The application of competition theory to invaders and biological control: A test case with purple loosestrife (*Lythrum salicaria*), broad-leaved cattail (*Typha latifolia*), and a leaf-feeding beetle (*Galerucella calmariensis*)

by

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Invasive species pose an enormous threat to native species and imposes substantial costs on the US economy. Although the threat of exotic species is well recognized, the general ecological mechanisms that underlie these invasions remain elusive. Predictions both for invasion success and the success of biological control remain poor. In this dissertation, I harness plant competition theory to predict the success of invasions and biocontrol, using a model system composed of invasive purple loosestrife (Lythrum salicaria), native broad-leaved cattail (Typha latifolia), and Galerucella calmariensis, a leaf-feeding beetle widely released to control loosestrife. In chapter 1, I introduce the problem and summarize my results. In chapter 2, I extend resource competition theory to competition for light: species coexistence is possible if one species is sufficiently taller and with less dense foliage than its competitor. This integrated model of competition for light is easily parameterized through measurements of light availability in monoculture and thus can easily be tested in the field. In chapter 3, I test the ability pf three models of plant competition (response to resource availability, plant size, and resource reduction) to predict competitive outcomes between loosestrife and cattail. My experimental design included monoculture mesocosms in which to measure plant traits, and mixture mesocosms in which to determine competitive outcomes. Surprisingly, while loosestrife was, on average, negatively affected by the presence of cattail, cattail was not, on average, negatively affected by loosestrife. Indeed, at high fertility, cattail was strongly negatively affected by loosestrife in the absence of insect herbivores of both species, yet was strongly facilitated when herbivores of both species were present. The facilitation of cattail by loosestrife was likely due to density dependent predation by cattail's natural enemies. Cattail abundance in mixture was not predicted by any of the three models, which is not surprising considering the lack of an overall competitive effect of loosestrife on cattail. In contrast, loosestrife abundance in mixture was well predicted by species height, as predicted by the plant size model. These results suggest that competitive traits may predict invasion success and biocontrol, but only when species interact only through competition for resources.

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1. Introduction

The invasion and spread of alien species throughout the world poses an enormous threat to the conservation of biodiversity and additionally imposes substantial costs on the US and global economies (Cox 1999, Enserink 1999). More than 2000 exotic species inhabit the US and an astounding 40% of the flora of Great Britain is composed of exotics (Ellis et al. 1994, Williamson 1996). One recent estimate places the cost to the US economy of harmful non-indigenous species at $137 billion per year (Pimentel et al. 2000), and exotics are considered a major threat to imperiled species in the US, second only to habitat loss (Wilcove et al. 1998). *Melaleuca*, Chinese tallow tree, garlic mustard, and the zebra mussel, among many other exotics, now form dense stands that typically exclude native species and reduce biodiversity (Di Stefano and Fisher 1983, Ewel 1986, Cameron and Spencer 1989, Mackie 1991, Gillis and Mackie 1994, Bruce et al. 1995, Cronk and Fuller 1995, Anderson et al. 1996, Jubinsky and Anderson 1996, Schloesser et al. 1996, Bruce et al. 1997, Williamson 1999, Ricciardi 2003). With increasing global commerce and the ease of international travel, we can expect introductions of non-native plant species to continue at an accelerated pace.

Although the threat of exotic species is well recognized, the general ecological principles and mechanisms that underlie these invasions have remained elusive (Roy 1990, Lodge 1993, Kareiva 1996b, Williamson 1999). Indeed, Kareiva (1996b) lamented the lack of sound theory to explain invasions and concluded that “predictions are still scarce” (see also Williamson 1999). Indeed, what Ehrlich (1989) concluded 15 years ago still holds true today, specifically that “ecologists cannot accurately predict the results of a single invasion or introduction event” (see also Williamson 1996).

Much of the effort to date to understand invasions has focused on characterizing life history traits of successful invaders (Di Stefano and Fisher 1983, Di Castri et al. 1990, Jones and Sharitz 1990, Mackie 1991, Lodge 1993, Schierenbeck et al. 1994, Cronk and Fuller 1995, Pysek et al. 1995, Rejmanek 1995, Tucker and Richardson 1995, Jubinsky and Anderson 1996, Rejmanek and Richardson 1996, Williamson 1996, Reichard and Hamilton 1997, Goodwin et al. 1999, Williamson 1999, Kolar and Lodge 2001, Pysek 2001, Kolar and Lodge 2002). This approach has been extremely valuable and has improved our ability to predict the life history traits that will allow an exotic species to invade a novel habitat, particularly if these habitats are disturbed. For example, Rejmanek and Richardson (1996) accurately characterized traits of 24 invasive and non-invasive pine species. They pointed out, however, that their classification applied most accurately to disturbed habitats. Furthermore, their method primarily identified species that would have traditionally been labeled “r” strategists and thus it was not unanticipated that these taxa would be capable of invading human dominated landscapes. In contrast, Goodwin, et al. (1999) compared the life history characters of 165 pairs of congeneric invasive/non-invasive species. They concluded that life history characters could not be used to predict the invasiveness of an additional 55 pairs of congenerics. Kolar and Lodge (2002) pushed this approach further by focusing on a specific ecosystem. They modeled past fish invasions in the great lakes with 87-94% accuracy. However, predictions for fish not yet introduced, based on discriminant analysis and categorical regression tree analysis, showed only 57% agreement, and two species known to be invasive elsewhere were predicted not to invade the great lakes; thus the results must be interpreted cautiously.

Overall, efforts to predict invasive potential based on character traits and correlative data are hampered by two central problems. Correlative analyses of invasive plant traits are biased by history, and these traits alone cannot elucidate the mechanism by which invasives out-compete native species (Roy 1990, Lodge 1993, Mack 1996, Williamson 1999). Past plant invasions have been the product of historical chance and biology (Di Castri 1990). The majority of past invasions have occurred because: 1) small seeds are easily dispersed by human activities, 2) human activity results in disturbed areas, 3) species which specialize on disturbed areas have small seeds and tend to be "r" strategists. In this way, the historical data are biased towards invaders that specialize on disturbed habitats and have high dispersal rates. Consequently, most invasions have been by "r" strategists colonizing disturbed habitats. Does this mean that species that are poor dispersers cannot become invasive? No, it only means that we have not yet inadvertently assisted such species by dispersing them into appropriate habitats in foreign lands. As invasions continue, we increase the likelihood that species will be introduced into “pristine” areas where they may be able to out-compete the dominant plant species in the local flora.

The correlative approaches described above are not able to identify a mechanism to explain how exotics displace native species. One obvious mechanism is that invaders are “good competitors.” Daehler (1998) found that exotic plants that invaded natural areas (as opposed to more disturbed landscapes) did not fall out neatly as “r” strategists. He concluded that plants with the highest potential to invade more pristine habitats were plants that typically might be considered good competitors including grasses, nitrogen fixers, and clonal trees. Indeed, it appears that species that can invade “undisturbed” or “pristine” habitats are species with large seeds and slower growth rates that would typically be classified further along the continuum towards a “k” strategist (Rejmanek and Richardson 1996). In fact, there are many cases of relatively large seeded species that appear to invade undisturbed habitats (Gade 1976, Hayashida

1989, Vitousek and Walker 1989, Bass 1990, Richardson et al. 1990, White and Stiles 1992, Biggeli and Hamilton 1993, Sallabanks 1993, Rejmanek 1996).

Purple loosestrife (*Lythrum salicaria* L.) is an herbaceous perennial of Eurasian origin that became established in North America in the early 1800's. It has spread aggressively throughout wetlands in the northeastern US, southeastern Canada, and the Great Lakes region. Loosestrife has also become a problem in the arid west and northwestern US (Thompson et al. 1987). Loosestrife forms nearly mono-dominant stands in wetlands supporting emergent macrophyte vegetation, and commonly displaces cattail species (*Typha latifolia* L. and *T. angustifolia*), among many others (Thompson et al. 1987). Loosestrife invasions threaten several declining species including bulrush, dwarf spike rush, the bog turtle, the black tern, and the canvasback, and provides poor habitat for wildlife including waterfowl and muskrat (Thompson et al. 1987, Malecki et al. 1993, Blossey et al. 2001b, Stark, Bunker and Carson, in prep., but see Hager and McCoy 1998).

Herbicides and mechanical methods have not successfully stopped the spread of Loosestrife. Loosestrife produces copious seed crops which form persistent seed banks which can contain more than 400,000 seeds/m2 (Thompson et al. 1987, Welling and Becker 1990). Consequently, killing or removing adult plants with herbicides, mechanical means, or burning results in rapid recolonization and recruitment from seed (Thompson et al. 1987, Malecki et al. 1993, Gabor et al. 1995, Gabor et al. 1996, Blossey et al. 2001b).

In 1992, *Galerucella calmariensis* L*.,* as well as *Galerucella pusilla* Duft., *Hylobius transversovittatus* Goeze,(a root-feeding weevil) and *Nanophyes marmoratus* Goeze (a flower-feeding weevil) were approved by USDA-APHIS for introduction in the US (Malecki et al. 1993, Blossey et al. 2001b). *G. calmariensis* has proven the easiest of the four species to rear, and this ongoing project has led to the release of hundreds of thousands of beetles (Blossey et al. 2001b). By 1995, the beetles had become established in the 10 states where they had been released and the weevil had become established in 6 of 9 states where they had been released (Hight et al. 1995). Malecki et al. (1993) predicted that these releases would cause a reduction in loosestrife abundance to 10% of its current level over 90% of its range. Following releases of both beetles in Virginia in 1992, McAvoy et al. (1997) found that although the beetles were well established and spreading, they were having minimal impact on loosestrife stands three years following their release. Dech and Nosko (2002) similarly censused *Galerucella* and loosestrife abundance at several sites in Ontario three years after initial releases and found that the impact on loosestrife was low. A survey of 46 release sites in New York, Pennsylvania and Ohio found that *Galerucella* damage to loosestrife was generally low, although loosestrife at some sites did experience intense defoliation by *Galerucella* (Brinker, Bunker and Carson, unpublished data). Overall, while we certainly expect *Galerucella* to have a substantial and beneficial impact on loosestrife, it is clear that the impact is not easily predicted and that the mechanism of impact has not been rigorously evaluated.

Biological control is often touted as the best long-term solution for the control of invasive species (McFadyen 1998, McFadyen 2000, Blossey et al. 2001b). Although biocontrol has brought into check numerous invasive plants worldwide (Harris 1988, Crawley 1989a, Crawley 1989b, Cronk and Fuller 1995, McFadyen 1998, McFadyen 2000), we generally do not understand why some biocontrol efforts are successful while the majority appear to fail. For example, of the 1128 insect introductions designed to control an invasive plant, only about 10% were considered successful in spite of the fact that the introduced insect was able to establish a viable population in more than 60% of the cases (Williamson 1996, Williamson and Fitter 1996).

Successful biological control is clearly a tricky business and indeed the causes for these failures were likely varied and complex. Still, because we lack a mechanistic understanding of what allows phytophagous insects to reduce the spread of invasive plants, we are often left guessing when and if a biological control agent will work. Biological invasions and biocontrol pose a timely and demanding challenge to ecological theory and practice. But as Kareiva (1996a) pointed out "ecology has <u>not</u> contributed much to the practice of biocontrol – instead biocontrol has taught ecology a great deal about species interactions." Indeed, Harper (1977) concluded that the biocontrol of St. Johns wort by a chysomelid beetle was "the most exciting experiment in the whole of the science of plant-animal relationships."

This dissertation brings to bear an ecological approach that is complementary to the trait-based approach described above. Specifically, I apply theories of plant competition that generate specific predictions for both the success of invasive species and the success of biological control (Shea and Chesson 2002). Several models have been developed in the field of community ecology to predict competitive ability from plant traits. Goldberg (1996) proposed that in natural communities competitive ability is primarily the ability to respond to low resource availability. Gaudet and Keddy (1988) argued that plant size (either biomass or height) is the best predictor of competitive outcomes, and demonstrated that both biomass and height predicted competitive effect among species competing in small pots. Classical resource competition theory formally models interactions between consumers and resources (Armstrong and McGehee 1976, Tilman 1980, Tilman 1982), and has been generalized to both specialist and generalist herbivores (Grover 1994, Holt et al. 1994, Grover 1995). Resource competition theory predicts that the species that is able to reduce the availability of the shared limiting resource to the lowest level, and persist at that level will win in competition (Tilman 1980, Tilman 1982).

However classical resource competition theory (Tilman 1980, Tilman 1982) assumes that resources are distributed uniformly, and thus cannot be applied directly to competition for light, which may be the key resource in many ecosystems (Grace and Wetzel 1981, Pacala et al. 1996, Twolan-Strutt and Keddy 1996, Nicotra et al. 1999). Because of this limitation, I begin by extending classical resource competition theory with a model of competition for light that integrates competitive ability vertically through the plant canopy (Chapter 2). My results show that two species can coexist when competing for a single resource when that resource (e.g., light) is non-uniformly distributed. For coexistence to occur, one species must be sufficiently taller and with sufficiently less dense foliage, essentially a gleaner-opportunist trade-off for light. When this is the case both species will experience greater light availability when rare and are shaded primarily by the canopy of their competitor. Thus both species will increase when rare and neither can be driven to extinction by the other. Importantly, this model can be parameterized through simple measurements of light availability in monoculture and thus can easily be tested in the field. I believe this approach represents a significant advance in theoretical models of competition for light, a subject whose progress has been limited by the vertical nature of light supply. I hope that my efforts will add to the progress already made and stimulate additional research in this area (Tilman 1988, Pacala et al. 1996, Huisman et al. 1997, Huisman et al. 1999b, Perry et al. 2003).

In chapter 3, I test the ability of six models of plant competitive ability (species height, biomass, response to low resource availability, total effect on resource availability and two versions of the integrated light model, with and without the effects of standing litter) to predict the performance of loosestrife and cattail in mixture, using a model system composed of purple loosestrife (*Lythrum salicaria* L.), broad-leaved cattail (*Typha latifolia* L.) and a leaf-feeding beetle (*Galerucella calmariensis* L.). I used large, 1000 liter mesocosms to grow each species in monoculture mesocosms to measure traits, and both species in mixture mesocosms to determine the competitive outcomes. Both monoculture and mixture mesocosms included treatments with insect herbivores of both species suppressed with an insecticide, and a gradient of herbivory on loosestrife by *Galerucella* when insects were not suppressed. To generalize across environments, I crossed all treatments with two levels of fertility.

My results show that, on average, loosestrife abundance was lower in mixture than in monoculture, demonstrating that competition is occurring for loosestrife. In contrast, cattail abundance, on average, was not lower in mixture relative to monoculture, demonstrating no overall competitive effect of loosestrife on cattail. Herbivory did alter competitive outcomes, but only for cattail at high fertility. When insect herbivores of both species were suppressed with insecticide, cattail abundance in mixture decreased by 70% relative to monoculture. With insect herbivores of both species present, cattail abundance increased with increasing abundance of *Galerucella*. At the highest level of *Galerucella* abundance, cattail was facilitated by loosestrife: cattail abundance in mixture was 110% greater than in monoculture. The strong facilitative effect of loosestrife on cattail is likely due to cattail escaping from natural enemies, which reduced cattail abundance in monoculture by more than 80%.

The trait implicated by the plant size hypothesis, species height, was the best predictor of competitive outcomes for loosestrife, explaining, along with loosestrife abundance in monoculture, 42% of loosestrife abundance in mixture. In contrast, no traits explained a significant amount of variation in abundance for cattail in mixture. This result is not surprising considering that facilitation through associational resistance, rather than competition for resources, appeared to be the major effect of loosestrife on cattail. Overall, my results suggest that traits associated with resource competitive ability can predict competitive outcomes, including the effect of herbivory on those outcomes, as long as competition for resources remains the primary interaction between species, as appeared to be the case for loosestrife. However, when interactions become facilitative, traits related to resource competitive ability are unlikely to be predictive without additional details of the mechanisms of facilitation.

Taken together, my research makes several important contributions to community ecology in general and to invasion biology and biocontrol in particular. First, I extend competition for light to species with complex canopies. This approach not only predicts coexistence on a single resource but also is easily parameterized from simple measurements in monoculture, allowing researchers to apply the model to real-world situations. My mesocosm experiment is the first experimental test of the ability of resource competition theory to predict the effect of higher trophic levels on the outcome of competition among higher plants. Finally, this work represents the first effort, to my knowledge, to simultaneously test the ability of multiple theories of plant competition to predict species invasions and the success of biocontrol. Importantly, measurements of light competitive ability in monoculture did reasonably predict competitive outcomes for loosestrife. In contrast, cattail abundance was not primarily structured by competitive interactions, but rather by facilitation through escape from natural enemies. Not surprisingly, traits related to competitive ability did not predict cattail abundance. This result suggests that the threat posed by an exotic species, and of the ability of insect herbivores to control invaders, may be accurately predicted by traits measured in monoculture, but only if those traits accurately reflect all mechanisms of interaction, including facilitation.

2. Competition for light between plant species with complex canopies: using invasibility criteria to predict competitive outcomes

2.1. Abstract

Traditional models of resource competition will fail to predict competitive outcomes when plants compete for light, because the directional nature of light and height asymmetry between competing species violate assumptions of uniform resource availability. Here I present a model that uses invasibility criteria to predict the outcome of competition for light and requires no assumptions about the vertical canopy structure of competing species. Traditional models predict that the species with the lowest resource availability in monoculture will invade and competitively exclude other species. Building on this approach, I vertically integrate the light available to a species that is at low abundance within the canopy of its competitor. If this quantity is greater than the light available in a conspecific canopy, then this species should show positive growth when at low abundance and invade its competitor. This approach is powerful because no assumptions about canopy structure are required, and the model can be parameterized based on simple field measurements of light availability in monoculture. In addition, with the simplifying assumptions that species differ only in height and foliage density, the model predicts that two species can coexist on a single resource, light, if they differ sufficiently in height and foliage density.

2.2. Introduction

Mechanistic models of resource competition predict that the species that reduces the equilibrial availability of the limiting resource to the lowest level will competitively exclude all other species (Tilman 1980, Tilman 1982, Grover 1997). This prediction has been well supported among species that compete for uniformly distributed resources such as phytoplankton and grasses (Tilman 1977, Tilman 1981, Tilman and Sterner 1984, Tilman and Wedin 1991, Wedin and Tilman 1993, Grover 1997, Fox 2002). However, competition for light structures many higher plant communities, including forests, old fields, and wetlands (Bazzaz and Pickett 1980, Grace and Wetzel 1981, Carson and Pickett 1990, Pacala et al. 1996, Twolan-Strutt and Keddy 1996, Carson and Root 2000, Coomes and Grubb 2000, Rebele 2000).

Light fundamentally differs from other resources because of its directional nature. Light availability declines with depth in a plant canopy, violating the assumption of uniform resource availability. For this reason, existing analytical models of competition for light have usually considered only the special cases where canopies completely overlap and have uniform foliage density (e.g., phytoplankton competing in a well mixed water column), or where one canopy is completely above the other (Reynolds and Pacala 1993, Huisman and Weissing 1994, Weissing and Huisman 1994, Huisman and Weissing 1995, Rees and Bergelson 1997, but see Huisman et al. 1999b for a treatment of phytoplankton competition in partially mixed water columns, Litchman and Klausmeier 2001, Perry et al. 2003).

However, in natural assemblages, plant canopies almost never overlap completely and rarely have uniform foliage distributions. For example, Figure 1 depicts light availability in monocultures of purple loosestrife (*Lythrum salicaria*) and broad-leaved cattail (*Typha latifolia*). Cattail is taller than loosestrife and therefore reduces light to lower levels than loosestrife in the upper canopy, whereas loosestrife reduces light to lower levels than cattail in the lower canopy. At the soil surface, loosestrife and cattail reduce light to equally low levels. Neither loosestrife nor cattail is predicted to win in competition if competitive ability is measured by absolute resource reduction (i.e., light at the soil surface) in monoculture. Resource availability at any particular height within the canopy may fail to successfully predict the outcome of competition because a single measure cannot account for differences in resource reduction throughout the canopy (Tilman 1988). Thus, any successful predictor of competitive outcomes must somehow integrate light availability as a function of height in the canopy.

Here I describe a model of plant competition where two competing species may have partially overlapping canopies as well as foliage distributions that vary with height. I approach the problem by asking whether one species can invade an established stand of the other, based on the amount of light the invading species would receive relative to the amount received in a conspecific stand. I begin with a general analytical model, and then develop both a specific analytical application as well as an empirical application. The analytical application assumes two competing species differ only in maximum height and foliage density, yet have uniform foliage distributions, and predicts coexistence between two species that differ sufficiently in height and foliage density. Unlike existing models that are limited by strict assumptions of canopy structure, the empirical application requires no assumptions of canopy structure and therefore allows prediction of competitive outcomes based on simple field measurements.

2.2.1. The model

Traditional models of resource competition predict that the species that reduces resource availability to the lowest level in monoculture will competitively exclude all other species

(Tilman 1980, Tilman 1982). This occurs simply because, within a monoculture of its competitor, resource availability is greater than the minimum required to balance losses and gains of the superior resource competitor, which will therefore increase when rare. Conversely, when at low abundance within a monoculture of the superior competitor, the inferior resource competitor does not experience sufficient resource availability to balance gains and losses, and thus declines to extinction. These principles should hold for species that compete for light: if light availability within a competitor's canopy is greater than the minimum required to balance gains and losses, then a species should increase when rare and successfully invade. This approach simply extends traditional resource competition models by quantifying the light available to a species when at low abundance within a canopy of its competitor, relative to the light available within a conspecific canopy where gains are balanced by losses.

Consider two competing plant species in a community that is light limited. When grown in monoculture, each species should increase in population or biomass density until losses equal gains. Now consider the ability of one species to invade the other. If species *a* receives more light when shaded only by species *b* (i.e., when it is infinitesimally rare and thus at the boundary condition) than it receives in its own canopy, then species *a* should increase when rare and invade species *b*. If both species can invade the other, then coexistence is predicted. If neither species can invade the other, then priority effects occur. If only one species can invade the other, then competitive exclusion is possible.

