsonian Environmental Research Center (SERC), Edgewater, MD to investigate asexual, sexual reproduction and seedling survival as explanations for the success of *R. phoenicolasius*. I compared the invasive to a native congener, *Rubus argutus*. A pollinator exclusion experiment demonstrated that the lack of pollinators had greater negative effect on *R. argutus* fruit production. *R. phoencolasius* also had significantly higher fruit production and more seeds per fruit than R. *argutus.* Greater numbers of fruits were removed, presumably by frugivores, from *R. phoenicolasius* demonstrating that its seeds are readily dispersed. Leaf litter additions significantly increased mortality of seedlings, but shading did not have a significant effect on seedling biomass. *R. phoenicolasius* seedlings inoculated with arbuscular mycorrhizal fungi (AMF) collected from roots of *R. argutus* and *R. phoenicolasius* did not grow as well as seedlings that were not inoculated. Seedlings inoculated with *R. argutus* AMF had significantly higher leaf weight, area and total biomass than seedlings with AMF from *R. phoenicolasius*. I observed negligible asexual reproduction for both species and observed no significant differences between species. Following

establishment, seed production, dispersal and seedling survival may be more important to the spread of the invasive *R. phoenicolasius* than asexual reproduction.

Introduction

The ability of invasive species to reach high densities in their non-native habitats may be a result of high levels of reproduction. Many successful invasive species are able to reproduce sexually through seed production and asexually through vegetative propagation to a greater extent than coexisting natives (Baker 1974, Meyer and Schmid 1999, Brundu *et al.* 2001, Sakai *et al.* 2001, Simberloff 2003). This allows for greater dispersal through seed production in addition to local spread through vegetative growth. The *Rubus* species compared in this study have similar life histories. Both the invasive, *R. phoenicolasius* and the native, *R. argutus* produce biennial shoots, hereafter referred to as canes, from perennial root stocks and are capable of sexual and asexual reproduction. Both species reproduce asexually producing new canes from rhizomes. In addition, the invasive *R. phoenicolasius* can sprout a new cane from the tip of an existing cane that comes into contact with the soil. I compared sexual and asexual reproduction of both *Rubus* species and investigated the requirements for seedling survival in the invasive, *R. phoenicolasius*.

Individuals that reproduce sexually are often dependent on local pollinators for pollen transfer (Parker 1997, Pan and Price 2002, Foreman and Kessili 2003). Some invasives negatively affect native sexual reproduction either by producing showy flowers which draw pollinators away from natives, or by contamination of native stigma with invasive

95

pollen (Brown and Mitchell 2001, Brown *et al*. 2002). Some invaders have a decreased

dependence on local pollinators, accomplished through self-compatibility or through

apomixis (Baker 1974, Rejmanek 1996, Rambuda and Johnson 2004). When individuals

reduce their dependency on pollinators there can be seed production even in isolated

populations or in habitats with a limited community of pollinators. High levels of fruit

and seeds aid invasives in their spread into local and neighboring communities (Foreman

and Kessili 2003, Foxcroft 2004, Kuhn *et al*. 2004).

The ability of invasive seedlings to survive in a range of habitats may help explain their

success (Gerlach and Rice 2003, Dietz *et al.* 1999). Seedlings of invasives have been

shown to survive in a range of light, water and nutrient conditions, which would allow

invasives to take advantage of many different habitats in their invaded range, or even

expand their range (Witkowski 1991). In addition, invasive species may be able to take

advantage of the soil community in their invaded habitat more so than in their native

habitat. This has been shown with invasive species and arbuscular mycorrhizal fungi

(AMF) (Zabinski *et al.* 2002, Callaway *et al.* 2004b). AMF are associations between

fungi and the roots of plants, where the plant provides carbon derived from

photosynthesis and the fungi facilitates uptake of nutrients, especially phosphorus (Bever

et al. 2001, Pringle and Bever 2002). The relationship between AMF and host plants

range from parasitic to mutualistic (Klironomos 2003). In a parasitic relationship, the

plant may suffer decreased growth and reproduction due to the association with the fungi

(Taylor and Harrier 2000). In mutualistic relationships the plant benefits from an

association with the fungi and produces greater biomass and higher reproductive output

96

(Lovelock and Miller 2002, Callaway *et al.* 2003). Invasives may also alter soil conditions to encourage a microbial community which then benefits further invasion (Kourtev *et al.* 2002 and 2003, Bever 1997).

Clonal reproduction may determine not only the establishment of a population but also the survival of that population (Hartnett and Bazzaz 1985a, 1985b, Tappeiner *et al.* 1991, Nishitani *et al.* 1999). The balance of sexual reproduction to asexual reproduction is often determined by the immediate habitat of the plant (Cain and Damman 1997, Harada *et al.* 1997, Kudoh *et al.* 1999). The plant and soil community, plant density, and abiotic features such as light, will determine the extent of clonal reproduction. In patches of *Solidago canadensis* colonizing old field habitats, lower density promoted asexual reproduction (Hartnett and Bazzaz 1985a). Both *Rubus* species can be found in patches: the density within a patch may discourage clonal growth inside the patch, whereas on the edge of the patch there may be greater clonal growth (Parker 2000, Wikberg and Svenson 2003, McDowell and Radosevich 2005). *R. phoenicolasius* and *R. argutus* can be found in a range of light levels which may affect their clonal reproduction (Whitney 1986, Ricard and Messier 1996).

In this study I compared sexual and asexual reproduction of both species to examine the role that each plays in population dynamics. I tested two hypotheses related to fruit production and dispersal. I hypothesized that fruit production of *R. phoenicolasius* would be less dependent on pollinators than the native *R. argutus* and that the invasive would benefit by having its fruits dispersed by local frugivores. Two seedling-related

hypotheses were also tested. I hypothesized that shading and litter additions would not affect seedling survival or growth of *R. phoenicolasius.* I further hypothesized that seedlings of the invasive would grow better when inoculated with AMF, especially AMF collected in populations of the invasive species. Two hypotheses focused on clonal growth. I hypothesized that there would be greater vegetative reproduction on the edges of the patches for both *Rubus* species but that, overall, the invasive species would produce more clonal ramets than the native species.

Methods

Study species

The invasive species, *Rubus phoenicolasius* is native in Japan, Korea and China. *R. phoenicolasius* was introduced to the United States in the 1890's, but it is in the last few decades that it has become a problem at the Smithsonian Environmental Research Center (SERC) (Hummer 1995). *R. phoenicolasius'* introduced range overlaps with the range of the native *Rubus argutus*. Both species can be found in fields and forests in the eastern United States. *R. phoenicolasius* and *R. argutus* have similar life history characteristics with biennial canes and a perennial rootstock and both are capable of sexual and asexual reproduction. The first year cane, primocane, is only vegetative while the second year cane, floricane, undergoes lateral branching and produces flowers and fruit. In the second year the perennial root stock will often send up another cane. Both species are able to reproduce clonally through underground rhizomes, but only *R. phoenicolasius* is capable of tip rooting (where the tip of the cane touches the ground, roots are produced and a new individual cane is produced).

Study site

The study was conducted at the Smithsonian Environmental Research Center (SERC), Edgewater, MD, USA (~10 km SSE of Annapolis, 38˚53' N, 76˚33' W). The 1,000 hectares that are part of the SERC property include agricultural fields, abandoned fields, and successional and mature forests that are typical of the region (Brush *et al.* 1980). Two non-contiguous forest habitats were used, locally known as Fox Point and Corn Island. Fox Point is a large tract of undisturbed mid-successional forest (60-70 years old). Corn Island is a narrow (50m x 1km) mid-successional forest (50-60 years old) between a dirt road and an agricultural field. Due to the fact that the Corn Island forest is primarily edge habitat, the Corn Island forest has higher light levels 13% GSF as compared to 10% GSF at Fox Point (Chapter 2, Meiners *et al.* 2002b). Corn Island also had higher soil nitrogen concentrations (Chapter 2) because the forest receives runoff from adjacent agricultural fields. Forest types were not replicated and with one high light and one lower light habitat there is a limit to the ability to generalize results.

Sexual reproduction

Four studies were conducted to examine the sexual reproduction of both species.

Pollinator limitations: A pollination study was conducted for three consecutive summers (2002 – 2004). In 2002 the study was conducted at both forests. Four patches of each species were selected and floricanes of five individuals of each species per site (5 individuals x 8 sites = 40 individuals for each species) were marked. Half the inflorescences on each individual were covered with a $6cm^2$ pollinator exclusion bag,

made of nylon fabric and secured with twist ties. The inflorescences were covered prior to floral opening and bags were left on for a 2-week period. The bags were removed at the end of the flowering period and plants were revisited once fruits developed to determine fruiting success, the percentage of flowers in each inflorescence that produced fruit. In 2003 and 2004 the experiment was repeated but only at Corn Island, due to low flowering rates in Fox Point. Five individual plants of each species were studied in three patches (5 individuals x 3 patches = 15 individuals for each species). Six inflorescences were tagged on each cane. Three inflorescences were covered with pollen bags, as in previous years, to prevent cross-pollination and three inflorescences were left uncovered.

