EXPLAINING VARIATION IN INSECT HERBIVORE CONTROL OVER PLANT COMMUNITIES

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Research has repeatedly demonstrated that herbivores can, at some times and in some places, control the distribution and abundance of plants. Consequently, explaining variation in herbivore control over plant communities is a central goal in ecology and evolutionary biology. Two major challenges have prevented theoretical progress in this area of research. First, although there are numerous hypotheses that attempt to explain variation in herbivore control over plant communities, theoretical reviews have focused on a single hypothesis. Thus, it has been unclear where these herbivore control hypotheses diverge in their predictions and rationale. Second, herbivore control hypotheses base their explanations on highly correlated vegetation characteristics, namely net primary productivity (NPP), plant vigor, plant apparency, plant tissue nitrogen, plant defenses, plant tolerance, and host plant concentration. Consequently, interpretations of field experiments and meta-analyses have been equivocal. To address the first problem, I simultaneously reviewed herbivore control hypotheses and their predictions and rationale. I demonstrate that these hypotheses can be synthesized into four central hypotheses based on NPP, plant size, resource availability, and host stem density. This provides researchers with few vs. many herbivore control hypotheses. To address the second problem, I simultaneously tested these hypotheses by experimentally manipulating resource availability, total stem density, plant species composition, and herbivore abundance under field conditions. I then monitored the response of herbivore abundance, damage to plants, and the reduction in plant mass due to herbivory. The experiments demonstrated that herbivory caused the strongest reductions in mean stem mass where per stem resource availability was lowest, regardless of where herbivore abundance and damage was greatest. This result supports the plant tolerance based resource availability hypothesis, which assumes that the ability of plants to tolerate herbivory increases as resource availability increases. In addition, herbivore control over both simple plant communities (i.e., monocultures) and complex plant communities (i.e., polycultures) was due to herbivory on the dominant plant species, *Solidago canadensis*. Together, these results suggest that future herbivore control hypotheses should focus on the effect of per-capita resource availability on the ability of dominant plants to tolerate herbivory.

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PREFACE

I am indebted to Aileen Butera, Melissa Faigeles, and Nicholas Zaorski. My dissertation would not have been possible without their assistance in the field ("die *canadensis* die!!"), their organizational skills ("James, do you have your wallet, phone, keys, and glasses"), and their unending comic relief ("What are trowels for?"). Your friendship has truly enriched my life. I am also grateful for the following people, who volunteered time to help maintain these experiments: J. Baker, S. Berman, A. Boulé, E. Deleon, C. Evenoski, J. Klosky, J. Lingenfelter, S. Papperman, A. Royo, A. Randel, N. Schoeppner, H. Schumacher, K. Walker, B. Walker, and M. Welsh. Finally, I also thank P. Morin, D. Bunker, S. Tonsor, E. Airoldi, and A. Zheng for statistical advice; N. Haddad, JC Cahill, and H. Schumacher for contributing data; and B. Issac, J. Rawlins, B. Androw, and C. Young at the Carnegie Museum of Natural History for help identifying arthropods and plant species.

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1.0 INTRODUCTION

In 1960, Hairston, Smith and Slobodkin provoked a heated debate about the relative importance of the factors that regulate plant communities. They hypothesized that herbivores do not control the structure of natural plant communities because predators keep herbivore populations at extremely low abundance. This hypothesis was provocative because it made a bold assertion about the relative importance of different factors that structure populations, communities, and ecosystems. Other researchers responded by hypothesizing that alternative factors, such as plant defenses, were more important factors that constrained herbivores. The ensuing debate has generated an enormous number of ecological and evolutionary hypotheses that try to predict when herbivores will have strong control over plants.

A major problem that has faced ecologists and evolutionary biologists is that these herbivore control hypotheses base their predictions on vegetation characteristics that are highly correlated (e.g., plant productivity, plant size, plant defenses). Consequently, tests of these hypotheses have remained equivocal because the factors are typically confounded in field experiments. This has resulted in very little progress toward determining which vegetation characteristics merit further theoretical attention (Chapter 2.0).

Although there has been a growing call for studies that simultaneously test these hypotheses, two issues have made this a daunting task. First, no study has simultaneously reviewed herbivore control hypotheses side-by-side. Therefore, where herbivore control hypotheses diverge in their predictions has not been made clear. I provide this review in Chapter 2.0, which synthesizes herbivore control hypotheses by showing how they explain patterns of herbivore control using five vegetation characteristics: plant productivity, plant tolerance, plant tissue quality, host plant concentration, and plant size. I also show that which vegetation characteristic is used to explain herbivore control is generally based on assumptions about herbivore diet breadth (e.g., specialists vs. generalists). This assumption, referred to as the consumer diet breadth hypothesis, predicts that specialist herbivore abundance responds to host plant characteristics (e.g., stem density, tissue N) while generalist herbivore abundance responds to community-level characteristics (e.g., net primary productivity) and plant defenses. Chapter 2.0 also reviews the current empirical evidence for herbivore control hypotheses. The empirical review shows that empiricists have provided weak explanations for observed patterns of insect herbivore control because empiricists only consider a single herbivore control hypothesis or, when they do consider multiple hypotheses, the alternative predictions are not explicitly or accurately described.

Given the need for empirical studies that simultaneously test multiple herbivore control hypotheses outlined in Chapter 2.0, I conducted field experiments that tested these hypotheses in old-field herbaceous plant communities using a diverse assemblage of naturally colonizing insect herbivores. Chapter 3.0 tests the consumer diet breadth hypothesis and shows that specialist herbivore abundance responded to host plant characteristics and, as diet breadth increased (i.e., became more generalized), plant community-level characteristics provided a better explanation for herbivore density. This evidence supports the consumer diet breadth hypothesis, demonstrating that the herbivore community in these experiments encompassed enough variation in herbivore diet breadth to provide a fair, simultaneous test of alternative herbivore control hypotheses.

In Chapter 4.0, I provide evidence that total insect herbivore density and damage to plants were all best explained by an effect of resource availability on *Solidago canadensis* tissue quality. This result supports the plant quality based resource availability hypothesis described in Chapter 2.0. Surprisingly, however, the strength of herbivore control over plant communities was always greater under low resource conditions, regardless of herbivore abundance or herbivore damage. In addition, herbivore control at the plant community-level was due to a decline in the tolerance of the dominant plant species, *S. canadensis*, as resource availabilities declined. This result supports the plant-tolerance based resource availability hypothesis (see Chapter 2.0). Overall, the results from Chapter 4.0 suggest that herbivore control over plant communities can be decoupled from herbivore density and damage. This sharply contrasts with the prominent view that a factor (e.g. resource availability) alters the strength of herbivore control over plant communities only through its affect on herbivore abundance (or consumption). These results suggest that future hypotheses should use the effect of resource availability on the tolerance of dominant plants as their foundation and then investigate how other processes (e.g. abiotic factors, predators, shifts in species composition) modify the outcome of this relationship.

2.0 HERBIVORE CONTROL HYPOTHESES: A THEORETICAL AND EMPIRICAL REVIEW

2.1 INTRODUCTION

More than 40 years ago, Hairston et al. (1960) provoked a heated debate about the relative importance of the forces that regulate primary producers (see Hairston 1991, Sih 1991, *Special Feature* Ecology 1992, Polis 1999). They hypothesized that the control of plant community structure by native insect herbivores is a rare and unnatural event because predators keep herbivore populations at extremely low abundance. This idea, that the presence or absence of higher trophic levels (e.g., predators, herbivores) controls plant communities, became known as 'top-down' control. The response to this provocative hypothesis was that other mechanisms, such as plant defenses or interference competition among herbivores, could be as important as predators in constraining herbivore control (e.g., Murdoch 1966, Ehrlich and Birch 1967, Feeny 1970, Arditi and Ginzburg 1989, Hartley and Jones 1997). This latter perspective, that resources regulate plant communities because vegetation characteristics (e.g., defenses) or consumer characteristics (e.g., interference competition) constrain herbivores, became known as 'bottom-up' control. Thus, at the inception of this debate, these alternative hypotheses predicted plant communities were controlled from the either the bottom-up or the top-down. Furthermore, Lawton and McNeill (1979) argued that insect herbivores were doubly constrained because they were trapped between predators and well-defended plants. Consequently insect herbivores were predicted to have weak control over plant community structure (Strong et al. 1995, Carson and Root 2000).

This dichotomous view, (i.e., bottom-up vs. top-down forces) was eventually discarded because numerous studies demonstrated that these forces vary spatially and temporally and interact to regulate primary producers (*Special Feature* 1992). Consequently, the primary objective of the bottom-up, top-down debate is to predict when and where herbivory will exert strong top-down control (Matson and Hunter 1992, Power 1992, Hunter and Price 1992, Letourneau and Dyer 1998, Chase et al. 2000a).

Unfortunately, the bottom-up, top-down debate has left us with numerous alternative herbivore control hypotheses. These hypotheses predict that the strength of herbivore control will vary along key vegetation gradients, such as net primary production (NPP: e.g., Oksanen et al. 1981), plant tolerance (e.g., Maschinski and Whitham 1989), host concentration (e.g., Janzen 1970, Long et al. 2003), plant diversity (e.g., Strong 1992), plant defenses (e.g., Stamp 2003), and plant size (e.g., Price 1991). The relative empirical importance of these hypotheses, however, remains unclear because these gradients are often highly correlated and thus typically confounded in field studies. Thus, there is a need to review these hypotheses side by side to clarify the issues facing empiricists that desire to simultaneously test these hypotheses.

Here, I review and synthesize herbivore control hypotheses and I assess their empirical support. I synthesize the current theoretical literature by distinguishing four central hypotheses that rely on different environmental gradients to predict the strength of herbivore control (i.e., the NPP hypothesis, the resource availability hypothesis, the host concentration hypothesis, and the plant size hypothesis). I support each central hypothesis by describing its sub-hypotheses, which are conceptually related but mechanistically distinct (e.g., Janzen 1970 vs. Root 1973). By doing so, I provide empiricists with a few (vs. many) hypotheses that, when simultaneously tested, can help to identify which mechanisms are most likely to explain patterns of herbivore control. Therefore, this review differs from previous theoretical reviews, which have focused on a single environmental gradient (e.g., NPP: Chase et al. 2000a) or a single mechanism (e.g., plant defenses: Stamp 2003). The major theoretical points are summarized in Table 1.

I also describe the empirical evidence for each hypothesis, focusing on insect herbivore control over terrestrial plant mass (summarized in Table 2). I focus on trophic interactions involving insect herbivores because these comprise the vast majority of trophic interactions in terrestrial systems (Strong et al. 1984, Hawkins and Lawton 1987, May 1988). In addition, terrestrial insect herbivores were at the center of initial top-down, bottom-up arguments (Nicholson 1933, Andrewartha and Birch 1954, Hairston et al. 1960, Lawton and McNeil 1979) and their role in structuring plant communities is still unclear (Strong et al. 1995, Carson and Root 2000, Fowler 2002, Fagan et al. 2004). Despite the focus on insect herbivores, the issues addressed here are also relevant to discussions of vertebrate herbivores, where explanations for their control over standing plant mass have also considered these hypotheses (see McNaughton 1979, Augustine and McNaughton 1998, Chase et al. 2000a).

2.2 HERBIVORE CONTROL HYPOTHESES

2.2.1 The net primary productivity hypothesis

The NPP hypothesis states that, because energy transfer from one trophic level to the next is inefficient, NPP will predict the standing density (mass or individuals) of higher trophic levels and consequently the reduction in standing plant mass by generalist herbivores (Fretwell 1977, 1987, Power 1992, Oksanen et al. 1995, Persson et al. 1996, Chase et al. 2000a,b). Note that this hypothesis distinguishes between the terms 'productivity' and 'standing' (Persson et al. 1996, Chase et al. 2000a). Productivity is the rate of mass production, whereas standing is the density of mass or individuals once foraging and food web dynamics (e.g., resource competition, predation) have played out. Thus, the NPP hypothesis uses net plant productivity to predict herbivore and predator densities (mass or individuals) and the reduction in standing plant mass by herbivores.

The NPP hypothesis was originally proposed to explain patterns of standing mass in closed food chains involving vertebrate herbivores (Oksanen et al. 1981). In other words, measures of standing mass for a given trophic level were considered the result of birth, growth, and death rates that were driven by mechanisms internal to that food chain (i.e., each food chain along an NPP gradient is considered independent of other food chains). More recently, the NPP hypothesis has formally addressed invertebrate herbivores (e.g., Wootton and Power 1993, Schmitz 1994) and open food chains (e.g., Wootton and Power 1993, Oksanen et al. 1995). The latter development recognizes that foraging behavior can generate differences in the density of individual consumers among patches that differ in NPP (e.g., Wootton and Power 1993, Oksanen et al. 1995). In a recent review, Chase et al. (2000a) distinguished three categories of NPP sub-hypotheses based on whether the reduction in standing plant mass due to herbivory is predicted to stay constant (i.e. resource controlled food chains), increase (i.e. consumer controlled food chains), or decrease (heterogeneous food webs) as NPP increases (Table 1). These differences arise because different NPP sub-hypotheses make different assumptions about plant, herbivore, and predator traits.

2.2.1.1 Resource controlled food chain sub-hypothesis

This NPP sub-hypothesis has two key assumptions. First, individuals within a trophic level are identical (e.g., all plants have the same traits, all herbivores have the same traits). Consequently, herbivores (and predators) are generalists: the plant community is edible for the entire herbivore community. Second, herbivores harvest a constant proportion of plant productivity regardless of plant, herbivore, or predator density (Chase et al. 2000a). Therefore, the reduction in standing plant mass by herbivory never changes as NPP increases. This is thought to occur when herbivores attack plants that do not contribute to plant productivity (e.g., post-reproductive or sick individuals; e.g., Pimm 1982) or when intra- and interspecific competition among herbivores increases as herbivore mass increases, which then decreases per capita herbivore consumption rates (e.g., Arditi and Ginzburg 1989). Irrespective, resource controlled food chains predict that plant mass, herbivore, and predator standing mass increase as NPP increases (due to the first assumption) but the proportional reduction in standing plant mass due to herbivory will not vary as NPP increases (due to the second assumption; Chase et al. 2000a).

2.2.1.2 Consumer controlled food chain sub-hypothesis

Consumer-controlled food chains also assume all individuals within a trophic level are identical. When functional responses are modeled linearly, consumer-controlled food chains predict that adjacent trophic levels exhibit decoupled patterns in standing mass along NPP gradients (i.e., standing plant mass increases, standing herbivore mass stays constant, standing predators mass increases; e.g., Oksanen et al. 1981). In contrast, hypotheses that allow for non-equilibrium (e.g., Oksanen et al. 1995) or non-linear functional responses (e.g., Abrams and Roth 1994) predict that adjacent trophic levels can exhibit parallel increases in standing mass as NPP increases. Despite these different patterns of standing mass, however, all consumer-controlled hypotheses predict that the reduction in standing plant mass due to herbivory will increase as NPP increases (Chase et al. 2000a).

2.2.1.3 Heterogenous food web sub-hypothesis

This sub-hypothesis also assumes that herbivores can reduce standing plant mass. In contrast to the other NPP sub-hypotheses, however, heterogeneous food webs assume that plant species differ in their traits due to trade-offs: some plant species are competitively superior but poorly defended while other plant species are competitively inferior but better defended (e.g., Holt et al. 1994, Leibold 1989, 1996). Herbivores are still considered generalists, however, they just cause smaller reductions in the mass of the better-defended plant species. Thus, in the absence of herbivores (i.e., at low NPP), competitively superior plant species dominate the plant trophic level. In the presence of herbivores (i.e., at relatively high NPP), however, better-defended plant species dominate the plant trophic level. Heterogeneous food webs predict that, as NPP increases, (1) plant and herbivore standing mass increases, (2) the elevated herbivore mass causes plant species composition to shift from poorly defended plant species to better defended plant species and, consequently, (3) the reduction in standing plant mass due to herbivory decreases as NPP increases (Chase et al. 2000a).

2.2.1.4 Empirical evidence for the NPP hypothesis

Insect herbivore performance (e.g., density, survival, growth, fecundity) has been shown to positively respond to plant growth. Waring and Cobb's (1992) literature review of fertility studies showed that plant growth (i.e. productivity) was the best predictor of herbivore performance (e.g., density, survivorship, see Waring and Cobb 1992: Table 2). Community-level empirical tests have reported evidence both for and against each NPP sub-hypothesis and in both open and closed systems (Table 2). Two meta-analyses did not find significant correlations between insect herbivore control over community-level standing plant mass and NPP and concluded that this did not support the NPP hypothesis, despite that the resource controlled sub-hypothesis predicts no change in herbivore control (Schädler et al. 2003, Coupe and Cahill 2003; also see Borer et al. 2005). In contrast, 73% of the community-level studies concluded that their data did support the NPP hypothesis. All of these tests were conducted across small spatial scales.

Table 2 shows NPP studies that used either fertilizer or placed plots along a standing plant mass gradient to manipulate NPP. Only one of these studies (Moran and Scheidler 2002) controlled for the effect of fertility on other vegetation characteristics (e.g., species diversity) that are also thought to control herbivore foraging behavior and population growth rates. Despite this issue, authors have suggested two general conclusions about the relationship between NPP and insect herbivore control. First, numerous authors have argued that the empirical evidence suggests that NPP ultimately regulates herbivore control by affecting rates of herbivore growth, reproduction, consumption, and foraging behavior and indirectly altering predation pressure (e.g., Schmitz 1994, Fraser 1998, Fraser and Grime 1997,1998,1999, Forkner and Hunter 2000, Moon and Stiling 2002a, Moon and Stiling 2002b, Moran and Scheidler 2002). Second, there is a consensus that the response of herbivore density to NPP will depend upon the identity of the insect herbivore, host plant, and predator (e.g., Forkner and Hunter 2000, Ritchie 2000, Schmitz et al. 2000, Denno et al. 2002, Moon and Stiling 2002a, Moran and Scheidler 2002). This suggests that if NPP is a critical component of plant-insect interactions, the NPP hypothesis will often be community and species dependent for all trophic levels.