It is useful to think of species *a* as a single stem that is so thin that self shading is negligible, within a matrix of stems of species *b* (Figure 2A). In this case, each leaf of species *a* receives light whose availability is controlled by species *b*. Two functions for each species, *i*, are required to describe the outcome of competition: the light available in monoculture as a function of height in the canopy, $f_i(h)$, and foliage density as a function of height, $d_i(h)$ (Figure 2B, C). In the general model, I make no assumptions about the form of either function except that light availability increases with height in the canopy, and that foliage density, d_i (the ability to capture light), is the product of biomass, w_i, and the light extinction coefficient, k_i, of that biomass. Thus, the amount of light received by species *a* when invading species *b* can be quantified by tallying the light available to the leaves of species *a* when light availability is controlled by the shading effect of species *b*. At any given height, *h*, the light captured by a single stem of species *a* will be equal to the light available within a stand of species *b*, $f_b(h)$, multiplied by the foliage density of species *a*, $d_a(h)$. The total light capture (equation 1) of this stem of species *a* in a canopy of species *b* can be found by integrating this product vertically through the canopy,

$$\int_{h=0}^{\hat{h}_a} f_b(h) d_a(h) dh \,, \tag{1}$$

where $\hat{h}_a$ is the height of species *a*. If this quantity is greater than the sum of light captured by a single stem of species *a* within a conspecific stand (equation 2)

$$\int_{h=0}^{\hat{h}_a} f_a(h) d_a(h) dh \,, \tag{2}$$

then species *a* will show positive growth and invade species *b*. Therefore, if the ratio of the total light capture by a stem of species *a* within a matrix of species *b* to the total light capture by a stem of species *a* within a conspecific matrix is greater than 1, then species *a* should invade species *b*. I define this ratio as $R_{a|b}$ (equation 3)

$$R_{a|b} = \frac{\int_{h=0}^{\hat{h}_a} f_b(h) d_a(h) dh}{\int_{h=0}^{\hat{h}_a} f_a(h) d_a(h) dh}. \qquad (3)$$

If species *a* is taller than species *b*, its light availability function, $f_a(h)$, will contain two terms, because the portion of species *a* that is entirely above species *b* experiences full sun (100% ambient light). Thus, equation 3 becomes

$$R_{a|b} = \frac{\int_{h=\hat{h}_b}^{\hat{h}_a} d_a(h) dh + \int_{h=0}^{\hat{h}_b} f_b(h) d_a(h) dh}{\int_{h=0}^{\hat{h}_a} f_a(h) d_a(h) dh}. \qquad (4)$$

The relative light available to the shorter species *b* within a stand of species *a* is

$$R_{b|a} = \frac{\int_{h=0}^{\hat{h}_b} f_a(h) d_b(h) dh}{\int_{h=0}^{\hat{h}_b} f_b(h) d_b(h) dh}. \qquad (5)$$

The metrics $R_{a|b}$ and $R_{b|a}$ together predict the outcome of competition. If $R_{a|b} > 1$, then species *a* will receive more light in competition with species *b* than in monoculture and thus will invade species *b*. If $R_{a|b} > 1$ and $R_{b|a} < 1$, then species *a* will invade species *b*, and species *b* will decline to extinction when at low abundance. If both $R_{a|b}$ and $R_{b|a}$ are greater than one, then the species will coexist. If both $R_{a|b}$ and $R_{b|a}$ are less than one, then priority effects occur, as neither species can invade established stands of the other.

2.2.2. Analytical application

To explore possible competitive outcomes and the consequences of life-history trade-offs between allocation to height versus allocation to foliage, I apply simplifying assumptions about the form of the light availability and foliage density distributions. Assuming that foliage is uniformly distributed and that light attenuation follows Lambert-Beer's law (Thornley and Johnson 1990), equation 4 becomes

$$R_{a|b} = \frac{d_a(\hat{h}_a - \hat{h}_b) + d_a \int_{h=0}^{\hat{h}_b} e^{-d_b(\hat{h}_b - h)} dh}{d_a \int_{h=0}^{\hat{h}_a} e^{-d_b(\hat{h}_b - h)} dh}, \tag{6}$$

and equation 5 becomes

$$R_{b|a} = \frac{d_b \int_{h=0}^{\hat{h}_b} e^{-d_a(\hat{h}_a - h)} dh}{d_b \int_{h=0}^{\hat{h}_b} e^{-d_b(\hat{h}_b - h)} dh}. \tag{7}$$

Integrating and simplifying equations 6 and 7 produce

$$R_{a|b} = \frac{d_a(\hat{h}_a - \hat{h}_b) + \frac{d_a}{d_b}\left(1 - e^{-d_b \hat{h}_b}\right)}{1 - e^{-d_a \hat{h}_a}} \tag{8}$$

and,

$$R_{b|a} = \frac{d_b\left(e^{d_a \hat{h}_b - d_a \hat{h}_a} - e^{-d_a \hat{h}_a}\right)}{d_a\left(1 - e^{-d_b \hat{h}_b}\right)}. \tag{9}$$

The condition for greater light availability for species a within species b, and thus positive growth when rare, is $R_{a|b}>1$. Thus, the zero net growth isocline for species a within b is $R_{a|b}=1$:

$$1=\frac{d_a(\hat{h}_a-\hat{h}_b)+\frac{d_a}{d_b}\left(1-e^{-d_b\hat{h}_b}\right)}{1-e^{-d_a\hat{h}_a}}. \tag{10}$$

For b within a the isocline is defined by $R_{b|a}=1$:

$$1=\frac{d_b\left(e^{-d_a(\hat{h}_a-\hat{h}_b)}-e^{-d_a\hat{h}_a}\right)}{d_a\left(1-e^{-d_b\hat{h}_b}\right)}. \tag{11}$$

While there is no simple analytical solution to these equations, we can compute a numerical solution to determine how competitive outcomes depend on model parameters. Because these equations contain four free parameters ($\hat{h}_a$, d_a, $\hat{h}_b$, and d_b), I reduce the dimensionality of the system by setting $n=\hat{h}_a/\hat{h}_b$, $x=d_b/d_a$, and $y=\hat{h}_b d_b$. Now n is the height of the taller species, a, relative to the shorter species, b; x is the foliage density of the shorter species, b, relative to the taller species, a; and y is the total foliage (leaf area index, LAI) of the shorter species, b. The isoclines (equations 10 and 11) now reduce to

$$1=\frac{yn-y+1-e^{-y}}{x(1-e^{-\frac{yn}{x}})}, \tag{12}$$

and

$$1=x\frac{e^{-\frac{yn}{x}+\frac{y}{x}}-e^{-\frac{yn}{x}}}{1-e^{-y}}, \tag{13}$$

for species *a* and *b*, respectively.

To find a numerical solution, I used XPPAUT (Ermentrout 2002) to solve both equations for *x* (relative foliage density) with respect to *n* (relative height) at several levels of *y* (LAI of the shorter species, *b*), which span the observed range of LAI in terrestrial plant communities (Gower et al. 1999, Turner et al. 1999). The results show a single point of unstable coexistence ($R_{a|b} = R_{b|a} = 1$) and a region of stable coexistence ($R_{a|b} > 1$, $R_{b|a} > 1$) at each level of LAI (y), as well as areas of dominance by each species (Figure 3). Priority effects ($R_{a|b} < 1$, $R_{b|a} < 1$) are not observed. Coexistence only occurs when competing species exhibit a tradeoff between allocation to height and allocation to foliage, such that the taller species allows sufficient light through its canopy to satisfy the minimum light requirement of the shorter competitor.

2.2.3. The empirical model

Perhaps the greatest utility of my general model is that it suggests a new method to quantify competitive ability for light based on field measurements. The empirical model simply sums light collected by one species when shaded by the other (as opposed to integrating it as in the analytical model), relative to light capture within a conspecific stand. Here, light available to species *a* within *b* is:

$$R_{a|b} = \frac{\sum_{s=0}^{\hat{s}_a} f_{b,s} d_{a,s}}{\sum_{s=0}^{\hat{s}_a} f_{a,s} d_{a,s}}, \tag{14}$$

where $f_{b,s}$ is the incoming light available to height segment s within species b's canopy, $d_{a,s}$ is the foliage density of species a within height segment s, and $\hat{s}_a$ is now the total number of height segments of the taller species.

Foliage density ($d_{a,s}$) within a height segment can be estimated by the relative reduction in light across segment s. Thus equation 14 becomes

$$R_{a|b} = \frac{\sum_{s=0}^{\hat{s}_a} f_{b,s}\left(\frac{f_{a,s} - f_{a,s-1}}{f_{a,s}}\right)}{\sum_{s=0}^{\hat{s}_a} f_{a,s}\left(\frac{f_{a,s} - f_{a,s-1}}{f_{a,s}}\right)}. \tag{15}$$

Note that this underestimates $d_{a,s}$ because of self shading within a height segment; as the vertical thickness of segment s approaches zero, this estimate approaches actual foliage area. In equation (15), the denominator is simply the total amount of light captured by the entire canopy, and thus reduces to

$$R_{a|b} = \frac{\sum_{s=0}^{\hat{s}_a} f_{b,s}\left(\frac{f_{a,s} - f_{a,s-1}}{f_{a,s}}\right)}{1 - f_{a,0}}. \tag{16}$$

Because this model can be parameterized entirely by light availability in monocultures of each species, it is a simple task to make clear predictions of competitive outcomes based on empirical data. To return to the example of loosestrife and cattail (Figure 1), loosestrife receives 13% more light when shaded by cattail ($R_{l|c} = 1.13$) and thus should increase when rare in a stand of cattail. In contrast, cattail receives 13% less light when shaded by loosestrife ($R_{c|l} = 0.87$) and thus should decline when rare. In other words, the outcome of competition should be the competitive exclusion of cattail by loosestrife.

2.2.4. Model assumptions

This model is based on several simplifying assumptions. I assume that light is the limiting resource, and that monocultures reach equilibrium, with losses balancing photosynthetic gains. I likewise assume that species have similar phenologies, that species traits are not plastic (i.e., morphology and physiology are constant between monoculture and polyculture), and that species populations are not size structured. I also assume a linear response of photosynthesis to light availability, and that all plant tissue has equal photosynthetic capacity. The assumption of no size structure is certainly violated for some species, but is likely robust for clonal perennials that dominate many grasslands, old-fields, and wetlands.

Violations of several of these assumptions can be quantified in the field, and then included in the empirical model. For instance, when two species have very similar phenologies, the model will likely be robust to seasonal changes in light availability and leaf area. If not, the assumption of no seasonality can be addressed by measuring light availability and foliage density throughout the growing season, and simply summing light capture throughout the growing season as well as throughout the canopy. The related assumptions of no seasonality, linear photosynthetic responses to light availability and equal photosynthetic capacity of plant tissue can also be addressed in the field, by measuring photosynthetic responses to light availability randomly throughout the canopy and through the growing season.

While the analytical model assumes a linear response of photosynthesis to light availability, a saturating response (e.g., Michaelis-Menton) is likely more realistic (Reynolds and Pacala 1993). However, predictions from traditional resource competition theory (Tilman 1980) do not require that Michaelis-Menton dynamics govern growth, but rather that growth is simply a monotonically increasing function of resource availability (Huisman 1994). Additionally, Armstrong and McGehee (1980) argue that non-linear growth functions can only increase the opportunity for coexistence. Thus while inclusion of Michaelis-Menton dynamics into my model framework will likely be a fruitful avenue for future research, my prediction of coexistence is likely conservative with the assumption of a linear response.

2.3. Discussion

This model of competition for light makes three important contributions to competition theory. First, I show that competition for a single resource can lead to coexistence when that resource is directional and therefore competition is asymmetric. Coexistence only occurs when species exhibit a logically appealing tradeoff between allocation to height and allocation to leaves (Figure 3). Second, my approach offers a direct application of competition theory to empirical tests of competition for light in terrestrial systems, where species have complex, overlapping canopies. Prior efforts to model competition for light have assumed that canopies either overlap completely or do not overlap at all; thus these models can be empirically applied only to special cases of terrestrial plant competition. Finally, my model conceptually unifies asymmetric approaches to modeling competition with symmetric resource reduction models. This model explicitly incorporates minimum resource requirements (i.e., the essential component of symmetric models of competition) and differences in species height (i.e., the essential component of asymmetric competition models).

This model is unique in that it is based upon boundary conditions and global stability arguments and that it treats species with incompletely overlapping canopies. However, predictions from this model are analogous to those of other quantitative descriptions of light competition that approach the problem with more restrictive assumptions. When phytoplankton compete for light in a well-mixed water column (i.e., canopies completely overlap), models predict that the species that reduces light availability to the lowest level at equilibrium will competitively exclude all others and that coexistence will not occur (Huisman and Weissing 1994, Weissing and Huisman 1994, Huisman and Weissing 1995). These models are well corroborated by experimental tests (Huisman et al. 1999a) and are analogous to the special case of my model where both species have the same height ($\hat{h}_a = \hat{h}_b$, n=1). This model similarly predicts that, among species of equal height and with uniform foliage densities (i.e., completely overlapping canopies), the species with higher foliage density at equilibrium (lower light availability) will competitively exclude all others and that coexistence will not occur (Figure 3). This model also makes similar predictions to Huisman et al. (1997), who modeled competition for light among terrestrial clonal plants with species canopies that do not overlap at all. In their model as well as ours, coexistence occurs only if the species exhibit a tradeoff between growing tall and growing dense foliage: the taller species must allow sufficient light through its canopy to meet the light requirement of the shorter species (Figure 3)(Huisman et al. 1997).

My results suggest that as ecosystem productivity and thus leaf area index increase, the opportunity for coexistence decreases (Figure 3). As values of LAI (y) for the shorter species increase across the range of naturally occurring LAI (Gower et al. 1999, Turner et al. 1999), the range of trait values allowing coexistence shrinks. Compared to my results at low productivity (Figure 3A), the shorter species must have far higher foliage density to coexist at higher levels of productivity (Figure 3D), for a given difference in relative height.

Priority effects, which were not observed, only arise in models of light competition that either incorporate size structure (Perry et al. 2003), competition for above and belowground resources (Reynolds and Pacala 1993), or both (Tilman 1988, Rees and Bergelson 1997). Because of this dichotomy, I suggest that when species compete for a single resource, priority effects may occur only among species with size structured populations, where the extent of asymmetry can vary with the order of species establishment.

As described above, most models of competition for light rely on assumptions that simplify vertical complexities in light availability such that clear predictions often cannot be generated for the complex canopies that characterize terrestrial plant communities. While the sole experimental test, to my knowledge, of competition for light in higher plants successfully predicted competitive outcomes based on light availability at the soil surface (Seabloom et al. 2003), the limitations of this approach have long been recognized (Tilman 1988). I currently have underway an experimental test of competition for light that compares several metrics of light competitive ability, including light availability at the soil surface, the response of species to low light availability (Goldberg 1996), above-ground biomass and maximum species height (Gaudet and Keddy 1988), in addition to the integrated metric presented here.

By investigating light competition with invasibility criteria, I developed a simple model that, for the first time, predicts outcomes of competition for light between species with complex, overlapping canopies. The predictive ability of competition theory has previously been hampered by a lack of models treating this ubiquitous competitive scenario. In terrestrial plant communities partially over-lapping canopies are not special cases but rather the norm (Harper 1977, Terborgh 1985, Tilman 1988, Pacala et al. 1996, Liira and Zobel 2000). This model has begun to surmount this limitation. The next step for light competition models will be to explicitly model the dynamics of plants competing with partially overlapping canopies, and to investigate dynamics away from the boundary condition.

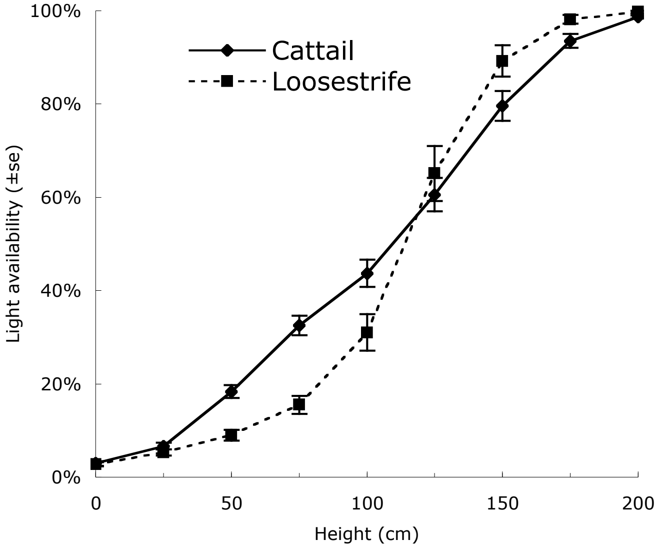


Figure 1. Light availability in broad-leaved cattail (Typha latifolia) and purple loosestrife (Lythrum salicaria) monocultures (mean ± se, n=6). At the soil surface, loosestrife and cattail reduce light to similar levels, yet cattail reduces light more than loosestrife in the upper canopy (150-175 cm), while loosestrife reduces light more than cattail in the lower canopy (50-100 cm). Measurement of light availability at any single height cannot adequately compare the light competitive ability of these species.

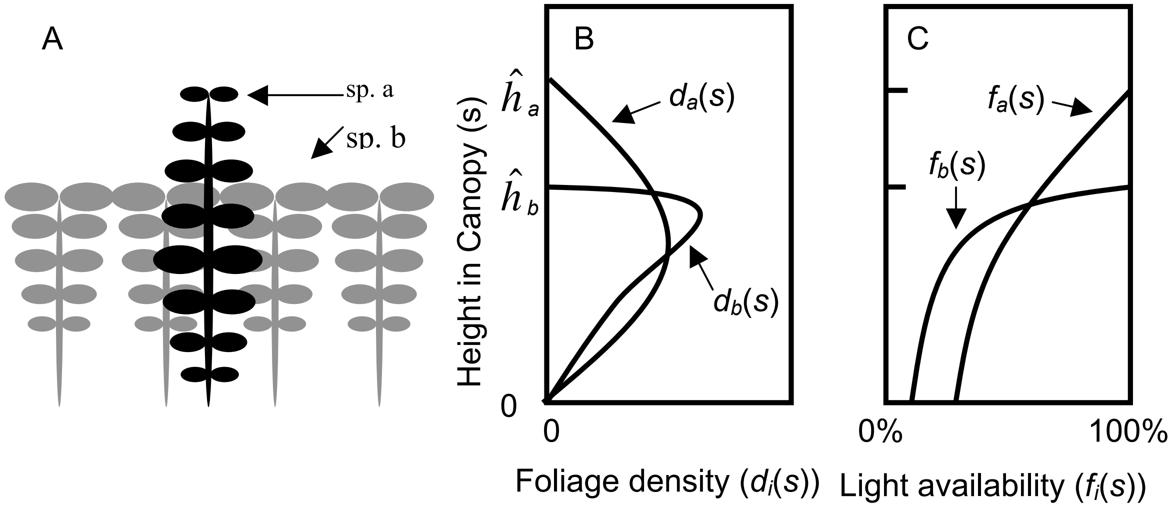


Figure 2. A) Two plant species that differ only in maximum height, h_i, and foliage density, $d_i(s)$. B) Foliage density, $d_i(s)$, as a function of height in canopy, s. C) Light availability, $f_i(s)$, as a function of height.

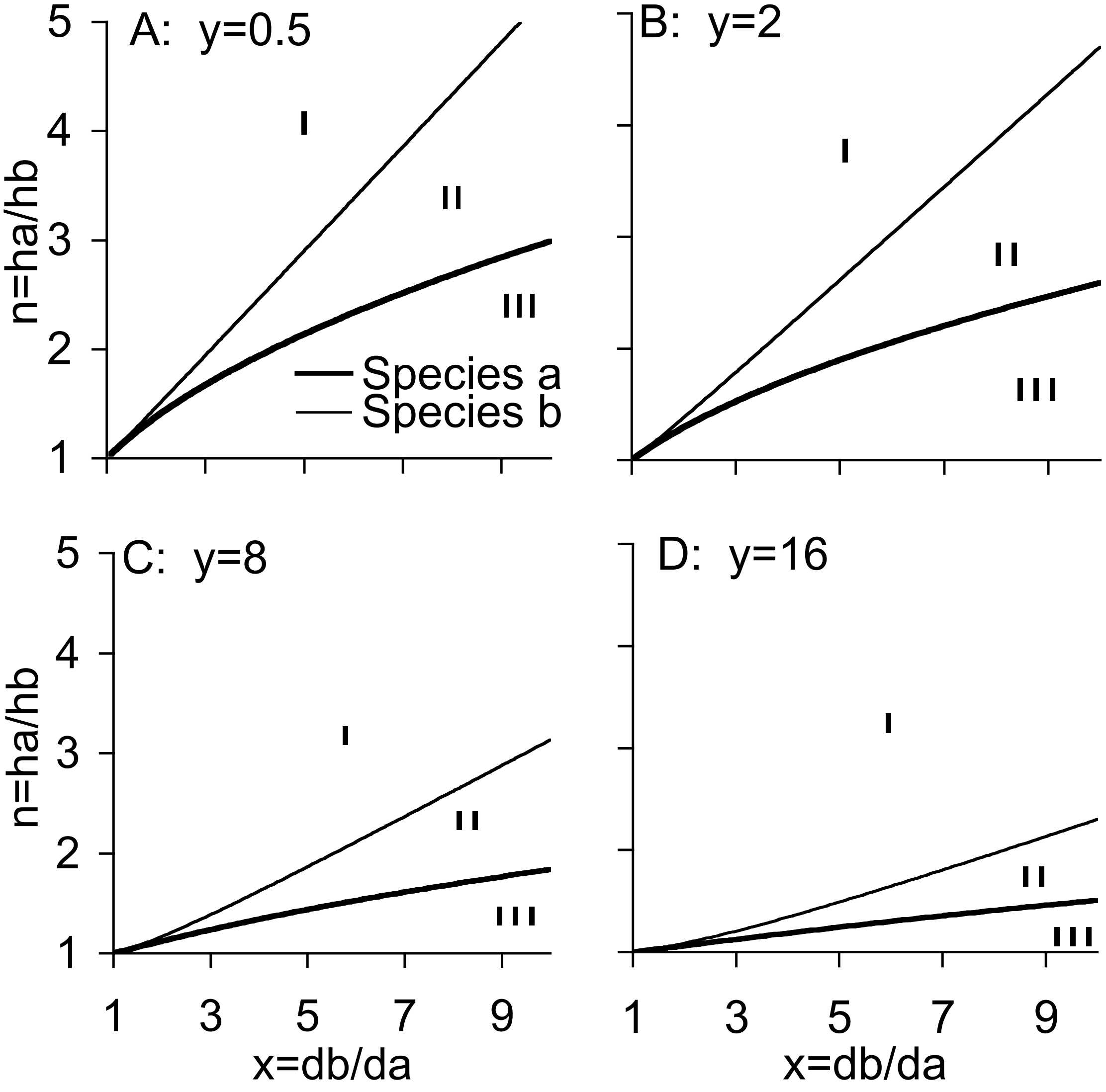


Figure 3. Zero net growth isoclines of a taller species, *a*, and a shorter species, *b*. *x* is the foliage density of the shorter species, *b*, relative to the taller species, *a*. *n* is the height of the taller species, *a*, relative to the shorter species, *b*. *y* is the leaf area index (height·foliage density) of the shorter species, *b*. *n* has a lower bound at 1 by definition. The taller species, *a*, always excludes the shorter species, *b*, when species *a* has denser foliage ($x<1$). In region I, species *a* has a positive growth rate when rare within a stand of species *b* ($R_{a|b}>1$), while species *b* has a negative growth rate when rare within a stand of species *a*; thus *a* excludes *b*. In region II, $R_{a|b}>1$ and $R_{b|a}>1$; thus species *a* and *b* coexist. In region III, $R_{a|b}<1$ and $R_{b|a}>1$; thus *b* excludes *a*.