In 2004 a control study was conducted to determine if bagging inflorescences had any affect on fruit production. Five individual plants of each species at the three sites in Corn Island were used for the experiment. Six flower groups from each plant were used, with one flower per group marked for cross pollination. Flowers were cross pollinated using picked flowers then either covered or left uncovered for one week. Plants were then revisited in 3 weeks to observe fruiting.

Fruit dispersal: In 2004 a fruit dispersal study was conducted at seven sites at Corn Island, four for *R. argutus* and three for *R. phoenicolasius*. Three floricanes were marked at each site, with the exception of the third site for *R. phoenicolasius* which had six floricanes. Each plant was numbered and each inflorescence was labeled. Plants were visited every other day during the flowering phenophases and the total number of buds, number of undeveloped flowers, number of aborted fruits and the total number of

developing fruits was noted. The number of flower buds and developing fruits that were missing from one sampling date to another were noted. Mature fruits were collected during each visit to the study sites.

Seed production: In 2002, thirty fruits of each species were collected at both forests and the number of seeds per fruit counted. In 2003 and 2004 the study was repeated but *R. argutus* did not produce any fruits at Fox Point in either year.

Sexual reproduction analysis: All analyses were conducted with SAS 8.2 using proc mixed (SAS 2004) with the exception of the fruit dispersal study, for which a T-test was used. For all analyses a P value of .05 or smaller was considered significant. The 2002 pollinator exclusion study was analyzed using a two-way ANOVA, with treatment and forest as fixed factors in the model. Data were arcsine transformed for homogeneity of variances. The 2003 and 2004 pollinator exclusion studies were analyzed using a one way ANOVA with the four treatments in the model and data arcsine transformed. Planned orthogonal comparisons were made with T-tests between covered and uncovered treatments within species and between species. The pollination control study was analyzed using a one-way ANOVA and the data were arcsin transformed. Data shown in graphs are untransformed. The fruit dispersal study was analyzed using a T-test comparing number of dead fruits and number of missing fruits between species. Data were arcsine transformed. The number of seeds per fruit measured in the 2002, 2003 and 2004 studies was analyzed using a one-way ANOVA.

Seedling survival and growth

Field experiment: Survival of *R. phoenicolasius* seedlings was determined at two sites in each forest. At each site I constructed a 1 x 0.4 m shade structure with shade cloth that removed 30% of the light at a height of 0.5m above ground level. Six 30cm^2 plots were established under each shade structure and a similar number of plots were established in a similar sized plot that was located 1m from the shade structure. The plots in each 1 x 0.4 m area were subdivided into four treatments: 1. shading and leaf litter added (SL), 2. shading and no leaf litter (SN), 3. no shading and litter added (NL), 4. no shading and no leaf litter (NN). Four cm of locally collected leaf litter was added to each of the SL and NL plots. In each plot, three seedlings of *R. phoenicolasius* were planted in June 20th 2004. Seedlings were harvested on August 20th and separated into roots, leaves, and stems. Each root was examined for mycorrhizal associations (methods described below). Leaf area was measured with a LiCor leaf area meter (Li-Cor, Lincoln Nebraska, USA) and leaf and stem biomass was determined after drying to a constant weight at 60°C.

Mycorrhizal study: *Rubus phoenicolasius* seeds were germinated in sterile soil and 8 week old seedlings (approx 4cm high) were transplanted to 8 cm diameter pots that contained a 75:25 mixture of sterilized Promix (peat bark based growing medium) and sand that had been autoclaved for two 1hour sessions at 120°C. After transplanting, the seedlings were allowed to acclimate for 3 days in the greenhouse at SERC. To obtain arbuscular mycorrhizal fungi (AMF) used in the study, roots of *R. argutus* and *R. phoenicolasius* were collected from SERC forests then screened to determine the presence of fungi. Roots from four individuals of each species with AMF present were

cut into pieces (<1cm) and mixed with sterile potting soil. Seedlings were then

transplanted into pots with treated soil.

The experiment had the following five treatments with 12 sterile seedlings of *R.*

phoenicolasius per treatment: 1. RPT = *R. phoenicolasius* seedlings inoculated with AMF

from *R. phoenicolasius*, 2. RAT = *R. phoenicolasius* seedlings inoculated with AMF

from *R. argutus*, 3. RPC = *R. phoenicolasius* seedlings inoculated with 5 ml of a filtrate

obtained by washing roots of *R. phoenicolasius* in distilled water and filtering the

solution through a 25 μl filter (Lovelock and Miller 2002). The filtrate inoculated the

seedling with microorganisms from the field soils but not AMF, 4. RAC = *R.*

phoenicolasius seedlings inoculated with filtrate from roots of *R. argutus* (procedure

same as described in 3), 5. C = Control, *R. phoenicolasius* seedlings received 5 ml of

distilled water. Treatments were started on July 6, 2004. The plants were watered every 2

days with distilled water, fertilized weekly with a 20-20-20 fertilizer, and rotated weekly

on the greenhouse tables. Plants were harvested after 6 weeks (August 18, 2004) and

separated into roots, stems and leaves. A 2 cm subsample of root of each seedling was

collected and analyzed for AMF infection. Roots were cleared in a 10% KOH solution

and autoclaved for 20 minutes at 120°C. Roots were then stained in a trypan blue 0.05%

in acidified glycerol dye for 20 minutes in the autoclave at 120°C. Roots were destained

for 3 days in a 50% glycerol and water solution then examined under a light microscope

to determine the presence of arbuscular mycorrhizal fungi (AMF) (Brundrett *et al.* 1996).

Percent infection was determined under a 10x microscope, by placing the roots on a grid.

At each point that a root crossed the horizontal and vertical lines on the grid, it was

counted as uninfected or infected. Total infection was calculated as: infected counts on lines / [total counts on lines] (Brundrett *et al.* 1996). Leaves were measured for area using a LiCor leaf area meter (Li-Cor, Lincoln Nebraska, USA). Plant parts were dried (at 60˚C) and then weighed. Specific leaf area (SLA) was calculated as leaf area/leaf weight and the root: shoot ratio was calculated as root biomass/shoot biomass.

Seedling survival and growth analysis: All analyses were conducted with SAS 8.2 using proc mixed. For all analyses a P value of .05 or smaller was considered significant. Data from the field study were analyzed with a one way ANOVA with treatment in the model. The four treatments are: shading and leaf litter additions (SL), shading and no leaf litter (SN), no shading and litter (NL) and no shading and no leaf litter (NN). Percent infection in roots was arcsin transformed and leaf area and weights were log transformed for homogeneity of variances. Untransformed data are shown in the graphs.

Data from the mycorrhizal study were analyzed with a one-way ANOVA with treatment in the model. Planned orthogonal comparisons were made with T-tests for differences in treatments to address the two hypotheses. First, *R. phoenicolasius* seedlings performed better with both RAT and RPT AMF treatments than in the control (C) treatment. Comparisons were made between the control and a combination of the RAT and RPT treatments. Second, *R. phoenicolasius* seedlings performed better with the RPT treatment than with the RAT treatment. Comparisons were made between RPT and RAT treatments. Percent infection in roots was arcsin transformed for homogeneity of

variances. Leaf weight, area, SLA, biomass and root:shoot ratios were all log transformed. Untransformed data are shown in the graphs.

Asexual reproduction: A study of clonal propagation was conducted in the summer of 2004 at both forests. Three patches of each species were selected at each forest. A single transect was extended through the center of each patch and all individuals within 30 cm (*R. phoenicolasius*) or 100 cm (*R. argutus*) of the transect were labeled. The center of each transect was marked and it was subdivided into six sections (outer, middle, center) of equal length. Data for transect, age (primocane or floricane), and number of fruits was recorded for each labeled plant. Plants were physically examined to determine if they had arisen from an existing root stock, from a rhizome offshoot of another plant, or from root tipping. If the cane was shared with any live and/or dead canes, it was identified as a shared perennial rootstock. The total number of canes sharing the rootstock of each cane were recorded. If the labeled cane did not share with any live and/or dead canes the individual was identified as a clonal rhizome and the underground parts were examined to determine which plant it was connected to and the length of the rhizome.