2.2.2 The resource availability hypothesis

The resource availability hypothesis states that resource availability to plants will predict herbivore control over standing plant mass because resource availability determines (1) the ability of a plant to cope with herbivory (i.e. plant tolerance) or (2) the quality of plant tissue (i.e., concentrations of nutrients or toxins; Table 1).

2.2.2.1 Plant tolerance sub-hypothesis

Plants tolerate herbivory when they regrow after experiencing herbivory by specialist or generalist herbivores (Strauss and Agrawal 1999). The plant tolerance sub-hypothesis assumes that the ability of a plant to regrow after herbivory is determined by the availability of plant resources (see McNaughton 1979, Maschinski and Whitham 1989, Strauss and Agrawal 1999). Plants growing in low resource environments are less able to regrow after herbivory compared to plants where resources are less limiting, and plants can compensate or overcompensate for herbivory when resources are not limited (Maschinski and Whitham 1989). Contrary to other herbivore control hypotheses (e.g., NPP-based heterogeneous food webs), the plant tolerance sub-hypothesis does not require herbivore abundance or herbivore consumption rates to change in order for herbivore control over plants to change. The plant tolerance sub-hypothesis only predicts that herbivory will (1) reduce stem mass at low resource levels, (2) the reduction in standing stem mass will decrease as resource levels increase and (3) herbivory will cause an increase in stem mass at high resource levels. Plant tolerance is typically explored at the level of individual stems (e.g., Strauss and Agrawal 1999, Hawkes and Sullivan 2001), but is expected to explain patterns of herbivore control over community-level measures of standing plant mass (see McNaughton 1979, Augustine and McNaughton 1998, Strauss and Agrawal 1999, Chase et al. 2000a,b, Stiling and Moon 2005).

2.2.2.2 Plant tissue quality sub-hypothesis

Resource availability to plants also affects plant tissue quality, which is predicted to alter herbivore abundance, herbivore consumption rates, and thus the strength of herbivore control over standing plant mass (e.g., White 1984, Herms and Mattson 1992, Stamp 2003, Throop and Lerdau 2004). There are two alternative types of plant quality mechanisms: nutrition-based hypotheses and defense-based hypotheses.

Nutrition-based plant quality. Here, resource (e.g., water, soil nitrogen) availability is assumed to (a) directly determine nitrogen concentrations in a plant’s tissue and (b) the tissue N concentrations subsequently determine both specialist and generalist herbivore load, herbivore damage per stem, and the reduction in stem mass due to herbivory (e.g., White 1984, Throop and Lerdau 2004). This sub-hypothesis was originally intended to explain insect herbivore population dynamics and typically has been explored at the level of herbivore performance on individual stems (e.g., Mattson 1980, Waring and Cobb 1992). Herbivore responses to nitrogen concentrations in plant tissue, however, are expected to explain patterns of herbivore control over community-level measures of standing plant mass (e.g., Ritchie 2000, Denno et al. 2002, Throop and Lerdau 2004, Stiling and Moon 2005). Depending on plant and herbivore traits, the reduction in standing plant mass by herbivory is predicted to either increase or decrease with resource availability.

There are two widely held perspectives about the relationship between resource availability, tissue nitrogen, and herbivore control. The first perspective focuses on soil nitrogen availability and predicts that increasing soil nitrogen directly increases tissue nitrogen concentrations (e.g., Ritchie 2000, Throop and Lerdau 2004). Increasing tissue nitrogen concentrations with increasing soil nitrogen, however, can either positively affect herbivores (e.g. Mattson 1980, Ritchie 2000, Stiling and Moon 2005, Throop and Lerdau 2004) or negatively affect herbivores (e.g., Mattson 1980, Throop and Lerdau 2004). Higher tissue N is predicted to have positive affects on herbivore abundance and consumptions rates if herbivores always attempt to acquire more nitrogen. In contrast, higher tissue N can also reduce herbivore abundance or consumption when tissue N either exceeds optimal levels for herbivores (e.g., becomes toxic) or because herbivores can acquire enough N in fewer bites when tissue N is high.

The second perspective considers that increasing resource availability can either increase or decrease tissue N concentrations, depending on whether plants become relatively more stressed at low vs. high resource availability (White 1984). Herbivores, however, always positively respond to increases in tissue nitrogen concentrations (White 1984). Therefore, herbivore loads or damage per stem and reduction in stem mass due to herbivory are predicted to either increase or decrease with availability as herbivores respond to a changing N pool (White 1984).

Irrespective, the nutrition-based plant quality hypothesis predicts that herbivore loads or damage per stem and the reduction in standing plant mass due to herbivory will *jointly* increase or decrease as resource availability (and thus tissue nitrogen) increases (Table 1).

Defense-based quality. Plants produce defenses that reduce the negative effect of herbivory on plant growth. Plants, however, might experience trade-offs between allocation to growth vs. allocation to defenses and the shape of the trade-off is assumed to depend on resource availability to plants (e.g., Bryant et al. 1983, Coley et al. 1985, Bazzaz et al. 1987, Herms and Mattson 1992, Stamp 2003). Resource-based plant defense hypotheses assume that plants are plastic in their allocation to defenses and that defenses reduce the effect of herbivory on plant growth (Stamp 2003). Consequently, plant defense hypotheses make testable predictions about herbivore damage per stem and the strength of herbivore control over stem mass. They do not, however, make explicit predictions about herbivore abundance.

Stamp (2003) rigorously reviewed plant defense theories and concluded that future research should focus on the Extended Growth-Differentiation Balance hypothesis (GDB: Herms and Mattson 1992) because it encompasses other, defense-based hypotheses. This hypothesis states that a limiting resource (or other factor) that slows plant growth more than it slows photosynthesis will increase the amount of resources, namely carbohydrates, available for allocation to defense related products (Stamp 2003). There are several assumptions made by

GDB (reviewed by Stamp 2003). First, defenses reduce herbivore damage and its affect on plant mass. Second, defenses are costly because they compete with growth related processes for photosynthate (or assimilates). Third, rapidly growing plants can compensate for mass lost to herbivory. Finally, plant defense theory also generally assumes that host plant defenses are more effective against generalist herbivores compared to its specialist herbivores (Cornell and Hawkins 2003; see also Dyer and Coley 2001). Below, I briefly outline how these assumptions generate predictions about changes in herbivore control over standing plant mass along three key gradients (Table 1). I first consider that defense is a function of either soil nutrients or light, because these resources have different effects on plant growth (Stamp 2003). In reality, however, defense concentrations are a function of the duel constraints of nutrient and light availability (Stamp et al. 2004). Therefore, I also describe the dual constraints of nutrients and light on plant growth along a stem density gradient.

Soil Nutrients: Growth depends heavily on nutrient (i.e., nitrogen, water) availability to drive the enzymatic activity that is necessary for cell division and expansion (Herms & Mattson 1992, Kursar & Coley 2003, Stamp 2003). The demand of growth for nutrients is assumed to be greater than that of photosynthesis, which causes low nutrient availability to slow plant growth much more than it slows photosynthesis (Herms & Mattson 1992, Stamp 2003). Thus, when the availability of soil nutrients is low, the limited photosynthate (or assimilates) produced is preferentially allocated to meet the demand of growth related processes vs. defense (Stamp 2003). The combination of low growth and low allocation to defenses results in moderate defense concentrations (Herms & Mattson 1992, Stamp 2003). At intermediate soil nitrogen levels, however, growth is still limited by nutrient availability but photosynthesis is less constrained. Therefore, excess photosynthate (or assimilates) is produced and can be allocated to defense at little cost to growth. This results in high concentrations of plant defenses at intermediate soil nutrient levels. At high soil nutrient levels, growth is no longer nutrient limited and thus photosynthate (or assimilates) is not being produced beyond what is required for growth. Consequently, rapid growth combined with low allocation to defenses results in low concentrations of defenses. In total, the independent effect of soil nutrients on plant growth predicts that defense concentrations will peak at intermediate soil nutrients (e.g., Fig. 3 in Stamp 2003). Consequently, damage per stem should be lowest at intermediate levels of soil nutrients.

The reduction in mean stem mass due to herbivory, however, should decrease as nutrients increase because fast growing plants can compensate for mass lost to herbivory.

Light. The rate of photosynthesis is assumed to respond more strongly to light availability compared to growth, which causes excess photosynthate (or assimilates) accumulate as light increases (Herms & Mattson 1992, Stamp 2003). The GDB predicts that independently increasing light levels will cause defense concentrations to increase linearly with light (Stamp 2003, Stamp et al. 2004). Consequently, damage per stem should decrease as light increases (Stamp 2003, Stamp et al. 2004). The reduction in stem mass due to herbivory should also decline as light increases because plants growing at high light are able to compensate for lost mass (Stamp 2003).

Plant density. Actual defense concentrations in plant tissue will be jointly constrained by declines in soil nutrients and light as stem density increases (Stamp et al. 2004). The bell shaped nutrient-defense relationship and the linear light-defense relationship generate a positive sigmoid relationship between plant density and defense: defense concentrations slightly increase across low plant density, then steeply increase across intermediate plant density, and finally plateau across high plant densities (Stamp et al. 2004). If so, then herbivore damage per stem will exhibit a negative sigmoid relationship with plant density. The reduction in stem mass due to herbivory, however, is predicted to increase with density (despite a decline in damage) because the low plant growth rates at high stem density do not allow plants to compensate for tissue lost to herbivory (see Herms and Mattson 1992, Stamp 2003).

2.2.2.3 Empirical evidence for the resource availability hypothesis

Stem level evidence. There is no doubt that tolerance, tissue N, and defense concentrations all change along resource availability gradients. For plant tolerance, the response to increasing resource availability is variable and can decrease (Strauss and Agrawal 1999, Hawkes and Sullivan 2001, Wise and Abrahamson 2003). Some of this variation is likely explained by life history differences (e.g., basal vs. apical meristem; Strauss and Agrawal 1999, Stowe et al. 2000, Hawkes and Sullivan 2001). More importantly, tolerance studies typically do not determine if the manipulated resource in the lab is actually most limiting to plant growth in the lab or if herbivory directly affects acquisition of the limiting resource in the lab, both of which determine plant tolerance responses (Wise and Abrahamson 2003). Regardless, current experimental evidence at the stem level does not consistently support the plant tolerance sub-hypothesis' prediction that tolerance will increase as resource supply increases.

Herbivore responses to changes in tissue nitrogen have mostly been explored in response to nutrient availability. Increasing soil nitrogen and decreasing water both consistently increase tissue N (Mattson 1980, White 1984, Waring and Cobb 1992, Ayers 1993, Throop and Lerdau 2004, Huberty and Denno 2004). In addition, there is evidence that increasing tissue N generally increases herbivore reproduction, growth, survivorship, and consumption (e.g., Mattson 1980, Scriber and Slansky 1981, Waring and Cobb 1992, Awmack and Leather 2002, Fagan et al. 2002, Throop and Lerdau 2004). Increasing tissue N, however, can also decrease insect herbivore performance when it surpasses optimal levels (e.g., becomes toxic; Mattson 1980, Throop and Lerdau 2004), can be resource-plant-insect specific (Ritchie 2000, Goranson et al. 2004), and may not affect population densities of insects despite significant effects on the performance and behavior of individuals (Kyto et al. 1996).

Resource availability also determines plant defense concentrations and research does support the assumptions of GDB (reviewed in Coley et al. 1983, Bryant et al. 1987, Herms and Mattson 1992, Berenbaum 1995, Cornell and Hawkins 2003, Stamp 2003). First, growth and defense processes do compete for photosynthate and metabolic machinery (Herms and Mattson 1992, Kursar and Coley 2003, Stamp 2003). In addition, growth is strongly reduced under low nutrient (e.g., nitrogen, water) availability while photosynthesis is less affected (reviewed in Herms & Mattson 1992). Second, numerous studies have shown that defense concentrations change when resource availability increases (see Stamp 2003). Third, there is a large body of evidence showing that plant defenses reduce herbivore damage (see Berenbaum 1995, Stamp 2003). Finally, Cornell and Haskins (2003) demonstrated that host plant defenses generally cause stronger reductions in generalist herbivore performance compared to specialist herbivores (also see Dyer and Coley 2001, Dyer et al. 2004). Unfortunately, there is little empirical evidence that mechanistically links resource availability, plant growth, defense levels, and herbivore damage. Only three experimental studies have used resource availability gradients that were large enough to test the GDB hypothesis (see Stamp 2003, Stamp et al. 2004). Both Mihaliak and Lincoln (1985) and Wilkens et al. (1996) found that several plant defenses peaked at intermediate levels of nitrate and at intermediate plant growth. Stamp et al. (2004) found that increasing stem density caused the concentrations of several allelochemicals to decrease sigmoidally, but did not find a significant relationship between plant growth and defense. Although these limited results largely support the defense-based plant tissue quality sub-hypothesis, none of these studies demonstrated that higher defense concentrations reduced herbivore damage or the negative impact of herbivory on plant growth.

Community-level evidence. There are five community-level studies of the resource availability hypothesis (Table 2). Each study considered nutrient-based mechanisms and tested this mechanism by manipulating soil fertility or by placing plots along a standing plant density or resource availability gradient (Table 2). Two of these studies considered that soil fertility could be confounded with other vegetation characteristics. Moran and Schielder (2002) manipulated soil fertility independent of species diversity. They found that, when predators were removed from old-fields, increasing soil fertility caused increases in the mass of the dominant herbivores and subsequently stronger reductions in standing plant mass. The presence of predators, however, prevented soil nitrogen additions from increasing herbivore control. They concluded that these results supported the NPP hypothesis, but they did not discuss if NPP and nutrition based mechanisms make different or similar predictions.

Stiling and Moon (2005) manipulated tissue N independent of host stem size and host stem density. They showed that increasing soil fertility caused higher host tissue N concentrations, which subsequently increased the density of a stem-galling insect and a leaf-feeding insect. Interestingly, though galling damage reduces host stem density in this system, they did not observe a decline in host plant stem density as galling damage increased with fertility. Thus, they suggested that host plants at high fertility tolerate higher levels of galling. The tolerance hypothesis, however, predicts that herbivores should cause stronger reductions in standing plant density at low fertility because plant are less able to regrow after herbivory under low resource conditions. They did not observe this pattern.

One study concluded that they found support for the nutrient-based plant quality sub-hypothesis. Fagan and Bishop (2000) and Bishop (2002) demonstrated that herbivore damage and densities are highest on lupine stems located in low stem density patches. Because low-density patches are concentrated along the edge of the population, herbivores reduce the expansion of the lupine population. Consequently, herbivores control community-level standing plant mass by suppressing lupine because lupine fixes nitrogen and its presence strongly regulates patterns of primary production. Fagan et al. (2004) recently demonstrated that nutrient concentrations of low-density lupine are high, which has a positive effect on herbivore performance. They concluded that this supported nutrient-based quality hypotheses (e.g., White 1984).

In total, there is good evidence that nutrients and defenses vary predictably with resource supply, which often has predictable effects on the performance of individual herbivores but does not always have similar effects at the herbivore population level or community-level (for divergent perspectives on this issue compare Kyto et al. 1996, Ritchie 2000, Throop and Lerdau 2004, Dyer et al. 2004). There is, however, very weak community-level evidence for the resource availability hypothesis. Of five studies, one (Fagan and Bishop 2000, Bishop 2002, Fagan et al. 2004) found evidence that supported its predictions about herbivore control.

2.2.3 The host concentration hypothesis

The host concentration hypothesis states that the reduction in standing plant mass due to herbivory increases as host plant concentration increases because specialist herbivores aggregate or outbreak whenever host plants reach high stem density (e.g., Janzen 1970, Connell 1971, Root 1973, Long et al. 2003, Carson et al. 2004). This mechanism focuses on specialist herbivore impacts on mean host plant mass, and this insect-host plant feedback mechanism is expected to scale up to explain herbivore control over community-level measures of standing plant mass (Carson et al. 2004).

2.2.3.1 Resource concentration sub-hypothesis

Root (1973) discovered that insect herbivores often reached high abundance when hosts are concentrated. He provided three possible explanations for this pattern: 1) immigration rates increase and emigration rates decrease 2) in situ reproduction increases due to a favorable microenvironment and/or 3) survival increases due to lowered predation pressure. More recently, Root's (1973) resource concentration hypothesis has been extended to explain the reduction in community-level measures of standing plant mass (Carson and Root 2000, Long et al. 2003, Carson et al. 2004). Whenever the absolute or relative stem density of a host becomes high in a plant community, specialist herbivores will aggregate or outbreak on that host and reduce host abundance. Because the host plant represents a large portion of the plant community, this will reduce standing plant mass (e.g., Carson and Root 2000, Long et al. 2003). While outbreaks of native insects are not required for the rule to operate (see Long et al. 2003) the influence of insects is assumed to be most pronounced during outbreak events whenever hosts are abundant, long-lived perennial plant species (Carson et al. 2004). Therefore, the extended resource concentration hypothesis strongly emphasizes a temporal component such that once a long-lived perennial plant species reaches high abundance it will *eventually* be found by specialist insect herbivores. Thus, the extended resource concentration hypothesis predicts that (1) specialist herbivore load, damage per stem, and reduction in mean host plant mass due to specialist herbivores will increase with absolute or relative host stem density, (2) the reduction in community-level standing plant mass due to herbivory also increases with absolute or relative host stem density, but (3) this herbivore control over the plant community is solely due to specialist herbivore control over the host (Long et al. 2003, Carson et al. 2004; Table 1).