3. Competition and facilitation between invasive purple loosestrife and native broad-leaved cattail: the critical effects of herbivory on interaction strength

3.1. Abstract

Invasive species threaten native diversity and cost the global economy billions of dollars per year. Biological control offers great hope for low-cost, long-term solutions for individuals invaders. However, our ability to predict invasions, as well as our ability to predict the efficacy of biological control, is woeful at best. Ecological theory offers several specific models of plant competition that may be applied to both invaders and biocontrol. The response to low resource availability model, the plant size model, and the resource reduction model all make specific predictions regarding the key traits of successful invaders. To evaluate the predictive power of these three broad models of plant competition, I tested three explicit hypotheses in a community composed of invasive purple loosestrife, native broad-leaved cattail, and *Galerucella calmariensis*, a leaf-feeding beetle widely released in an effort to control loosestrife. First, competition is occurring and thus inter-specific interactions reduce the abundance of loosestrife and cattail. Second, herbivory alters competitive outcomes. And third, traits measured in the absence of inter-specific interactions can predict those competitive outcomes. My experimental design included monoculture mesocosms in which I measured plant traits, and mixture mesocosms in which I quantified the effect of inter-specific interactions on species abundance. Both monocultures and mixtures included gradients of insect herbivory on loosestrife and cattail. I also included two levels of fertility in order to generalize across environments.

My results show that, on average, loosestrife abundance was lower in mixture than in monoculture, demonstrating that competition is occurring. In contrast, cattail abundance, on average, was not reduced by competition. Herbivory did alter competitive outcomes, but only

for cattail at high fertility. When insect herbivores of both species were suppressed with insecticide, cattail abundance in mixture decreased by 70% relative to monoculture. With insect herbivores of both species present, cattail abundance increased with increasing abundance of *Galerucella*. At the highest level of *Galerucella* abundance, cattail was facilitated by loosestrife: cattail abundance in mixture was 110% greater than in monoculture. The strong facilitative effect of loosestrife on cattail is likely due to cattail escaping from natural enemies; insect herbivores reduced cattail abundance in monoculture by more than 80%.

The trait implicated by the plant size hypothesis, species height, was the best predictor of competitive outcomes for loosestrife, explaining, along with loosestrife abundance in monoculture, 42% of loosestrife abundance in mixture. In contrast, no traits explained a significant amount of variation in abundance for cattail in mixture. This result is not surprising considering that facilitation through associational resistance, rather than competition for resources, appeared to be the major effect of loosestrife on cattail. Overall, my results suggest that traits associated with resource competitive ability can predict competitive outcomes, including the effect of herbivory on those outcomes, as long as competition for resources remains the primary interaction between species, as appeared to be the case for loosestrife. However, when interactions become facilitative, traits related to resource competitive ability are unlikely to be predictive without additional details of the mechanisms of facilitation.

3.2. Introduction

Invasive species pose a great challenge to ecologists, threatening many native species and inflicting substantial economic costs (Wilcove et al. 1998, Pimentel et al. 2000). In spite of the widespread concern over invasive species, ecologists are generally unable to predict which species are likely to become invasive (Williamson 1999). Many efforts to predict invasiveness have used broad-scale correlative approaches to identify traits associated with invaders versus unsuccessfully introduced species or native congeners (Reichard and Hamilton 1997, Goodwin et al. 1999, Kolar and Lodge 2001, Pysek 2001, Kolar and Lodge 2002). While these approaches have greatly increased our knowledge of the "average" invader, they still may fail to predict the success of individual exotic species. Indeed, some have concluded that "predicting the behavior of a species in a new environment may be effectively impossible" (Williamson 1999). Similarly, our ability to predict successful biological control is lacking, as most attempts to control invasive plants with insect herbivores have failed (Crawley 1989a, Crawley 1989b, Williamson and Fritter 1996, but see McFadyen 1998, for a more positive analysis). Clearly, we need approaches that can identify potential invaders before they wreak havoc on native ecosystems, as well as insect herbivores that will effectively control invaders.

One alternative to the broad-scale, correlative approach is to apply theories of community ecology (Tilman 1982, Miller and Werner 1987, Gaudet and Keddy 1988, Tilman 1988, Keddy and Shipley 1989, Goldberg 1996, Shea and Chesson 2002, Seabloom et al. 2003) to predict the success of invasive species. By identifying the critical traits for competitive success in a particular habitat, we may be able to identify the exotic species that pose the greatest threat. For instance, invaders of highly disturbed habitats may be superior competitors for regeneration sites by producing large quantities of well dispersed seeds (Seabloom et al. 2003, Chase and Leibold

2004). In contrast, invaders of later successional habitats may displace natives because they tolerate low resource availability or reduce the availability of limiting resources to very low levels (Tilman 1982, Goldberg 1996). For instance, invaders of forest understories may be better able than natives to tolerate low light availability. By identifying the traits that allow species to succeed in specific habitats, this approach allows for better precision in identifying the species that are most threatening to those habitats.

Community ecology offers several theories of plant competition that generate specific, testable predictions for the success of exotic species in native communities, as well as for the success of biological control (Shea and Chesson 2002). These theories can be grouped into three general models: 1) the response to low resource availability model, 2) the plant size model, and 3) the resource reduction model.

Response to low resource availability - Goldberg (1996) argued that "the long-term response of populations at equilibrium" (i.e., species abundance in many natural communities), will be best predicted by the ability of juvenile individuals to tolerate the depleted resource levels imposed by established stands of vegetation. The logic behind this prediction is clear: for one species to invade another, the invader's propagules must be able to persist under the resource-limited conditions imposed by the established stand. For instance, the prevailing model of forest dynamics predicts that shade tolerance drives succession towards species with increasing ability to survive deep shade (e.g., Kobe et al. 1995, Pacala et al. 1996, Walters and Reich 1996, Davies 2001). In other words, the species best able to respond to low resource levels (i.e., survive or grow), will eventually invade and displace all others. According to Goldberg (1996), the "ability of individuals to deplete resources is irrelevant to the equilibrial outcome of competition for a single resource and only ability to tolerate low levels of the resource determines the outcome" (Goldberg 1996, citing Vandermeer and Goldberg, unpublished results).

Plant size - Both Keddy and colleagues (Gaudet and Keddy 1988, Keddy and Shipley 1989) and Miller and Werner (1987) have argued that plant species with larger individuals (either biomass or height) are better competitors. This model is based on the idea that larger individuals or species are able to capture more of the limiting resource and thereby deny other species or individuals access to that resource (Miller and Werner 1987, Gaudet and Keddy 1988, Keddy and Shipley 1989). This model is not directly mechanistic, in that neither resource availability nor resource capture are actually measured. Rather, it assumes that plant size synthetically summarizes the ability of an individual or species to compete for resources (Miller and Werner 1987, Gaudet and Keddy 1988). Gaudet and Keddy (1988) demonstrated that both biomass and height predict competitive effect among species competing in pots. Because Miller and Werner (1987) used relatively few species, they could not directly test the ability of plant size, measured in the absence of inter-specific competition, to predict competitive outcomes or community abundance. Nonetheless, their results are consistent with the plant size model (Miller and Werner 1987).

Resource reduction - Classical resource competition theory mathematically models interactions between consumers and resources (Armstrong and McGehee 1976, Tilman 1980, Tilman 1982). Resource competition theory predicts that the species that is able to reduce the availability of the shared limiting resource to the lowest level at equilibrium, and persist at that level, will win in competition (Tilman 1980, Tilman 1982). Because of the mathematical nature of the model and its equilibrial solution, a species' effect on, and response to, resource availability are equivalent: a population draws resources down to a minimum level, and then proceeds to persist at that level of resource availability. The resource reduction model, while well supported by studies of phytoplankton and zooplankton (see Grover 1997, for review), has received only limited support in higher plants. Wedin and Tilman (Tilman and Wedin 1991, Wedin and Tilman 1993) found that the ability of four grass species to reduce soil nitrogen availability predicted competitive outcomes, but only in low nitrogen plots. In fertilized plots, competitive outcomes were dependent on initial conditions (Wedin and Tilman 1993).

Here, I report results from a long-term mesocosm experiment designed to test the ability of these three models to predict the outcome of competition between a widespread invader (Purple loosestrife, *Lythrum salicaria* L.) and a dominant native species (Broad-leaved cattail, *Typha latifolia* L.) that it often displaces, as well as the effect on that outcome of an insect released in an effort to biologically control the invader (*Galerucella calmariensis* L.). I included two levels of fertility to determine whether my results are generalizable across environments. All three models make specific predictions for competitive outcomes and invasion success, based on the trait values associated with each hypothesis. The *response to low resource availability* model (Goldberg 1996) predicts that the success of an invader will be positively correlated with its survival at low resource availability, relative to the survival of its native competitors. Similarly, the *plant size* model (Miller and Werner 1987, Gaudet and Keddy 1988) predicts that the competitive success of an exotic species will be positively correlated with the size asymmetry of the exotic relative to its native competitors. The *resource reduction* model (Tilman 1980, Grover 1995, Chapter 2) predicts that the success of an exotic species will be positively correlated with its ability to reduce the availability of the limiting resource relative to the resource reduction ability of its native competitors. The specific predictions for each of these general hypotheses can be logically extended to include the effects of herbivores on competitive outcomes (e.g., Grover 1994, Holt et al. 1994, Grover 1995). If the traits described above (height, response to low resource availability, etc.) define competitive ability for plants, then insect herbivores must, short of simply killing their host outright, alter those traits in order to alter the outcome of competition. To test these models I addressed three specific hypotheses: 1) competition does, in fact, occur (i.e., species' abundance is lower in mixture than in monoculture); 2) *Galerucella* herbivory on loosestrife alters competitive outcomes; and 3) competitive outcomes for loosestrife and cattail can be predicted by the traits implicated by each of the models of plant competition outlined above.

3.3. Methods

3.3.1. Study system

Purple loosestrife is an herbaceous perennial from Eurasia that invades fertile marshes throughout North America (Thompson et al. 1987, Malecki et al. 1993, Blossey et al. 2001b). Loosestrife threatens many native plant and animal species and is widely considered one of the most successful invaders in North America (Thompson et al. 1987, Malecki et al. 1993, Blossey et al. 2001b, Landis et al. 2003) However, the limited experimental evidence of the impact of loosestrife suggests widely varying effects of loosestrife on native species richness (Morrison 2002, Landis et al. 2003), and the observational evidence of loosestrife's impact is often conflicted (Hager and McCoy 1998, Treberg and Husband 1999, Farnsworth and Ellis 2001).

Broad-leaved cattail is a common, native herbaceous perennial that often dominates fertile marshes in North America. Broad-leaved cattail frequently co-occurs with loosestrife, and is thought to be often displaced by loosestrife invasions (Thompson et al. 1987). Loosestrife and cattail are herbaceous perennials that senesce all above-ground biomass each winter, and display similar vegetative phenologies throughout the growing season (Bunker and Carson, unpublished data). Both species are common near Pymatuning Laboratory of Ecology, Linesville, Crawford County, PA, where this study was conducted.

Galerucella calmariensis (Chrysolmelidae) is a leaf-feeding beetle native to Eurasia that has been widely released in the U.S. and Canada since 1992 in an effort to biologically control purple loosestrife (Malecki et al. 1993, Blossey et al. 2001b). Both adults and larvae of *Galerucella* feed on loosestrife, with the larvae causing the majority of damage (D. Bunker, pers. obs.). While *Galerucella* appears to achieve successful control of loosestrife at some release sites, the effect of *Galerucella* is more often minimal, causing less than 10% leaf-area damage to loosestrife (Hight et al. 1995, McAvoy et al. 1997, Katovich et al. 2001, Dech and Nosko 2002, Landis et al. 2003, Brinker, Bunker and Carson, unpublished data). For instance, Landis et al. (2003) quantified effects of *Galerucella* at 24 release sites and found that while native species richness increased at some sites, *Galerucella* did not have clear impacts at the majority of release sites (13 of 24). Surprisingly, I have found no published studies where experimental releases have been compared to control sites.

In the highly fertile marshes where loosestrife and cattail occur, light availability at the soil surface is very low (Figure 4), and is comparable to light availability in both temperate and tropical forest understories (Grace and Wetzel 1981, Pacala et al. 1996, Twolan-Strutt and Keddy 1996, Nicotra et al. 1999). In such highly fertile systems, light is more likely to be limiting than below-ground resources (Grace and Wetzel 1981, Schmitt et al. 1986, Gaudet and Keddy 1988, Tilman 1988, Twolan-Strutt and Keddy 1996, Carson and Root 2000). For these reasons I concluded that loosestrife and cattail are likely to be most limited by light availability and thus if resource competition occurs, it occurs as competition for light.

Loosestrife, cattail, and *Galerucella* make an ideal model system with which to test the ability of competition theory to predict the success of both invasions and biological control. Both plant species are well studied and can be manipulated both in mesocosms and in the field (Grace and Wetzel 1981, Grace and Harrison 1986, Grace 1987, Weiher and Keddy 1995, Mal et al. 1997, Weihe and Neely 1997). *Galerucella* has been identified as a likely successful biocontrol agent, has been widely released in an effort to control loosestrife, and has few non-target effects (Malecki et al. 1993, Blossey et al. 2001a, Blossey et al. 2001b, Schooler et al. 2003). Because loosestrife and cattail occur in habitats that are likely to be light limited, this system also offers an excellent opportunity to test the ability of light reduction throughout the canopy to predict the outcome of competition (see Chapter 2).

3.3.2. Experimental overview

To test the ability of the *response to low resource availability, plant size* and *resource reduction* models to predict the outcome of competition, four goals must be achieved: 1) species performance must be quantified in monoculture (i.e., in the absence of inter-specific interactions); 2) competitive outcomes must be quantified by comparing species performance in mixture (i.e., in the presence of potential competitors) with performance in monoculture; 3) plant traits must be quantified in the absence of inter-specific interactions; and 4) the ability of plant traits to predict outcomes must be tested by regressing competitive outcomes against species' traits. Note that inter-specific interactions may result in competition or facilitation, or may have no effect at all on the abundance of species. I use the term "competitive outcome" in a broad sense that includes all possible effects of inter-specific interactions.

To accomplish these goals, I used two experiments: the *response to low resource availability experiment* and the *mesocosm experiment*. In the *response to low resource availability experiment*, I quantified species' response to low resource availability by growing loosestrife and cattail in pots under a gradient of experimentally manipulated light availability. This experiment allowed me to quantify the trait implicated by the *response to low resource availability* model, specifically, seedling survival at low light availability (Goldberg 1996). In the *mesocosm experiment*, I used 1000 L cattle tanks to create experimental wetland mesocosms, including monocultures of each species and mixtures containing both species, in a substitutive design. In the monocultures I quantified the traits implicated by the *plant size* (height and standing crop) and *resource reduction* (light availability) models, as well as species abundance in the absence of inter-specific interactions. In mixture I quantified each species' performance in the presence of the other species. Together, these two experiments allowed me to quantify the specific traits that are critical to the ability of plant species to compete for light, as implicated by the three models of competition, and also to quantify competitive outcomes. Both experiments included herbivory treatments to quantify effects of herbivory on traits and competitive outcomes. Because fertility is a critical environmental factor that has strong effects on the structure of wetland ecosystems (Morris 1991, Bedford et al. 1999), I replicated both experiments at two levels of fertility to generalize my results to multiple environments.

3.3.3. Response to low resource availability experiment

Goldberg (1996) argues that the response of juveniles to low resource availability determines long-term competitive outcomes, because in order to displace a competitor, juveniles must be able to establish under conditions of reduced resource availability imposed by competing adults. While cattail, and to some extent loosestrife, can spread vegetatively within a site, initial establishment at a given site must be from seed. Thus, to quantify their ability to survive at low resource availability, I grew seedlings of both species in pots under a wide gradient of light availability, at both high and low fertility, and inflicted three levels of simulated herbivory on loosestrife.

The experiment utilized a split-plot design, with five replicates of each of seven light environments (the main-plot factor), and with all combinations of two soil fertility treatments and four species-herbivory treatments (split-plot factors), randomized within each main-plot (280 experimental units). The species-herbivory treatment included cattail without herbivore damage, and loosestrife with three levels of damage, inflicted by mechanically removing 0, 25 or 50% of each leaf. To control insect herbivore damage, I sprayed all individuals weekly with the insecticide esfenvalerate (see *Herbivory treatments*, below, for further justification). The seven light environments ranged from 1% to 90% of ambient light, and were manipulated with neutral density shade cloth. Soil fertility was manipulated with a one-time addition (0, 16 g N m^{-2} yr^{-1}) of urea (NH_2-CO-NH_2) to each pot. The 8.6 L pots were filled to 2 cm below the rim with low-fertility topsoil and additionally fertilized with potash (8 g K_2O m^{-2} yr^{-1}) and phosphate (8 g P_2O_5 m^{-2} yr^{-1}). The pots lacked drain holes, and soils were maintained in a fully saturated state for the duration of the experiment. The fertility treatments, topsoil and flooding regime were identical to those used in the mesocosm experiment (see *Mesocosm establishment and fertility treatments*, below).

On May 27, 2003 I placed ~200 seeds of loosestrife or cattail in each pot, which was placed in full sun during the germination period. After germination, I thinned each pot to 5-7 individuals. On June 26, I fertilized each pot as above. On July 16, I randomly thinned each pot to one individual and placed the pot in a randomly assigned light environment (main-plot). At this time loosestrife was 5-10 cm tall and cattail 15-25 cm tall. On August 1, I inflicted herbivore damage to loosestrife and censused the height (and stem diameter for loosestrife) of each individual. In early September, I determined survivorship and harvested all individuals.

3.3.4. Mesocosm experimental design: monocultures and mixtures

The mesocosm experiment served four purposes in testing the hypotheses outlined above. In monoculture, I quantified species abundance and also quantified species traits in the absence of inter-specific interactions. In mixture, I quantified species abundance in the presence of inter-specific interactions. Together, these data allowed me to: 1) quantify competitive outcomes by comparing species abundance in mixture with that in monoculture, 2) determine whether insect herbivory altered competitive outcomes, 3) quantify traits implicated by the three models of competition, and 4) quantify the ability of the three models of competition to predict competitive outcomes by regressing species abundance (standing crop g m^{-2}) in mixture against trait values and monoculture abundance.

The design of the mesocosm experiment (Table 1) was a partial factorial, with three species combinations (monocultures of each species and two-species mixtures), two fertilities, and four herbivory treatments (only two of the herbivory treatments were applied to cattail monocultures, see *Herbivory treatments*, below), and six replicates, for a total of 120 mesocosms. The experiment utilized a randomized complete block design, with each treatment combination replicated once within each of six blocks.

3.3.5. Mesocosm establishment, fertility treatments, and mixture design

I initiated the mesocosm experiment in May 2000 at the Pymatuning Lab of Ecology of the University of Pittsburgh, Linesville, Crawford County, PA. The mesocosms were constructed within 1000 L polyethylene cattle tanks that were 164 cm in diameter and 50 cm in height and had 2.1 m^2 of surface area. I filled each mesocosm with 30 cm nutrient poor commercial topsoil (Powell Sanitation, Meadville, PA, 42 ppm P, 200 ppm K, 3 ppm NH_4, 7 ppm NO_3). I fertilized each mesocosm in early June of each year with 0 or 16 g N m^{-2} (added as urea) for low and high fertility treatments, respectively. I manipulated nitrogen because nitrogen is most often the limiting nutrient in the marsh ecosystems where loosestrife and cattail naturally occur (Morris 1991, Bedford et al. 1999). I also fertilized all mesocosms with 8 g P_2O_5 m^{-2} y^{-1} and 8 g K_2O m^{-2} y^{-1} (added as triple super-phosphate and muriate of potash, respectively) to ensure that nitrogen was the limiting soil resource. The water level was maintained at the soil surface during the growing season (May-August) and at 10 cm above the soil surface for over-wintering (Day et al. 1988, Weiher and Keddy 1995). To minimize edge effects in the light environment, I surrounded each mesocosm with a skirt made of green shade cloth that blocked 60% of ambient light and extended 90 cm above the soil and 65 cm above the edge of the cattle tank. The mixture mesocosms were divided in half vertically, from the top of the tank to the bottom of the soil, with a removable black plastic sheet oriented from North-East to South-West, and species were randomly planted into one side or the other.