Asexual reproduction analysis: All analyses were conducted with SAS 8.2 using proc mixed. For all analyses a P value of .05 or smaller was considered significant. Differences between species and forest were examined with a two-way ANOVA. A two-way ANOVA was also used to examine number of ramets per rootstock with species, area of transect and forest in the model. Comparisons were made between species in each

section of the transect looking at mean differences which were sequential Bonferroni adjusted.

Results

Sexual Reproduction

In 2002, there was no significant difference between forest type in the number of fruits produced but there was a significant difference between treatments at both forests (Corn Island: $F_{3,264}$=111.61, P<.001; Fox Point $F_{3,164}$=33.46, P<.001). At Corn Island flowers of *R. argutus* that were not bagged produced more fruits ($T_{1,264}$=11.31, P<.001) but there was no significant difference between bagged and unbagged *R. phoenicolasius* flowers ($T_{1,264}$=0.48, P>.05) (Fig. 1). The same results were found at Fox point with significant treatment differences only for *R. argutus* ($T_{1,167}$=2.58, P=.011) (Fig. 1). *R. phoenicolasius* produced more fruits than *R. argutus* at both forests (Corn Island - $T_{2,264}$=15.02, P<.001; Fox Point -$T_{1,167}$= 9.57, P<.001) (Fig. 1).

In 2003 there was a significant difference in the number of fruits produced by treatment ($F_{3,131}$=43.82, P<.001). Flowers of both species that were not bagged produced more fruits (*R. argutus* - $T_{1,131}$=3.60, P<.001; *R. phoenicolasius* - $T_{1,131}$=2.53, P=.012) and the invasive species produced more fruits than the native species ($T_{1,131}$=10.53, P<.001) (Fig. 2)

In 2004 there also was a significant species difference ($F_{3,74}$=20.09, P<.001) but there was no significant difference between bagged and unbagged treatments for either species

(*R. argutus* - $T_{1,74}=0.28$, P>.05; *R. phoenicolasius* - $T_{1,74}=0.03$, P>.05). Similar to the other years, the invasive species produced more fruits than the native ($T_{1,74}=7.59$, P<.001) (Fig. 3).

In the 2004 study there was no significant within-species effect of covering flowers with bags (*R. argutus* - $T_{1,94}=.00$, P>.05; *R. phoenicolasius* - $T_{1,94}=0.45$, P>.05). There was a significant difference between species in the number of fruits produced ($T_{1,94}=3.53$, P<.001) (Fig. 4).

R. argutus produced fewer fruits than *R. phoenicolasius.* In addition, there were significantly more unfilled seeds and fruit desiccation in *R. argutus* as compared to *R. phoenicolasius* ($T_{1,406}=29.30$, P<0.001). Significantly more ripe fruits of the invasive species were removed by frugivores ($T_{1,213}=4.66$, P<0.001) (Fig. 5).

Comparisons of the number of seeds per fruit were made across four treatment types 1. *R. argutus* at Corn Island, 2. *R. argutus* at Fox Point, 3. *R. phoenicolasius* at Corn Island, 4. *R. phoenicolasius* at Fox Point. In 2002 there was a significant difference ($F_{3,156}= 201.87$ P<.001) in the four treatments and a significant difference between *R. argutus* and *R. phoenicolasius* ($T_{1,156}= 32.19$, P<.001) with *R. phoenicolasius* having greater number of seeds per fruit. In 2003 and 2004 there was a significant difference between the three treatments 1. *R. argutus* in Corn Island, 2. *R. phoenicolasius* in Corn Island, and 3. *R. phoenicolasius* in Fox Point (2003 - $F_{2,87}= 63.21$, P<.001, 2004 - $F_{2,87}= 54.84$, P<.001). The number of seeds per fruit again differed significantly between species with *R.*

phoenicolasius having significantly more seeds per fruit (2003 - $T_{1,87} = 9.43$, P<.001, 2004 - $T_{1,87} = 10.40$, P<.001) (Fig. 6).

Seedling growth and survival

There was greater seedling survival in the plots without litter ($F_{3,44}=7.05$, P<.001, $T_{1,44}=4.58$, P<.001) (Fig. 7). However, there were no differences in seedling leaf weight ($F_{1,14}=0.32$, P>.05) and area ($F_{1,14}=0.42$, P>.05) between the SN and NN treatments (Figs. 8 and 9). There was also no significant difference in the percentage of roots infected with AMF (Forest - $F_{1,17}=1.38$, P>.05; treatment - $F_{1,17}=3.88$, P>.05).

All seedlings survived in the mycorrhizal study and there was a significant difference in the infection across treatments ($F_{4,55}=3.64$, P=.01). Compared to the control, the RAT and RPT treatments had significantly higher infection ($T_{1,55}=2.46$, P=.017). There was no significant difference in infection rate between RPT and RPC ($T_{1,55}=0.90$, P>.05), nor was there a significant difference between the infection rate of RAT and RAC ($T_{1,55}=1.73$, P>.05). Neither was there a significant difference between the infection rate of RAT and RPT ($T_{1,55}=1.50$, P>.05) (Table 1).

There were significant differences across treatments for seedling leaf area, leaf weight, root weight and total biomass. For leaf weight, root weight and total biomass, control seedlings were significantly larger than the treatment seedlings.

Leaf area differed significantly across the five treatments ($F_{4,55} = 3.25$, P=.040) but there was no significant difference between the controls and the RPT and RAT treatments ($T_{1,55} = 1.77$, P>.05). RAT leaf area was significantly larger than RPT ($T_{1,55} = 2.10$, P<.05). Leaf weight also differed significantly across all treatments ($F_{4,55}=3.77$, P<.01) and there was a significant difference between the control and RPT and RAT treatments with the control seedlings having greater leaf weights ($T_{1,55}= 2.18$, P=.033). RAT seedlings had significantly greater leaf weights than the RPT treatment ($T_{1,55}=2.18$, P=.034). SLA did not differ significantly across treatments ($F_{4,55}=1.80$, P>.05) (Table 1).

There were significant differences in root weights across treatments ($F_{4,53}=3.07$, P=.024) and a significant difference between controls and the RPT and RAT treatments with the control having greater root weights ($T_{1,53}=2.78$, P=.007). There was no significant difference between RAT and RPT, but there was a trend of RAT having greater root weights ($T_{1,53}=1.54$, P>.05) (Table 1).

There were significant differences in total biomass across all treatments ($F_{4,53}=2.73$, P=.039) and a significant difference between the control and RPT and RAT ($T_{1,53}=2.12$, P=.038), with the control having greater biomass than both treatments. There was no significant difference between RPT and RAT treatments. There were no significant differences between treatments in the root:shoot ratio ($F_{4,53}=1.85$, P>.05) (Table 1).

Clonal propagation

The native species only produced two ramets from underground rhizomes and the invasive species produced none (Table 2). There was no significant difference between the two forests for any of the metrics ($F_{1,9}>0.00$, $P>.05$) nor was there a significant difference between species ($F_{1,9}=2.19$, $P>.05$) in the number of clonal ramets produced. Since the majority of individuals arose from rootstocks that already supported other canes, I examined the size of individuals in terms of number of canes per rootstock as it related to the location of rootstocks within patches (Fig. 10). In the center and the outside of the patch individuals of *R. phoenicolasius* produced a significantly greater number of canes than *R. argutus* ($T_{1,173}= 2.92$, $P=.004$) and ($T_{1,173}= 2.85$, $P=.005$) respectively, but there was no significant difference between species in the area between the center and outside of the patch ($T_{1,173}= 0.95$, $P>.05$) (Fig. 11).

Discussion

In 1974, Baker compiled a list of 12 qualities for successful weeds; included in this list are self-compatibility and rapid vegetative growth. Since Baker's publication, no consensus has emerged regarding breeding system traits and invasiveness. An invasive species which reproduces sexually as well as asexually would be able to disperse to new habitats, as well as maintaining vigorous growth in its current habitat (Eriksson 1994). Self-compatibility would also aid in the invasion of island habitats, where pollinators or suitable mates may be limited (Schueller 2004). 100% self-compatibility was found in a survey of 17 invasive species in South Africa (Rambuda and Johnson 2004). Success of the invasive *Senecio squalidus* was attributed to plasticity in breeding systems, including

self-compatibility (Hiscock 2000). In contrast, Parker (1997) found that self-compatibility was not necessary for the success of the invasive *Cytisis scoparus*, although the lack of self-compatibility may slow its ability to spread. In examining plant databases Sutherland (2004) found that counter to Baker's predictions non-invasive weeds had greater self-compatibility than invasive weeds. Self-incompatible plants may still succeed in novel habitats through general mutualisms with native or invasive insect pollinators, or through wind pollination (Barthell 2001, Ghazoul 2002).