2.2.3.2 Janzen-Connell sub-hypothesis

The Janzen-Connell hypothesis also predicts that specialist herbivores cause a greater reduction in per host plant growth and survivorship as host plant concentration increases (Janzen 1970, Connell 1971). Originally proposed to explain the maintenance of species diversity in tropical forests, the Janzen-Connell hypothesis assumes that adult plants have size refugia from herbivores: large adults act as sources for herbivores that attack smaller juveniles. This assumption of adult size refugia causes Janzen-Connell predictions to diverge slightly from the resource concentration hypothesis. While both hypotheses predict that herbivores will strongly reduce mean per host plant mass (i.e., herbivore impact averaged across all juveniles and adults), the reduction in standing plant mass due to herbivory will be small when adults have size refugia because most of the host's mass is concentrated in large, resistant individuals (i.e., adults). Thus, both Janzen-Connell and resource concentration hypotheses predict that reductions in mean host plant mass and standing plant mass due to herbivory will increase as host stem density increases. Janzen-Connell, however, predicts relatively smaller herbivore reductions in community-level standing plant mass.

2.2.3.3 Trophic complexity sub-hypothesis

Strong (1992) also hypothesized that strong top-down control in terrestrial plant communities will be restricted to low diversity systems because these systems have a few strong, direct links between consumers (e.g., herbivores) and their resources (e.g., host plants). In these low diversity systems, top-down control by any one species or trophic level can easily cascade to other species and other trophic levels. In contrast, in high diversity systems, the impact of any species or trophic level is strictly limited because of the reticulate, interconnected nature of diverse food webs. Thus, this reticulate food web hypothesis predicts that the reduction in standing plant mass due to herbivory will decline as plant diversity increases (Table 1; also see McCann et al. 1998). The main mechanism thought to strengthen consumer-resource interactions, particularly for trophic interactions involving insect herbivores, is when the entire plant trophic level is dominated by a plant species that is edible at least one herbivore in the community (see Strong 1992, Polis 1999, Polis et al. 2000, McCann et al. 1998). Thus, this hypothesis uses diversity to predict herbivore control, but the main underlying mechanism is the resource concentration hypothesis.

2.2.3.4 Empirical evidence for the host concentration hypothesis

There is evidence for positive feedbacks between herbivore density per host and host abundance: insects are known to aggregate or out-break in high host stem density/low diversity stands (e.g., Root 1973, Risch et al. 1983, Andow 1991, Coll and Bottrell 1994, Morris et al. 1996, Carson and Root 2000, Long et al. 2003, Carson et al. 2004). There is, however, high variability in herbivore responses to host concentration. For example, Andow (1991) found that only 45% (27/59) of specialist herbivore species had statistically lower population sizes when hosts were in polyculture (see Table 2 in Andow 1991). Other reviews have also found highly variable responses among herbivore species, although these studies did not distinguish between specialist and generalist herbivores (Risch et al. 1983, Yamamura 2002, Rhainds and English-Loeb 2003). Recently, Otway et al. (2005) found that (1) the probability of nine specialists occurring in patches of vegetation increased as host mass increased but (2) the load (i.e., # insects per g host mass m^{-2}) of all nine specialists declined as host mass increased. While strong positive feedbacks between herbivores and host plant density may not universal (Otway et al. 2005), dominant host plants only need to have a single herbivore that responds to host concentration. In addition, most studies are conducted over short time periods, which might prevent researchers from observing a positive feedback between herbivore abundance and host plant abundance. When positive feedback is observed between a host and insect herbivore, there is evidence that this leads to greater per stem damage levels that subsequently cause stronger reductions of host-plant mass (e.g., Bach 1980, Carson and Root 2000, Long et al. 2003). Carson et al.'s (2004) review of the literature suggests this may be common in over 30 plant communities worldwide, particularly for long-lived perennial species that are vulnerable to repeated insect herbivore outbreaks.

Five community-level studies have tested the host concentration hypothesis (Table 2). Working in herbaceous old-field plant communities, Carson and Root (2000) and Long et al. (2003) found that insect herbivores (*Microrhoplala vittata, Trirhabda virgata*) attacked a dominant plant (the goldenrod *Solidago altissima*) and thereby reduced standing plant mass. Both studies showed that herbivore density and/or damage per *S. altissima* stem increased as *S. altissima* density increased. Long et al. (2003) further demonstrated herbivore control was a function of host-plant density: increases in herbivore load and damage per stem caused stronger reductions in goldenrod mass.

In contrast, Stiling and Moon (2005), Coupe and Cahill (2003), and Fagan and Bishop (2000) did not find support for the host concentration hypothesis. Stiling and Moon (2005) found that herbivore abundance and control did not significantly vary with the stem density of a dominant, widespread host plant, which they had manipulated independently of host tissue N and host plant size. Because the study was conducted in monoculture, it is unclear if herbivores will not respond to relative host stem density or if the non-significant main stem density effect also means that herbivores did not respond NPP (i.e., NPP probably increased with stem density). Irrespective, this study did not support the host concentration hypothesis. As described above, Fagan and Bishop (2000) and others (Bishop 2002) demonstrated that herbivores decrease community-level standing plant mass in diverse natural communities by attacking low-density patches of the host plant. This is the exact opposite pattern predicted by host concentration. Finally, Coupe and Cahill's (2003) meta-analysis found that plant species richness did not explain any variation in herbivore control over standing plant mass, suggesting that herbivore-host plant interactions are not more tightly coupled when host plants were concentrated (also see Borer et al. 2005).

In total, while there is evidence for a positive feedback between insect and host plant, there is little evidence that this mechanism will consistently lead to stronger herbivore control at high host concentrations. Only two studies, which were conducted in the same system, found evidence for the host concentration hypothesis. Except for Carson & Root 2000, however, this these studies have been short term and therefore they have not addressed the temporal component inherent to the resource concentration sub-hypothesis.

2.2.4 The plant size hypothesis

The plant size hypothesis states that absolute or relative plant size determines the strength of herbivore control over standing plant mass due to herbivory because relative plant size determines plant 'vigor' (Price 1991) or plant 'apparency' (e.g., Feeny 1975, 1976).

2.2.4.1 Plant vigor

This hypothesis assumes that herbivores prefer large, vigorous plants because plant size is strongly, positively correlated with plant quality (Price 1991). In addition, relatively large plants are assumed to allocate little to defenses because they invest more resources into growth (Price 1991). Finally, relatively large, vigorously growing plants are assumed to have a greater ability to regrow after experiencing herbivory compared to small plants (Price 1991). In total, this hypothesis is very similar to the resource availability hypothesis, in that vigor is an indication of both tolerance and plant quality. It differs from the resource availability hypothesis, because it makes no assumptions about resource availability gradients. It also does not make any assumptions about which plant trait determines plant quality (e.g., vigor can either be high tissue N or low plant defenses). Thus, the plant vigor hypothesis predicts plant quality increases with plant growth, which subsequently increases herbivore load and damage. The reduction in stem mass due to herbivory, however, is predicted to decrease as relative stem size increases, with plants strongly overcompensating at relatively large stem sizes.

2.2.4.2 Plant apparency

Large plants might also be more apparent to herbivores, particularly specialists, simply because they are relatively easily to find (e.g., Feeny 1975, 1976; also see Thompson 1994, 2005). This differs from the vigor hypothesis because herbivores are not responding to variation in plant quality associated with plant size. Though the original apparency hypothesis has an evolutionary component, which considers that apparent plants allocate more to defenses (see Stamp 2003), I do not consider this here. It is well recognized that apparency theory does not adequately or usefully describe patterns of plant defense allocation (reviewed in Stamp 2003). Hence, apparency, as described here, predicts that large stems, regardless of quality, will have greater herbivore density and damage per stem, which subsequently reduces stem mass.

2.2.4.3 Empirical evidence for the plant size hypothesis

Stem level evidence. Plant size often provides a good indicator of quality. For example, large vigorous stem or species often have relatively higher tissue N and low defenses (see Waring and Cobb 1992, Wilkens et al. 1996, Reich et al. 1999, Forkner and Hunter 2000, Ruel and Whitham 2002, Kursar and Coley 2003, Shipley et al. 2005). In addition, herbivores often preferentially attack larger, rapidly growing stems or species that can compensate for lost tissue (e.g., Coley et al. 1985, Price 1991, Feller 1995, Forkner and Hunter 2000, Price et al. 2004, Nakamura et al. 2006). There are also examples where vigorous plant species vastly under compensate for tissue lost to herbivores (e.g., Ruel and Whitham 2002, Letourneau et al. 2004). Thus, there are patterns that fit both the vigor and apparency sub-hypotheses. There are some cases where insects do not discriminate based on plant size, or even prefer small, less vigorous stems, which occurs when herbivore phenology is decoupled from periods of high variation in plant size (e.g., insects emerge prior to bud-break: Price et al. 2004) or when there are significant ecological costs to selecting the most vigorous stems (e.g., predators: Moon and Stiling 2006).

Unfortunately, authors often simply showed a positive correlation between plant quality or plant size and herbivore density, performance, or damage (e.g. Goranson et al. 2004). Other studies considered both the vigor hypothesis and an alternative hypothesis (e.g., plant defenses) as potential explanations for their results (e.g., Letourneau et al. 2004). The alternative hypothesis, however, was often based on a plant trait (e.g., defenses) that is correlated with plant size. Because they vigor hypothesis considers that any aspect of quality can be positively correlated with plant size (Price 1991), these studies are not actually considering alternative hypotheses. In addition, the vigor hypothesis is sometimes used to explain why large, vigorously growing stems experience stronger reductions in mass by herbivores (e.g., Ruel and Whitham

2002, Letourneau et al. 2004). This, however, clearly contradicts the plant vigor hypothesis, which predicts that, despite higher load and damage on vigorous plants, vigorous plants should over-compensate (Price 1991). In total, stem-level patterns typically support the plant size hypothesis but there is a good deal of confusion regarding its application.

Community-level evidence. One community-level study considered the plant size hypothesis (Table 2). Fagan and Bishop (2000) and Bishop (2002) demonstrated that herbivore damage and densities were highest on lupine stems located in low stem density patches. More recently, Fagan et al. (2004) demonstrated that nutrient concentrations of low-density lupine are high, which has a positive effect on herbivore performance. Although Fagan et al. (2004) considered the plant vigor hypotheses (Price 1991), they concluded the positive effect of tissue quality on herbivore performance was better explained by nutrient-based quality hypotheses (e.g., White 1984). In total, despite evidence at the stem level, there are no community-level studies that have concluded their results supported the plant size hypothesis.

2.3 THEORETICAL AND EMPIRICAL SUMMARY

Despite an abundance of well-cited hypotheses linking herbivore density and damage to patterns of standing plant mass, these hypotheses can be classified into one of four central hypotheses (Table 1). This synthesis highlights several important patterns that have not been made clear by previous reviews (Power 1992, Strong 1992, Polis 1999, Chase et al 2000a,b, Schmitz et al. 2000, Halaj and Wise 2001, Shurin et al. 2002, Borer et al. 2005).

2.3.1 A call for experiments to simultaneously test multiple herbivore control hypotheses.

Current theory expects that patterns of herbivore control can be explained by the response of herbivore density and damage to five vegetation characteristics (Table 1): productivity (i.e., NPP hypothesis), plant tolerance and tissue quality (i.e., resource availability hypothesis), stem density (i.e. host concentration hypothesis), and plant size (i.e., the plant size hypothesis). While these are not mutually exclusive (e.g., tolerance is a component of NPP, resource availability, and plant size hypotheses), each of these hypotheses predicts that herbivores respond to different vegetation characteristics. Therefore, theoretical progress requires that we first empirically determine the relative importance of these vegetation characteristics for explaining herbivore density and damage to plants. Next, empirical studies need to determine if herbivore responses to vegetation characteristics are linked to patterns of herbivore control since patterns of herbivore abundance and damage can be decoupled from patterns of herbivore control, as with the plant tolerance sub-hypothesis (Table 1).

Unfortunately, previous experimental approaches prevent us from assessing the relative importance of these vegetation characteristics. Experiments typically considered a single hypothesis (Table 2). Those studies that did consider multiple hypotheses either did not explicitly describe or contrast the alternative predictions (e.g., Moran and Scheidler 2002), incorrectly supported hypotheses (e.g., Stiling and Moon 2005, Letourneau et al. 2004) or actually considered a single hypothesis (e.g., Letourneau et al. 2004). Only two studies were designed to explicitly test multiple herbivore control hypotheses (Coupe and Cahill 2003, Stiling and Moon 2005; also see Dyer and Coley 2001, Borer et al. 2005 for insect herbivore & non-insect herbivore examples). Finally, the vast majority of studies used experimental fertility gradients or plots located along standing plant density or resource availability gradients without controlling for other gradients (e.g., host concentration) thought to affect herbivore density and damage (Table 2).

The above problems stem from the trend of testing for blanket ‘bottom-up effects’ relative to ‘top-down effects’ (e.g., Forkner and Hunter 2000, Denno et al. 2002). This prevents researchers from rigorously testing alternative herbivore control hypotheses. For example, Denno et al. (2002) state that they manipulated fertility because it increases tissue nutrients, but make predictions referring to both tissue nutrients and productivity, and then use NPP and tissue quality interchangeably throughout the explanation of their results. Other studies conclude that herbivore density or damage was controlled by either NPP or plant quality, citing previous evidence that herbivores are known to respond to productivity or tissue N (Table 2). The cited supporting evidence, however, is often equally ambiguous. For example, Waring and Cobb’s (1992) extensive literature review of fertilization studies is widely cited as evidence that herbivores respond to tissue N (e.g., Fraser and Grime 1999, Moon and Stiling 2005). Waring and Cobb (1992) did show that tissue N was correlated with herbivore performance, but they also showed that plant growth was a better estimate of herbivore performance than tissue N (Waring and Cobb 1992: Table 2 and 5). I note that Waring and Cobb (1992) highlighted that few studies also considered the effect of resources on allocation to plant defenses.

Even when studies did experimentally control for multiple vegetation characteristics, they did not discuss or recognize its importance. For example, Moon and Stiling (2006) tested the plant vigor hypothesis (Price 1991), which predicts that there should be a positive correlation between plant size and quality, which subsequently causes herbivore density and damage to increase with plant size. They previously demonstrated, however, that the same herbivore species responded to the quality of the same host plant independent of host plant size (Stiling and Moon 2005). In other words, despite that these authors already provided one of the best studies to date demonstrating that herbivores actually tracked plant tissue quality independent of host plant size, they went on to test the plant vigor hypothesis, indicting that they do not realize the importance of their initial findings and how they relate to the plant vigor hypothesis.

In total, empiricists have provided very weak explanations for the observed patterns in herbivore density and damage. Even when an experiment finds a pattern of herbivore control that matches the prediction of a given herbivore control hypothesis, it is unclear if herbivores are responding to the vegetation characteristic under study or one confounded with it. Progress requires that empiricists clearly define plant quantity, plant quality, and 'bottom-up effects' and provide explicit, alternative hypotheses. Designing experiments to test those predictions will be challenging, but is not impossible. Given the clear need to explicitly test multiple herbivore control hypotheses, I suggest several additional steps below that may help to develop a more rigorous and informative approach to explaining patterns of herbivore control.

2.3.2 Scale dependent relationships between vegetation characteristics and herbivore control.

The relationships between herbivores and vegetation characteristics such as NPP, stem density, plant size and tissue quality, are likely to be scale dependent (see McGeoch and Price 2005). First, patterns of herbivore control might result from herbivores responding to any of these vegetation characteristics at the stem, plant population, or the plant trophic level. For example, herbivores might not respond to NPP, but they might respond to the productivity of a single host plant or the mean stem productivity of a plant community. Alternatively, herbivores might not respond to host stem density, but they might respond to total stem density. Therefore, empiricists should test these possibilities.

Second, patterns of herbivore control are expected to result from herbivores responding at the individual, population, or trophic levels (Table 1). Knowing what aspect of herbivore demography was observed is critical because herbivore responses at one level (e.g., individual foraging behavior) do not always accurately describe patterns of herbivore density and damage at another level (e.g., population level; Otway et al. 2005, McGeoch and Price 2005). Some authors address this problem by describing their test as being conducted in either an open food web, where variation in herbivore control is driven by immigration and emigration rates, vs. a closed food web, where variation in herbivore control is driven internally by herbivore birth, growth, and death rates (Table 2). Other authors do not provide this information (Table 2), which makes it difficult to determine if appropriate measures of herbivore density were used. If the food web is open, the measure that describes foraging behavior is the number of herbivore foraging incidences, not a measure of herbivore mass density, which obscures individuals and confounds foraging with somatic and reproduction (e.g., Wootton and Power 1993, Oksanen et al. 1995).

Finally, many studies are conducted over short time periods, which may not be adequate to observe the patterns predicted by several of these hypotheses (e.g., host concentration). Thoughtful consideration of these issues will provide a more in depth picture of patterns of herbivore control as it might reveal consistent scale dependent relationships between herbivore demographic parameters and vegetation characteristics.