In June 2000, I sowed seed of loosestrife and cattail into each mesocosm at densities of ~40,000 seeds m^{-2}. To ensure a broad sample of local genetic diversity for both species, I collected and pooled mature flower heads from eight populations of each species near the Pymatuning Laboratory of Ecology. I then separated seed from fruit, using the method described by McNaughton (1968) to separate cattail seed. At the end of the first growing season, loosestrife and cattail stem densities were 24.5±1.4 and 22.7±2.6 individuals/m^2 (mean±se) respectively. In May 2001, I removed the plastic barrier to allow the species to compete fully.

3.3.6. Herbivory treatments

The four herbivory treatments included: 1) insecticide treated, hereafter "insects suppressed," 2) manual removal of *Galerucella*, hereafter "(-)Beetles," 3) ambient levels of herbivory, including herbivory by *Galerucella*, hereafter "Ambient herbivory," and 4) manual addition of *Galerucella*, hereafter "(+)Beetles." I initially stocked each mesocosm during May of the second growing season with 0, 8, 16 or 32 adult beetles per 100 m of loosestrife stem, for the four herbivory treatments respectively. A pilot project established in 1999 estimated second-year loosestrife abundance at 194 and 128 m of loosestrife stem per mesocosm, at high and low fertility, respectively. Thus, into each loosestrife monoculture mesocosm, I placed 0, 16, 31, or 62 adults at high fertility and 0, 10, 20, or 41 at low fertility, for the four herbivory treatments, respectively, and half as many in each mixture mesocosm. Beetle adults were obtained from the USDA-APHIS rearing facilities in Niles, Michigan.

Throughout the peak egg laying period each year (late May and early June), I manually aspirated adults from the (-)beetles mesocosms and placed them in the (+)beetles mesocosms, repeating the process twice each week until no further *Galerucella* could be harvested from the (-)beetles mesocosms. Because *Galerucella* do not feed on cattail (Malecki et al. 1993, Blossey et al. 2001a, Blossey et al. 2001b, Schooler et al. 2003, D. Bunker, personal observation), I established monocultures of cattail with only the insect suppression treatment and the ambient herbivory treatment (Table 1). Insects of all other species were allowed to colonize all herbivory treatments according to their own natural history. Ambient herbivory on cattail was primarily inflicted by the noctuid moth *Bellura obliqua*. Japanese beetles (*Popillia japonica*) occasionally fed on loosestrife late in the season, but generally caused little damage.

The insect suppression treatment consisted of weekly applications of esfenvalerate (trade-name: AsanaXL, a synthetic pyrethroid, DuPont, Wilmington, Delaware) at the label recommended rate of 0.04 ml/m^2, during the period of *Galerucella* activity (May through July). At the same time, an equivalent amount of water was sprayed on the three other herbivory treatments. I chose Esfenvalerate because it contains a single isomer of the insecticide Fenvalerate, an insecticide whose effects are well known (Adelsbach and Tjeerdema 2002). Fenvalerate is highly effective at low concentrations and does not cause experimental artifacts (Cain et al. 1991, Root 1996, Carson and Root 2000). Fenvalerate kills insects on contact and continue to be effective for 7-10 days following application because residues remain on plants acting as anti-feedants and oviposition repellents (Stark 1983, Gist and Pless 1985). Fenvalerate neither stimulates plant growth nor does it have any phytotoxic effects on the plant species so far tested (Root 1996, Carson and Root 2000).

3.3.7. Loosestrife leaf-area damage censuses – evaluating the effects of herbivory treatments

I censused loosestrife leaf-area damage in early July of each year, after larvae had begun to pupate, by randomly selecting one leaf from the lower, middle and upper portions of 6-18 stems of loosestrife per mesocosm (depending on loosestrife abundance) in a stratified random manner. Damage was estimated by visually comparing leaves with leaf templates with known percentages of damage. I then averaged across all leaves sampled within a mesocosm. Although the herbivory treatments significantly affected leaf-area damage to loosestrife (see *results*, below), there was substantial variability within treatments. For this reason, I included both herbivory treatment and leaf-area damage to loosestrife in further analyses. Because insect herbivore damage to cattail was expected to be low, I did not census cattail for leaf area damage. Future work will include quantification of damage to cattail.

3.3.8. Plant abundance censuses

To estimate above-ground standing crop, I censused each mesocosm in late July of each year. I sub-sampled the monoculture mesocosms by randomly choosing four pie-shaped sampling quadrats, each 1/16th of the entire mesocosm. Within each quadrat, I measured the height (and, for loosestrife, the diameter) of each stem. In the mixture mesocosms, I placed six sampling quadrats systematically, such that three were on the side originally occupied by cattail and three on the side originally occupied by loosestrife. On each side, two quadrats were placed opposite each other and adjacent to the original divide between the species, while the third was placed perpendicular to the original divide. To avoid destructive harvests, I calculated standing crop using allometric relationships developed from individuals harvested from separate mesocosms. For cattail, maximum height was a good predictor of per-stem biomass (r^2=0.92, $F_{1,26}$=307, p<0.0001). For loosestrife, stem diameter, maximum height, and their interaction were used to predict per-stem dry mass (r^2 = 0.97, $F_{3,77}$=948, p<0.0001). For each mesocosm, I applied these allometric equations to each sampled stem, and then summed across all sampled stems to calculate per-species standing crop for each mesocosm (g m^{-2}).

3.3.9. Quantifying competitive outcomes – the response ratio

The hypotheses outlined above predict that: 1) if competition is occurring, then species abundance in mixture will be less than abundance in monoculture; 2) if insect herbivory alters the outcome of competition, then the abundance of species in mixture, relative to monoculture, will change among herbivory treatments and/or with loosestrife leaf-area damage; and 3) if any of the three models of competition predict competitive outcomes, then relatively "better" traits will be associated with greater abundance in mixture, relative to monoculture. All three predictions require a measure of species abundance in mixture relative to monoculture.

Thus, to quantify the effect of inter-specific interactions on species abundance, I used the response ratio (*RR*) (Goldberg et al. 1999, Hedges et al. 1999, Osenberg et al. 1999),

$$RR_i = \left(\frac{Y_{ix}}{Y_{im}}\right), \qquad (1)$$

where $Y_{i\mathrm{x}}$ is the standing-crop of species i in mixture and $Y_{i\mathrm{m}}$ is the standing-crop of species i in monoculture. The response ratio is simply the abundance of species i in mixture relative to monoculture, and is bounded by 0 and infinity. If RR_i is less than 1 (100%), then inter-specific interactions have reduced the abundance of species i and competition has occurred; if RR_i is greater than 1 (100%), then inter-specific interactions have increased the abundance of species i and facilitation has occurred. When the response ratio is log-transformed, its sampling distribution is approximately normal, and thus the response ratio is a reasonable metric for parametric statistical analysis (Hedges et al. 1999).

3.3.10. Quantifying species abundance in the absence of inter-specific interactions

To calculate measures of interaction intensity, such as the response ratio, some experimenters have paired mixture replicates with monoculture replicates within the same block of an experiment, effectively treating blocks as replicates (Greiner La-Peyre et al. 2001, Howard and Goldberg 2001). However, my design does not lend itself well to that approach, because leaf-area damage to loosestrife varies within herbivory treatments, and is likely a critical covariate. Thus, to obtain a null prediction of abundance for each mixture (i.e., standing crop in the absence of competitive effects, and the denominator of the response ratio, *RR*), I used least squares estimates of monoculture abundance (g m^{-2}), using data from the 2003 plant abundance census.

For cattail, I used an ANOVA model to calculate least squares mean abundance for each fertility by herbivory treatment combination. Because *Galerucella* do not feed on cattail (Malecki et al. 1993, Blossey et al. 2001a, Blossey et al. 2001b, Schooler et al. 2003, D. Bunker, personal observation), cattail monocultures in the ambient herbivory treatment provided null predictions of abundance for cattail in the (-)Beetles, Ambient herbivory, and (+)Beetles mixtures. For loosestrife, I used an ANCOVA model to calculate least squares estimates of mean abundance, adjusted to the observed leaf-area damage in each mixture. Thus, the cattail model used fertility and herbivory treatments, and their interaction as effects to estimate cattail abundance, while the loosestrife model used fertility and herbivory treatments, as well as loosestrife leaf-area damage (the three year mean) and all interactions to estimate loosestrife abundance.

I did not include a block effect in these models, because including block both when generating the null predictions as well as when quantifying outcomes (see below) would effectively introduce a block by culture (monoculture vs. mixture) interaction, which I wanted to avoid. I excluded one loosestrife monoculture from the loosestrife model because it experienced complete defoliation in both 2002 and 2003, and had virtually zero abundance in 2003. As a result this monoculture replicate had enormous leverage, and also caused the residuals to be heteroscedastic. Because my goal was to build a predictive model for standing crop in mixture, where mean damage did not exceed 37%, removing this monoculture made my estimates more conservative and more accurate over the range of damage observed in mixture, and allowed my analyses to meet the assumptions of homoscedasticity. Analyses were conducted in JMP (version 5.01, SAS Institute, Cary, N.C.); response variables and leaf-area damage were transformed as necessary to meet the assumptions of normality and homoscedasticity.

3.3.11. Quantifying the effects of species, treatments and leaf area damage on competitive outcomes

I used standard ANCOVA procedures (SAS Proc Mixed, version 6.12, SAS Institute, Cary, NC, Littell et al. 1996) to quantify the effects of species, fertility, herbivory treatment, and leaf-area damage to loosestrife, as well as all interactions, on the response ratio (*RR*). Because species' responses may be correlated within an individual mixture mesocosm, I used a repeated measures approach by including the mixture itself as a random effect (Littell et al. 1996). I also included block as a random effect. I tested whether competition (or facilitation) is occurring simply by determining whether the 95% confidence interval of the treatments means overlap 1 (100%). Significant main effects of, or interactions with, herbivory treatment or leaf area damage indicate that herbivory is changing the outcome of competition. Where such significant effects were found, I used orthogonal contrasts to identify significant differences between species and among treatments.

3.3.12. Quantifying species traits associated with the three models of competition

The three models of plant competition predict that a species' performance in mixture (i.e., where performance is measured as abundance in mixture relative to monoculture) will be positively associated with that species' trait value and negatively associated with the trait value of its competitor. For instance, if species *a* is shorter than species *b* in low fertility monocultures, but taller than species *b* in high fertility monocultures, then the "performance" of species *a* in mixture should be greater at high fertility than at low fertility. Note that neither the absolute nor the relative difference in species' traits makes any prediction about the overall magnitude of competitive effects. To be truly predictive, traits must be measured in the absence of inter-specific interactions. Thus, to estimate trait values for each species in each mixture, I used methods similar to those used to estimate the null prediction for abundance in the absence of inter-specific effects (see *Quantifying species abundance in the absence of inter-specific interactions*, above).

Response to resource availability model

Goldberg (1996) argues that competitive outcomes in undisturbed communities are determined by the response of juveniles to low levels of the limiting resource, because juveniles must be able to survive conditions of low resource availability imposed by adults of competing species. I quantified species' response to low resource availability as seedling survival at low light, at both high and low fertility and with a gradient of simulated herbivore damage to loosestrife (see *response to resources experiment*, above). All individuals survived at both 18 and 39% light availability. Thus, I defined "low resource availability" as light availability below 18%, and pooled all treatments below that level (1, 3, 7, and 12% light availability). This resulted in a total of 155 individuals (n=38, 40, 38 and 39, for loosestrife with 0%, loosestrife with 25%, loosestrife with 50%, and cattail with 0% damage, respectively; 5 pots were inadvertently placed in the incorrect light environment, and therefore removed from the analysis).

To estimate survivorship at low light for each species, I used a generalized linear mixed model to conduct logistic regression (SAS Proc Mixed Glimmix Macro, version 6.12, SAS Institute, Cary, N.C., Littell et al. 1996). For cattail, I used least-squares mean survival at each fertility level. For loosestrife, I estimated the linear relationship between percent leaf-area damage and survival at each level of fertility. I then used these models to calculate predicted survival at low light for each species in each mixture.

Plant size model

I quantified plant size using two different plant traits measured in monoculture: mean height and standing crop. Both standing crop and height have been invoked as traits summarizing competitive ability (Miller and Werner 1987, Gaudet and Keddy 1988, Keddy and Shipley 1989), and both correlate well with competitive effect (Gaudet and Keddy 1988, Keddy and Shipley 1989). Both Gaudet and Keddy (1988) and Miller and Werner (Miller and Werner 1987) argue that plant size predicts competitive ability particularly where light is most likely to be limiting.

For standing crop, I used the same estimates developed above for the null predictions of abundance in the absence of inter-specific effects (see *Quantifying species abundance in the absence of inter-specific interactions*, above). For height, I applied the same methodology used to obtain null predictions of abundance in the absence of inter-specific effects to estimate mean height for each species in each mixture (see *Quantifying species abundance in the absence of inter-specific interactions*, above). These estimates were based on the mean stem height within each monoculture, collected during the 2003 plant abundance census (see *plant abundance censuses*, above).

Resource reduction model

I used three metrics to evaluate the resource reduction model: one utilizes total effect on light availability, and the other two utilize the light model proposed in chapter 2, above. The three metrics incorporate increasing complexity in the measurement of the effect of each species on light availability.

I collected light availability measurements at 25 cm intervals from the soil surface to the top of the canopy within each monoculture using a Li-Cor line quantum sensor (100 x 1 cm) referenced to ambient light simultaneously sampled with a Li-Cor point sensor (Li-Cor, Lincoln, Nebraska). All light measurements were collected under diffuse light conditions (dawn, dusk, or overcast). Growing season light availability was measured in monoculture mesocosms in late June, during the middle of the 2003 growing season. Spring light availability (see Metric 3, below), when light is controlled only by standing dead litter, was collected in monoculture mesocosms in late April, 2004.

Metric 1: Light availability at the soil surface: This approach uses the traditional interpretation of resource competition theory, which assumes that resources are homogenously distributed (Tilman 1982). Even though light clearly violates the assumption of a homogenously distributed resource (e.g., Tilman 1988), the theory may nonetheless be robust to such violations because juveniles must endure these depleted light levels during establishment. Additionally, light at the soil surface is easy to measure. To estimate light availability at the soil surface for each mixture, I applied the same methodology used to obtain null predictions of abundance in the absence of inter-specific effects (see *Quantifying species abundance in the absence of inter-specific interactions*, above).

Metric 2: The standard light model - Light capture throughout the canopy: I parameterized the standard light model using equation 15, chapter 2, which quantifies the light captured by species a when shaded only by species b, ($R_{a|b}$):

$$R_{a|b} = \frac{\sum_{s=0}^{\hat{s}_a} f_{b,s}\left(\frac{f_{a,s} - f_{a,s-1}}{f_{a,s}}\right)}{\sum_{s=0}^{\hat{s}_a} f_{a,s}\left(\frac{f_{a,s} - f_{a,s-1}}{f_{a,s}}\right)} , \qquad (2)$$

where $\hat{s}_i$ is the maximum number of height segments of species i, and $f_{i,s}$ is light availability in a monoculture of species i at the top of height segment s.

Metric 3: The light model with litter effect – Light capture throughout the canopy, assuming litter is non-photosynthetic: The standard light model assumes that all biomass that captures light is equally photosynthetic. However, cattail monocultures develop substantial standing dead litter that captures large amounts of light, whereas loosestrife does not (Figure 5). Standing dead litter can strongly alter competition for light because litter casts shade as does live tissue, yet a species is not deprived of light when its litter is shaded. Thus, litter decreases light available to competitors, yet shading *of* litter does not decrease photosynthesis. If litter is assumed to be photosynthetic, then the light captured by an individual of a species is overestimated. For these reasons, I parameterized the light model a second time to account for the lack of photosynthetic capacity by standing dead litter. I did so by quantifying the leaf-area of standing dead litter for both species through measures of light availability collected in late April 2004, before emergence. By subtracting standing dead leaf-area from growing-season leaf-area, I removed the light captured by standing dead from the model predictions. Recall equation 14 from chapter 2:

$$R_{a|b} = \frac{\sum_{s=0}^{\hat{s}_a} f_{b,s} d_{a,s}}{\sum_{s=0}^{\hat{s}_a} f_{a,s} d_{a,s}}, \tag{3}$$

noting that $d_{a,s}$ is leaf-area in height segment s. To remove the leaf-area of standing litter, I subtract litter leaf area from growing season leaf area:

$$R_{a|b} = \frac{\sum_{s=0}^{\hat{s}_a} f_{b_g,s} \left(d_{a_g,s} - d_{a_l,s} \right)}{\sum_{s=0}^{\hat{s}_a} f_{a_g,s} \left(d_{a_g,s} - d_{a_l,s} \right)}, \tag{4}$$

where g denotes growing season and l denotes litter. Note that now light availability is parameterized only by growing season light availability, and thus includes the effect of both live and dead foliage, while leaf-area includes only live foliage. Expressing equation (4) solely in terms of light availability yields equation (5), which I used to parameterize the light model under the assumption that litter is non-photosynthetic:

$$R_{a|b}=\frac{\sum_{s=0}^{\hat{s}_a} f_{b_g,s}\left(\left(\frac{f_{a_g,s}-f_{a_g,s-1}}{f_{a_g,s}}\right)-\left(\frac{f_{a_l,s}-f_{a_l,s-1}}{f_{a_l,s}}\right)\right)}{\sum_{s=0}^{\hat{s}_a} f_{a_g,s}\left(\left(\frac{f_{a_g,s}-f_{a_g,s-1}}{f_{a_g,s}}\right)-\left(\frac{f_{a_l,s}-f_{a_l,s-1}}{f_{a_l,s}}\right)\right)} . \qquad (5)$$

To parameterize the light model, I required estimates of light availability throughout the canopy based on light availability in monoculture, as functions of fertility, herbivory treatment, and for loosestrife, leaf-area damage. Cattail and loosestrife vary widely in maximum height both within and among fertility and herbivory treatments. If incorporated into a single model, the complete lack of variance at higher heights for some treatment combinations (where all values are 100%) results in highly non-normal residuals. Thus I used separate models for groups of treatments that had similar maximum heights, using SAS Proc Mixed (SAS Institute, Cary, NC, Littell et al. 1996). I used a logit-transformation of light availability to meet the assumptions of normality and homoscedasticity.

3.3.13. Quantifying the ability of traits to predict outcomes in mixture

Using each mixture as a replicate, I used multiple regression to quantify the variability in observed abundance in mixture explained by: 1) monoculture abundance in the absence of inter-specific interactions, 2) the trait value of the species in question, and 3) the trait value of the competing species. Monoculture abundance and traits were estimated for each mixture as described above (see *Quantifying species abundance in the absence of inter-specific interactions*, and *Quantifying species traits associated with the three models of competition*, above). To test the explicit hypothesis that traits explain variation in abundance in mixture, above and beyond that explained by abundance in monoculture, I used sequential sums of squares (Type I), first adding abundance in monoculture and then adding the traits simultaneously in a single group (Kleinbaum et al. 1998). For the trait "standing crop", monoculture abundance and the species' trait are the same, and thus I included this variable only once in the analysis. For light captured throughout the canopy, both with and without the effect of standing dead litter, the light model incorporates traits of both species, and therefore only light captured by the species in question is incorporated in the regression. Multiple regression was conducted using JMP (version 5.01, SAS Institute, Cary, N.C.). All variables were log- or logit-transformed to meet the assumptions of normality and homoscedasticity.

3.4. Results

3.4.1. Effects of herbivory treatments on leaf-area damage to loosestrife

Insect herbivores caused increasing leaf-area damage to loosestrife with increasing abundance (Table 2, Figure 6). Suppression of insect herbivores with insecticide reduced leaf-area damage (averaged over the three years) from 10% under ambient herbivory to 3% (t=-6.26, p<0.0001, Table 2, Figure 6). Manual removal ((-)Beetles) of *Galerucella* reduced leaf-area damage relative to manual addition ((-)Beetles) of *Galerucella* (8% vs. 12%, t=-2.15, p=0.035, Table 2, Figure 6), but not relative to Ambient herbivory (10%). Leaf-area damage to loosestrife also varied yearly among herbivory treatments (Table 2, Figure 6), and was higher overall in monoculture than in mixture (8.6% and 6.1%, respectively, Table 2). Because leaf area-damage to loosestrife varied considerably within herbivory treatments (Figure 6), I included both herbivory treatment and leaf-area damage in further analyses.

3.4.2. Effects of treatments and loosestrife leaf-area damage on traits in the absence of inter-specific interactions.

Survival at low light: results from the response to low resource availability experiment

Cattail had significantly lower survival at low light than undamaged loosestrife ($F_{1,127}$=6.28, p=0.0135), but when loosestrife was mechanically damaged, this difference disappeared (cattail vs. loosestrife with 25% damage, $F_{1,124}$=0.00, p=0.95; cattail vs. loosestrife with 50% damage, $F_{1,124}$=0.32, p=0.57; Table 3, Figure 7). Mechanical damage caused a significant decline in loosestrife survival (Table 3). Survival never varied with fertility (Table 3).

Standing crop: results from the monoculture mesocosms

Cattail standing crop increased strongly in the insecticide treatment relative to the ambient herbivory treatment, and more so at high fertility than at low fertility (Table 4, Figure 8). Neither fertility, leaf-area damage, nor *Galerucella* abundance (i.e., herbivory treatment) significantly altered loosestrife standing crop in monoculture (Table 4, Figure 8).

The statistical significance of the results for loosestrife should be interpreted cautiously, because leaf-area damage is correlated with herbivory treatment (Table 2, Figure 6). The variance inflation factor for leaf-area damage was low, demonstrating that collinearity between leaf-area damage and the other factors in the model (fertility and herbivory treatments) was weak, and therefore did not limit the accuracy of the estimates obtained (Kleinbaum et al. 1998). Nonetheless, type III sums of squares test the significance of an effect while holding other factors constant. Thus, significant effects of leaf-area damage indicate an effect over and above that of the herbivory treatments. However, my goal here is not to test hypotheses, but rather to obtain least squares estimates of species' abundance and traits in monoculture. This cautionary note should be considered when interpreting treatment effects on other loosestrife traits as well.