I hypothesized that the invasive *R. phoenicolasius* would be self-compatible which would enable it to more easily establish itself in habitats with low pollinator service or a lack of mates. Consistent with this hypothesis, I found that *R. phoenicolasius* had less dependence on cross-pollination to set fruit than *R. argutus*. In all three years that I bagged flowers, seed set was either not different or higher in bagged flowers compared to unbagged flowers of *R. phoenicolasius*. The first two years, excluding pollinators significantly reduced fruit production in the native, but in the final year of the study there was no effect of bagging.

In addition to self-compatibility and reduced pollinator dependence I expected the invasive to produce high numbers of fruits and seeds. The success of invasives spreading into new habitats has been correlated with high numbers of seeds (Foxcroft *et al*. 2004, Kuhn *et al*. 2004). *Fallopia japonica*, another invasive capable of asexual and sexual reproduction, produced large numbers of seeds (Foreman and Kessili 2003). In invaded habitats invasive species have been shown to have greater reproductive output than in

their native habitats (Wolfe *et al*. 2004). In all three years I observed significantly greater fruit production in the invasive *R. phoenicolasius* than the native *R. argutus*. The higher rate of fruit production was also observed in a demographic study conducted at the same time. In addition seed numbers per fruit were higher in the invasive (Grotkopp *et al*. 2002, Richardson and Rejmanek 2004).

In addition to greater fruit production in *R. phoenicolasius,* a greater number of these fruits were removed prior to desiccation or rotting. Seeds of both species need to pass through an animal gut or require a long period in the seed bank to germinate (Swartz 2002). There were significantly greater numbers of fruits taken from the invasive *R. phoenicolasius* than from the native *R. argutus*. *R. phoenicolasius* fruits are also displayed in a tighter grouping than the native, which may look more attractive to potential fruit dispersers (Sallabanks 1993, Schmidt *et al*. 2004). Another comparative study between native and invasive congeners also demonstrated the preference of invasive fruits over native fruits in the genus *Carpobrutus* (Vila and D'Antonio 1998).

Due to the potential for greater spread of seeds of the invasive *R. phoenicolasius* through high seed number and frugivore dispersal, it was important to investigate the growth and survival of seedlings. In the seedling study I expected to see equal survival of *R. phoenicolasius* in all of the treatments. In the invasives *Allaria petiolata and Celastrus orbiculatus,* seedlings were not affected by litter manipulations (Meekins and McCarthy 2001, Ellsworth *et al*. 2004). In contrast, I observed almost 100% mortality in the treatments with litter addition. This may not only be due to the lack of light. In addition

112

the litter would increase the moisture levels around the seedling, possibly causing the seedling to rot. One of the reasons that I have not observed a large number of seedlings in established plots in the interior of the forest is that the presence of litter may negatively affect seedling survival.

I found no significant difference in growth between shade treatments. This may be due to the fact that my shading treatment only reduced light by 30% and this may be within the range for normal seedling growth (Whitney 1986). Seeds of *R. phoenicolasius* fall from or are removed from plants in July so they are on the ground well before leaves fall. In spring, when seeds would be germinating they would be buried under several centimeters of leaf litter. Survival of *R. phoenicolasius* may be limited to areas with low litter cover, which may explain their presence in edges and trails.

With the prevalence of mycorrhizal associations between fungi and forest plants in the eastern deciduous forest, I was curious how soil fungi may affect *R. phoenicolasius*. I believed that in the soils where *R. phoenicolasius* had become established the seedlings would be less susceptible to pathogens and more capable of taking advantage of local fungi. I predicted that arbuscular mycorrhizal fungi (AMF) would aid in the survival and growth of *R. phoenicolasius* seedlings. However I found no difference in survival between any AMF additions and controls. I also observed significantly greater leaf weight, root weight and total biomass in control seedlings compared to treatments inoculated with *R. argutus* AMF and *R. phoenicolasius* AMF. There have been other studies that have found similar patterns with AMF additions to *Rubus* species. In one

113

study 9 species of fungi had more negative effects than positive effects on *R. ideaus* (Taylor and Harrier 2000). Another study conducted on *Rubus* saw no increase in biomass with the presence of mycorrhiza (Hughes *et al.* 1979). Another greenhouse study observed greater mortality and lower growth in the invasive *Ammophila arenaria* grown in locally collected California dune soils as compared to sterilized soils (Beckstead and Parker 2003). AMF had a negative effect on biomass of *Lythrum salicaria*, however there was a positive effect on the flowers of *L. salicaria* which produced greater amounts of pollen (Philip *et al.* 2001). West (1996) found that only when the invasive was put in a competitive treatment with a native plant did the fungi help the invasive. Other authors have concluded that the impacts of AMF may not be direct and may only be elucidated in observing the invasives' interactions with the community (Marler *et al* 1999, Callaway *et al.* 2004a).

Invasive species affect the soil community, potentially changing it from that associated with native species (Kourtev *et al*. 2002 and 2003). Different communities of AMF have different impacts on plant growth (Lovelock and Miller 2002). My second prediction was that AMF obtained from *R. phoenicolasius* would lead to greater seedling growth compared to AMF from the native *R. argutus*. In fact, I observed the opposite, with *R. phoenicolasius* AMF treatment causing greater negative effects on seedlings than the *R. argutus* AMF treatment. There was no significant difference in the colonization of seedling roots between these two species, so it is possible that the composition of the AMF community associated with *R. argutus* provides less negative impacts to the invasive. Given that both species collected for inoculation were collected within 20 m of

114

each other, this may be occurring in the field. However studies collecting roots from both species and identifying species of fungi associated with each would be required to definitively answer this question.

Although seedling survival plays a role in the success of a clonal invasive, asexual reproduction is also important. Again vegetative reproduction is one of the characteristics Baker attributed to successful weeds in 1974. I predicted that the invasive would have higher levels of asexual reproduction. I also predicted that plant density in the center of a patch would deter clonal growth, so I expected to see higher rates of clonal propagation at the edges of plots (Parker 2000). However this pattern was not observed. Out of approximately 90 individuals surveyed in each species I only found 2 individuals of the native *R. argutus* that had arisen from clonal growth in the year leading to the study. So there were no significant differences between species, or forest. *Rubus argutus* and *R. phoenicolasius* often produce new canes each season from an existing root stock; this is the most common form of growth that was observed. The lack of clonal growth may be due to the fact that the patches observed were over five years old and clonal activity is decreasing. Small, newly established patches may demonstrate greater levels of clonal propagation. This has been observed in *Solidago*: as density of individuals' increased, clonal reproduction was decreased (Harnett and Bazzaz 1985a, Harnett and Bazzaz 1985b).

Conclusion

There is agreement that a successful invasive is capable of spreading quickly, yet specific characteristics of invasive species are still debated (Kuhn *et al*. 2004). My results for sexual reproduction are in agreement with previous studies on invasive species, demonstrating high rates of fruiting and seed production (Grotkopp *et al*. 2002, Morris *et al*. 2002, Foreman and Kessili 2003, Foxcroft *et al*. 2004, Kuhn *et al*. 2004, Richardson and Rejmanek 2004, Wolfe *et al*. 2004). In addition I found the invasive to have higher rates of self-compatibility, decreasing its dependence on local pollinators (Baker 1974, Hiscock 2000, Rambuda and Johnson 2004, Schueller 2004). Also in agreement with prior studies is the finding that invasive fruits were removed in greater numbers than native fruits (Vila and D'Antonio 1998). Counter to previous studies on invasive seed survival I found that leaf litter negatively affected seedling survival and that seedlings were not dependent on, nor benefited from fungal additions (Meekins and McCarthy 2001, Lovelock and Miller 2002, Zabinski *et al.* 2002, Callaway *et al.* 2003, Klironomos 2003, Callaway *et al.* 2004a, Ellsworth *et al*. 2004). The sensitivity to litter could limit the distribution of *R. phoenicolasius* seedlings, but the lack of dependence on AMF could allow for a wider range of potential habitats. Although I did not find much evidence for clonal reproduction, this may be explained by the fact that all of my plots have been established for over 5 years (Harnett and Bazzaz 1985a).