2.3.3 Vegetation characteristics and herbivore diet breadth

Herbivore control hypotheses expect that herbivore diet breadth will typically determine whether herbivores respond to a given vegetation characteristics (Table 1). Many studies, however, were conducted in food webs that included diverse herbivore assemblages (Table 2). Some studies get around this issue by assembling food webs with herbivores that have specific diet breadth (e.g., Schmitz 1993, 1994, Fraser and Grime 1998, 1999). Indeed, this approach has been extremely informative to theory (Schmitz 2004). Natural herbivore communities, however, have a range of herbivore diet breadths, and these herbivores can respond in different directions to different vegetation characteristics (e.g., Ritchie 2000, Huberty and Denno 2005, Dyer et al. 2004). Dyer and colleagues (Dyer and Coley 2001, Letourneau et al. 2004, Dyer et al. 2004) have studied trophic interactions in natural, complex food webs and have demonstrated that herbivore diet breadth determines whether herbivore performance and rates of herbivory respond to plant defenses, and that these differences bear on patterns of herbivore control. Thus, studies that simultaneously test multiple herbivore control hypotheses should first test the underlying assumption that herbivores of different diet breadths respond to different vegetation characteristics (see chapter 2). Testing this consumer diet breadth hypothesis would demonstrate that, given that the key vegetation characteristics are experimentally manipulated, there is sufficient variation in herbivore diet breadth to fairly test alternative herbivore control hypotheses.

2.4 CONCLUSIONS

There is a growing call for experiments to test general theories that predict the relative importance of vegetation characteristics for determining the strength of top-down control by insect herbivores (e.g., Moon et al. 1999, Mulder et al. 1999, Dyer and Coley 2001, Long et al. 2003, Dyer et al. 2004, Borer et al. 2005). This arises from the inability to determine causal mechanisms that regulate plant-herbivore interactions because key vegetation characteristics (i.e. productivity, tissue quality, plant tolerance, host concentration, plant size) are often confounded. The available empirical studies have not met this challenge (but see Stiling and Moon 2005). This review suggests that theoretical progress can be made by studies designed to simultaneously test a few central hypotheses and by thoughtful consideration of (1) the scale at which herbivores interact with vegetation characteristics and (2) the role of herbivore diet breadth.

Table 2.1 A summary of herbivore control hypotheses

This table describes the four central hypotheses (NPP, resource availability, host concentration, and plant size) and their sub-hypotheses (e.g. the resource controlled NPP sub-hypothesis). For each sub-hypothesis, the key assumptions are listed, namely herbivore diet breadth (e.g., polyphagous), the vegetation character (e.g., productivity) affecting herbivore abundance and damage, and the biological scale at which herbivores respond to that vegetation character (e.g., trophic level). Finally, the gradients (e.g., NPP) used by each sub-hypothesis to predict responses (● = no change as gradient increases, △ = increases, ▽ = decreases) of herbivore abundance, herbivore damage, and the reduction in plant mass.

						Predictions for insect herbivore		
	Sub-hypothesis	**Diet breadth†**	**Vegetation character**	**Scale of herbivore response**	**Gradient**	**Abundance**	**Damage**	**Reduction plant mass**
NPP	Resource controlled	P	Productivity	Trophic level, individual	NPP	△	na	●
	Consumer controlled	P			NPP	● or △	na	△
	Heterogenous	P			NPP	△	na	▽
Resource availability	Tolerance	M, O, P	Regrowth	na	Light / fertility	na	na	▽**
	Tissue quality	M, O, P	Nutrition	Individual, population	any resource	If ▽	or ▽	then ▽
						If △	or △	then △
		P > M, O	Defenses	Individual, population	Nutrients	na	convex	▽*
					Light	na	▽	▽*
					Stem m^{-2}	na	▽sigmoid	△*

Table 2.1 (continued)

Host Concentration	Resource concentration	M	Stem density	Individual, population	# or % host stems m^{-2}	△	△	△
	Janzen-Connell	M	Stem density		# or % host stems m^{-2}	△	△	△
	Reticulate Foodweb	M, O, P	Host Abundance		Diversity	na	▽	▽
Plant Size	Plant Apparency	M > O, P	Stem size	Individual	Stem size	△	△	△
	Plant Vigor	M, O, P	Stem size		Stem size	△	△	▽**

† M = monophagous, O = oligophagous, P = polyphagous

* compensate or ** overcompensate at high end of the gradient

Table 2.2 Empirical studies of insect herbivore control over plant community mass

For each study, the central hypothesis tested (reviewed in Table 2.1) is indicated (e.g., NPP), the type of plant community (e.g., closed, polyculture), and the diet breath of the herbivore(s). Also listed are the type of manipulations used to test the hypothesis, alternative explanations the authors could statistically rule out (e.g., plant diversity), and the conclusions drawn by the authors regarding what controlled herbivore density, damage, and control over plant biomass.

						Conclusion* about herbivore	
Hypo-theses*	**Citation**	**System†**	**Diet breadth‡**	**Manipu-lation§**	**Statistically ruled out§**	**Density or damage**	**Control over plant biomass**
NPP	Schmitz 1993	Pc	P	Fertility		NPP	NPP
NPP	Schmitz 1994	Pc	P	Fertility		NPP	NPP
NPP	Fraser & Grime 1997	M/P?	M,O,P	Site		NPP	NPP
NPP	Fraser 1998	M/P?	M,O,P	Site		NPP	NPP
NPP	Fraser & Grime 1998	Pc	P	Fertility		NPP	NPP
NPP	Fraser & Grime 1999	Pc	P	Fertility		NPP	NPP
NPP	Schädler et al. 2003	M/Po	M,O,P	Site			not NPP
NPP	Uriarte & Schmitz 1998	Pc	M,O,P	Site			NPP
NPP, RA	Moran & Scheidler 2002	P?	M,O,P	Fertility	H’	NPP	NP
NPP, RA	Denno et al. 2002	Mo/c	M	Fertility Litter		NPP/RA	HC
NPP, HC	Coupe & Cahill 2003	M/Pc	M,O,P	Site, H’			not NPP or HC
RA, PS	Letourneau et al. 2004	Po	M,O,P	Site		PS	not RA or PS

Table 2.2 (continued)

HC, RA	Stiling & Moon 2005	M?	M	Fertility, HSD	PS, HSD	RA	RA
HC	Carson & Root 2000	Po	M			HC	HC
HC	Long et al. 2003	P?	M	Litter		HC	HC
HC, RA, PS	Fagan and Bishop 2000 Bishop 2002 Fagan et al. 2004	P?	M	Site		RA	RA

* Authors considered the following hypotheses: NPP = net primary productivity; RA = resource availability; HC = host concentration; PS = Plant size

† M= monoculture, P = polyculture; c = closed (i.e., herbivore response driven by birth, growth, & death); o = open (i.e., herbivore response driven by herbivore foraging); ? = unclear

‡ M = Monophagous; O = oligophagous (feeding on species within a genus); P = polyphagous.

§ To test the hypothesis, each study manipulated either herbivores and/or predators and: Fertility (experimental manipulation of soil nutrients), Site (plots located along a natural standing plant density or resource gradient), H' (plant diversity), Litter, or HSD (host stem density).

3.0 PREDICTING INSECT HERBIVORE ABUNDANCE ALONG VEGETATION GRADIENTS: EXPERIMENTAL FIELD TESTS OF THE CONSUMER DIET HYPOTHESIS

By James Patrick Cronin

ABSTRACT

Trophic interaction hypothesis assume that herbivore diet breadth (e.g., specialist vs. generalist) determines which vegetation characteristics will control herbivore abundance, diversity, and the strength of herbivore control over plants. Therefore, I tested the diet breadth hypothesis, which states that herbivore diet breadth (e.g. specialist vs. generalist) determines which resource characteristics explain herbivore abundance. This hypothesis predicts that specialist herbivores respond to host plant characteristics (e.g., stem density, productivity, and tissue quality) and generalist herbivores respond to community-level vegetation characteristics (e.g., total stem density, net primary productivity, community-level plant tissue quality, and diversity). Critical tests of this hypothesis are lacking because the key host plant characteristics and key community-level characteristics that are required to test this prediction are highly correlated and thus typically confounded in empirical studies. I experimentally tested the consumer diet breadth hypothesis by simultaneously manipulating fertility, total stem density, and species composition in old-field vegetation dominated by *Solidago* spp. and *Aster* spp. for two years and recording the abundance of naturally colonizing insect herbivores. I classified insect herbivore species as monophagous (i.e., feeding on *S. canadensis*), oligophagous (i.e., feeding on *Solidago* spp.), or polyphagous (i.e., feeding on *Solidago* spp. and *Aster* spp.). The abundance of monophagous insects was weakly explained by *S. canadensis* (i.e., host plant) characteristics. The abundance of oligophagous herbivores was strongly explained by a ratio of mean non-*S. canadensis* stem

mass of mean *S. canadensis* stem mass. The abundance of polyphagous herbivores was weakly explained by the community-level characteristic of total stem density. Thus, these results provide some support the consumer diet breadth hypothesis: as herbivore diet breadth increased, herbivore abundance responded more strongly too community-level vegetation characteristics. The host and community-level vegetation characteristics, however, explained little variation in monophagous and polyphagous herbivore abundances, respectively. Therefore, I discuss the utility of diet breadth for explaining variation in herbivore abundances along vegetation gradients. I conclude that the diet breadth mechanisms that currently define trophic interaction hypotheses might not predict patterns of insect herbivore diversity and control over plant communities and suggest alternative herbivore traits (e.g., feeding guild, body size) and demographic parameters (e.g., probability of occurrence) that might provide better explanations for patterns of herbivore abundance, herbivore diversity, and herbivore control over plant communities.

3.1 INTRODUCTION

Trophic interaction hypothesis often assume that herbivore diet breadth (e.g., specialist vs. generalist) determines which vegetation characteristics will control herbivore abundance, diversity, and the strength of herbivore control over plants. For example, specialist herbivore abundance is often predicted to increase with particular characteristics of host plants, such as host stem density, host productivity, and host tissue quality (e.g., Janzen 1970, Connell 1971, Root 1973, White 1984, Long et al. 2003, Joshi et al. 2004, Carson et al. 2004). Consequently, many trophic interaction hypotheses based on specialist herbivores predict that increasing plant species richness will increase herbivore diversity but decrease herbivore control over plant communities (Abrams 1995, Siemann 1998, Haddad et al. 2001, Long et al. 2003, Carson et al. 2004). In contrast, generalist herbivore abundance is often predicted to increase with particular characteristics of whole plant communities, such as total stem density, net primary productivity (NPP), or total plant quality (e.g., Oksanen et al. 1981, Holt et al. 1994, Leibold 1996, Wootton and Power 1993, Chase et al. 2000, Haddad et al. 2001, Joshi et al. 2004). Consequently, many trophic interaction hypotheses based on generalist herbivores predict that increasing total plant abundance will increase herbivore diversity and potentially alter herbivore control (Abrams 1995, Siemann 1998, Chase et al. 2000). I refer to these contrasting responses of generalists and specialists as the consumer diet breadth hypothesis whereby specialist consumers respond to host characteristics vs. generalist consumers that respond to community-level characteristics.

Empirical tests of the consumer diet breadth hypothesis are extremely difficult because the key host plant and community-level characteristics are highly correlated and thus typically confounded in field studies (e.g., see Moon et al. 1999). For example, increasing soil nitrogen in terrestrial systems increases net primary productivity but can also change plant tissue quality, host concentration, and total stem density (see White 1984, Tilman and Pacala 1993, Waide et al. 1999, Mittelbach et al. 2001, Stevens and Carson 1999a,b, Haddad et al. 2001, Throop and Lerdau 2004). Despite this, the vast majority of relevant studies have focused on the effects of a single host plant or community-level characteristic (e.g., Risch et al. 1983, Andow 1991, Yamamura 2002, Rhainds and English-Loeb 2003). Although more recent studies have simultaneously tested the effects of two or more host or community-level characteristics on herbivore abundances, these studies were observational or did not investigate the effects of host plant characteristics vs. community-level characteristics on herbivore species with different diet breadths (e.g., Jonsen and Fahrig 1997, Siemann 1998, Siemann et al. 1999, Knops et al. 1999, Koricheva et al. 2000, Steffan-Dewenter and Tscharntke 2000, Symstad et al. 2000, Haddad et al. 2001, Richardson et al. 2002, Pfisterer et al. 2003, Stiling and Moon 2005, Perner et al. 2005, Otway et al. 2005, Östergård and Ehrlén 2005). Thus, we currently lack studies that simultaneously test the independent effects of key host vs. community-level characteristics on the abundance of consumers with different diet breadths.

I experimentally tested the consumer diet breadth hypothesis using a combination of stem density, fertility, and species composition treatments to independently manipulate key community characteristics (i.e., total plant tissue quality, total stem density, NPP) vs. key host characteristics (i.e., host tissue quality, absolute and relative host stem density and productivity). Next, I recorded the abundance of naturally colonizing herbivores and I assigned a subset of these herbivores to three different diet breadth classes based on their host associations in the experiments: monophagous on the host plant *Solidago canadensis*, oligophagous on *Solidago* spp., or polyphagous on *Solidago* and *Aster* spp. I then tested whether host characteristics or community level characteristics explained the abundance of each diet class. By comparing the results for each diet class, I determined whether herbivores responded to community-level characteristics as diet became more generalized. Of course, other factors have also been hypothesized to determine herbivore abundance, namely species diversity (e.g., Strong 1992), predators (e.g., Schmitz 2003, Singer and Stireman 2005), plant size (e.g., Rhoades 1979, Price 1991), and the abundance of inedible stems (e.g., Holt et al. 1994). Therefore, I quantified how these variables naturally varied along the experimental gradients and determined whether they also contributed to the abundance of different herbivores.

3.2 METHODS

3.2.1 Model system and experimental design

I conducted this study at the University of Pittsburgh's Pymatuning Laboratory of Ecology (Crawford Co, Pennsylvania, USA) in an early successional old-field dominated by *Solidago canadensis* where other *Solidago* and *Aster* spp. were also common (see Table 3.1 for plant species composition and relative abundance). *S. canadensis* is a native, herbaceous, clonal perennial that dominates (~30-40 stems m^{-2}) old-fields throughout the eastern United States and Canada (Werner et al. 1980, Carson and Root 1999). Both insect herbivore and arthropod predators have been well studied in old-fields (see Root and Cappuccino 1992, Schmitz 2003). The herbivore community was dominated by Dipterans (e.g., Agromyzidae, Cecidomyiidae) and Lepidopterans (e.g., Lyonetiidae, Tortricidae) and was typical of old-fields in the northeast (USA) in terms of species composition, dominance rankings, and guild structure (Tables 3.2, 3.3). Common arthropod predators included spiders (e.g., Gnaphosidae, Thomisidae, Pholcidae) and ladybird beetles (Coleoptera: Coccinellidae).

My goal was to experimentally create major gradients in host stem density, host productivity, and host tissue quality that were independent of community-level gradients in total stem density, net primary productivity, and tissue quality. Therefore, I experimentally manipulated fertility, stem density, and species composition in two full-factorial experiments: The Monoculture Experiment (left half of Fig. 1a) and The Polyculture Experiment (right half of Fig. 1a). In both experiments, I manipulated plant density in $4m^2$ plots at four levels: 8, 16, 24 or

32 stems m^{-2} (as depicted across the bottom in Fig. 1a). In monocultures, every stem was *Solidago canadensis*. As the absolute abundance of *S. canadensis* increased in monoculture, its relative abundance was of course always 100% (as depicted across the top of the monoculture half of Fig. 1a). In contrast in polyculture, *S. canadensis* stems m^{-2} was held constant at 8 stems m^{-2} as total stems m^{-2} increased. Consequently, as shown across the top of the polyculture half of Fig. 1a, *S. canadensis*' relative abundance declined (100% - 25%) in polyculture as total stems m^{-2} increased. In addition, as shown on the left side of Fig. 1a, I crossed these density treatments with three fertility levels. Finally, the right side of Fig. 1a shows that half of the plots were sprayed with insecticide so that I could estimate plant productivity (and quantify herbivore impact on mean stem mass, see Chapter 4.0).

I established this design in spring 2003 by selecting 294 $4m^2$ plots from 600 plots containing old-field vegetation (Fig. 1b). To ensure all plots were of similar quality, I only selected plots of moderate extant *S. canadensis* stem density and that were similar in height (*unpublished data*, JP Cronin). Thus, my results are not due to confounding historical differences in plot quality with treatment effects. The selected plots were thinned to appropriate densities and fertilized. Neighboring plots were paired and randomly assigned the following treatments:

Spray. During the growing season, I applied esFenvalerate, a synthetic pyrethroid, at recommended application rates every 7-10 days. The use of insecticides in general, and esFenvalerate in particular, has been previously justified in detail (Root 1996, Carson and Root 2000, Siemann et al. 2004).

Fertility. I applied a slow release fertilizer (Osmocote, [The Scotts Company, Marysville, Ohio]; 8:6:12 NPK), half in May and half in June, at a rate and a ratio similar to other old-field studies (Tilman 1987, Carson and Pickett 1990, Stevens and Carson 1999a). I fertilized evenly across the 4, $1m^2$ quadrants at 0g, 8g, or 16g N m^{-2} per year.

Stems m^{-2}. Plots were divided into 16, $0.25m^2$ subplots and repeatedly weeded during the growing season, leaving weeded mass in the plot. In polycultures, I kept other forbs in the plots in addition to *S. canadensis*. I kept only perennial plant species that were common throughout the site (Table 3.1) in order to minimize both among plot variation in non-*S. canadensis* plant species composition and within season stem turnover. I haphazardly assigned non-*S. canadensis* species to stems within each $0.25m^2$ subplot by keeping the stem of every third acceptable species (i.e., common perennials) encountered, without species replacement, until the treatment stem density was reached.