Species height: results from the monoculture mesocosms

Increasing fertility increased the height of loosestrife, whereas neither herbivory treatment nor damage significantly altered loosestrife height (Table 5, Figure 9). Excluding insect herbivores significantly increased cattail height, particularly at high fertility (Table 5, Figure 9).

Resource reduction I – light at the soil surface: results from the monoculture mesocosms

Leaf-area damage to loosestrife increased light availability at the soil surface (Table 6, Figure 10). In contrast, increasing herbivore abundance did not increase light availability at the soil surface beyond the effects of leaf-area damage, nor did increasing fertility decrease light availability at the soil surface (Table 6, Figure 10). In cattail monocultures, neither increasing fertility nor insect suppression reduced light availability at the soil surface (Table 6, Figure 10).

Resource reduction II – light availability throughout the canopy during the growing season: results from the monoculture mesocosms

With insect herbivores suppressed with insecticide, loosestrife generally reduced growing season light availability to lower levels than cattail in the lower canopy, while cattail reduced growing season light to lower levels in the upper canopy (Figure 5, Table 7). In the presence of insect herbivores, leaf-area damage to loosestrife consistently increased light availability during the growing season, however the effect of leaf-area damage on light availability was generally greater at high fertility (i.e., either damage alone or the damage by height interaction was significant, Table 7, Figure 11). At high fertility (Figure 11A), loosestrife cast deeper shade than cattail throughout the canopy when damage was minimal; when damage was severe, cattail cast deeper shade in the upper canopy. At low fertility (Figure 11A), loosestrife cast nearly as much shade as cattail in the upper canopy, even at the highest level of damage.

When insect herbivores of both species were suppressed with insecticide, the standard light model predicted that, at both high and low fertility, loosestrife captures more light (R) when shaded by cattail than when shaded by conspecifics (Figure 12). In contrast, cattail was predicted to capture less light when shaded by loosestrife than when shaded by conspecifics (Figure 12).

In the presence of insect herbivores of both species (pooled across the (-)Beetles, Ambient herbivory, and (+)Beetles treatments), the standard light model predicted that, at high fertility, the light captured by loosestrife (R) when shaded by cattail would decline sharply with increasing leaf-area damage to loosestrife, and that the light captured by cattail would increase sharply with damage to loosestrife (Figure 13). At low fertility, the effects of leaf-area damage were far weaker than at high fertility (Figure 13). If loosestrife and cattail interacted only through their effects on the light environment, the standard light model predicted that loosestrife would dominate and eventually exclude cattail at high fertility when damage is less than ~30% (Figure 13). At low fertility the model predicted that loosestrife would exclude cattail even at 50% damage (Figure 13).

Resource reduction III – the effects of standing dead litter on light availability throughout the canopy: results from the monoculture mesocosms

In the spring, before loosestrife and cattail emerged from the soil, and thus light was controlled only by standing dead litter, the effects of species on light availability were generally reversed, with cattail reducing light to lower levels near the soil surface (Figure 5, Figure 14).

When this standing dead litter was assumed by the light model to be non-photosynthetic, the relative light captured by cattail when shaded by conspecifics (*R*) changes strongly. When insect herbivores are suppressed, cattail was predicted to capture slightly more light when shaded by loosestrife than when self-shaded, at both high and low fertility (*R*>100%, Figure 15, compare with Figure 12). Thus, the light model predicted that individuals of both species will capture more light when shaded by the other species, and thus that they would coexist. In the presence of insect herbivores, cattail was predicted to capture more light when shaded by loosestrife (the curve moves upward), and thus only ~15% damage to loosestrife was required to prevent eventual competitive exclusion (Figure 16A, compare with Figure 13A). At low fertility, the model predicted that cattail and loosestrife would coexist when damage to loosestrife was above 30% (Figure 16B, compare with Figure 13B). In contrast, altering this assumption had little effect on light captured by loosestrife, at either high or low fertility (Figure 15, Figure 16).

3.4.3. Competitive outcomes

Does competition happen?

Overall, competitive effects were not strong: loosestrife abundance was reduced 26% in mixture relative to monoculture (*RR* = abundance in mixture / abundance in monoculture =0.74, upper 95% ci=0.88), while cattail abundance was not different between monoculture and mixture

(*RR*=0.97, lower 95% ci=0.82, upper 95% ci=1.14; Figure 17). Competition reduced the abundance of loosestrife more than the abundance of cattail (26 vs. 3%, respectively, t=-2.25, p=0.0269, Table 8, Figure 8, Figure 17). Note that analysis of covariance demonstrated that the effect of percent leaf-area damage to loosestrife on *RR* did not vary significantly among treatment combinations, nor did percent leaf-area damage have a significant overall effect on *RR*. Therefore, percent leaf-area damage was removed from the analysis, and treatment effects on *RR* were quantified with analysis of variance (Littell et al. 1996). Thus, damage did not have an additional effect on competitive outcomes (*RR*) beyond the effect of the herbivory treatments.

Can herbivores alter the outcome of competition?

Herbivores did alter the outcome of competition (significant species by herbivory interaction, Table 8). Specifically, at high fertility, cattail abundance in mixture relative to monoculture (*RR*) decreased when all insect herbivores were suppressed with insecticide (insecticide treatment vs. (-)Beetles, Ambient herbivory and (+)Beetles pooled, $F_{1,80}$=26.73, p<0.0001, Figure 17A), and increased with increasing beetle abundance when cattail experienced ambient herbivory (i.e., cattail abundance (*RR*) was higher in the (+)Beetles treatment relative to the (-)Beetles treatment t=-2.9, p=0.0048, Figure 17A). Indeed, with insect herbivores suppressed, cattail abundance in mixture was reduced by 70% relative to monoculture abundance (Figure 17). In contrast, in the (+)Beetles treatment, cattail was facilitated by loosestrife, as its abundance was 110% higher than in monoculture (Figure 17A).

However, at low fertility, neither suppression of all insects nor beetle abundance affected cattail performance in mixture (Figure 17B). Furthermore, neither suppression of all insects nor beetle abundance altered loosestrife performance in mixture (*RR*) at either high or low fertility

(Figure 17A, B). The presence of cattail significantly decreased loosestrife abundance (*RR*<1) only at low fertility and only in the Ambient herbivory and (+)Beetles treatments (Figure 17A, B). Cattail abundance was never significantly reduced (or increased) by the presence of loosestrife at low fertility (Figure 17B).

Do traits predict of competitive outcomes?

Each of the three models of plant competition suggest specific traits predict competitive outcomes. Of the six traits considered, three (survival at low light availability, height, and light at the soil surface) explained significant variation in loosestrife abundance in mixture, above and beyond that explained by monoculture abundance (Table 9). No traits explained significant variation in cattail abundance in mixture (Table 10).

Height in monoculture was the best predictor of loosestrife abundance in mixture (adjusted r^2=0.42, Table 9). As predicted by the *plant size* model (Miller and Werner 1987, Gaudet and Keddy 1988, Keddy and Shipley 1989), loosestrife abundance in mixture was positively associated with loosestrife height (scaled estimate=0.33, Table 9). In contrast, the estimated effect of cattail height on loosestrife abundance was small (scaled estimate=0.01, Table 9). Light availability at the soil surface also significantly predicted loosestrife abundance (adjusted r^2=0.36, Table 9). However, loosestrife abundance was positively associated with light availability at the soil surface in loosestrife monocultures (scaled estimate=0.20, Table 9), and negatively associated with light availability at the soil surface in cattail monocultures (scaled estimate=-0.23, Table 9), which is the exact opposite of the predictions of the *resource reduction* model (Tilman 1982). Survival at low light availability was the third best predictor of loosestrife abundance in mixture (adjusted r^2=0.35, Table 9). As predicted by the *response to low resource* *availability* model (Goldberg 1996), loosestrife abundance in mixture was positively associated with loosestrife survival at low light availability (scaled estimate=0.10, Table 9), and negatively associated with cattail survival at low light availability (scaled estimate=-0.12, Table 9).

3.5. Discussion

3.5.1. Does competition happen?

To my surprise, cattail abundance, on average, was not lower in mixture relative to monoculture, demonstrating no overall effect of competition on cattail (Table 8, Figure 17). In contrast, loosestrife abundance, on average, was 26% lower in mixture relative to monoculture, demonstrating that competition was negatively affecting loosestrife (Table 8, Figure 17). These results are surprising considering the large swaths of natural marsh once occupied by native species such as cattail that are now dominated by loosestrife (Thompson et al. 1987, Malecki et al. 1993, Blossey et al. 2001b).

3.5.2. Can herbivory alter the outcome of competition?

Herbivory did alter the outcome of competition, but only for cattail at high fertility. The effect of cattail on loosestrife abundance (*RR*) never varied with herbivory, nor did the effects of loosestrife on cattail vary with herbivory at low fertility (Table 8, Figure 17).

The effects of inter-specific interactions on cattail abundance at high fertility were complex, shifting from strongly competitive when all insect herbivores were suppressed, to strongly facilitative when herbivores were present (Figure 17A). In monoculture, cattail abundance was sharply reduced by ambient herbivores, (Figure 8C, D, Table 4). Thus, it appears that the facilitation of cattail by loosestrife was due to a reduced impact of natural enemies on cattail. The mechanism of facilitation may be density-dependent predation on cattail by larvae of the noctuid moth *Bellura obliqua* (D. Bunker, pers. obs.). However, resource competition may also have occurred, as cattail abundance did increase with *Galerucella* abundance (Figure 17A). *Galerucella* are unlikely to be benefiting cattail directly, but rather may be benefiting cattail by limiting the resource competitive ability of loosestrife. Note however that *Galerucella* may benefit cattail via indirect effects mediated through higher trophic levels (e.g., Stiling et al. 2003).

In contrast to the effects of inter-specific interaction on cattail, loosestrife abundance is never significantly reduced by cattail at high fertility (i.e., loosestrife's *RR* is never significantly below 1, Figure 17A). At low fertility, the results appear to be much simpler. Cattail abundance is neither reduced nor increased through association with loosestrife (Figure 17B). While this demonstrates no net effect of loosestrife on cattail, there may still be both a competitive effect and a facilitative effect of loosestrife on cattail, if these forces balance each other. Loosestrife is only affected by competition with cattail in the Ambient herbivory and (+)Beetles treatments ($RR<1$), yet *RR* does not differ significantly among herbivory treatments. To summarize the results at low fertility, herbivores have no net effect on the outcome of inter-specific interactions for either species (Figure 17).

3.5.3. Which competition models, and associated traits, best predict competitive outcomes and invasion success?

Three traits (response to low light availability, height, and total effect on light) significantly predicted the abundance of loosestrife in mixture, with loosestrife abundance in monoculture as a covariate (Table 9). The model that included species height in monoculture explained the most variation (adj. r^2=0.42, Table 9). No trait contributed significantly towards predicting the abundance of cattail in mixture, with cattail abundance in monoculture as a covariate (Table 10). This contrast is not surprising. Overall, competition was occurring for loosestrife (mean *RR*=74%, upper 95% ci=88%, Figure 17), and thus traits related to competitive ability should predict the effect of competition. In contrast, there was no net effect of inter-specific interactions on cattail (*RR*=97%, lower 95% ci=82%, upper 95% ci=114%; Figure 17). Thus, competition for resources is not the primary force controlling the abundance of cattail. Rather, it appears that cattail's own natural enemies have a strong effect on cattail abundance, as can be seen by the strong decrease in cattail abundance in monoculture when insect herbivores are not suppressed with insecticide (Figure 8C, D). Thus, it is not surprising that traits related to competitive ability for light do not predict the combined effects of competition and facilitation on cattail.

The response to low resource availability model

For loosestrife, my results agree well with the *response to low resource availability* model (Goldberg 1996), as juvenile survival under resource-limited conditions was indeed a good predictor of competitive outcomes (Table 9). As predicted, loosestrife abundance in mixture was positively associated with loosestrife survival at low light and negatively associated with cattail survival at low light (Table 9). While loosestrife must establish from seed to invade the cattail portion of the mixtures, cattail may spread vegetatively. Because loosestrife abundance was negatively associated with cattail survival, seedling survival at low light may be a good predictor of competitive outcomes, even among clonal perennials. Indeed, these results agree well with those of Howard and Goldberg (2001), who found that, among eight old-field *perennials*, the germination, growth and survival of seedlings were better predictors of natural abundance than the growth and survival of adults.

The plant size model

For loosestrife, my results also provide strong support for the *plant size* model (Miller and Werner 1987, Gaudet and Keddy 1988, Keddy and Shipley 1989), as species height was the best predictor of loosestrife abundance in mixture (Table 9). These results compare well with those of Keddy and Shipley (1989), who found that the relative difference in plant height explained 37% of the variation in competitive outcomes and those of Gaudet and Keddy (1988), who found that height explained 64% of the variation in competitive outcomes. In my experiment, height explained 37% of the residual variation (the variation not explained by monoculture abundance). This result is impressive considering the fact that height varied only 0.3 orders of magnitude in my experiment compared to 2.9 and 1.8 orders of magnitude in the Keddy and Shipley (1989) and Gaudet and Keddy (1988) experiments, respectively. However, in contrast to the results of Gaudet and Keddy (1988), who found that competitive outcomes were even more strongly correlated with plant biomass (r^2=0.81) than with plant height, I found that standing crop (biomass) was not a good predictor of competitive outcomes for loosestrife (Table 9).

The resource reduction model

Although light availability at the soil surface was a good predictor of competitive outcomes, its effects on competitive outcomes were the opposite of those predicted by theory: loosestrife abundance in mixture was positively associated with light availability at the soil surface in loosestrife monocultures and negatively associated with light availability at the soil surface in cattail monocultures (Table 9). This paradoxical relationship may possibly be due to two features of the effect on light availability by loosestrife and cattail. First, at low fertility, loosestrife allowed *more* light to reach the soil surface when insects were suppressed than when *Galerucella* were present (Figure 10B). *Galerucella* often damage the apical meristem of loosestrife, causing loosestrife to lose apical dominance and develop a shorter, shrubbier stature, as a result reduce light to lower levels deep in the canopy (D. Bunker, pers. obs.). Second, cattail most effectively reduced light at the soil surface at high fertility and when herbivores were suppressed (Figure 10B). Thus, these traits predict that loosestrife will not perform particularly well when insects were suppressed, yet loosestrife abundance was somewhat less affected by cattail in these treatments (Figure 17).

Neither the standard model of competition for light throughout the canopy, nor the light model refined to account for the lack of photosynthesis by standing dead litter, explained a significant amount of variation in loosestrife abundance in mixture (Table 9). To my knowledge only one other study has experimentally tested the resource reduction model among species competing for light (Seabloom et al. 2003). Seabloom et al. (2003) found that even though native California perennial grasses reduced light, nitrogen, and water availability more than their exotic annual competitors, they were still less abundant in natural communities, due to strong recruitment limitation. When this recruitment limitation was experimentally overcome, the native species strongly reduced exotic abundance.

3.5.4. Can traits predict invasions and the success of biological control?

These results suggest that plant traits, and height in particular, may make good predictions of competitive outcomes when species interact primarily through mutually limiting resources, as appeared to be the case for loosestirfe (Tilman 1982, Miller and Werner 1987, Gaudet and Keddy 1988, Keddy and Shipley 1989, Goldberg 1990, Goldberg 1996). In addition, height predicted competitive outcomes for loosestrife in the face of substantial herbivory. This suggests that the effect of herbivores on competitive ability is mediated, at least in part, via plant traits, and therefore that the effects of herbivores on competitive outcomes can be predicted by their effects on plant traits. Thus, traits related to competitive ability may well predict invasion success and the success of biological control in communities structured primarily by competition for resources.

However, when plant species traits, or the effects of herbivores on those traits, vary with plant species density, then measurements of traits in monoculture may fail to make accurate predictions. The accuracy of these predictions may be improved by accounting for the functional or numerical response of herbivores to host plant density or host plant quality (Holt et al. 1994, Grover 1995, see Bolker et al. 2003, for review). Alternatively, the problem of density dependence can be avoided by directly measuring and/or manipulating herbivore load, and then comparing this gradient to naturally occurring herbivore loads. Indeed, this is the approach I used by manipulating *Galerucella* and measuring leaf-area damage directly, and this may account for the difference in the ability of traits to predict outcomes for loosestrife and cattail.

3.5.5. Implications for the effect of insect herbivores on long-term competitive outcomes between loosestrife and cattail

My results suggest that loosestrife and cattail may coexist in these experimental mesocosms when insect herbivores are present. If so, it appears that loosestrife will continue to dominate, as loosestrife standing crop is twice that of cattail in mixture, even when the abundance of *Galerucella* was greatest (i.e., in the (+)Beetles treatment, Figure 8). It is important to note that my observed results may be transient, even after three full seasons of competition and herbivory: cattail may find a temporary respite from its natural enemies by associating with loosestrife, yet loosestrife may eventually drive cattail to exclusion. On the other hand, the competitive ability of cattail may increase as it continues to escape its natural enemies. Only competitive exclusion (or perhaps long-term coexistence) will provide a definitive answer. For this reason I will continue to monitor this experiment for at least one additional season.

In natural marshes, my results may be applicable to the extent that environmental and biological conditions resemble the natural marshes where loosestrife and cattail co-occur. The critical environmental factor that defines these marshes (in addition to flooding regime) is nitrogen availability (Day et al. 1988, Morris 1991, Bedford et al. 1999). These marshes tend to have high rates of nitrogen mineralization and assimilation (Morris 1991), and thus may be more similar to my high fertility mesocosms, where I added 16 g N m^2 y^{-1}. The critical biological factor is herbivore abundance, for both cattail and loosestrife. In the absence of *Galerucella*, loosestrife experiences very low levels of herbivore damage (Malecki et al. 1993, Blossey and Notzold 1995, D. Bunker, pers. obs.). Where *Galerucella* has been released, herbivore damage varies widely, from no damage to complete defoliation (Dech and Nosko 2002, Landis et al.

2003, Brinker, Bunker and Carson, unpublished data). Few published data exist on insect herbivore load on cattail in the wild. Penko and Pratt (1987) found that 15% of cattail stems showed insect damage in nineteen cattail stands in Minnesota. This rate of attack is far lower than the ~80% of stems damaged by insects in my mesocosms with ambient herbivory (D. Bunker, pers.obs.).

My results at high fertility with insects suppressed may reasonably reflect natural dynamics in the absence of *Galerucella*. Here, where insect attack on cattail was suppressed below levels seen in nature, loosestrife still sharply reduced cattail abundance (Figure 8, Figure 17), as it also does in natural marshes in the absence of *Galerucella* (Thompson et al. 1987, Blossey et al. 2001b). In contrast, none of my treatments accurately reflect both the natural insect herbivore load on cattail and *Galerucella* abundance, as cattail rarely experiences insect attack at the high rates found in my mesocosms.

3.5.6. Implications for the effects of herbivory on plant community structure

My results demonstrate that insect herbivores can have strong effects on plant community structure. The Host Concentration Model (*sensu* Carson et al. 2004) argues that herbivores will have the greatest effects on plant community structure when hosts are aggregated in dense patches, because herbivores will locate dense host populations more easily, reproduce at higher rates within dense patches of hosts, and/or be less likely to leave dense patches of hosts (Janzen 1970, Connell 1971, Root 1973, Letourneau 1986, Carson and Root 2000, Hamback et al. 2000, Klironomos 2002, Stiling et al. 2003, Carson et al. 2004). My results support this model, as cattail appears to be escaping from its natural enemies by associating with loosestrife (Figure 17).

3.5.7. Conclusions

Predicting the abundance and distribution of species has been a long-standing goal of community ecology (Harper 1977, Morin 1999). Species interactions such as competition, facilitation and herbivory are often considered critical factors influencing the realized abundance of species within a given community. However, because the number of pair-wise interactions between species in a community increases exponentially, predictions based on all pair-wise interactions are often not feasible. This has led to many attempts to identify traits that may predict competitive outcomes (Tilman 1982, Miller and Werner 1987, Gaudet and Keddy 1988, Keddy and Shipley 1989, Goldberg 1990, Goldberg and Landa 1991, Tilman and Wedin 1991, Wedin and Tilman 1993, Goldberg 1996, Howard and Goldberg 2001).

Here, I have built upon and extended this body of work in several important ways. First, I have simultaneously compared the predictive power of the specific traits implicated by three prominent models of the mechanisms of plant competition. These include the *response to low resource availability* model (Goldberg 1996), the *plant size* model (Miller and Werner 1987, Gaudet and Keddy 1988, Keddy and Shipley 1989), and the *resource reduction* model (Tilman 1982). Second, I have extended the *resource reduction* model to better describe competition for light by both incorporating the effect of species on light availability throughout the canopy, as well as quantifying the role of standing dead litter in species' effect on, and response to, light availability. Third, I extended this trait-based approach to include trophic complexity by experimentally testing the ability of traits to predict the effects of herbivores on competitive outcomes between their plant hosts. In particular, the incorporation of trophic complexity is essential if we are to make accurate predictions of the abundance and distribution of plant species in natural communities.

My results show that, for cattail, insect herbivory fundamentally altered the outcome of competition from strongly competitive in its absence to strongly facilitative in its presence. When interactions between plants were competitive, as was the case for loosestrife, the plant traits implicated by the plant size and response to low resource availability models were good predictors of competitive outcomes, while the resource reduction model was a poor predictor of competitive outcomes. However, when inter-specific interactions were not generally competitive, as was the case with cattail, traits related to competitive ability were not good predictors of the effects of inter-specific interactions.

The predictive power of traits measured in the absence of inter-specific interactions may be limited in a number of ways. Most importantly, traits, in the broadest sense, must be predictable from observations in the absence of inter-specific interactions. For instance, plasticity of plant traits must be either minimal or predictable (Callaway et al. 2003). The traits of herbivores must also be predictable, in that the functional and numerical responses of the herbivores to their hosts must either be controlled or directly incorporated into a predictive model (Janzen 1970, Connell 1971, Root 1973, Letourneau 1986, Grover 1994, Holt et al. 1994, Grover 1995, Carson and Root 2000, Hamback et al. 2000, Klironomos 2002, Stiling et al. 2003, Carson et al. 2004). For traits to predict effects of facilitation, traits that confer facilitative effects or responses must also be considered (e.g., Callaway et al. 1991, Callaway 1994).