# Figure 1. Percent fruit production in relation to pollinator exclusion in 2002
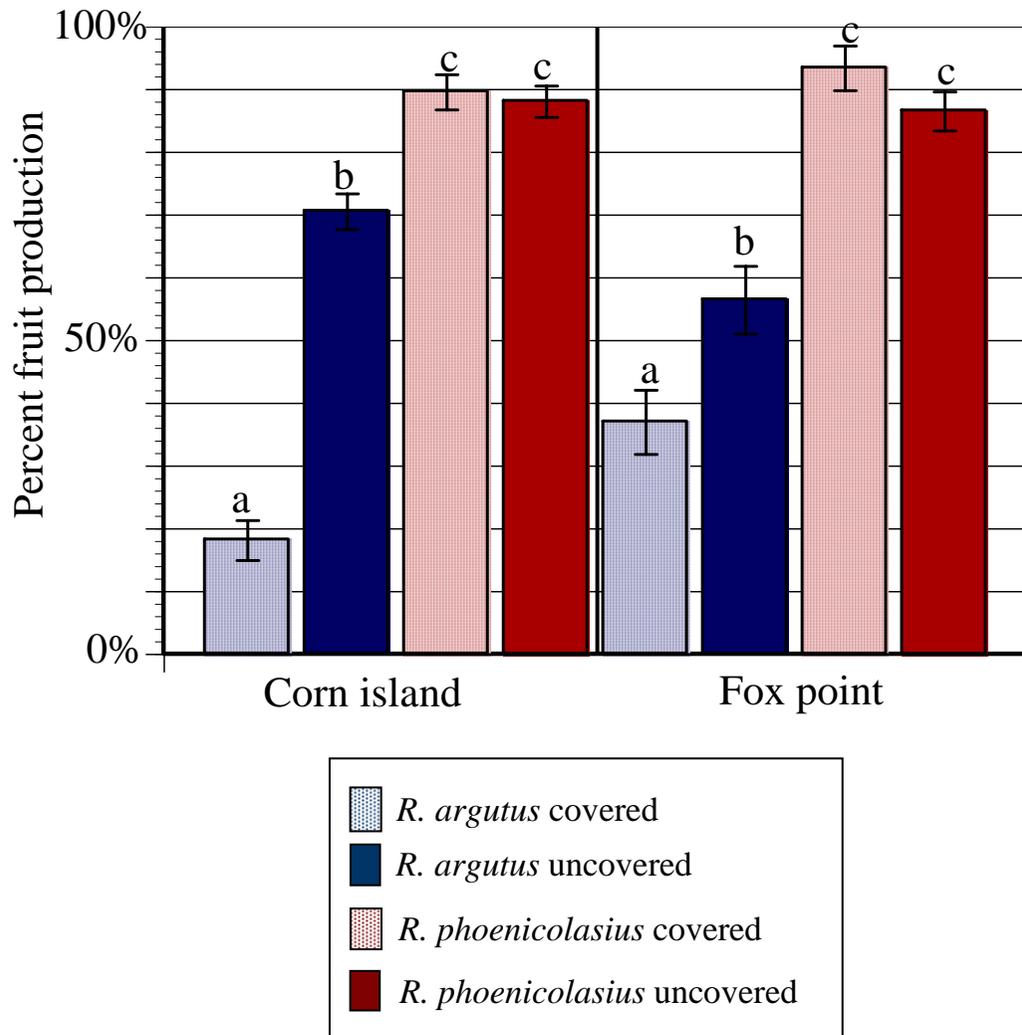
Figure 1. Percent fruit production for each treatment, there were four treatments: *R. argutus* covered, *R. argutus* uncovered, *R. phoenicolasius* covered and *R. phoenicolasius* uncovered. In both Corn Island and Fox Point there is a significant difference between the *R. argutus* treatments but no difference between the *R. phoenicolasius* treatments. Data shown are mean ± SEM.

# Figure 2. Percent fruit production in relation to pollinator exclusion in 2003
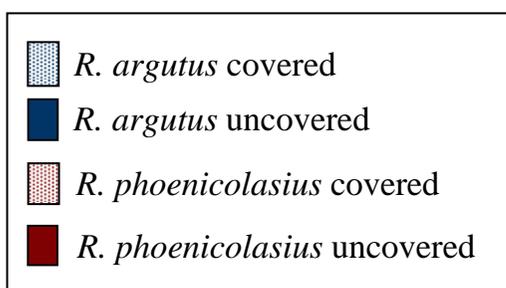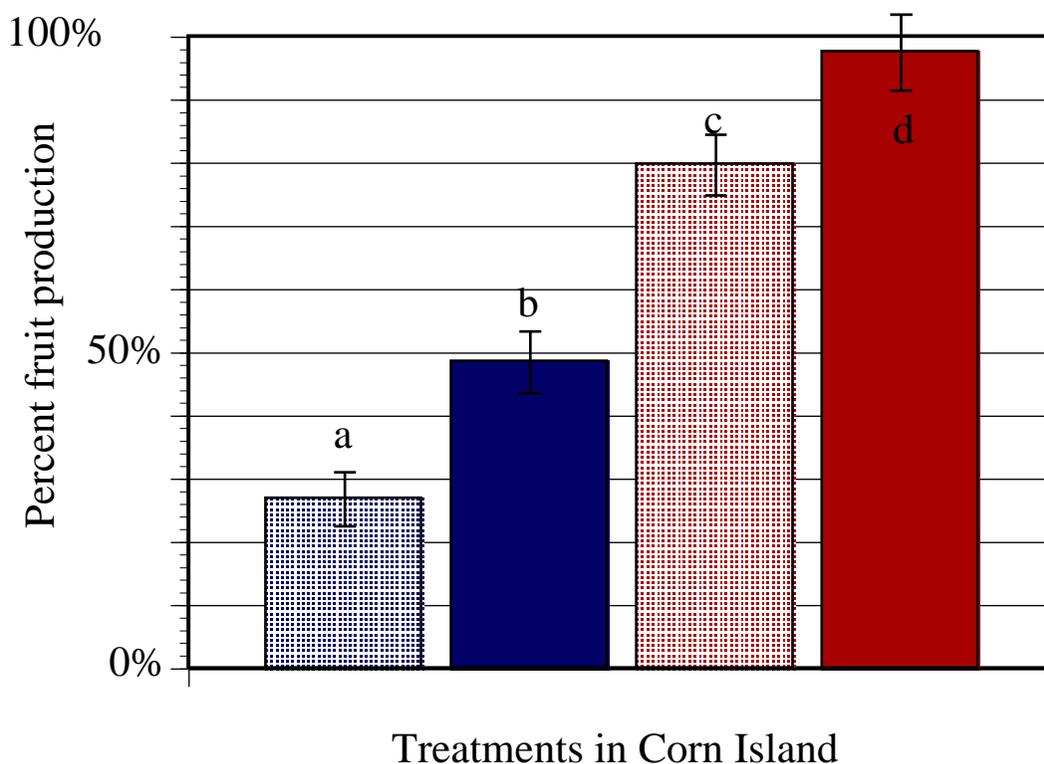

Figure 2. In 2003 in Corn Island there was a significant difference between the *R. argutus* treatments and between the *R. phoenicolasius* treatments. Data shown are mean ± SEM.

Figure 3. Percent fruit production in relation to pollinator exclusion in 2004
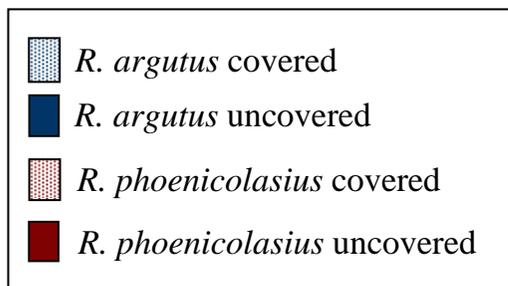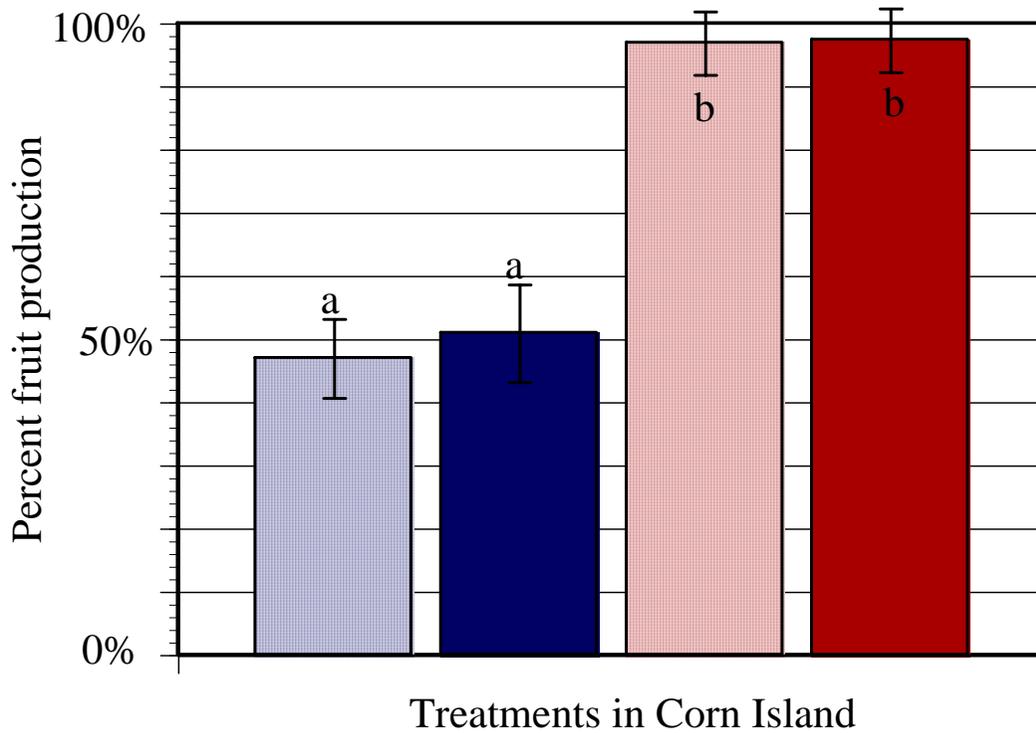

Figure 3. Percent fruit production for each treatment, in both Corn Island in 2004 there was no significant difference between the *R. argutus* treatments and no difference between the *R. phoenicolasius* treatments. Data shown are mean ± SEM.