General Site Condition. In spring 2003, I repeatedly mowed a 3-5 m buffer between plots to eliminate *S. canadensis* and other tall forbs from the buffer zones. The width of this buffer is well beyond the length of the vast majority of rhizomes in these communities (Cain et al. 1991, Bazzaz 1996). By late summer of 2003, my 4m^2 experimental patches were scattered throughout a matrix of mowed vegetation that was devoid of *S. canadensis*, dominated by forbs and perennial monocots, and fenced to exclude large vertebrates (mainly white-tailed deer, *Odocoileus virginianus*).

3.2.2 Response variables

3.2.2.1 Vegetation characteristics

In August of 2003 and 2004, I recorded the identity and size of each stem in the center 1m^2 of each plot. Species-specific allometric regressions of mass on size (Table 3.1) were then used to estimate aboveground mass for each stem. I used allometry rather than harvesting because harvesting would have changed the treatment densities. Although final mass estimates do not precisely quantify plant growth or NPP, my plots were composed of perennial species that emerge in early spring, persist well into September, senesce all aboveground mass in the fall, and were maintained at specific densities. Furthermore, previous studies have shown that single point estimates accurately capture relative differences in productivity (e.g., Tilman 1987, Inouye et al. 1987, Carson and Pickett 1990). Thus, my mass estimates should adequately describe relative differences in plant productivity.

3.2.2.2 Herbivore abundance

Herbivore sampling protocol followed that of Root and Cappuccino (1992), which was specifically designed for *Solidago* dominated old-fields. In mid- to late June, when herbivore activity is at its highest, I sampled ~2 *S. canadensis* stems in each of the 16, 0.25m^2 subplots. In polyculture, I sampled an additional ~2 non-*S. canadensis* stems per subplot. I searched each stem for insect herbivores (and predators). Herbivore-host association data allowed 42% of the herbivores sampled to be classified into one of three diet categories (Table 3.2; also see Root and

Cappuccino 1992). Insect species were classified as monophagous on *S. canadensis* if >95% of the individuals were found only on *S. canadensis* (Table 3.2). Insect species that were sampled on just *Solidago* spp. (23.8% of stems, Table 3.1) were classified as oligophagous (see Table 3.2). Insect species that were sampled on *Solidago* and *Aster* spp. (50.7% of stems, Table 3.1) were considered polyphagous (see Table 3.2).

3.2.3 Testing the herbivore diet breadth hypothesis

Because I experimentally controlled the stem density of *S. canadensis* in both monocultures and polycultures, I was able to manipulate host plant characteristics independent of community-level characteristics. I focused on the response of herbivore abundances to three key vegetation characteristics:

3.2.3.1 Host stem density vs. total stem density

Specialist herbivores are predicted to increase with absolute or relative host stem density (reviewed in Carson et al. 2004). If herbivores that specialize on *S. canadensis* respond to absolute *S. canadensis* stem density, their abundance in monoculture will increase as *S. canadensis* stem density increases. In contrast, because *S. canadensis* absolute stem density remains constant in polyculture (Fig. 1a), specialist herbivore abundance on *S. canadensis* in polyculture will stay constant as total stem density increases in polyculture. On the other hand, if *S. canadensis* specialists respond to relative *S. canadensis* stem density, their abundance will stay constant in monoculture as *S. canadensis* stem density increases. In polyculture, however, if *S. canadensis* specialists respond to relative host stem density, their abundance on *S. canadensis* in polyculture will decline as total stem density increases in polyculture (i.e., as *S. canadensis* relative stem density decreases, Fig. 1a).

The diet breadth hypothesis predicts that, as diet breadth increases, herbivores will respond to community-level vegetation characteristics because these herbivores are assumed to respond to all plant species. If so, then polyphagous herbivore abundance (i.e., herbivores that feed on *Solidago* spp. and *Aster* spp.) is predicted to increase as total stem density increases in both monoculture and polyculture (*Solidago* spp. and *Aster* spp. constituted 74% of the non-*S. canadensis* stems, Table 3.1). Because oligophagous herbivores do not feed on just *S.*

canadensis, or on 76% of the non-*S. canadensis* stems in the polycultures (Table 3.1), I predicted there would be no or weak correlations between total stem density and oligophagous herbivore abundances. Thus, I first looked for significant correlations between total stem density and measures of herbivore abundance for each diet class, (while controlling for other key factors thought to influence herbivore abundance: see *Statistical Analyses* below). I then compared the monoculture results to the polyculture results to determine if herbivores were responding to either absolute or relative *S. canadensis* stem density or total stem density.

3.2.3.2 Host productivity vs. net primary productivity

Specialist herbivores are also predicted to increase with absolute or relative host productivity (see Chapter 4.0). If specialist herbivores respond to absolute host productivity, then their abundance will increase with total mass m^{-2} in monoculture but will not increase with total mass m^{-2} in polyculture. On the other hand, if specialist herbivores respond to relative host productivity, then their abundance will not vary with total mass m^{-2} in monoculture (where relative *S. canadensis* productivity was held constant: Fig. 1a) but will decline on *S. canadensis* in polyculture as total mass m^{-2} increases (or increase as the % *S. canadensis* mass m^{-2} increases).

As diet breadth increases, herbivores are predicted to respond to NPP rather than the productivity of a single host plant (e.g., Holt et al. 1994, Leibold 1996). If so, then polyphagous herbivores will increase with total mass m^{-2} in both monoculture and polyculture. Because oligophagous herbivores do not feed on just *S. canadensis*, or on 76% of the non-*S. canadensis* stems in the polycultures (Table 3.1), I predicted there would be no or weak correlations between total mass m^{-2} and oligophagous herbivore abundance. Thus, I looked for correlations between total mass m^{-2} (or % *S. canadensis* mass m^{-2} in polyculture) and measures of herbivore abundance for each diet class (again, while statistically holding constant a suite of other key factors thought to influence herbivore abundance, see *Statistical Analyses* below). I then compared the monoculture results to the polyculture results to determine if herbivores were responding to either absolute or relative *S. canadensis* productivity or NPP.

3.2.3.3 Host tissue quality vs. Community-level tissue quality

Specialist herbivores are also predicted to respond to host plant tissue quality (e.g., White 1984, Throop and Lerdau 2004). Plant tissue quality (i.e., tissue N, plant defenses) changes as soil nitrogen increases and this can either positively affect herbivores (e.g. Mattson 1980, Ritchie 2000, Stiling and Moon 2005, Throop and Lerdau 2004) or negatively affect herbivores (e.g., Mattson 1980, Throop and Lerdau 2004). Higher tissue N is predicted to have positive affects on herbivore abundance and consumptions rates if herbivores always attempt to acquire more nitrogen. In contrast, higher tissue N can also reduce herbivore abundance or consumption when tissue N either exceeds optimal levels for herbivores. Finally, the effect of nutrient availability on growth-differentiation trade-offs is predicted to cause plant defenses to peak at intermediate fertility levels (Herms & Mattson 1992, Stamp 2003, Stamp et al. 2004).

Because of these herbivore responses to the effects of fertility on tissue N and plant defenses, I predicted that specialist herbivore abundance in both monoculture and polyculture would significantly vary on *S. canadensis* as fertility increased. As diet breadth increases, however, herbivores are predicted to respond to community-level plant tissue quality of all plant species (e.g., Haddad et al. 2001, Joshi et al. 2004). Therefore, I predicted that polyphagous herbivore abundance would significantly vary with fertility in monoculture, on *S. canadensis* stems in polyculture, and on non-*S. canadensis* stems in polyculture (74% of which were *Solidago* spp. and *Aster* spp.). Finally, I predicted that oligophagous herbivore abundance would also significantly vary with fertility because of the effect of fertility on the tissue quality of *Solidago* spp. in both monoculture and polyculture.

Although fertility universally alters plant quality by increasing tissue nitrogen content in plants or altering plant defenses (Ayers 1993, Throop and Lerdau 2004, Stamp 2003), I acknowledge that fertility also alters plant productivity. I, however, was able to use fertility as a proxy for plant tissue quality because I controlled for the effect of fertility on plant productivity by including mean stem mass and NPP in my statistical models (see *Statistical Analyses* below). Thus, by comparing the monoculture results to the polyculture results, I determined if herbivores were responding to either *S. canadensis* or total plant quality.

3.2.3.4 Other factors

To evaluate whether other factors were important in determining herbivore abundances, I also calculated final mean stem mass (i.e., a proxy for plant vigor [Price 1991] and plant apparency [Feeny 1975, 1976]), plant species diversity using Shannon's Diversity Index (H', Molles 1999), a ratio of mean non-*S. canadensis* stem mass / mean *S. canadensis* stem mass (as a measure of the plant apparency), percent inedible stems m^{-2} (e.g., Holt et al. 1994, Leibold 1996), and the number of predators per plot (e.g., Schmitz 2003).

3.2.3.5 Statistical analyses

To test for correlations between herbivore abundance, herbivore damage, or herbivore control and the gradients, I separately analyzed the monoculture, polyculture community-level, S. canadensis in polyculture, and non-S. canadensis stems in polyculture. Analyses are based on year 2, when my experiments were fully established. I constructed mixed models that included both fixed treatment effects and random effects. All treatment effects were considered fixed while all unmanipulated but measured effects were considered random (Table 4.4). A variety of transformations of response variables were used to meet the assumptions of linear mixed models (Sokal and Rohlf 1999; *see Results*). Mixed model regression analysis was performed using JMP's (5.0.1.2) mixed model REML procedure. These analyses produced mean squares estimates for fixed effects and variance components for random effects. Percentages of variance explained (i.e., r^2s) can only be calculated on fixed effects and not on random effects. Therefore, in keeping with mixed model conventions, the ANOVA tables report F-ratios and associated r^2s for fixed effects while Variance Components are reported for random effects (JMP 5.0.1.2). In addition, 'Percents of Total' (where $\% = VC_i / \sum VC_{ij}$) are also reported for random effects (JMP 5.0.1.2). Note that r^2 values, which are calculated using sum of squares, estimate the proportion of the total variance explained by a fixed effect (Sokal and Rohlf 1999). The % value for a random effect, however, is calculated as the ratio of the random effect in question divided by the summed random effects and their residual only (JMP 5.0.1.2). Since % values are not estimates of the proportion of the total variance explained by a random effect, % values should not be compared to r^2 values or considered an estimate of the total variance explained (JMP 5.0.1.2). The % values should only be used to compare the relative magnitude among random effects.

For many random effects, the REML procedure either resulted in a negative variance component estimate or failed to estimate the 95% confidence interval. Both cases are commonly discussed in the statistical literature and are indicative of numerical instabilities that may arise when the true variance component is zero (i.e., when x explains no variation in y and therefore x does not contribute to the fit of the model: Smith and Murray 1984, Searle et al. 1992, Gould and

Nichols 1998, JMP 5.0.1.2). A statistically acceptable solution is to remove the offending random effects (justified since the variance component is zero anyway) and re-run the model (Searle et al. 1992). If a random effect is listed in Table 4.4 but is not shown for an analysis reported in an ANOVA table, that random effect was removed from that analysis because its variance component estimate indicated that it did not contribute to the fit of the model. I validated models reduced in this way, however, based on goodness-of-fit tests and likelihood ratio tests (Sokal and Rohlf 1999), which tests for lack of significant reduction in explanatory power of the model when the effect is removed relative to the inclusive model. Correlations among predictor variables (Appendix A), however, indicated caution in deciding what variable to remove in these cases. Therefore I further validated the REML results by re-testing the variance components for the offending random effects using a variety of models. These included models that only contained the offending random effect. I also examined models in which correlated random effects were removed but the offending effect left in the model, in case this would result in variance shifting from the correlated random effect to the offending random effect. Finally, I ran models with only the offending random effect and the full set of fixed treatment effects. The vast majority of models that contained random effects either did not explain any variation in response variables, or explained little variation relative to the fixed effects (*unpublished data*, JP Cronin). There were cases where a model that only contained the offending random effect was significant, but the random effect was not significant when fixed effects were also included in the model. In addition, in no cases did removal of correlated effects shift meaningful variance to the offending random effect. This indicates that these offending random effects had no explanatory power beyond their relationship with the fixed treatment effects. Thus, my removal of a random effect from a model with non-convergent MLE or zero-tending variance appears to be fully justified.

3.3 RESULTS

I successfully created substantial variation in the key characteristics (Table 3.4). The portion of variance in herbivore abundance that was explained was low in some cases, but herbivores of different diet breadth did significantly respond to very different vegetation characteristics (Fig.

2). Monophagous herbivores preferred low stem density, low fertility patches in both monoculture, polyculture, and on *S. canadensis* in polyculture (Table 3.5, Fig. 3.2a,b,c). Monophagous herbivores on *S. canadensis* in polyculture also preferred high density, intermediate fertility plots (Fig. 3.2c). Interestingly, the rare instances when monophagous herbivores were found on non-*S. canadensis* stems (<10 out of 908 monophagous herbivore occurrences) increased as fertility increased (Fig. 3.2d) and increased as relative *S. canadensis* mean stem mass increased (i.e., as the ratio of non-*S. canadensis* stem mass to *S. canadensis* stem mass approached 1, Table 3.5). The only other significant effect for monophagous herbivores was a small positive correlation with predator abundance in polyculture (Table 3.5).

Oligophagous herbivore abundance did not significantly vary along any of the gradients in monoculture (Table 3.6). In polyculture, however, oligophagous herbivores did increase as relative non-*S. canadensis* stem mass increased (i.e., as the ratio of non-*S. canadensis* stem mass to *S. canadensis* stem mass approached 1, Fig. 3.2e). None of the other variables explained any variation in oligophagous herbivore abundance.

Polyphagous herbivores declined as total stem density increased in both monoculture (Fig. 3.2f) and polyculture (Fig. 3.2g). Polyphagous abundance on *S. canadensis* also increased with mean stem mass in monoculture and with predators in polyculture, but these explained little variation (Table 3.7). No other variables explained variation in polyphagous abundance.

3.4 DISCUSSION

The results provide some empirical support for the consumer diet breadth hypothesis. For monophagous herbivores, fertility and stem density interacted to determine herbivore abundance in both monoculture and polyculture (Fig. 2), although this explained little variation in monophagous herbivore abundance. I suggest that the simplest explanation for this result is that monophagous herbivores are potentially responding to changes in *S. canadensis* tissue quality. Increasing soil nitrogen universally alters tissue quality by increasing plant tissue nitrogen concentrations as well as altering plant defenses (Waring and Cobb 1992, Herms and Mattson 1992, Ayers 1993, Stamp 2003, Throop and Lerdau 2004). In addition, increasing stem density potentially altered tissue quality: increasing density has been shown to decrease tissue nitrogen concentrations and alter plant defenses (Mattson 1980, Herms and Mattson 1992, Stamp et al. 2004). Thus, fertility likely interacted with density to determine *S. canadensis* tissue quality. My experiments, however, were not designed to distinguish between nutritional hypotheses vs. defense hypotheses. Irrespective, research has repeatedly demonstrated that herbivores respond to changes in plant tissue quality. Whether herbivore abundance increases or decreases, however, depends on what herbivores consider 'optimal' tissue quality (Mattson 1980, Scriber and Slansky 1981, White 1984, Throop and Lerdau 2004). Interestingly, monophagous herbivores found on non-*S. canadensis* stems also increased with fertility and with relative non-*S. canadensis* stem mass. Monophagous herbivores found on non-*S. canadensis* plants, however, were rare (<10 individuals in 908 occurrences) and therefore contributed little to patterns in total monophagous herbivore abundance. Importantly, the fact that monophagous herbivores were defined as herbivores of low abundance on non-*S. canadensis* plants does not prevent non-*S. canadensis* vegetation characteristics (e.g. relative non-*S. canadensis* stem mass, species diversity) from explaining total monophagous herbivore abundance. If non-*S. canadensis* vegetation characteristics influenced monophagous abundance, then these vegetation characteristics would have significant effects on monophagous herbivores found on *S. canadensis* in polyculture. I did not find evidence for this. Thus, I concluded that monophagous herbivore responses to fertility and density were most likely explained by changes in *S. canadensis* tissue quality.

Oligophagous herbivore abundance did not significantly vary in monoculture, but it did strongly increase in polyculture as ratio of mean non-*S. canadensis* stem mass to mean *S. canadensis* stem mass increased (i.e., as the ratio approached 1, Fig. 2e). I suggest that the simplest explanation for this result is that oligophagous herbivores preferred communities where rare host plants were relatively large. Oligophagous herbivores might prefer relatively large non-*S. canadensis* stems because large stems are relatively easy to locate (i.e., more apparent *sensu* Feeny 1975) or because these large stems are of higher quality (i.e., more vigorous *sensu* Price 1992). Indeed, changes in relative plant mass might indicate a change in relative growth rate, which is known to be correlated with changes in tissue N (e.g., Mattson 1980, Reich et al. 1999, Shipley et al. 2005) or plant defenses (e.g., Herms and Mattson 1992, Stamp 2003). If herbivores were responding to changes in non-host tissue quality (vs. plant apparency), there should also be significant effects of fertility on oligophagous herbivore abundance because increasing fertility also causes changes in tissue N (Throop & Lerdau 2004) and plant defense concentrations (Herms & Mattson 1992, Stamp 2003). I, however, did not find significant effects of fertility on oligophagous abundance in either experiment. Thus, the simplest explanation for oligophagous abundance was that oligophagous herbivores preferred communities where rare host plants were as apparent as the dominant host plant. This result is interesting because it suggests that oligophagous herbivore abundance responds to aspects of vegetation characteristics that lie between individual host-level characteristics and community-level characteristics, which further supports the hypothesis that herbivore diet breadth determines which scale (i.e., from the host plant scale to the plant community scale) herbivores will respond to plants.