While these limitations certainly pose a challenge to predictive ecology, we do have the tools and theory to overcome this challenge (see Bolker et al. 2003, for reviews, Berlow et al. 2004). While I have met these challenges with respect to the effects of herbivory on loosestrife, the facilitative effects of loosestrife on cattail remain enigmatic. To further address the multi-faceted interactions between loosestrife, cattail, and their respective herbivore communities, my future research will attempt to identify the specific mechanisms of facilitation of cattail by loosestrife.

Table 1. Experimental design and treatment combinations for the *mesocosm experiment*.

		Insects suppressed		(-) Beetles		Ambient herbivory		(+) Beetles	
		Fertility							
Culture	Species	Low	High	Low	High	Low	High	Low	High
Monoculture	Loosestrife	6	6	6	6	6	6	6	6
	Cattail	6	6	na	na	6	6	na	na
Mixture	Both	6	6	6	6	6	6	6	6

Notes: Insects were suppressed with weekly applications of insecticide. Adult *Galerucella* were manually removed from the (-)Beetles treatment and transplanted into the (+)Beetles treatment. Neither *Galerucella* nor other insects were manipulated in the Ambient herbivory treatment. *Galerucella* do not feed on cattail, and thus the (-)Beetles and (+)Beetles treatments were not applied to cattail monocultures. na=not applicable. Table values indicate number of replicates.

Table 2. ANOVA results for the effect of year, culture (mixture vs. monoculture), fertility, and herbivory treatments on loosestrife leaf-area damage in the *mesocosm experiment*.

Source	NDF	DDF	Type III F	P<F
Culture	1	75	7.31	**0.0085**
Fertility	1	75	0.41	0.5238
C*F	1	75	0.18	0.6708
Herbivory	3	75	20.12	**0.0001**
C*H	3	75	0.97	0.4122
F*H	3	75	1.47	0.2289
C*F*H	3	75	1.96	0.1271
Year	2	160	81.31	**0.0001**
Y*C	2	160	2.39	0.0952
Y*F	2	160	0.06	0.9402
Y*C*F	2	160	1.87	0.1574
Y*H	6	160	3.21	**0.0053**
Y*C*H	6	160	0.82	0.5581
Y*F*H	6	160	0.61	0.7240
Y*C*F*H	6	160	1.30	0.2582

Notes: NDF is numerator degrees of freedom; DDF is denominator degrees of freedom.

Table 3. ANOVA results of effects of species-herbivory and fertility on survival at low light, and ANCOVA results for effects of percent leaf-area damage and fertility on loosestrife survival at low light.

Test	Source	NDF	DDF	Type III F	Pr > F
ANOVA	**S**pecies-Herbivory	3	125.9	3.29	**0.0229**
	Fertility	1	124.7	2.27	0.1347
	S*F	3	124.7	1.20	0.3124
ANCOVA	**%D**amage	1	92.8	6.9	**0.0101**
	D*F	1	89.5	0.29	0.5894
	Fertility	1	89.7	0.14	0.7099

Notes: NDF is numerator degrees of freedom; DDF is denominator degrees of freedom, which was calculated using the Satterwaithe approximation (Littell et al. 1996). Because all individuals survived at 18% light availability, light treatments with lower light availability were pooled.

Table 4. ANOVA and ANCOVA results for effects of fertility and herbivory treatments (as well as percent leaf-area damage on loosestrife) on standing crop in monoculture mesocosms.

Species	Source	df	SS	F	P
Loosestrife	%**D**amage	1	0.014	1.79	0.1912
	F*D	1	0.007	0.92	0.3457
	H*D	3	0.058	2.51	0.0773
	F*H*D	3	0.036	1.58	0.2135
	Fertility	1	0.001	0.11	0.7407
	Herbivory	3	0.062	2.72	0.0616
	F*H	3	0.026	1.13	0.3536
	Error	31	0.237		
Cattail	**F**ertility	1	0.068	2.33	0.1423
	Herbivory	1	3.271	111.68	**<.0001**
	F*H	1	0.174	5.96	**0.0241**
	Error	20	0.037		

Notes: Loosestrife and cattail were analyzed separately using ANCOVA and ANOVA, respectively. Percent damage was centered prior to analysis.

Table 5. ANOVA and ANCOVA results for effects of fertility and herbivory treatments (as well as percent leaf-area damage on loosestrife) on mean height in monoculture mesocosms.

Species	Source	df	SS	F	P
Loosestrife	%**D**amage	1	0.001	0.92	0.3440
	F*D	1	0.000	0.28	0.5999
	H*D	3	0.004	1.89	0.1516
	F*H*D	3	0.003	1.47	0.2424
	Fertility	1	0.003	4.94	**0.0336**
	Herbivory	3	0.005	2.67	0.0649
	F*H	3	0.001	0.35	0.7865
	Error	31	0.021		
Cattail	**F**ertility	1	0.001	0.66	0.4271
	Herbivory	1	0.108	58.54	**<.0001**
	F*H	1	0.010	5.43	**0.0303**
	Error	20	0.037		

Notes: Loosestrife and cattail were analyzed separately using ANCOVA and ANOVA, respectively. Percent damage was centered prior to analysis.

Table 6. ANOVA and ANCOVA results for effects of fertility and herbivory treatments (as well as percent leaf-area damage on loosestrife) on light availability at the soil surface in monoculture mesocosms.

Species	Source	df	SS	F	P
Loosestrife	%**D**amage	1	0.263	4.32	**0.0461**
	F*D	1	0.028	0.46	0.5023
	H*D	3	0.203	1.11	0.3582
	F*H*D	3	0.027	0.15	0.9304
	Fertility	1	0.040	0.66	0.4216
	Herbivory	3	0.261	1.43	0.2535
	F*H	3	0.013	0.07	0.9749
	Error	31	1.889		
Cattail	**F**ertility	1	0.119	2.39	0.138
	Herbivory	1	0.037	0.75	0.3972
	F*H	1	0.024	0.49	0.4936
	Error	20	0.994		

Notes: Loosestrife and cattail were analyzed separately using ANCOVA and ANOVA, respectively. Percent damage was centered prior to analysis.

Table 7. ANOVA and ANCOVA results for effects of species, fertility, height and 2003 loosestrife leaf-area damage on light availability in monoculture mesocosms.

Species	Herbivory treatments	Season	Fertility	Effect	NDF	DDF	F	p
Loosestrife	(-) Beetles, Ambient, and (+) Beetles, pooled	Growing	High	%**D**amage	1	15.9	1.8	0.1989
				D*H	5	80	3.0	**0.0156**
				Height	5	80	50.8	**0.0001**
		Litter	High	%**D**amage	1	13.6	0.2	0.6741
				D*H	6	96	0.3	0.9307
				Height	6	96	25.9	**0.0001**
		Growing	Low	%**D**amage	1	79.9	30.6	**0.0001**
				D*H	4	75.1	1.7	0.1553
				Height	4	75.1	357.1	**0.0001**
		Litter	Low	%**D**amage	1	15.9	38.3	**0.0001**
				D*H	5	80	7.7	**0.0001**
				Height	5	80	308.7	**0.0001**
Loosestrife	Insecticide treatment	Both	High	**H**eight	6	65	389.7	**0.0001**
				Season	1	65	312.7	**0.0001**
				S*H	6	65	80.9	**0.0001**
			Low	**H**eight	5	55	302.2	**0.0001**
				Season	1	55	59.7	**0.0001**
				S*H	5	55	31.3	**0.0001**
Cattail	Insecticide treatment	Both	High	**H**eight	6	65	432.5	**0.0001**
				Season	1	65	6.3	**0.0145**
				S*H	6	65	8.5	**0.0001**
			Low	**H**eight	5	55	253.0	**0.0001**
				Season	1	55	4.2	**0.0458**
				S*H	5	55	6.5	**0.0001**
Cattail	Ambient herbivory	Both	Both	**F**ertility	1	5	0.2	0.7183
				Season	1	110	79.3	**0.0001**
				F*S	1	110	3.9	0.0507
				Height	5	110	542.9	**0.0001**
				F*H	5	110	0.7	0.6252
				S*H	5	110	11.0	**0.0001**
				F*S*H	5	110	1.8	0.1143

Notes: Horizontal lines separate individual ANOVAs and ANCOVAs. NDF is numerator degrees of freedom; DDF is denominator degrees of freedom, calculated using the Satterwaithe approximation (Littell et al. 1996).

Table 8. ANOVA results for effects of species, fertility and herbivory treatment on response ratio (*RR*, standing crop in mixture mesocosms relative to standing crop in monoculture mesocosms).

Source	df	Type III *F*	*P*
Fertility	1	1.12	0.2923
Herbivory	3	1.89	0.1384
F*H	3	3.34	**0.0234**
Species	1	5.08	**0.0269**
F*S	1	0.97	0.3276
H*S	3	6.29	**0.0007**
F*H*S	3	1.66	0.1829

Notes: Error df=80. Note that analysis of covariance demonstrated that the effect of percent leaf-area damage to loosestrife on *RR* did not vary significantly among treatment combinations, nor did percent leaf-area damage have a significant overall effect on *RR*. Thus, percent leaf-area damage was removed from the analysis and effects on *RR* were analyzed with analysis of variance (Littell et al. 1996).

Table 9. Multiple regression results for effects of species traits and monoculture abundance on loosestrife abundance in mixture mesocosms.

Trait	Source	Scaled estimate	df	Type I SS	F	P	r^2	Adj. r^2
Survival	Monoculture abundance	0.034	1	0.222	10.1	0.003		
	Loosestrife Survival	0.101	2	0.400	9.12	**0.0005**		
	Cattail Survival	-0.115						
	Error		44	0.964				
	Whole model			0.622	9.47	**<.0001**	0.39	0.35
Standing Crop	Monoculture abundance	0.147	1	0.222	7.92	**0.007**		
	Cattail standing crop	0.067	1	0.100	3.58	0.065		
	Error		45	1.263				
	Whole model			0.323	5.75	**0.006**	0.20	0.17
Height	Monoculture abundance	-0.273	1	0.222	11.4	0.002		
	Loosestrife height	0.328	2	0.503	12.9	**<.0001**		
	Cattail height	0.013						
	Error		44	0.861				
	Whole model			0.725	12.36	**<.0001**	0.46	**0.42**
Light at the soil surface	Monoculture abundance	0.092	1	0.222	10.3	0.0002		
	Loosestrife % light	0.197	2	0.413	9.53	0.0004		
	Cattail % light	-0.226						
	Error		44	0.951				
	Whole model			0.635	9.79	**<.0001**	0.40	0.36
Standard light model	Monoculture abundance	0.113	1	0.222	7.97	0.007		
	Loosestrife ($R_{l\|c}$)	0.100	1	0.11	3.91	0.054		
	Error		45	1.25				
	Whole model			0.33	5.94	**0.0051**	0.21	0.17
Light model with effect of standing dead litter	Monoculture abundance	0.136	1	0.222	7.75	0.007		
	Loosestrife ($R_{l\|c}$)	0.080	1	0.073	2.56	0.116		
	Error		45	1.291				
	Whole model			0.300	5.16	**0.0096**	0.18	0.15

Notes: Sequential sums of squares (Type I) were used to test whether traits explained additional variation beyond that explained by monoculture abundance. Where traits of both species are included, their combined effect was tested by adding them to the model simultaneously. Scaled estimates are regression coefficients for effects re-scaled to have a mean of zero and a range of two, and represent half the predicted response change as the regression factor travels its whole range. Theory predicts that, with the exception of light at the soil surface, loosestrife traits will be positively correlated with abundance in mixture (i.e., the scaled estimate will be positive), and that cattail traits will be negatively correlated with abundance in mixture. The trait "standing crop" for loosestrife is redundant with monoculture abundance, and thus is not included. The light model incorporates light availability in monocultures of both species, and thus ($R_{c|l}$) is not included. Horizontal lines separate individual regressions.

Table 10. Multiple regression results for effects of species traits and monoculture abundance on cattail standing crop in mixture mesocosms.

Trait	Source	Scaled estimate	df	Type I SS	F	P	r^2	Adj. r^2
Survival	Monoculture abundance	0.189	1	0.747	5.37	**0.025**		
	Loosestrife Survival	-0.098	2	0.100	0.36	0.70		
	Cattail Survival	0.033						
	Error		44	6.113				
	Whole model			0.846	2.03	0.123	0.12	0.06
Standing Crop	Monoculture abundance	0.200	1	0.747	5.56	**0.023**		
	Loosestrife standing crop	-0.175	1	0.174	1.30	0.260		
	Error		45	6.038				
	Whole model			0.921	3.43	**0.041**	0.13	0.09
Height	Monoculture abundance	1.636	1	0.747	5.68	0.022		
	Loosestrife height	-0.197	2	0.431	1.64	0.21		
	Cattail height	-1.457						
	Error		44	5.782				
	Whole model			1.177	2.99	**0.041**	0.17	**0.11**
Light at the soil surface	Monoculture abundance	0.213	1	0.747	5.38	**0.025**		
	Loosestrife % light	0.044	2	0.102	0.37	0.69		
	Cattail % light	0.064						
	Error		44	6.111				
	Whole model			0.848	2.04	0.122	0.12	0.06
Standard light model	Monoculture abundance	0.175	1	0.747	5.62	0.022		
	Cattail ($R_{c\mid l}$)	0.141	1	0.239	1.80	0.19		
	Error		45	5.974				
	Whole model			0.985	3.71	0.032	0.14	0.10
Light model with effect of standing dead litter	Monoculture abundance	0.140	1	0.747	5.45	**0.024**		
	Cattail ($R_{c\mid l}$)	0.083	1	0.046	0.33	0.566		
	Error		45	6.167				
	Whole model			0.792	2.89	0.066	0.11	0.07

Notes: Sequential sums of squares (Type I) were used to test whether traits explained additional variation beyond that explained by monoculture abundance. Where traits of both species are included, their combined effect was tested by adding them to the model simultaneously. Scaled estimates are regression coefficients for effects re-scaled to have a mean of zero and a range of two, and represent half the predicted response change as the regression factor travels its whole range. Theory predicts that, with the exception of light at the soil surface, cattail traits will be positively correlated with abundance in mixture (i.e., the scaled estimate will be positive), and that loosestrife traits will be negatively correlated with abundance in mixture. The trait "standing crop" for cattail is redundant with monoculture abundance, and thus is not included.

The light model incorporates light availability in monocultures of both species, and thus ($R_{l|c}$) is not included. Horizontal lines separate individual regressions.

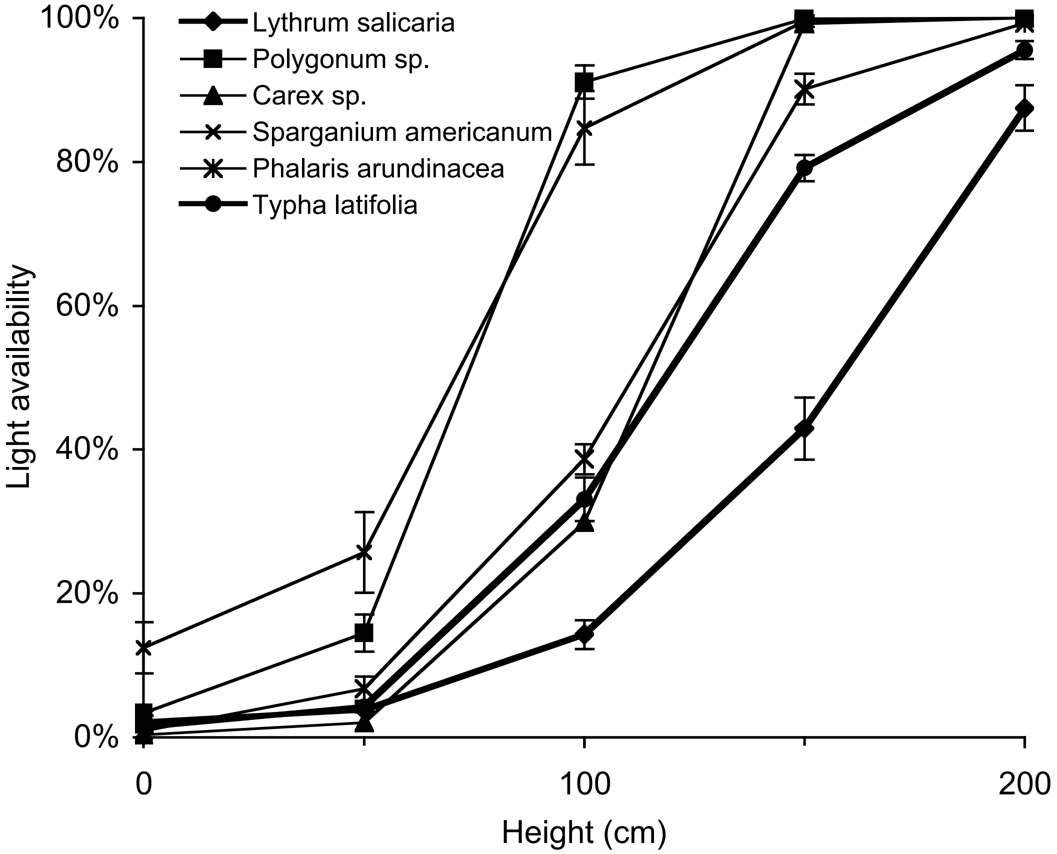
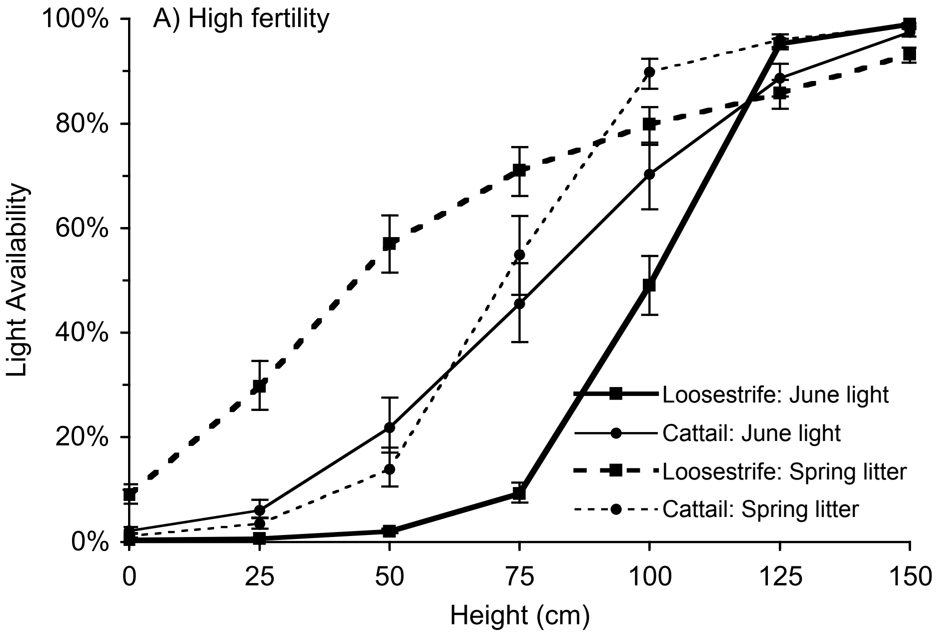


Figure 4. Light availability in natural stands of marsh dominants (mean ± se). Loosestrife (*Lythrum*) and cattail (*Typha*) reduce light to less than 3% at the soil surface and also dominate the light environment in the upper reaches of the canopy (n=32, 16, 12, 4, 4, and 32 for *Lythrum, Polygonum, Carex, Sparganium, Phalaris* and *Typha*, respectively).



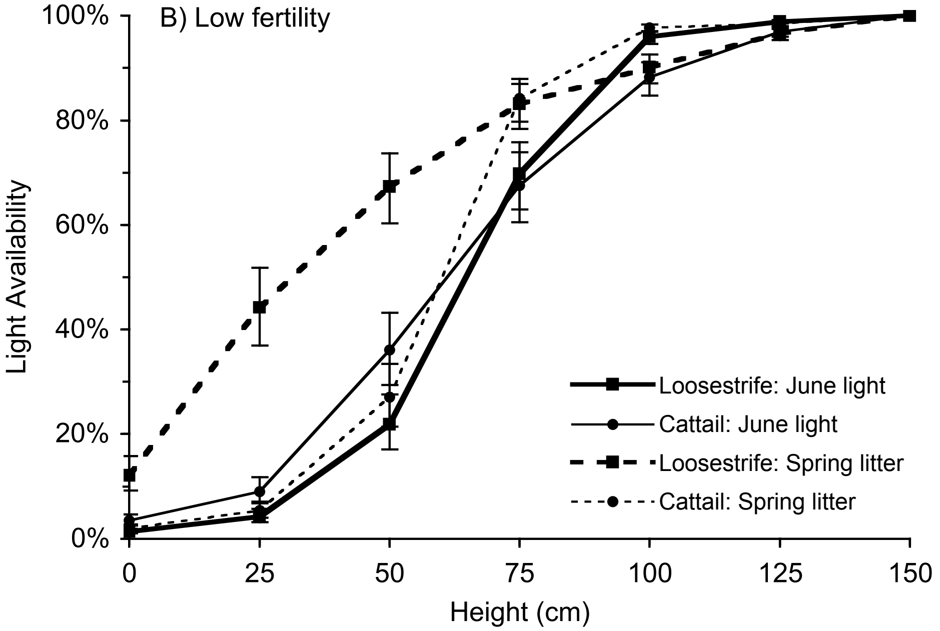


Figure 5. Light availability in cattail and loosestrife monoculture mesocosms with insects suppressed with insecticide (lsmean ± 1 se, n=6), at A) high and B) low fertility. During the growing season (June), cattail reduces light to lower level than loosestrife in the upper canopy, while loosestrife reduces light to lower levels in the lower canopy. In the spring, when light availability is affected only by standing dead litter, this pattern is reversed, because cattail has dense litter below ~75 cm, while loosestrife has thin, yet relatively tall litter.