Figure 4. Control for pollinator exclusion study in 2004

Percent fruit production

Treatments in Corn Island
(all individuals cross-pollinated)

R. argutus covered
R. argutus uncovered
R. phoenicolasius covered
*R. phoenicolasius* uncovered
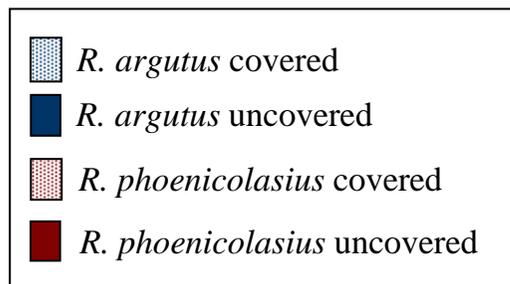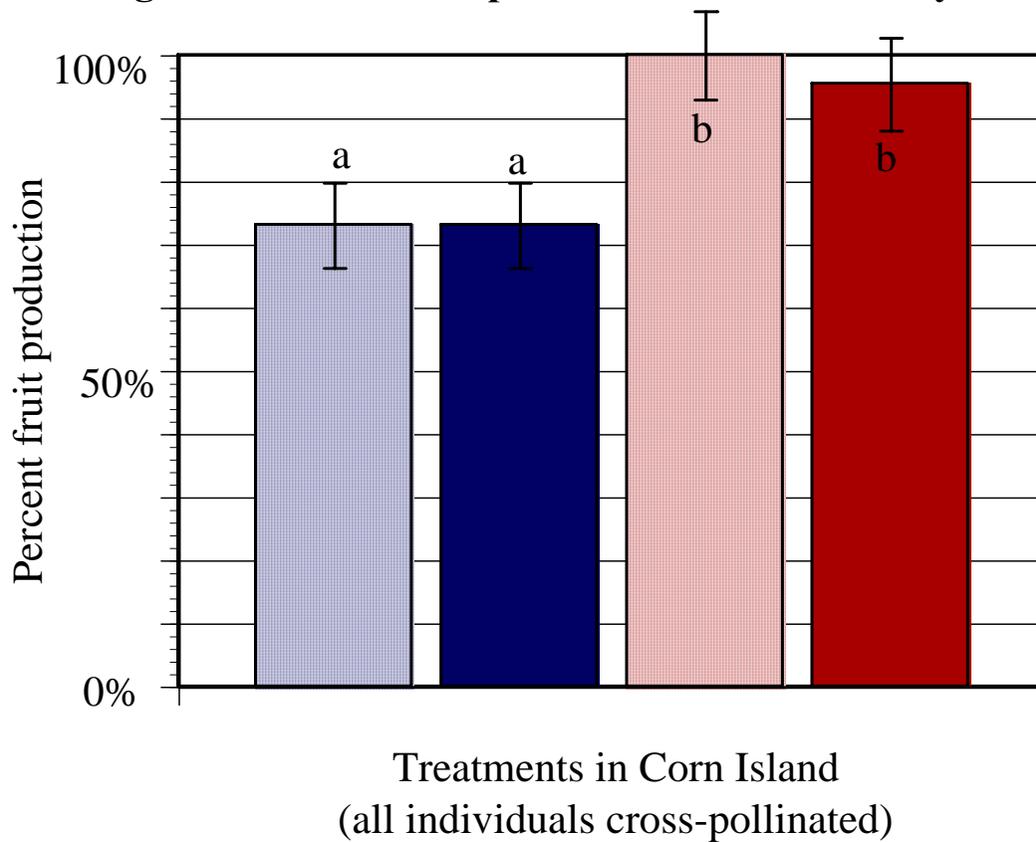
Figure 4. In the control study there was no difference between the *R. argutus* treatments and no difference between the *R. phoenicolasius* treatments. Data shown are mean ± SEM.

Figure 5. Percent fruit removed from plants out of the total number of fruits
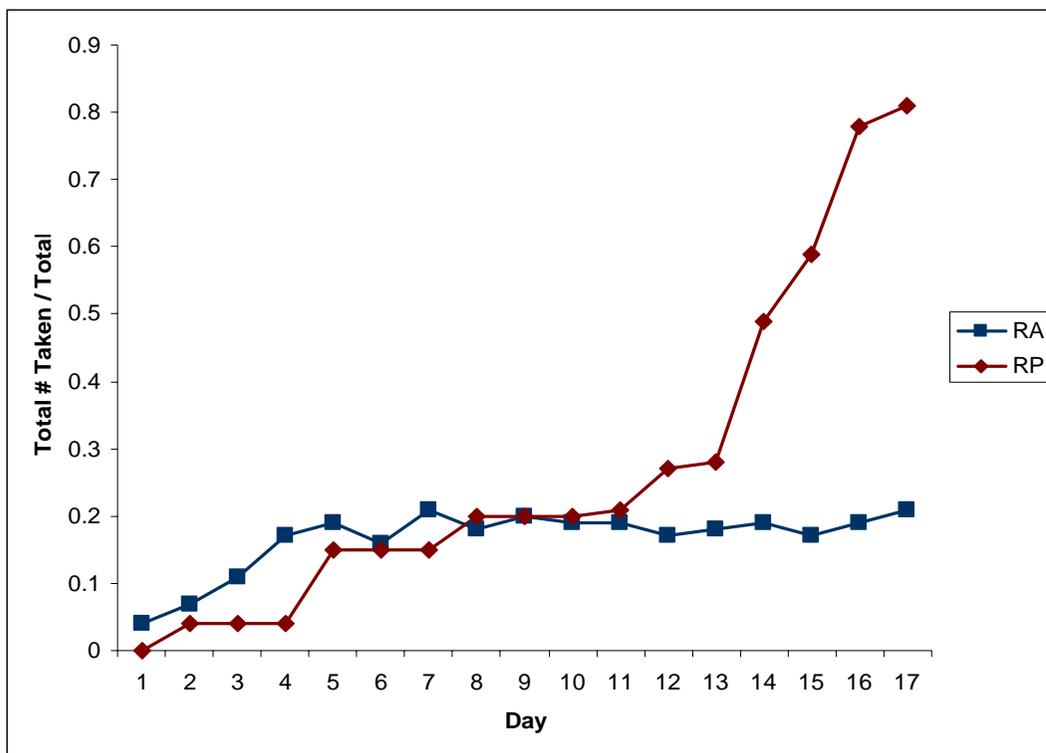

Figure 5. The percent of fruits removed from plants out of total number of fruits.