Polyphagous herbivore abundance declined in both experiments as total stem density, a plant community-level characteristic, increased. It was not clear, however, what aspect of total stem density influenced polyphagous herbivore abundance. If polyphagous herbivores were responding to plant quality, I also expected to find significant effects of fertility on polyphagous herbivore abundance. Because I did not see this pattern, I concluded that polyphagous herbivores were not responding to changes in plant quality as density increased. Therefore, I was unable to make suggestions as to why this community-level characteristic affected polyphagous herbivore abundances.

3.4.1 The utility of diet breadth

These results suggest that monophagous herbivore abundance responded to host plant characteristics (e.g., tissue quality), but host plant characteristics explained a small portion of the variance in monophagous herbivore abundance. Community-level characteristics (e.g., plant apparency, total stem density) provided better explanations of herbivore abundance as diet breadth increased, but community-level characteristics also explained a small portion of variation in polyphagous herbivore abundance. Thus, while these results provide some support for previous studies that suggested specialist and generalist herbivores respond to different vegetation characteristics (e.g., Andow 1991, Östergård and Ehrlén 2005), the diet breadth mechanisms that define trophic interaction hypotheses might not predict natural patterns of insect herbivore diversity and control over plant communities. Trophic interaction hypotheses typically emphasize either specialists (e.g., Root 1973, Janzen 1970, Long et al. 2003, Carson et al. 2004) or generalists (e.g., Oksanen et al. 1981, Holt et al. 1994, Leibold 1996). Natural herbivore communities, however, are comprised of both specialist and generalist species whose abundances respond in different directions to different vegetation characteristics (e.g., Fig. 2). Even herbivore species with the same diet breadth do not consistently respond in the same direction to a given vegetation characteristic. For example, Andow's (1991) widely cited review of herbivore responses to monocultures vs. polycultures is striking because it showed strong evidence that monophagous and polyphagous herbivores differentially responded to monocultures vs. polyculture. He classified, however, only 45% (27/59) of specialist herbivore species as statistically having relatively lower population sizes when hosts were in polyculture and only 33% (7/21) of polyphagous herbivores as statistically having relatively larger populations in polyculture (see Table 2 in Andow 1991). Other reviews have also found highly variable responses among herbivore species, though these studies did not account for differences in diet breadth (Risch et al. 1983, Yamamura 2002, Rhainds and English-Loeb 2003). Finally, field studies that simultaneously test multiple vegetation characteristics often explain small portions of variance in herbivore abundance (e.g., this study, Koricheva et al. 2000, Perner et al. 2005), even when conducted at larger spatial and temporal scales than this study (e.g., Haddad et al. 2001). Thus, while diet breadth might determine herbivore response to plants, heterogeneity in herbivore population responses to vegetation characteristics might prevent diet breadth mechanisms from explaining community level patterns of herbivore diversity and control.

This issue has made interpreting empirical tests of trophic interaction hypotheses problematic, particularly for diversity studies that investigate bottom-up effects of community-level vegetation characteristics on herbivore diversity (e.g., Knops et al. 1999, Symstad et al. 2000, Koricheva et al. 2000, Haddad et al. 2001). Unfortunately, current multivariate studies are not sufficient to indicate any consistent relationships between herbivore diet breadth and vegetation characteristics, the portion of variance in herbivore abundance explained, or the direction of herbivore responses (Table 3.8). Addressing several issues might resolve this problem. First, other traits, such as feeding guild (e.g., Haddad et al. 2001) and body size (e.g., Siemann et al. 1996, 1999) might provide more explanatory power compared to herbivore diet breadth. Second, post-colonization population growth might be less useful for predicting community-level patterns compared to other demographic parameters, namely immigration and emigration rates. In other words, understanding how species occurrence probabilities vary in response to specific vegetation characteristics (e.g., Otway et al. 2005) might provide a better explanation for the observed shifts in total herbivore abundance, diversity, and control along vegetation gradients (e.g., Karieva 1983, Siemann 1998, Knops et al. 1999, Carson and Root 2000, Haddad et al. 2001, Long et al. 2001, Perner et la. 2005). Resolving these issues requires empirical studies that are designed to determine if host plant and community-level vegetation characteristics differentially affect the demography of herbivores with different traits and then determine if the observed herbivore responses actually scale up to explain a significant amount of variation in herbivore diversity and control.

3.5 CONCLUSIONS

To my knowledge, this is the first study to directly test the consumer diet breadth hypothesis. Not only did I compare a range of diet breadths, I also simultaneously tested their response to host vs. community-level characteristics under field conditions. Although I found evidence supporting the diet breadth hypothesis, the general utility of diet breadth for predicting insect herbivore diversity and control over plant communities has not been demonstrated.

Table 3.1 Plant species composition and species-specific allometric regressions

Relative stem density was calculated for non-*S. canadensis* species pool in polyculture plots over two years. For species that lack allometric regressions, the number of stems per species recorded during the mass census is indicated in () under 'Regression' (27 stems over 2 years).

Species (Gleason & Cronquist 1991)	% Stems	R^2	Regression*
Ambrosia artemisiifolia	0.02	-	(1)
Apocynum cannabinum†	0.29	0.713	ln(y) = -2.128972+0.036814*x
Arctium lappa	0.05	-	(2)
Aster lanceolatus	21.9	0.811	ln(y) = -0.786634 + 0.0232804 * x-0.0000432 * (x-105.486)^2
Aster lateriflorus	18.9	0.848	ln(y) = -2.198723 + 0.0409084 * x-0.000244 * (x-73.7349)^2
Aster novae-angliae†	1.0	0.873	y = -1.307077 + 0.0670814 * x + 0.0009038 * (x-47.2097)^2
Aster pilosus	8.7	0.839	ln(y) = -1.493424 + 0.032735 * x-0.000102 * (x-91.9333) ^ 2
Aster prenanthoides†	0.18	0.734	y= -0.388134 + 0.0370978 * x + 0.0007961 * (x-26.612)^2
Calystegia sepium†	0.64	0.576	y = ln(-5.81950204610813 + 1.47483685803348 * x)
Carex annectens (inedible)	0.04	-	(2)
Carex spp b (inedible)	0.02	-	(1)
Cirsium discolor	0.13	-	(6)
Dipsacus sylvestris	0.07	-	(4)

Table 3.1 (continued)

Euthamia graminifolia	12.4	0.771	$\ln(y) = -0.846092 + 0.0333567 * x - 0.0003145 * (x-94.6578)^2$
Hieracium aurantiacum	0.02	-	(1)
Juncus tenuis (inedible)	18.9	0.786	$\ln(y) = -0.443645 + 0.0747702 * x - 0.0006031 * (x-24.902)^2$
Sisyrinchium angustifolia	0.22	-	(10)
Solanum carolinensis†	4.9	0.560	$y = -0.094014 + 0.0223518 * x + 0.00024 * (x-21.425)^2$
Solidago canadensis	-	0.803	$\ln(y) = 0.0760538 + 0.0197548 * x - 0.0000735 * (x - 143.113)^2$
Solidago gigantea	7.5	0.793	$\ln(y) = -0.792124 + 0.0246924 * x - 0.0000373 * (x - 124.785)^2$
Solidago rugosa	3.9	0.866	$\ln(y) = -0.974031 + 0.0262044 * x - 0.0001235 * (x - 105.692)^2$

* y = total aboveground dry mass (g stem, leaf and flowers). x = height (cm), except for J. tenuis (x = diameter; mm) and C. sepium (x = length of longest leaf; cm). $n \approx 100$ individuals per species. Stem were harvested on site, dried and weighed. *Apocynum cannabinum* and *Calystegia sepium* data were obtained from JC Cahill and H. Schumacher, respectively.

† y = above ground stem and leaf dry mass (g).

Table 3.2 Insect herbivore species composition

Described are the insect herbivores observed on all plant species in this study. Species #1-18 were identified as a single species in the field while insects #40-46 could not identified as a single species in the field. Also described are the insect herbivores observed in a 6-year survey of *S. altissima* stems in 16 old-fields in New York, USA (Root and Cappuccino 1992). For insects observed in the current study, the feeding guild, diet, abundance (# sampled), and host association are described. Species #1-18 are ranked according to their abundance in year two of the current study. Species with * were used to test the herbivore diet breadth hypothesis. To compare species composition and species dominance rankings in this experimental study to those of natural field conditions, Root and Cappuccino's (1992) rankings for the abundance, temporal variability, and spatial variability among old-fields are described (except #33-46, which Root and Cappuccino 1992 could not identify to species in the field). Of the herbivores identified to species in my experiments, 9 were found in the current study and in Root and Cappuccino (1992). Some of the differences in species composition are due to the inability to either study to identify individuals to species (e.g., I did not identify most leaf chewing and tip-boring Lepidoptera to species in the field because this would have damaged plants, but Root & Cappuccino 1992 did for many Lepidoptera). In addition, Root and Cappuccino (1992) only sampled *S. altissima*. Both studies had similar dominant herbivore species (e.g., *A. carbonifera and M. vittata*). Differences in the rankings of 11 other dominant old-field herbivores are likely explained by either high variability of specific insect species in space in time (*T. virgatta, E. canadensis, G. solidaginis*), present but low abundance in the current study (*C. solidaginis, E. solidaginis*), not present or not identified to species (*C. magna/vulgaris, A. gothica, Emposaca spp., Dichomeris spp, and O. conferta*), or because the species was present at my field site, but peaked prior to my herbivore census (*P. spumarius*). *P. spumarius* was predominantly observed by JP Cronin feeding on non-*Solidago* spp., namely *Trifolium pratense*, in the buffer zones among the experimental plots.

Table 3.2 (continued).

						Current Study		**Root & Cappuccino (1992) rankings §**		
#	**Insect herbivore species**	**Order**	**Family**	**Guild †**	**Diet ‡**	**# sampled (% on non-*S. canadensis*)**	**Primary Hosts (secondary hosts)**	**# (load)**	**Temporal variation**	**Spatial variation**
1	*Asteromyia carbonifera**	Diptera	Cecidomyiidae	LG		2186 (7)	*S. canadensis* (*S. gigantea, S. rugosa, A. lanceolatus, A. pilosus, E. graminifolia, A. lateriflorus*)	1	9	2
2	Miscellaneous (Unknown D)*	Diptera	?	LG		667 (12)	*S. canadensis* (*E. graminifolia, S. gigantea, A. lanceolatus, S. rugosa, A. pilosus*)	-	-	-
3	*Asphondylia bifolia**	Diptera	Cecidomyiidae	LG		621 (<1)	*S. canadensis* (*A. lanceolatus*, *S. gigantea, A. lateriflorus, A. pilosus*)	3	13	3
4	*Rhopalomyia solidaginis**	Diptera	Cecidomyiidae	SG		429 (7)	*S. canadensis* (*S. gigantea, E. graminifolia*)	2	16	3
5	*Microrhopala vittata**	Coleoptera	Chrysomelidae	LM		361 (11)	*S. canadensis* (*E. graminifolia, S. gigantea, S. rugosa*)	8 (3)	6	10
6	*Corimelaena pulicaria (sp)*	Hemiptera	Thyreocoridae	SF		322 (20)	*S. canadensis* (*A. lateriflorus, A. pilosus, A. lanceolatus*)	-	-	-
7	Miscellaneous (Unknown C)*	Diptera	?	LG		272 (100)	*E. graminifolia* (*S. gigantea, A. lateriflorus, A. pilosus*)	-	-	-

Table 3.2 (continued).

8	*Paria thoracica* (sp)	Coleoptera	Chryso-melidae	LC	?	266 (46)	*S. canadensis* (*A. lanceolatus, A. lateriflorus, A. pilosus, E. graminifolia, S. gigantea, S. rugosa, J. tenuis, A. novae-angliae*)	-	-
9	Miscellaneous (Unknown B)*	Diptera	?	LG	O	172 (5)	*S. canadensis* (*S. rugosa, S. gigantea*)	-	-
10	*Eurosta solidaginis**	Diptera	Tephri-tidae	SG	M	161 (<1)	*S. canadensis* (*A. lateriflorus*)	7 (4)	17
11	Miscellaneous (Unknown E)*	Homoptera	Psyllidae sp.	LG	P	136 (99)	*E. graminifolia* (*A. lanceolatus, S. gigantea, S. canadensis*)	-	-
12	*Cremastobombycia solidaginis**	Lepidoptera	Gracillar-iidae	LM	M	79 (2)	*S. canadensis* (*E. graminifolia, S. gigantea*)	5	10
13	*Melanagromyza* spp. B*	Diptera	Agromy-zidae	LM	P	38 (16)	*S. canadensis* (*A. pilosus, A. lanceolatus, S. gigantea, E. graminifolia*)	-	-
14	*Gnorimoschema gallaesolidagis**	Lepidoptera	Gelech-iidae	SG	M	32 (0)	*S. canadensis*	21 (7)	21
15	Miscellaneous (Unknown F)*	Diptera	?	LG	P	22 (77)	*S. gigantea* (*A. lanceolatus, S. canadensis*)	-	-
16	Miscellaneous (Unknown A)*	Orthoptera	?	LC	O	14 (7)	*S. canadensis* (*S. gigantea*)	-	-
17	*Exema canadensis**	Coleoptera	Chryso-melidae	LC	M	2 (0)	*S. canadensis*	9	5

Table 3.2 (continued).

18	*Trirhabda virgata**	Coleoptera	Chrysomelidae	LC	*M*	2 (0)	*S. canadensis*	3 (1)	2	11
19	*Adaina montana*	Lepidoptera	Pterophoridae	LC	*P*	--	--	19	23	5
20	*Agonopteryx pulvipennella*	Lepidoptera	Oecophoridae	LC	*P*	--	--	20	22	3
21	*Amphiigonalia gothica*	Hemiptera	Cicadellidae	SF	*O*	--	--	6	19	4
22	*Calycomyza solidaginis*	Diptera	Agromyzidae	LM	*O*	--	--	15	8	4
23	*Corythucha marmorata*	Hemiptera	Tingidae	SF	*P*	--	--	16	7	12
24	*Craspedolepta magna/vulgaris*	Hemiptera	Psylidae	SF	*M*	--	--	4	14	3
25	*Empoasca* spp.	Hemiptera	Cicadellidae	SF	*P*	--	--	10	1	4
26	*Epiblema scudderiana*	Lepidoptera	Tortricidae	SG	*O*	--	--	18	18	3
27	*Lygus lineolaris*	Hemiptera	Miridae	SF	*P*	--	--	14	4	6
28	*Oidaematophorus homodactylus*	Lepidoptera	Pterophoridae	LC	*O*	--	--	23	20	8
29	*Phaneta formosana*	Lepidoptera	Tortricidae	SG	*O*	--	--	11	11	5
30	*Philaenus spumarius*	Hemiptera	Cero-pidae	SF	*P*	--	--	2 (2)	12	5

Table 3.2 (continued).

31	*Publilia concava*	Hemiptera	Membracidae	SF	*M*	--	--	22	15	20
32	*Scrobipalpula sacculicola*	Lepidoptera	Gelechiidae	LM	*?*	--	--	17	3	8
33	Miscellaneous	Hemiptera	Membracidae	SF	?	--	--	--	--	--
34	Miscellaneous	Hemiptera	Homptera	SF	?	--	--	--	--	--
35	Miscellaneous	Hemiptera	Miridae	SF	?	--	--	--	--	--
36	Miscellaneous	Hemiptera	Heteroptera	SF	?	--	--	--	--	--
37	*Ophraella conferta*	Coleoptera	Chrysomelidae	LC	?	--	--	-- (6)	--	--
38	Miscellaneous	Coleoptera	-	LC	?	--	--	--	--	--
39	*Dichomeris* spp	Lepidoptera	Gelechiidae	LC	?	--	--	-- (5)	--	--
40	*Uroleucon spp**	Hemiptera	Aphididae	SF	P	290 (11)	*S. canadensis* (*A. lanceolatus*, *S. rugosa, S. gigantea*, *A. pilosus*, *E. graminifolia*, *A. lateriflorus*, *A. novae-angliae*)	---	---	---
41	Miscellaneous	Lepidoptera	?	TB	?	1343 (9)	*S. canadensis* (*A. lanceolatus, E. graminifolia, A pilosus, A. lateriflorus, S. gigantea, S. rugosa*)	---	---	---
42	Miscellaneous	Lepidoptera	?	LC	?	185 (18)	*S. canadensis* (*A. lanceolatus, E. graminifolia, S. gigantea, A. lateriflorus, A pilosus*)	---	---	---

Table 3.2 (continued).