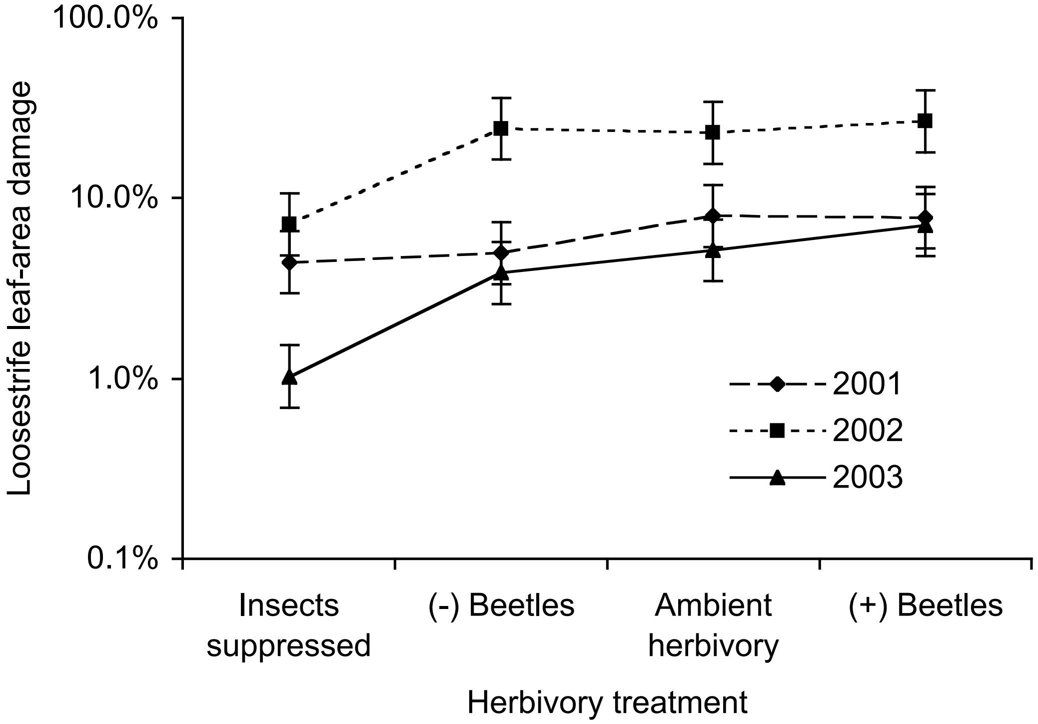


Figure 6. Effects of herbivory treatment and year on leaf-area damage (mean ± 95% ci, n=12). Insects were suppressed with weekly applications of insecticide during the growing season. During the egg laying period, *Galerucella* adults were manually removed from the (-)Beetles treatment and transplanted into the (+)Beetles treatment. The Ambient herbivory treatment was not manipulated. Insects of any species were allowed to colonize the four treatments. Insecticide reduced leaf-area damage to loosestrife relative to the other three treatments ($F_{1,75}$=55.68, p<0.0001). The hand removal and addition of beetles significantly affected leaf area damage: loosestrife in the (+)Beetles treatment experienced greater leaf-area damage than in the (-)Beetles treatment (t=-2.15, p=0.035).

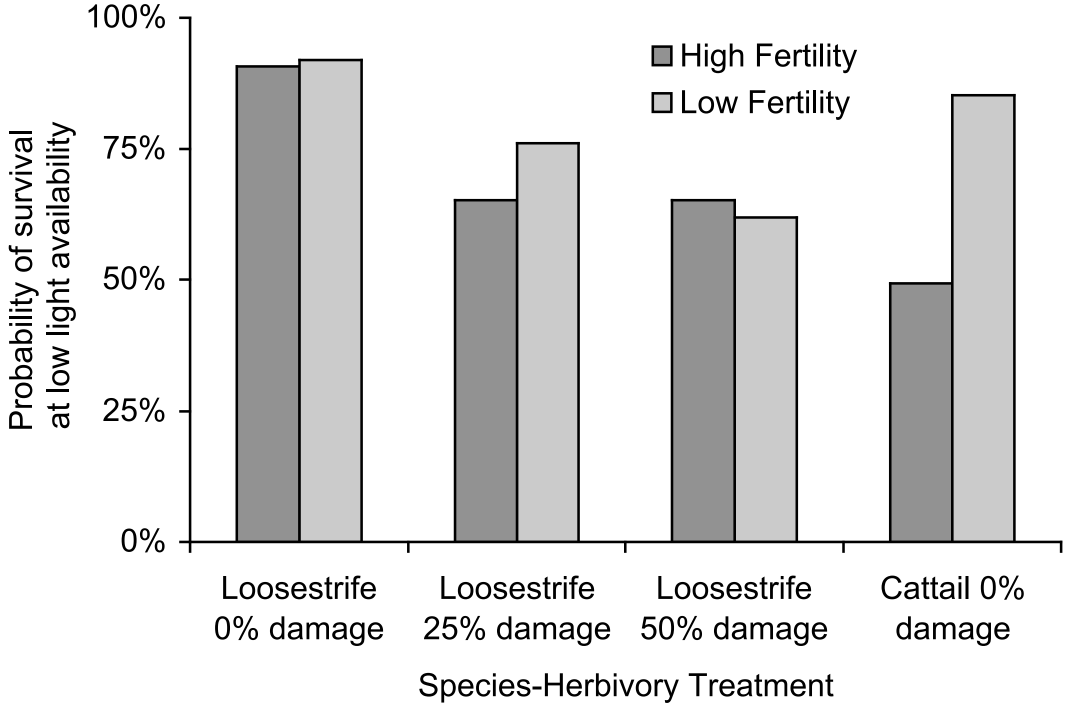


Figure 7. Survival probability of seedlings at low light availability as a function of species – herbivory treatment and fertility. Herbivory on loosestrife was simulated by mechanically removing 0, 25 or 50% of each leaf. Individuals were grown in pots under seven levels of light availability. Survival was significantly affected only by species-herbivory treatment ($F_{1,126}$=3.29, p=0.0229). Cattail had lower survival than undamaged loosestrife ($F_{1,127}$=6.28, p=0.0135), but survival did not significantly differ between cattail and loosestrife with either 25 ($F_{1,124}$=0.00, p=0.95) or 50% ($F_{1,124}$=0.32, p=0.57) leaf-area damage. Survival did not vary with fertility.

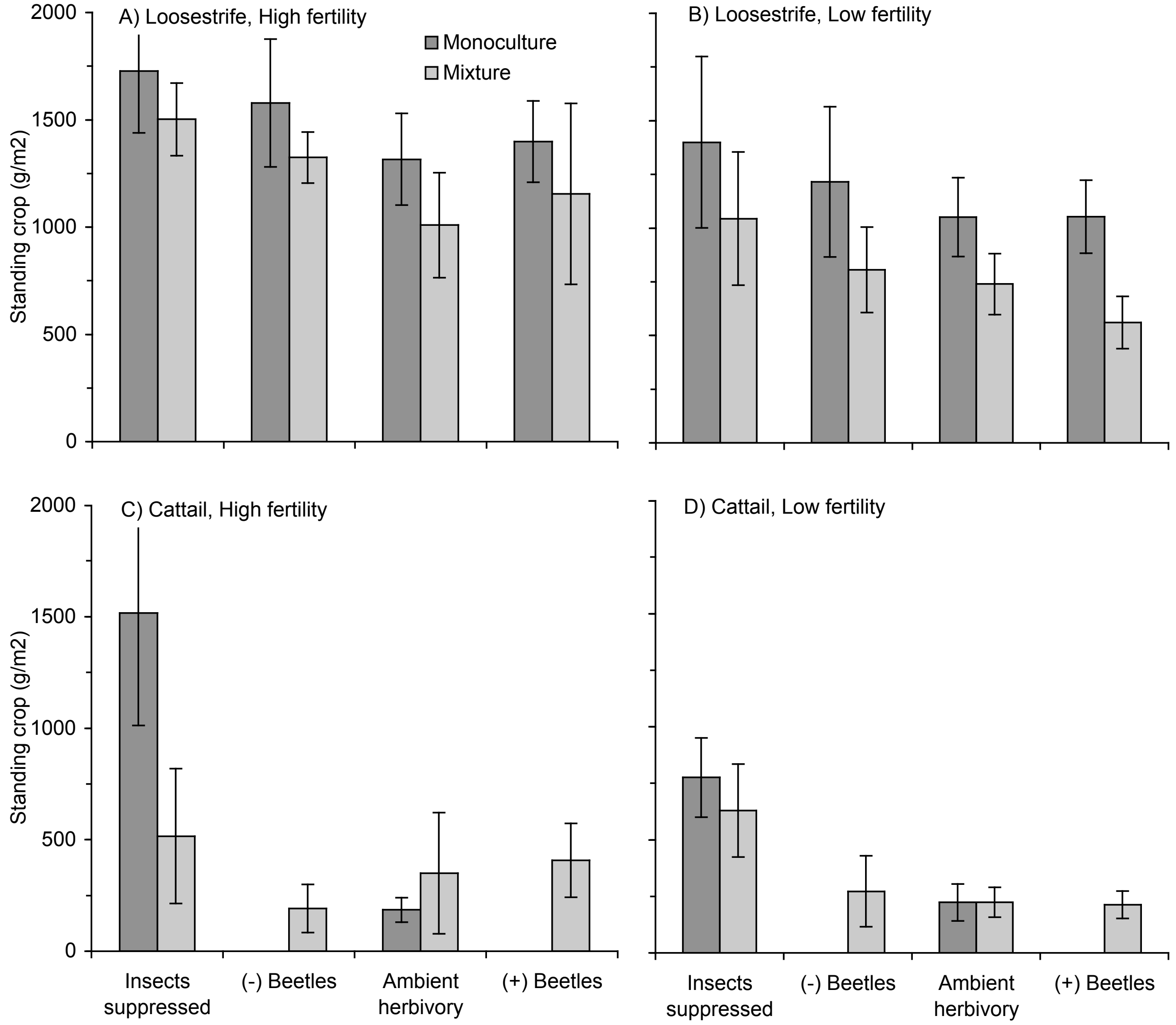


Figure 8. Standing crop (mean ± 95% ci, n=6) of loosestrife (A, B) and cattail (C, D) in monoculture and mixture mesocosms at high (A, C) and low (B, D) fertility. Insects of any species were allowed to colonize the hand manipulated treatments ((-)Beetles, Ambient herbivory and (+)Beetles). *Galerucella* were manually removed from the (-)Beetles treatment and added to the (+)Beetles treatment. Note that *Galerucella* do not feed on cattail, and thus the (-)Beetles and (+)Beetles treatments were not applied to cattail monocultures. Insect herbivory dramatically reduced cattail biomass in monoculture (C, D; compare insecticide treated vs. ambient).

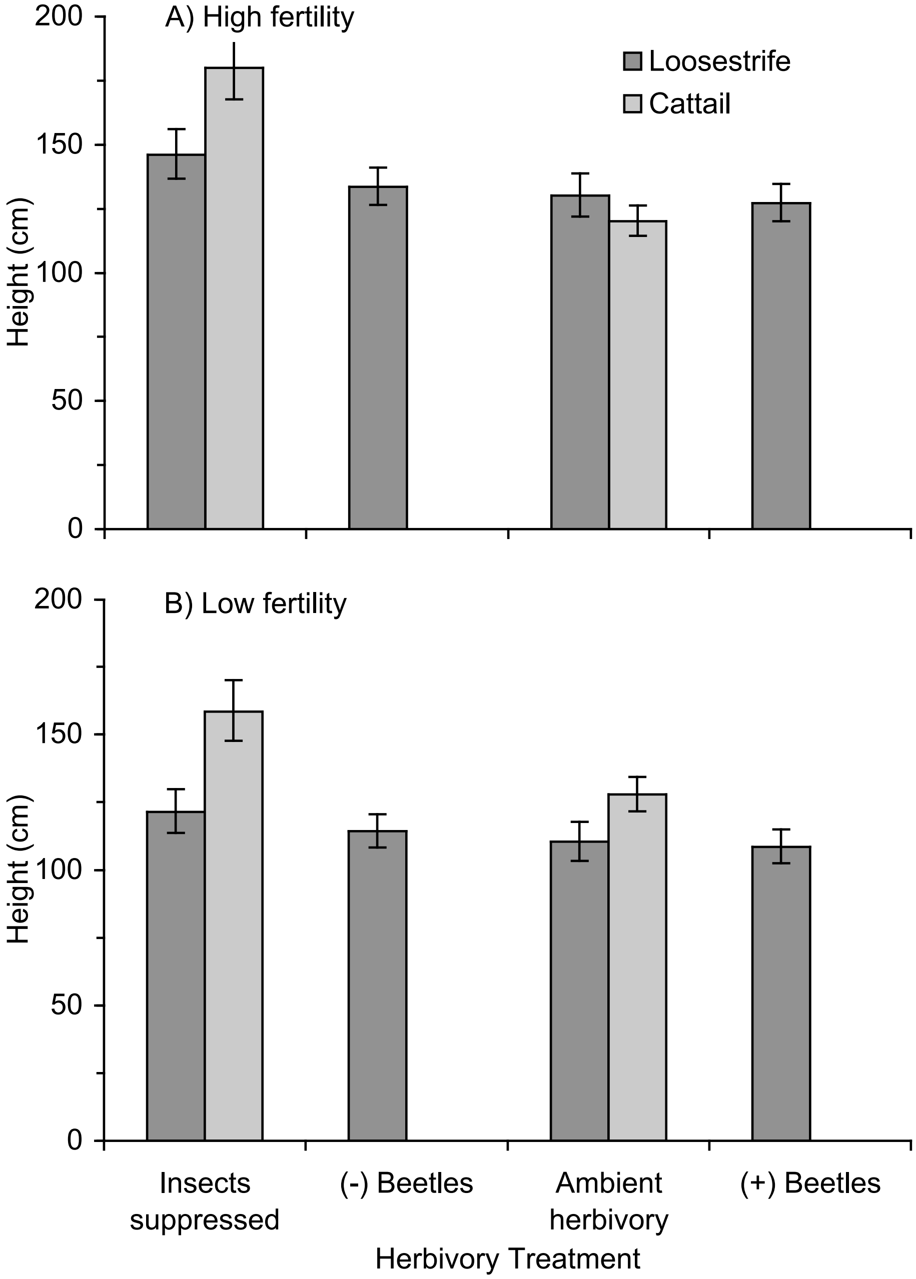


Figure 9. Species height in monoculture mesocosms (mean ± 95% ci) as a function of insect abundance at high (A) and low (B) fertility. Insect herbivores did not significantly decrease the height of loosestrife ($F_{1,31}$=2.67, p=0.06), but loosestrife height did increase significantly with fertility ($F_{1,31}$=4.94, p=0.34). Insect herbivores significantly decreased the height of cattail at high and low fertility, but had a greater impact at high fertility (significant herbivory by fertility interaction, $F_{1,20}$=5.43, p=0.03). Insects of any species were allowed to colonize the hand manipulated treatments ((-)Beetles, Ambient herbivory and (+)Beetles). *Galerucella* were manually removed from the (-)Beetles treatment and added to the (+)Beetles treatment. Note that *Galerucella* do not feed on cattail, and thus the (-)Beetles and (+)Beetles treatments were not applied to cattail monocultures.

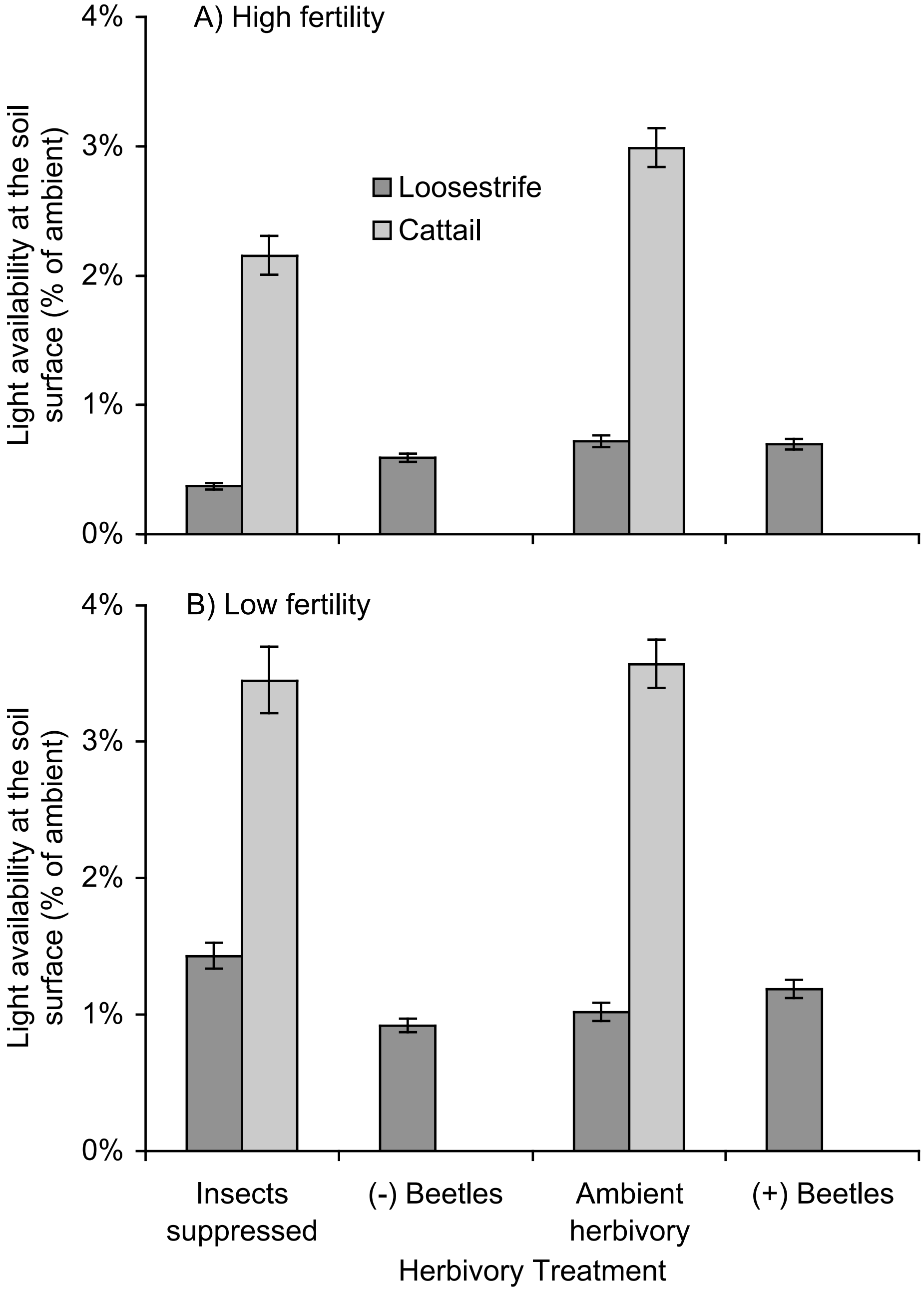


Figure 10. Light at the soil surface in monocultures of loosestrife and cattail (mean ± 95% ci) as a function of herbivory treatments at high (A) and low (B) fertility. Leaf-area damage to loosestrife did increase light at the soil surface ($F_{1,31}$=4.32, p=0.046), however herbivory treatments did not describe any variation beyond that explained by damage. Note that damage to loosestrife increases with beetle abundance. Insect herbivores did not significantly increase light at the soil surface in cattail monocultures. Insects of any species were allowed to colonize the hand manipulated treatments ((-)Beetles, Ambient herbivory and (+)Beetles). *Galerucella* were manually removed from the (-)Beetles treatment and added to the (+)Beetles treatment. Note that *Galerucella* do not feed on cattail, and thus the (-)Beetles and (+)Beetles treatments were not applied to cattail monocultures.

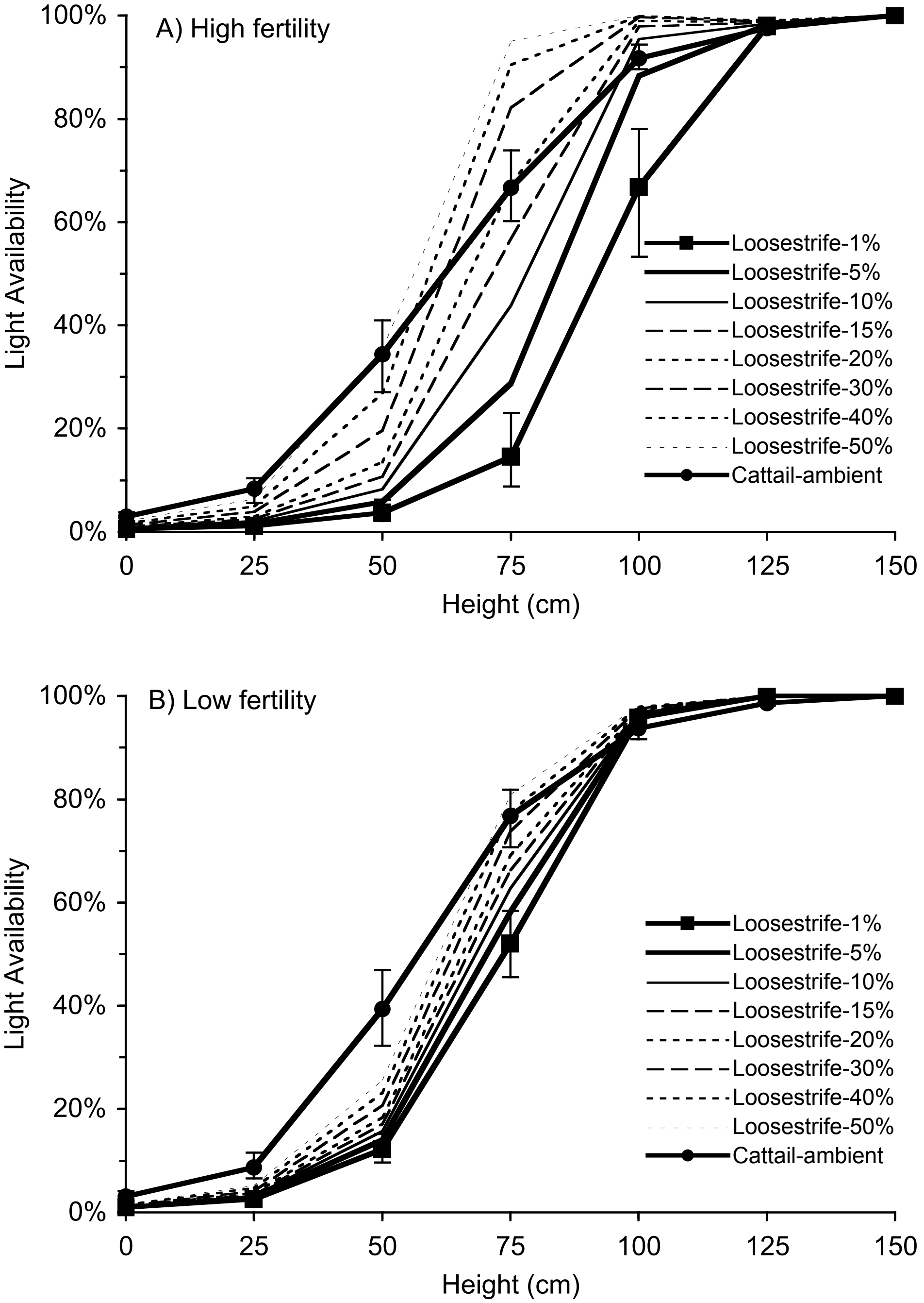


Figure 11. Growing season light availability (least-squares means ± se) in non-insecticide treated cattail (Ambient herbivory, n=6) and loosestrife (pooled across (-)Beetles, Ambient herbivory and (+)Beetles treatments, n=18) monoculture mesocosms as a function of height at A) high and B) low fertility. For loosestrife, least-squares means are presented across a range of leaf-area damage, from 1 to 50% damage. Some error bars excluded for clarity.