Figure 6. Seed counts per fruit for each species
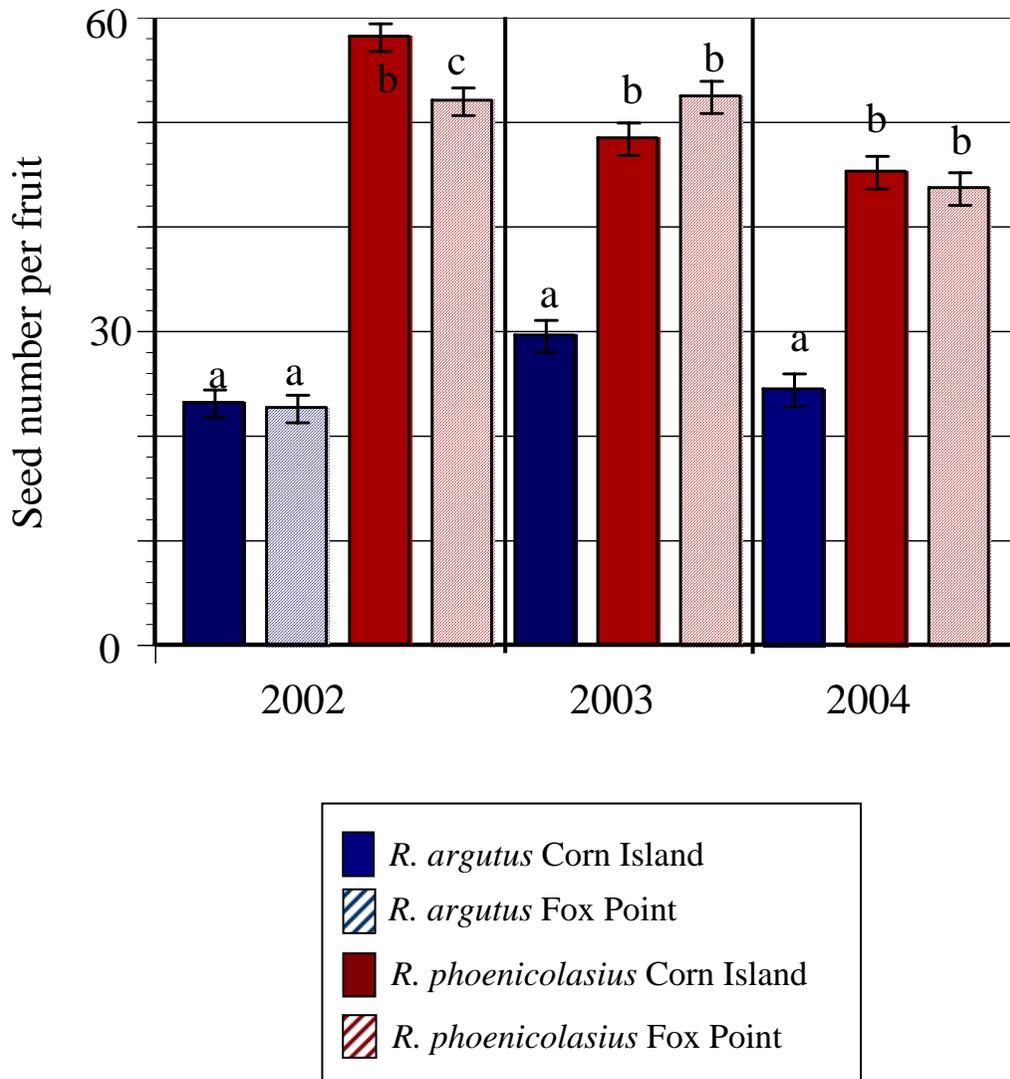
Figure 6. In all three years there were significant differences between *R. argutus* and *R. phoenicolasius*. Data shown are mean ± SEM.

Figure 7. Seedling mortality rates across treatments
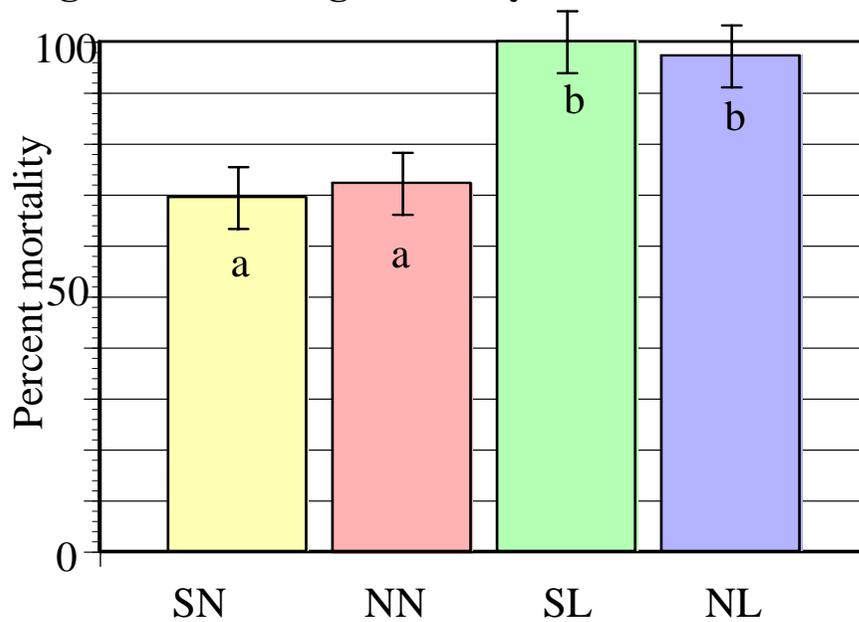
Figure 7. Percent mortality calculated for each treatment, There were four treatments: shading and no leaf litter (SN), no shading and no leaf litter (NN), shading and leaf litter additions (SL) and no shading and litter (NL). There is a significant difference between the treatments without litter and with litter additions. All data shown are mean ± SEM.

Figure 8. Seedling leaf areas
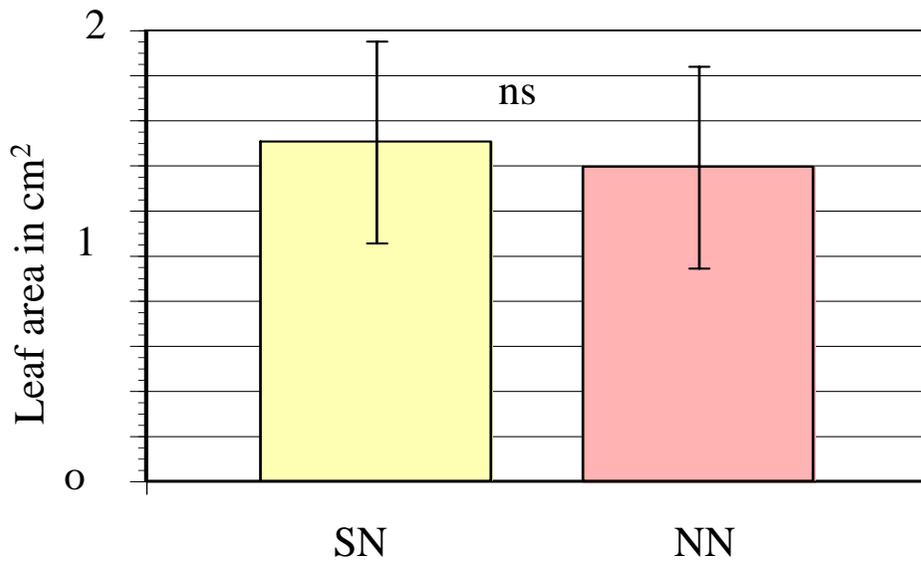
Figure 8. Seedling lead areas between the two treatments: shading and no leaf litter (SN), no shading and no leaf litter (NN), there is no significant difference between treatments. All data shown are mean ± SEM.

Figure 9. Seedling leaf weights
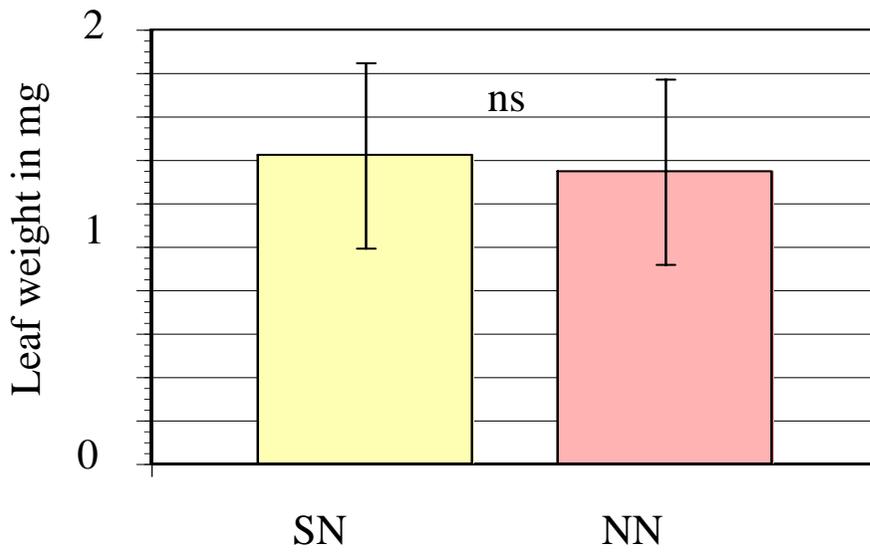
Figure 9. Seedling leaf weight for the two treatments: shading and no leaf litter (SN), no shading and no leaf litter (NN), there was no significant difference between treatments. All data shown are mean ± SEM.