43	Miscellaneous	Diptera	Agromyzidae	LM	?	2850 (10)	*S. canadensis* (*A. lanceolatus, A pilosus, S. gigantea, A. lateriflorus, E. graminifolia, A. novae-angliae, S. rugosa)*	---	---	---
44	*Melanagromyza* spp. A & *Cerodontha* spp. A	Diptera	Agromyzidae	LM	?	283 (12)	*S. canadensis* (*A. lanceolatus, S. gigantea, A. pilosus, A. lateriflorus, A. novae-angliae, E. graminifolia*)	-	-	-
45	*Bucculatrix* spp.	Lepidoptera	Lyonetiidae	LM	?	34 (100)	*A. lanceolatus* (*A. pilosus, A. lateriflorus, A. novae angliae*)	-	-	-
46	Miscellaneous	?	?	?	?	109 (25)	*S. canadensis* (*E. graminifolia, A. lanceolatus, S. gigantea, A. lateriflorus, A. pilosus, J. tenuis*)	-	-	-

† LG = leaf galler; SG = stem galler; LM = leaf miner; SF = sap feeder; LC = leaf chewer; TB = tip borer

‡ P = polyphagous on *Solidago* spp & *Aster* spp, more than 1 family, or on Composites; O = Oligophagous on *Solidago* spp.; M = monophagous on *S. canadensis*. Diet breadth was determined from observations, Root & Cappuccino 1992, or published literature.

§ Abundance rankings: 1 = highest median mean abundance vs. 23 = lowest abundance: see Fig 2 in Root and Cappuccino 1992; Temporal variability: 1 = highest variability over time vs. 23 = lowest variability over time: see Fig 4 in Root and Cappuccino 1992; Spatial variability: 1 = greatest randomness in distribution among field sites vs. 20 = more clumped, see Fig. 6 in Root and Cappuccino 1992.

- = not sampled/identified in Root and Cappuccino (1992); -- = not sampled/identified in current study; --- sampled in both Root and Cappuccino (1992) and in current study, but information was not provided by Root & Cappuccino (1992).

Table 3.3 Insect herbivore guild composition

Described are the relative abundances (# sampled) of the feeding guilds from the insects sampled in the current study (see #1-18 & #40-46 in Table 3.2). Also described are the abundance rankings of feeding guilds from Root and Cappuccino's (1992) six year survey of 16 old-field in New York, USA. This table demonstrates that the herbivore community in the current study was similar in guild structure compared to other old-field communities. This study, however, was more strongly dominated by gallers and leaf miners compared to Root and Cappuccino's (1992), who observed dominance of leaf chewers and miners (June) or gallers and sap feeders (September). This suggests that my census was conducted during species compositional turnover between June and September.

	Current Study		**Ranking of guilds (see Fig 8 in Root and Cappuccino 1992)**	
Guild†	**# sampled (% on non-*S. canadensis*)**	**% of total abundance**	**June Abundance**	**September Abundance**
Leaf chewers	469 (33.4)	4.3	1	3
Leaf miners	3645 (11)	33.5	2	4
Sap feeders	612 (15.7)	5.6	3	2
Gall makers	5217 (13.6)	55.5	4	1
Leaf gallers	4076 (16.4)	37.5	?	?
Stem gallers	622 (5.1)	5.7	?	?
Tip borers	1343 (9)	12.3	?	?
Miscellaneous	109 (25)	1	?	?

Table 3.4 Descriptive statistics for the predictor variables used to construct mixed models Using these predictor variables, mixed models were constructed for each response variable. Monoculture mixed models initially included the first six predictor variables listed and an interaction between fertility and density. Polyculture mixed models (either at the community, *S. canadensis,* or non-*S. canadensis* levels) initially included all of the predictor variables listed and an interaction between fertility and density. Random effects (†) were removed from models when JMP's (5.0.1.2) REML procedure estimated the variance component as zero, which is indicated by negative variance estimates or failure to estimate 95% confidence interval. Note that which random effects were removed differed among response variables. The final model for a response variable can be determined by looking at the effects that are reported in the ANOVA table for that response variable. For example, the final model for the monoculture analysis of monophagous herbivore abundance (Table 3.6) included fertility, density, fertility*density, and predators. The final model for polyculture community-level analysis of monophagous herbivore abundance (Table 3.6) included fertility, density, fertility*density, predators, and mass^{-2}.

	Monoculture		**Polyculture**	
Predictor Variable	**mean +/- stdev**	**range**	**mean +/- stdev**	**range**
Plant mass m^{-2} (g) †	491.7 +/- 234.7	154.3 - 1119.9	346.7 +/- 108.5	154.3 – 644.5
Plant Stems m^{-2}	-	8 - 32	-	8 - 32
Fertility (g N m^{2} yr^{-1})	-	0 - 16	-	0 - 16
Light (DIFN) †	0.32 +/- 14	0.12 – 0.72	0.42 +/- 0.14	0.15 - 0.72
Mean stem mass (g) †	24.7 +/- 7.1	8.5 - 45.7	20.3 +/- 7.4	8.2 – 42.5
# predators per plot†	2.05 +/- 1.8	0 - 8	1.46 +/- 1.46	0 - 8
Plant diversity (H') †	0	0	1.04 +/- 0.65	0 – 1.89
% *S. canadensis* mass m^{-2} (g)†	1	1	0.69 +/- 0.21	0.22 - 1
% inedible stems m^{-2}†	0	0	0.066 +/- 0.07	0 – 0.31
Relative non-*S. canadensis* stem mass†	0	0	0.35 +/- 0.24	0 – 0.99

Table 3.5 REML results for number of monophagous herbivores per control plot

Random effects† that lack statistics (or not shown here) were removed from a model because that random effect did not contribute to the fit of the model (see *Statistical Analyses*; e.g. mean stem mass was excluded from all four analyses, diversity was only included in the polyculture community analysis). Values in () indicate the percent increase (+) or decrease (-) in y as x increased.

Analysis		Statistic	Full Model	Fertility	Stems m^{-2}	Fertility* Stems m^{-2}	# Preda-tors†	Diver-sity†	Plant mass m^{-2} †	% inedible stems m^{-2}†	Relative non-*S. canadensis* stem mass†
	Mono-culture	*F* or *VC*†	**2.57***	**4.8***	0.57	**4.7***	0.0009				
		r^2 or %†	0.11	0.05	-	0.05 (see Fig 1)	-				
Polyculture	Comm-unity	*F* or *VC*†	**10.7*****	**6.2***	**5.3***	**10.6****	**0.11***	1.1	<0.001		
		r^2 or %†	0.44	0.04	0.036	0.07 (see Fig 1)	0.02 (+)	-	-		
	S. cana-densis	*F* or *VC*†	**2.8***	3.3	**3.8***	**3.7***	0.003			2.9	
		r^2 or %†	0.15	0.035	0.04	0.04 (see Fig 1)	-			-	
	Non-*S. cana-densis*	*F* or *VC*†	**2.9***	**6.9****	1.1	0.5					**0.41***
		r^2 or %†	0.16	0.1 (+98%)	-	-					0.82 (+87%)

† Variance Components (VC) and Percent of Total (%) are reported for random effects (vs. F ratios and r2 for fixed effects). '–' not reported because factor was non-significant, * means 0.01<P < 0.05, ** means 0.001 < P < 0.01, *** means P < 0.001. Data ln(y+1) transformed for monoculture: (df = 1, 79; n = 84), Polyculture community level (df =1,77; n = 84), *S. canadensis* in polyculture (df = 1,78; n = 84) and non-*S. canadensis* stems (df = 1, 58; n = 63 because the 8 stem m-2 treatment was not included).

Table 3.6 REML results for the number of oligophagous insect herbivores per control plot

Analysis		Statistic	Full Model	Fer-tility	Stems m^{-2}	Fertility* Stems m^{-2}	Relative non-*S. canadensis* stem mass†	% *S. canadensis* m^{-2}†	% inedible stems m^{-2} †	Mean stem mass†	# Preda-tors†	Diver-sity†
Mono-culture		*F* or *VC*	0.23	0.14	0.33	0.2						
		r^2 or %	-	-	-	-						
Polyculture	Commun-ity	*F* or *VC*	**5.3*****	0.0013	0.8	0.05		1.96	2.6	**0.001***		0.12
		r^2 or %	0.32	-	-	-		-	-	0.003 (+)		-
	S. cana-densis	*F* or *VC*	1.17	0.0075	0.44	2.1			4.1	0.0008		
		r^2 or %	-	-	-	-			-	-		
	Non-*S. canadensis*	*F* or *VC*	**2.3***	0.12	0.07	0.77	**11.5***	3.1	8.8		0.09	
		r^2 or %	0.26	-	-	-	0.42 (+87)	-	-		-	

Symbols as in Table 3.5. Data were ln(y+1) transformed for Monoculture: (df = 1,80; n = 84), Polyculture community level (df =1,76; n = 84) and *S. canadensis* in polyculture (df = 1,78; n = 84). Data were SQRT(y)+SQRT(y+3/4) transformed for non-*S. canadensis* stems in polyculture (df = 1, 55; n = 63 because the 8 stem density treatment is not included as it is a monoculture of *S. canadensis*).

Table 3.7 REML results for the number of polyphagous insect herbivores per control plot

Analysis		Statistic	Full Model	Fertility	Stems m^{-2}	Fertility* Stems m^{-2}	# Predators †	Mean stem mass†	Plant mass m^{-2} †
Mono-culture		*F* or *VC*†	**3.7****	0.16	**4.0***	0.03	0.0007	**0.0004***	
		r^2 or %†	0.18	-	0.04 (-24)	-	-	0.002 (+)	
Polyculture	Commun-ity	*F* or *VC*†	**3.6***	0.27	**10.1****	0.4			
		r^2 or %†	0.12	-	0.11 (-44)	-			
	S. cana-densis	*F* or *VC*†	**2.9***	0.57	0.04	1.8	**4.3****		
		r^2 or %†	0.13	-	-	-	0.05 (+)		
	Non-*S. canadensis*	*F* or *VC*†	0.43	0.51	1.1	0.17			9.45e^{-7}
		r^2 or %†	-	-	-	-			

Symbols as in Table 3.5. Data were ln(y+1) transformed for Monoculture: (df = 1, 78; n = 84), Polyculture community level (df =1, 80; n = 84) and non-*S. canadensis* stems in polyculture (df = 1, 58; n = 63 because the 8 stem density treatment is not included as it is a monoculture of *S. canadensis*). Data was not transformed for *S. canadensis* in polyculture (df = 1, 79; n = 84).

Table 3.8 Previous studies on insect herbivore abundance and vegetation characteristics

Field experiments that controlled for the effects of multiple vegetation characteristics on insect herbivore abundances in wild (i.e. non-cultivated) systems. Herbivore abundance was not explained by any vegetation characteristic for 13.9% of the species.

Diet breadth (# species)	Host Plant character	Community-level vegetation character	% species responding	Direction of slope (r^2)	Citation
M (9)	mass		100%	- (0.39-0.96)	Otway et al. (2005)
		# species	0%		
M (2)		Fertility (tissue quality)	100 %	+ (nr)	Stiling & Moon (2005)*
		stem density	0%		
M (2)		# functional groups	100%	- (nr)	Haddad et al. (2001) †
		# species	0%		
		mass m^{-2}	50%	+ (nr)	
		C:N	0%		
O (6)		# functional groups	67%	- (nr)	
		# species	16.6%	+ (nr)	
		Biomass	33%	- (nr)	
		C:N	0%		
		Note: 2 species did not significantly respond to any variable			
P (10)		# functional groups	70%	- (nr)	
		# species	40%	+ (nr)	
		Biomass	50%	-,+ (nr)	
		C:N	50%	- (nr)	
		Note: 2 species did not significantly respond to any variable			

* Because the study was conducted in monocultures, it is unclear if the herbivores track host plant or community-level vegetation characteristics. Thus, I chose to categorize the vegetation characteristics in this study as 'community-level'.

† Species listed in Table 5 of Haddad et al. (2001). Diet breadth data provided by N. Haddad.

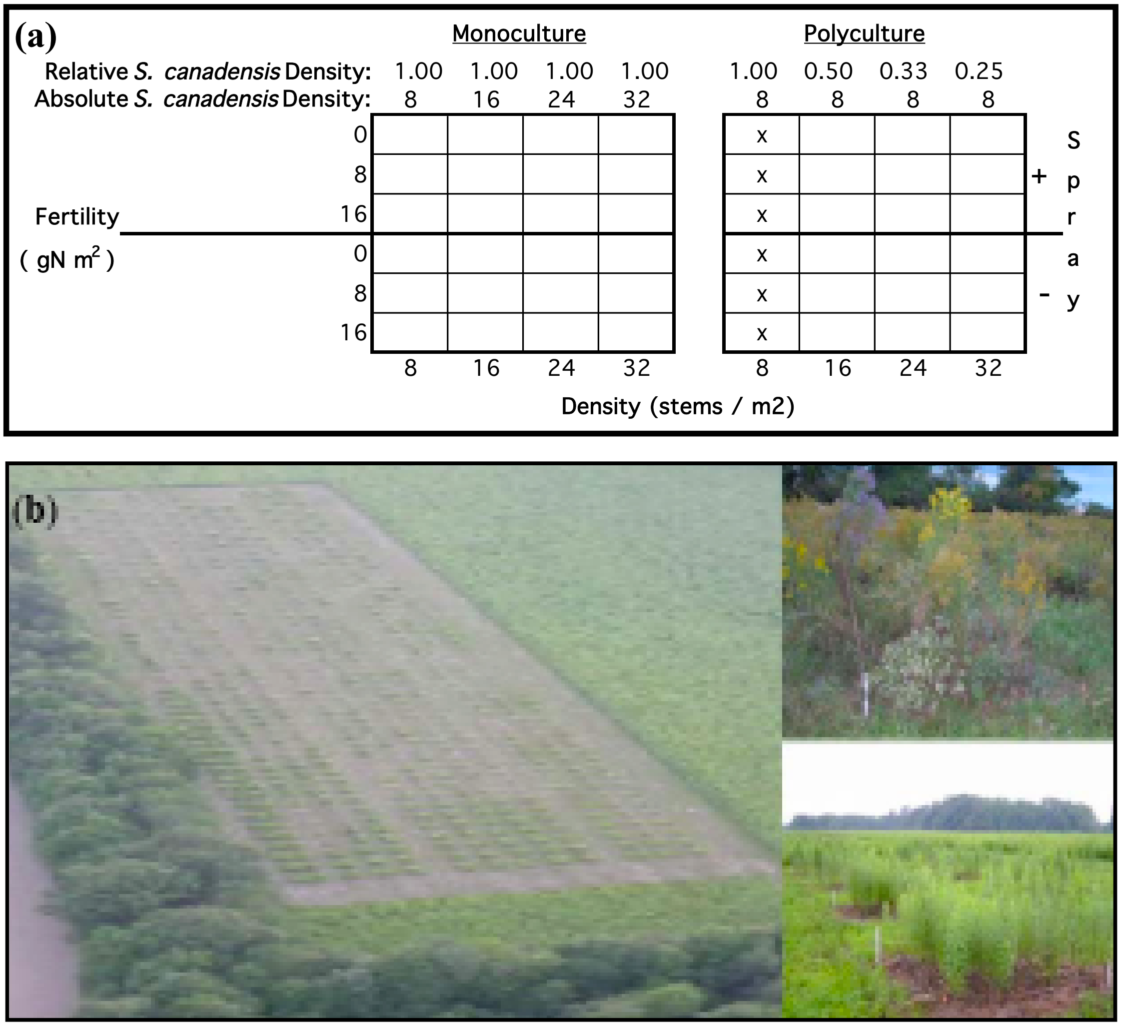

Figure 3.1. Experimental design and study site

(a) Design for the Monoculture and Polyculture Experiments. The 8 stem density polyculture treatments (represented with an 'x') were monocultures and were not replicated in the field. Instead, the data from the 42, 8 stem monoculture plots were used for both the monoculture and polyculture analyses. (b) Aerial photo of the common garden containing 600 4m^2 plots, 294 of which were used in the experiment (photo: A. Turner). Plots were separated by 2-5m mowed-buffers. The right-top and right-bottom photos show examples of a 24-stem density polyculture and monoculture, respectively.