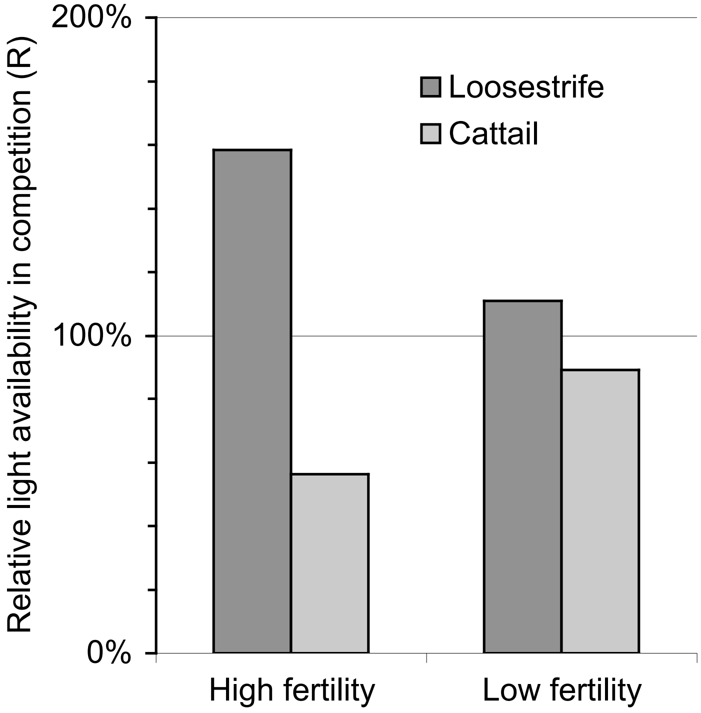


Figure 12. Standard light model predictions with insect herbivores suppressed with insecticide. *R* is light captured by a species when at low abundance within a monoculture of the other species (i.e., when it is shaded only by its competitor), relative to the light captured in a con-specific stand ($R_{as|b}$, Chapter 2). When *R* is greater than 100%, then that species should increase when rare within a canopy of the other species. If R>100% for both species, then the species should coexist. The model predicts that, if light is limiting and species interact only through light availability, loosestrife will competitively exclude cattail at both high and low fertility. The standard light model assumes that standing dead litter has photosynthetic capacity equal to live tissue.

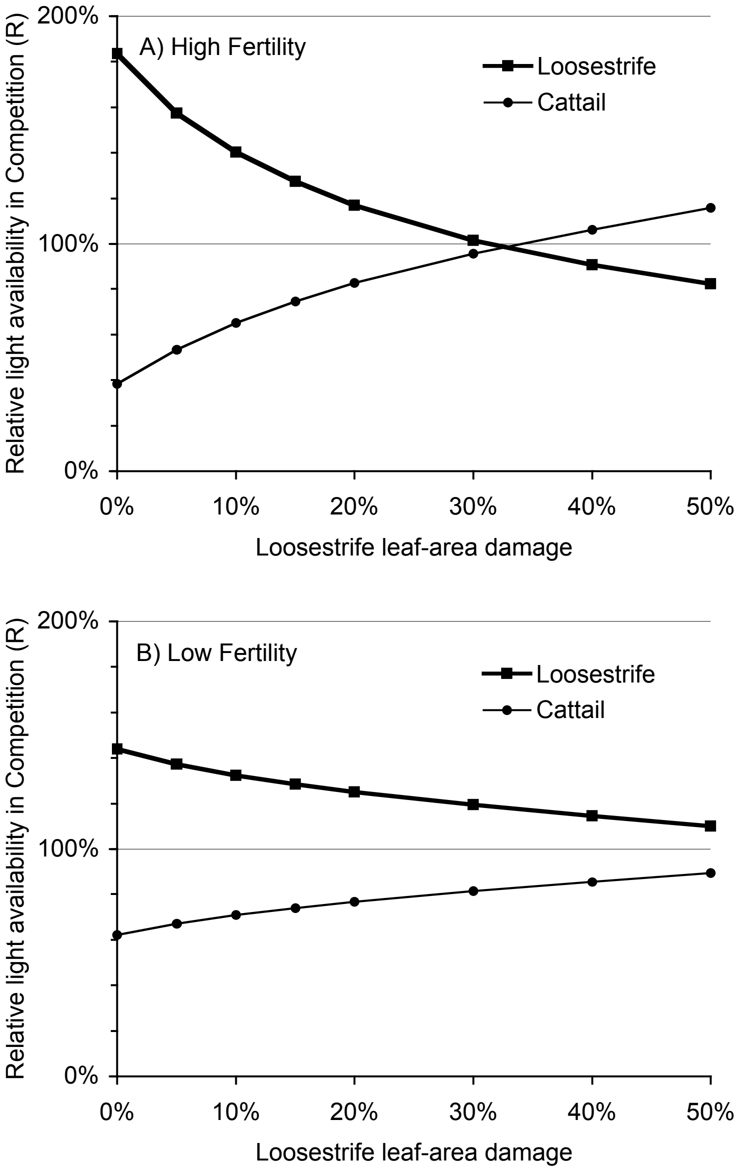


Figure 13. Standard light model predictions in the presence of insect herbivores (include the (-)Beetles, Ambient herbivory and (+)Beetles treatments). R is relative light captured by an individual when shaded only by the canopy of its competitor, as a function of leaf-area damage to loosestrife ($R_{as|b}$, Chapter 2). When R is greater than 100%, then that species should increase when rare within a canopy of the other species. If R>100% for both species, then the species should coexist. The standard light model assumes that standing dead litter has photosynthetic capacity equal to live tissue. At high fertility (A), more than 30% leaf-area damage is required to reverse the hierarchy of light competitive ability. At low fertility (B), even 50% leaf area damage to loosestrife is not sufficient to allow cattail to coexist in the presence of loosestrife.

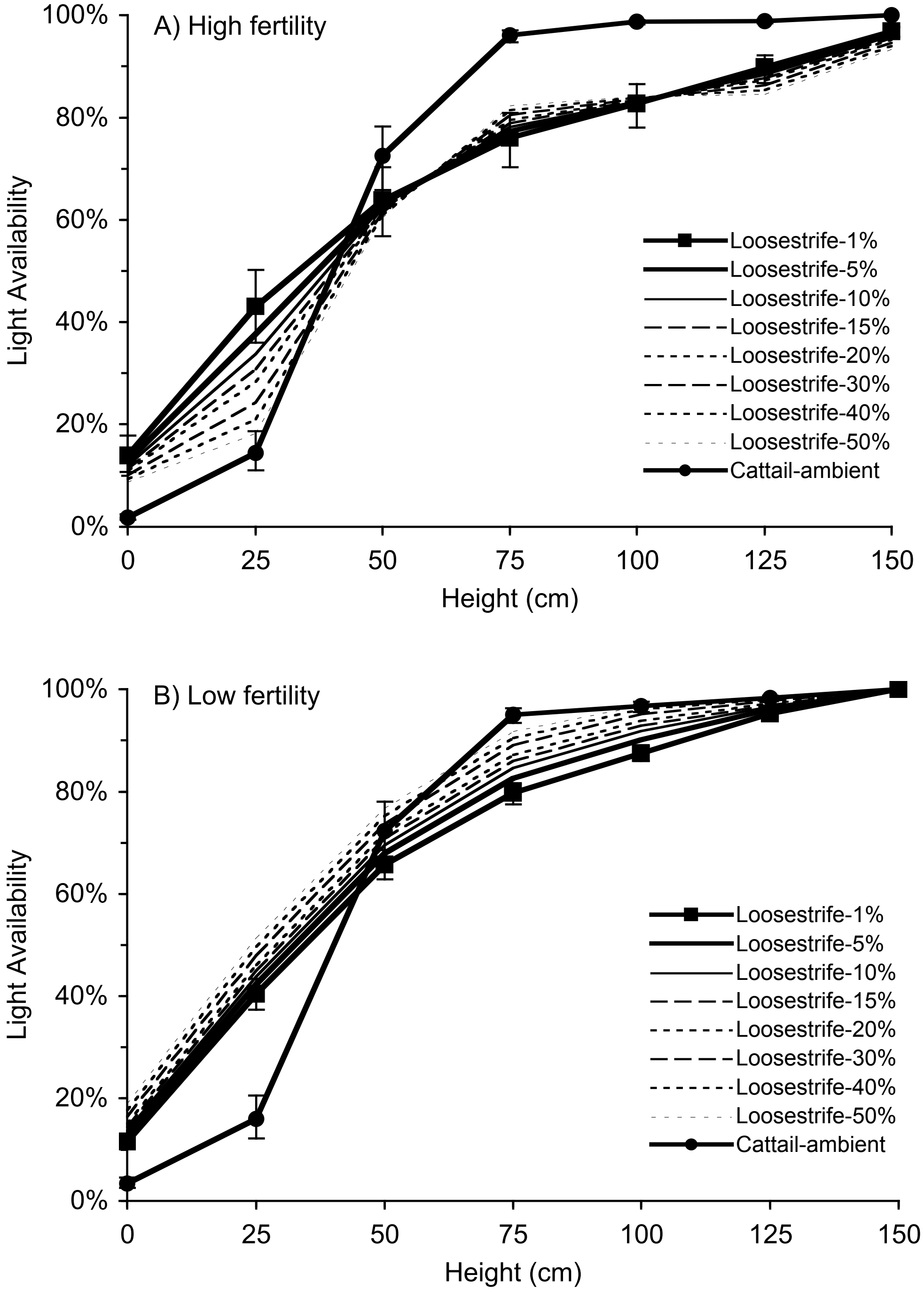


Figure 14. Spring light availability (when light is only controlled by standing dead liter, least-squares means ± se) in non-insecticide treated cattail (Ambient herbivory, n=6) and loosestrife (pooled across (-)Beetles, Ambient herbivory and (+)Beetles treatments, n=18) monoculture mesocosms as a function of height at A) high and B) low fertility. For loosestrife, least-squares means are presented across a range of leaf-area damage, from 1 to 50% damage. Some error bars excluded for clarity.

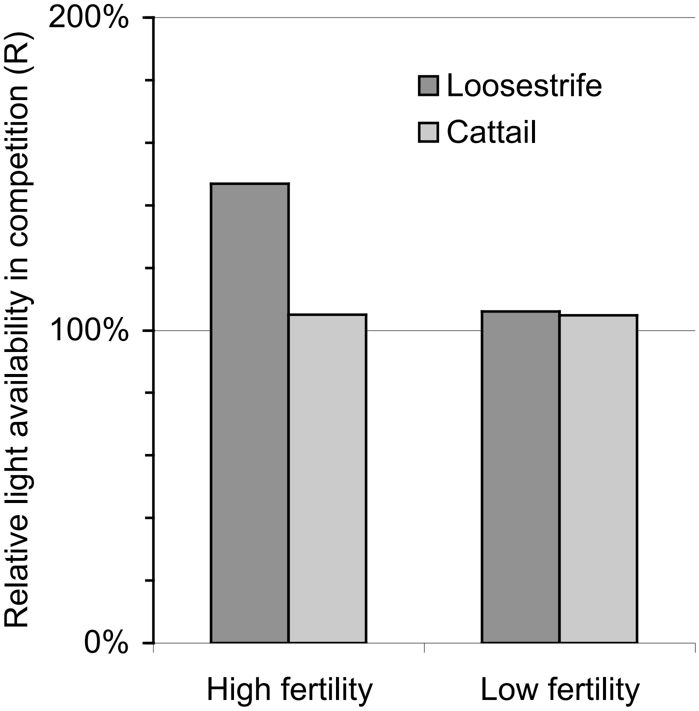


Figure 15. Light model predictions when insect herbivores are suppressed with insecticide, and assuming litter has no photosynthetic capacity, at high and low fertility. *R* is light captured by an individual when shaded only by its competitor, relative to the light captured in a con-specific stand ($R_{as|b}$, Chapter 2). When *R* is greater than 100%, then that species should increase when rare within a canopy of the other species. If R>100% for both species, then the species should coexist. With litter assumed to be non-photosynthetic, the model predicts loosestrife and cattail will coexist at both high and low fertility.

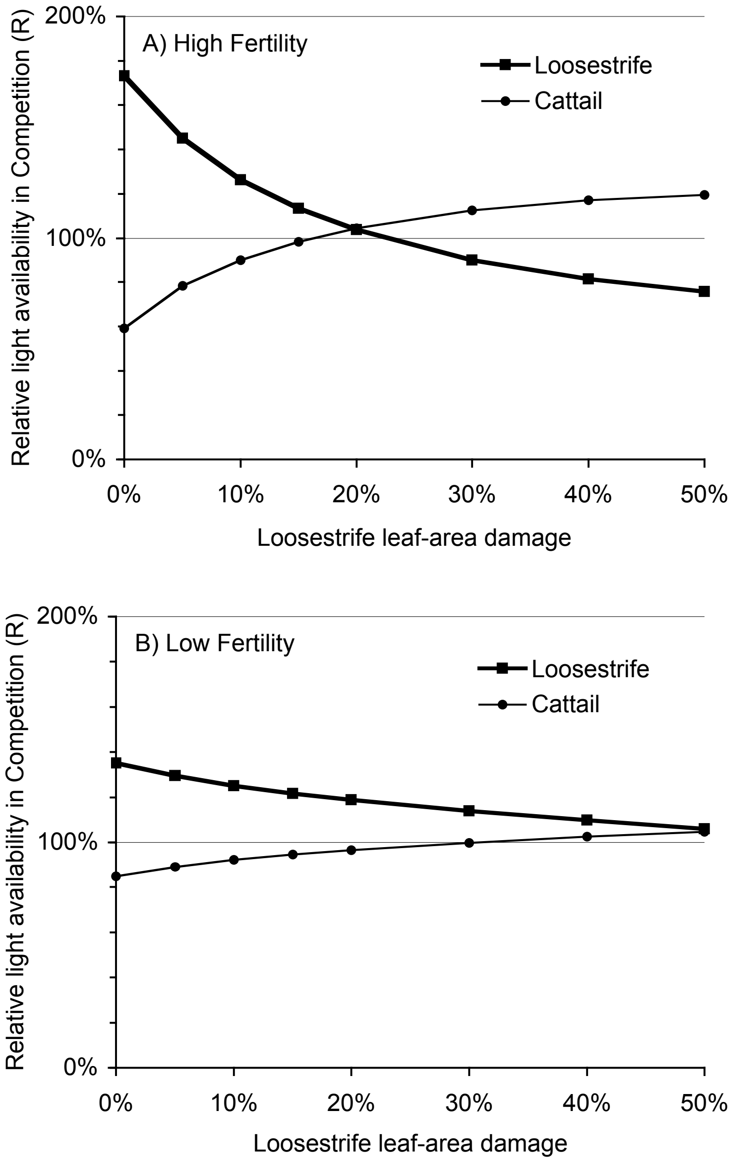


Figure 16. Light model predictions in the presence of insect herbivores (including (-)beetles, ambient herbivory and (+)beetles treatments), assuming that standing dead litter is non-photosynthetic. R is light captured by an individual when shaded only by the canopy of its competitor, relative to light captured when shaded by conspecifics, as a function of leaf-area damage to loosestrife ($R_{as|b}$, Chapter 2). When R is greater than 100%, then that species should increase when rare within a canopy of the other species. If R>100% for both species, then the species should coexist. Without leaf-area damage (0%), loosestrife receives far more light when shaded by cattail than when shaded by con-specifics, and cattail receives far less light when shaded by loosestrife. At high fertility (A), roughly 20% leaf-area damage is required to reverse the hierarchy of light competitive ability. At low fertility, even 50% damage is not sufficient to cause loosestrife to receive less light in competition compared to monoculture, however only 30% damage is required for cattail. A broad range of stable coexistence occurs with more than 30% damage to loosestrife.

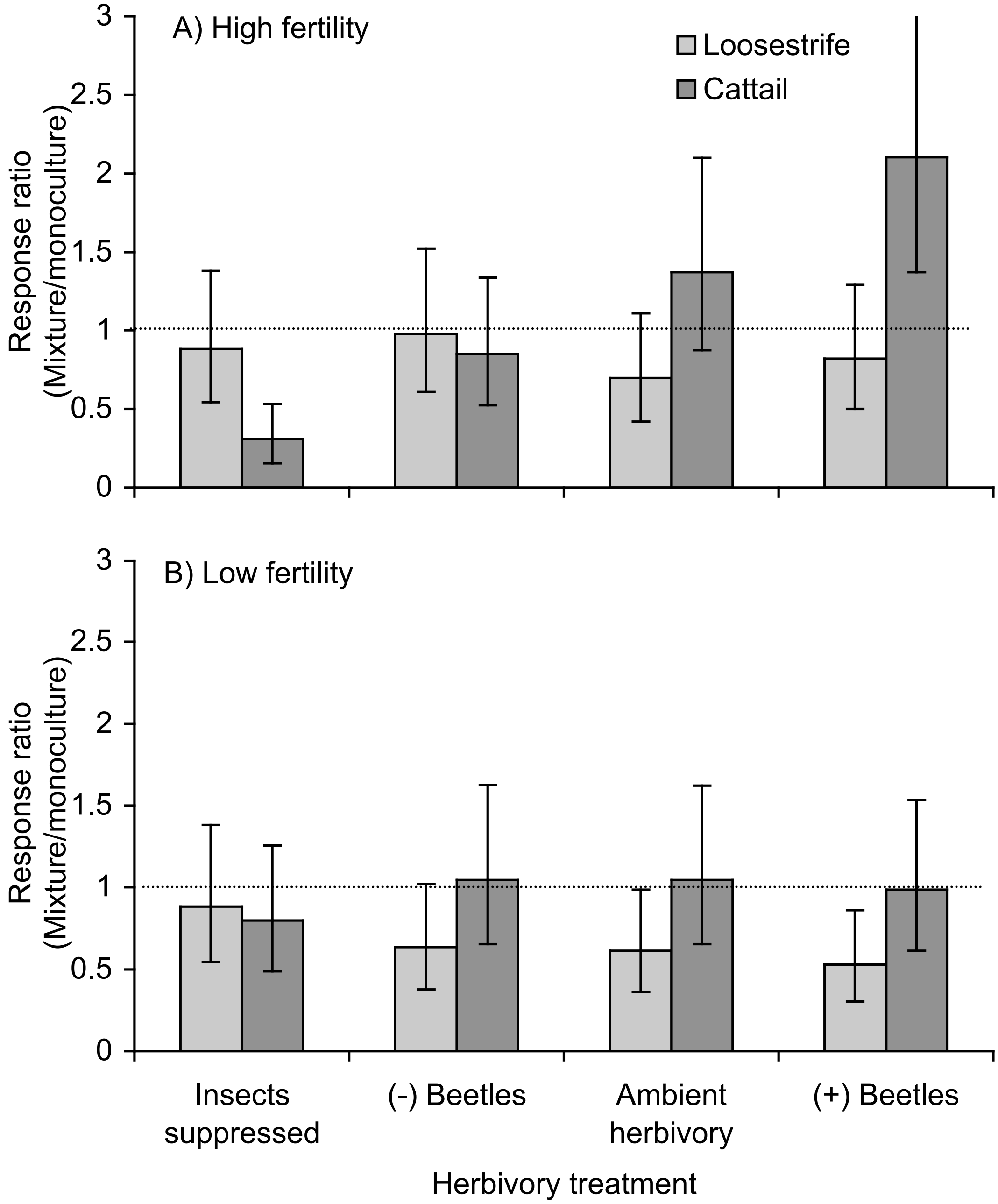


Figure 17. Response ratio (*RR*, mean ± 95% ci) of loosestrife and cattail in each of four herbivory treatments at high (A) and low (B) fertility. Response ratio (*RR*) is abundance in mixture mesocosms relative to abundance in monoculture mesocosms. A response ratio below 1 (100%) indicates an effect of competition on abundance. A response ratio above 1 indicates facilitation. Insects were suppressed with insecticide application. *Galerucella* were manually removed from the (-)Beetles treatment and added to the (+)Beetles treatment. Note that analysis of covariance demonstrated that the effect of percent leaf-area damage to loosestrife on *RR* did not vary significantly among treatment combinations, nor did percent leaf-area damage have a significant overall effect on *RR*. Thus, percent leaf-area damage was removed from the analysis and effects on *RR* were analyzed with analysis of variance (Littell et al. 1996).

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