Table 1. Seedling response to mycorrhizal additions

Measure	Control	*R.a.* Control	*R.a.* Treatment	*R.p.* Control	*R.p.* Treatment
Infection %	0.286 ± .0363	0.273 ± .0363	0.389 ± .0363	0.362 ± .0363	0.437 ± .0363
Leaf area (cm²)	10.67 ± 3.78	16.11 ± 3.78	10.93 ± 3.78	14.94 ± 3.78	5.06 ± 3.78
Leaf weight (g)	0.0178 ± .0060	0.0250 ± .0060	0.0159 ± .0060	0.0246 ± .0060	0.00847 ± .0060
SLA	591.7 ± 36.5	645.2 ± 36.5	677.9 ± 36.5	647.8 ± 36.5	729.0 ± 36.5
Root weight (g)	0.0065 ± .0012	0.0075 ± .0012	0.0039 ± .0012	0.0053 ± .0012	0.0031 ± .0012
Biomass (g)	0.0297 ± .0067	0.0396 ± .0067	0.0246 ± .0067	0.0252 ± .0067	0.0157 ± .0067
Root/shoot	0.231 ± .0246	0.185 ± .0246	0.188 ± .0246	0.201 ± .0246	0.190 ± .0246

Table 1. The mean response of seedlings to 5 mycorrhizal treatments: Control, *R.a.* control, *R.a.* treatment, *R.p.* Control, *R.p.* Treatment. Data shown are mean ± SEM.

Table 2. Number of individuals arising from clonal growth

	Corn Island		Fox Point	
	R. argutus	*R. phoenicolasius*	*R. argutus*	*R. phoenicolasius*
Clonal Rhizome	1	0	1	0
Perennial Rootstock	41	45	45	46

Table 2. Distribution of reproduction in *R. argutus* and *R. phoenicolasius*, there was only two incidences of reproduction with clonal rhizomes.

Figure 10. Transect set up for clonal study
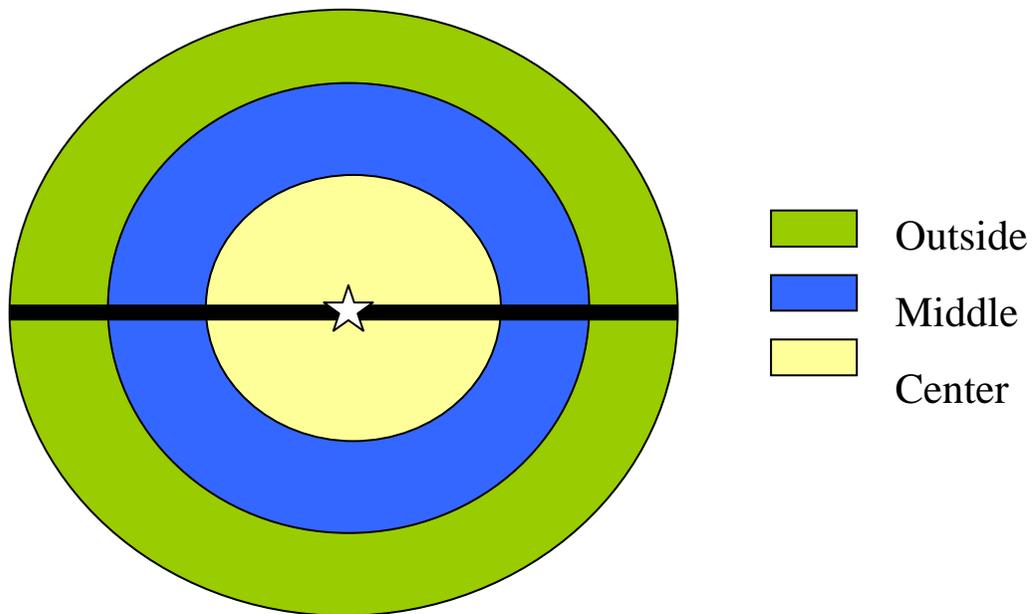
Figure 10. A transect was put through the entire patch of either *R. argutus* and *R. phoenicolasius*.

Figure 11. Number of canes per individuals in transect
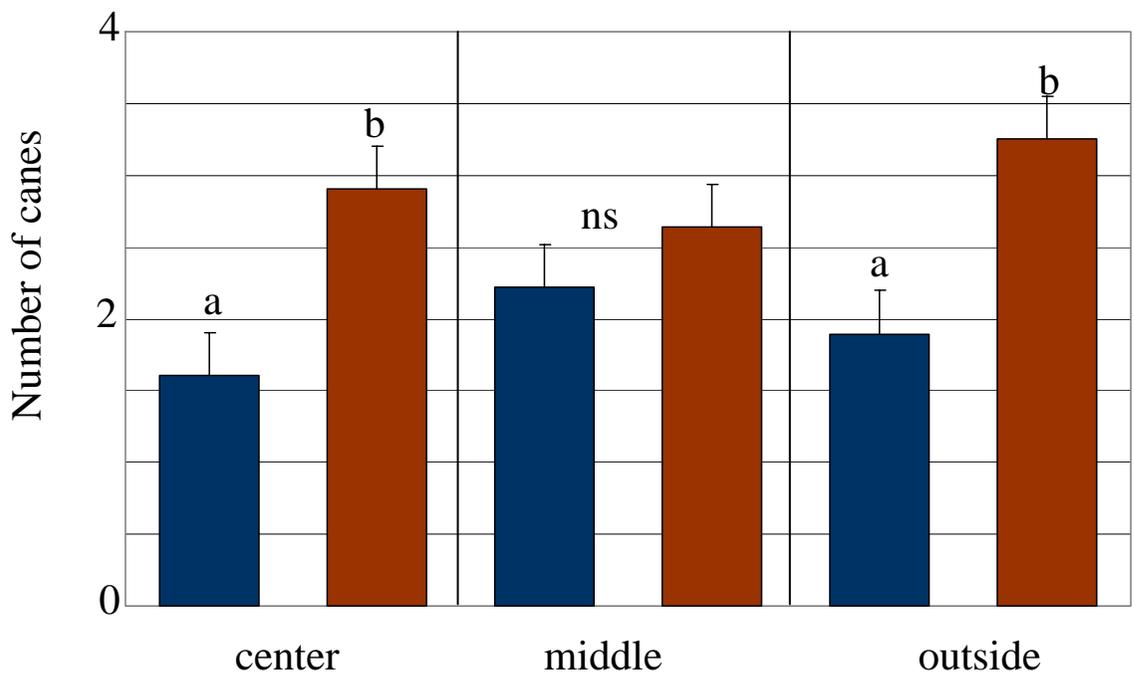
Figure 11. Multiple comparisons were made and were sequential Bonferroni adjusted. There was significant difference between species in total shared canes per individual (P<.0001). Specifically, there was significance between species in center and outside sections (center: P<.01; outside: P<.01). Data shown are mean ± SEM.

Summary

**Comparative ecology of the invasive *Rubus phoenicolasius*
and the native *Rubus argutus***

This work sought to identify plant traits that distinguished an invasive shrub, *R. phoenicolasius* from a closely related native congener, *R. argutus*. I tested the hypothesis that more efficient photosynthetic gas exchange responses would aid the success and survival of *R. phoenicolasius* as an invasive in the eastern deciduous forest of the United States (Meekins and McCarthy 2001). I examined the relationship between habitat characteristics and the ecology of an invasive and a native to determine if varying resource availability benefited the invasive (Davis *et al*. 2000). I quantified the population demographics of an invasive and native congener to determine if the invasive had greater potential for population growth (Parker 2000). Fungal components of soil communities were investigated for their role in the establishment and growth of invasive seedlings (Kourtev 2002).

I found that the invasive species *R. phoenicolasius* had greater impacts on a naturalized understory herb, *D. indica*, than the native *R. argutus*. These results suggest that the invasive species may have a greater impact on understory vegetation. *R. phoenicolasius* had greater potential for photosynthetic carbon gain per unit weight through higher specific leaf area and leaf nitrogen. Both species had higher photosynthetic rates in the higher light Corn Island forest as compared to the Fox Point forest. In both forests, *R. phoenicolasius* had significantly higher numbers of fruiting individuals with greater fruit

130

density per plot than *R. argutus*. Seedlings of the invasive did not require nor did they benefit from arbuscular mycorrhizal fungi (AMF) which indicates the absence of fungi would not limit the establishment of *R. phoenicolasius* in new habitats.

The first two years of the study were extreme precipitation years with drought conditions followed by heavy precipitation. The invasive, *R. phoenicolasius* had significantly lower mortality than *R. argutus* in Corn Island, which demonstrates the ability of the invasive to recover following drought. In addition, the variation in precipitation may have led to the low levels of clonal growth measured over the three year period.

In concert with previous studies on invasive species, I found the invasive to have more efficient photosynthetic gas exchange responses, greater competitive impacts on local species and a higher potential for population growth with lower mortality and greater rates of sexual reproduction than the coexisting native species.

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