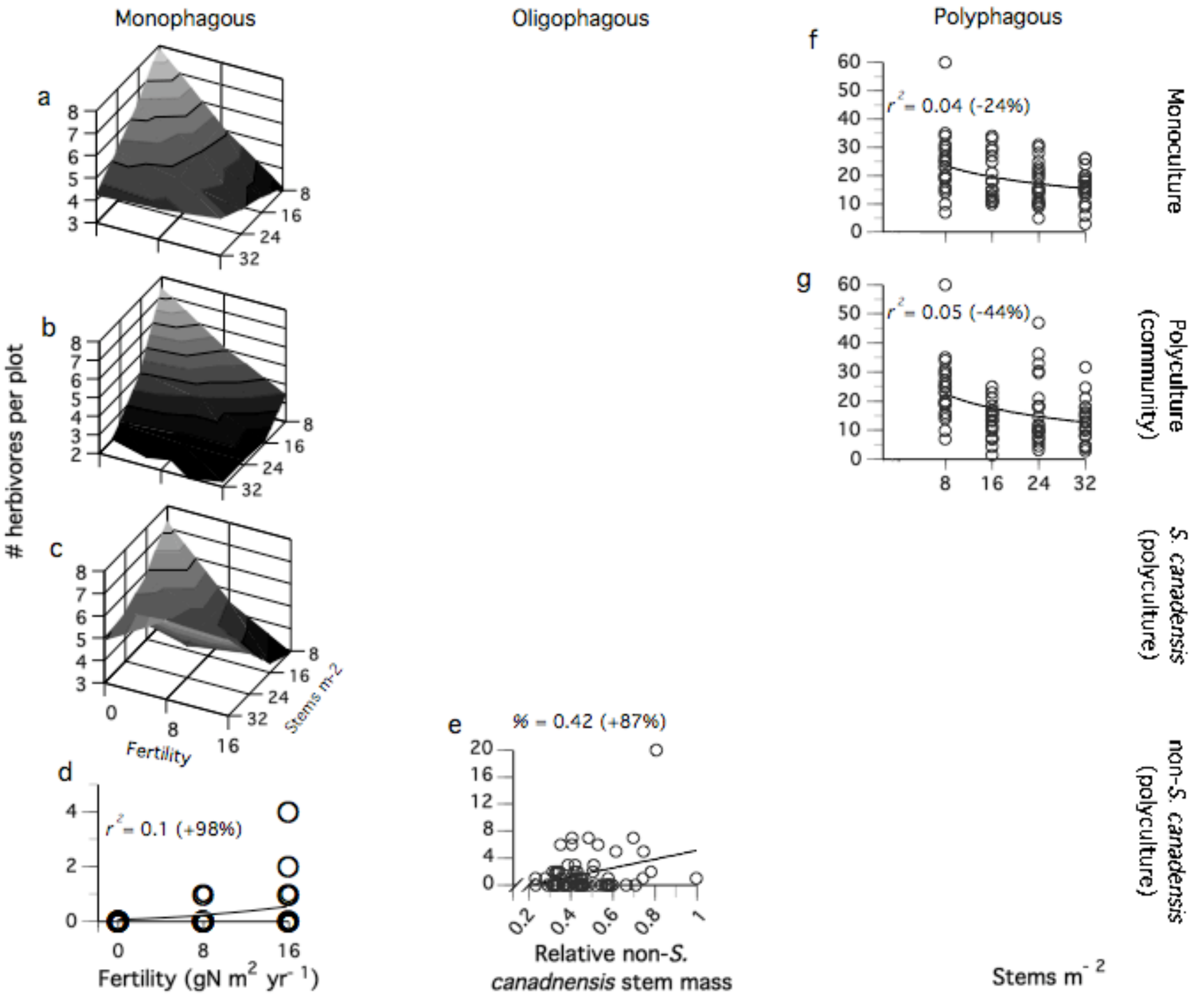

Figure 3.2 Monophagous, oligophagous, and polyphagous herbivore abundance in controls Monophagous herbivore abundance was explained by fertility*density interactions in (a) monoculture, (b) polyculture, and (c) on *S. canadensis* in polyculture. Rare instances when monophagous herbivores foraged on non-*S. canadensis* stems (<10 of 908 occurrences) were explained by either fertility (d) or relative non-*S. canadensis* mass (not illustrated, see Table 3.5). Oligophagous herbivore abundance increased on non-*S. canadensis* stems as relative non-*S. canadensis* stem mass increased (i.e., as ratio of non-*S. canadensis* stem mass to *S. canadensis* stem mass approached 1; e). Polyphagous herbivore abundance declined with stems m^{-2} in both (f) monoculture and (g) polyculture. The () following r^2s (fixed effects) and Percent of Total (% for random effects) indicate the % increase (+) or decrease (-) in y as x increases.

4.0 PREDICTING THE STRENGTH OF HERBIVORE CONTROL OVER PLANT COMMUNITIES: EXPERIMENTAL FIELD TESTS OF THE HERBIVORE CONTROL HYPOTHESES

By James Patrick Cronin

ABSTRACT

Trophic interaction hypotheses attempt to predict herbivore abundance, damage levels, and control over plant mass using a variety of biogeochemical gradients, namely resource availability to plants, net primary production, and the concentration of dominant plants. The relative empirical importance of these factors remains unclear, however, because they are often highly correlated in field studies. Here, I report results from the first field experiments that simultaneously manipulate these factors to determine which of these hypotheses, if any, predicted insect herbivore abundance, insect herbivore damage, and the strength of insect herbivore control over plant communities. I also tested other factors that are hypothesized to be important, namely plant size, plant species diversity, plant apparency, the abundance of inedible species, and predators. I found that insect herbivore abundance, damage to plants, and control over mean stem mass were all best explained by an effect of resource availability on *Solidago canadensis* tissue quality and the ability of *S. canadensis* to tolerate herbivory. Surprisingly, herbivores always caused the greatest reduction in mean stem mass under low resource conditions, regardless of herbivore abundance or herbivore damage. These results suggest that future hypotheses should use the effect of resource availability on the tolerance of dominant plants as their foundation and then investigate how other processes (e.g., abiotic factors, predators, shifts in species composition) modify the outcome of this relationship.

4.1 INTRODUCTION

Herbivore control over the structure and dynamics of plant communities varies spatially and temporally. Consequently, an enormous number of hypotheses have been generated in an attempt to explain variation in the strength of herbivore control over plants (e.g., see Hairston et al. 1960, Hunter and Price 1992, Power 1992, Strauss and Agrawal 1999, Chase et al. 2000, Stamp 2003, Weisser and Siemann 2004). All of these hypotheses predict that herbivore control will vary along key environmental gradients, namely net primary productivity (NPP: e.g., Oksanen et al. 1981, 1995, Wootton and Power 1993), host plant concentration (e.g., Janzen 1970, Long et al. 2003), and resource availability (e.g., White 1984, Maschinski and Whitham 1989).

Despite numerous informative tests of these hypotheses, the empirical evidence has remained equivocal because these gradients are often correlated and thus typically confounded in field experiments. For example, increasing soil nitrogen in terrestrial systems increases net primary productivity but can also change plant quality, plant tolerance to herbivory, host concentration, and total stem density (see White 1984, Tilman and Pacala 1993, Waide et al. 1999, Strauss and Agrawal 1999, Mittelbach et al. 2001, Stevens and Carson 1999a,b, Haddad et al. 2001, Throop and Lerdau 2004). Thus, these gradients can be highly confounded, making any test of the above theories extremely difficult.

This problem has led some to question the conclusions of experiments (e.g., Moon et al. 1999) and prevents meta-analyses from disentangling the influence of one gradient vs. another (e.g., Schmitz et al. 2000, Halaj and Wise 2001, Schädler et al. 2003, Coupe and Cahill 2003). Consequently, little progress has been made toward determining which environmental gradients (e.g., NPP vs. host concentration) actually explain variation in herbivore control and thus merit further theoretical attention (Hunter and Price 1992, Polis 1999, Moon et al. 1999, Mulder et al. 1999, Ritchie 2000, Halaj and Wise 2001, Schädler et al. 2003, Carson et al. 2004).

To address this problem, I simultaneously manipulated NPP, total plant density, host concentration, and resource availability under field conditions. I evaluated whether my experimental manipulations could predict herbivore abundance, herbivore damage, and herbivore impact on mean plant mass. Of course, numerous other gradients have also been proposed to predict herbivore control over plant communities, namely plant species diversity (e.g., Strong

1992), predators (e.g., Bernays and Graham 1988), plant size (e.g., Feeny 1975, Price 1991), and the abundance of inedible stems (e.g., Holt et al. 1994). These additional biological gradients can also be highly correlated, and further complicate interpretations of herbivore control studies. Therefore, I also quantified how these variables naturally varied along my experimental gradients and whether they contributed to variation in herbivore control. In doing so, I conducted first study to simultaneously test the major gradients thought to determine herbivore control over plants.

4.2 METHODS

4.2.1 Model system and experimental design

I conducted this study at the University of Pittsburgh's Pymatuning Laboratory of Ecology (Crawford Co, Pennsylvania, USA) in an early successional old-field dominated by *Solidago canadensis* where other *Solidago* and *Aster* spp. were also common (see Table 4.1 for plant species composition and relative abundances). *S. canadensis* is a native, herbaceous, clonal perennial that dominates (~30-40 stems m^{-2}) old fields throughout the eastern United States and Canada (Werner et al. 1980, Carson and Root 1999). Both insect herbivore and arthropod predators have been well studied in old fields (see Root and Cappuccino 1992, Schmitz 2003). The herbivore community was dominated by Dipterans (e.g., Agromyzidae, Cecidomyiidae) and Lepidopterans (e.g., Lyonetiidae, Tortricidae) and was typical of old-fields in the northeast (USA) in terms of species composition, dominance rankings, and guild structure (Tables 4.2, 4.3). Common predators included spiders (e.g., Gnaphosidae, Thomisidae, Pholcidae) and ladybird beetles (Coleoptera: Coccinellidae).

My goal was to experimentally create major gradients in fertility, NPP, total stem density, and host concentration (i.e., host relative and absolute abundance). Therefore, I experimentally manipulated fertility, stem density, and species composition in two full-factorial experiments: The Monoculture Experiment (left half of Fig. 1a) and The Polyculture Experiment (right half of Fig. 1a). In both experiments, I manipulated plant stem density in 4 m^2 plots at four levels: 8, 16, 24 or 32 stems m^{-2} (as depicted across the bottom in Fig. 1a). In monocultures, every stem was

Solidago canadensis. As the absolute abundance of *S. canadensis* increased in monoculture, its relative abundance was of course always 100% (as depicted across the top of the monoculture half of Fig. 1a). In contrast in polyculture, *S. canadensis* stems density was held constant at 8 stems m^{-2} as total stems density increased. Consequently, as shown across the top of the polyculture half of Fig. 1a, *S. canadensis'* relative abundance declined (100% - 25%) in polyculture as total stems density increased. In addition, as shown on the left side of Fig. 1a, I crossed these density treatments with three fertility levels. Finally, the right side of Fig. 1a shows that half of the plots were sprayed with insecticide so that I could quantify herbivore impact on mean stem mass.

I established this design in spring 2003 by selecting 294 $4m^2$ plots from 600 plots containing old-field vegetation (Fig. 1b). To ensure all plots were of similar quality, I only selected plots of moderate extant *S. canadensis* stem density and that were similar in height (*unpublished data*, JP Cronin). Thus, my results are not due to confounding historical differences in plot quality with treatment effects. The selected plots were thinned to appropriate densities and fertilized. Neighboring plots were paired and randomly assigned the following treatments:

Spray. During the growing season, I judiciously applied esFenvalerate, a synthetic pyrethroid, at recommended application rates every 7-10 days. The use of insecticides in general, and esFenvalerate in particular, has been previously justified in detail (Root 1996, Carson and Root 2000, Siemann et al. 2004).

Fertility. I applied a slow release fertilizer (Osmocote, [The Scotts Company, Marysville, Ohio]; 8:6:12 NPK), half in May and half in June, at a rate and a ratio similar to other old-field studies (Tilman 1987, Carson and Pickett 1990, Stevens and Carson 1999a). I fertilized evenly across the 4, $1m^2$ quadrants at 0, 8, or 16g N m^{-2} per year.

Stems m^{-2}. Plots were divided into 16, $0.25m^2$ subplots and repeatedly weeded during the growing season, leaving weeded mass in the plot. In polycultures, I kept other forbs in the plots in addition to *S. canadensis*. I kept only perennial plant species that were common throughout the site (Table 4.1) to minimize both among-plot variation in non-*S. canadensis* plant species composition and within-season stem turnover. I haphazardly assigned non-*S. canadensis* species to stems within each $0.25m^2$ subplot by keeping the stem of every third acceptable species (i.e., common perennials) encountered, without species replacement, until the treatment stem density was reached.

General Site Condition. In 2003, I repeatedly mowed a 3-5 m buffer between plots to eliminate *S. canadensis* and other tall forbs from the buffer zones. The width of this buffer is well beyond the length of the vast majority of rhizomes in these communities (Cain et al. 1991, Bazzaz 1996). By late summer of 2003, my 4m^2 experimental patches were scattered throughout a matrix of mowed vegetation that was devoid of *S. canadensis*, dominated by forbs and perennial monocots, and fenced to exclude large vertebrates (mainly white-tailed deer *Odocoileus virginianus*, Fig. 1b).

4.2.2 Testing herbivore control hypotheses

In August of 2003 and 2004, I recorded the identity and size of each stem in the center 1m^2 of each plot. Species-specific allometric regressions of mass on size (Table 4.1) were then used to estimate aboveground mass for each stem. I used allometry rather than harvesting because harvesting would have changed the treatment densities. Although final mass estimates do not precisely quantify plant growth or NPP, my plots were composed of perennial species that emerge in early spring, persist well into September, senesce all aboveground mass in the fall, and were maintained at specific densities. Furthermore, previous studies have shown that single point estimates accurately capture relative differences in productivity (e.g., Tilman 1987, Inouye et al. 1987, Carson and Pickett 1990). Thus, my mass estimates should adequately describe relative differences in plant productivity.

Using the species identity, plant size, and allometry data sets, I tested:

4.2.2.1 Community-level hypotheses

NPP-based hypotheses predict that as NPP increases adjacent trophic levels either show decoupled/stepwise patterns in abundance (e.g., plant abundance increases, herbivore abundance stays constant, predator abundance increases) or all trophic levels simultaneously increase in abundance (Chase et al. 2000). Depending on the hypothesis, however, herbivore control over mean stem mass can increase (Consumer controlled food chains), decrease (Heterogeneous food webs), or stay constant (Resource controlled food chains) as NPP increases (sensu Chase et al. 2000). To test these predictions, I estimated NPP as total mass m^{-2} in sprayed plots.

Community-level hypotheses have typically considered gradients of NPP, not gradients of total stem density. Since total stem density and NPP could be confounded (Steven and Carson 1999, 2000), it might be that herbivores are responding to total stem density (vs. NPP). Here I extend the predictions of community-level NPP-based hypotheses to also address total stem density. Thus, I tested if either NPP or total stem density affected herbivore abundance, damage, and control.

4.2.2.2 Host concentration hypotheses

Host concentration hypotheses predict that whenever a host plant reaches high stem density, herbivores will aggregate or outbreak on that host and reduce host abundance (see Carson et al. 2004). Because the host plant represents a large portion of the plant community, increased herbivore density and damage per host stem will reduce mean stem mass at the community-level (Long et al. 2003, Carson et al. 2004). Because I controlled the stem density of *S. canadensis*, I was able to manipulate host concentration (i.e., absolute or relative *S. canadensis* stems m^{-2}) independent of other community-level characteristics (i.e., total stem density, total mass m^{-2}, plant species diversity and composition). Thus, if herbivore control is determined by absolute *S. canadensis* stem density, herbivore control over *S. canadensis* in monoculture will increase as *S. canadensis* stem density increases. In contrast, because *S. canadensis* absolute stem density remains constant in polyculture (Fig. 1a), herbivore control over *S. canadensis* in polyculture (and thus polyculture communities) will stay constant as total stem density increases in polyculture. On the other hand, if herbivore control is best explained by relative *S. canadensis* stem density, herbivore control should stay constant in monoculture as *S. canadensis* stem density increases. In polyculture, however, if herbivore control is best explained by relative host concentration, herbivore control over *S. canadensis* in polyculture (and thus polyculture communities) should decline as total stem density increases in polyculture (Fig. 1a). Thus, I first tested for correlations between total stem density and measures of herbivore abundance, damage, and control over plants. I then compared the monoculture results to the polyculture results to determine if herbivores were responding to either absolute or relative *S. canadensis* stem density.

Host concentration hypotheses have typically considered host stem density, not host plant productivity. Since some host plants can become extremely abundant, it may be that herbivores are responding to the mass production of their host plant (vs. host stem density). Here I extend host concentration models to include the productivity of dominant plant species. Thus, I tested whether the absolute or relative productivity vs. the absolute or relative stem density of *S. canadensis* predicted herbivore abundance, damage and control.

4.2.2.3 Resource availability hypotheses

Resource availability may determine the degree to which individual plants cope with herbivory (e.g., Maschinski and Whitham 1989, Strauss and Agrawal 1999, Stowe et al. 2000). Thus, plant tolerance-based resource availability hypotheses predict that herbivore control will increase as resource availability per plant decreases (Maschinski and Whitham 1989, Strauss and Agrawal 1999, Stowe et al. 2000). Resource availability might also directly alter nutrient or defense concentrations in plant tissue, causing herbivore activity and control to jointly increase or decrease with resource availability (e.g., White 1984, Stamp 2003, Throop and Lerdau 2004). To test these hypotheses, I manipulated the availability of soil nutrients using fertility treatments. I also measured sub-canopy light levels (mean diffuse non-interceptance, DIFN) in the center of each plot at the soil surface in mid-August using a LAI-2000 (Li-cor, Lincoln, Nebraska; e.g., Carson and Root 2000). DIFN estimates the probability (0-1) that diffuse light reaches the sensor (LAI-2000 manual 1992). I controlled for edge effects by using the sensor's two center rings, which only measured light directly above the sensor (LAI-2000 manual 1992).

4.2.2.4 Other factors

To statistically evaluate whether other factors were important in determining the strength of herbivore control, I also calculated plant species diversity using Shannon's Diversity Index (H', Molles 1999), percent inedible stems m^{-2}, the number of predators per plot, and final mean stem mass in addition to a ratio of mean non-*S. canadensis* stem mass / mean *S. canadensis* stem mass (a measure of plant vigor [Price 1991] and plant apparency [Feeny 1975]).

4.2.3 Response Variables

4.2.3.1 Herbivore and predator abundance

Sampling protocol followed Root and Cappuccino (1992), which was specifically designed for *Solidago*-dominated old fields. In mid- to late June, when herbivore activity is at its highest, I sampled ~2 *S. canadensis* stems in each of the 16, 0.25m^2 subplots. In polyculture, I sampled an additional ~2 non-*S. canadensis* stems per subplot. I searched each stem for insect herbivores and predators. I then calculated the number of herbivore and predator per plot.

4.2.3.2 Herbivore damage

During mid-June, I quantified damage on eight leaves per stem on the same stems that were sampled for herbivore abundance. Percent leaf area damaged was visually estimated by comparing the actual damage to artificial leaf templates that had a range of damage levels (e.g., 1%, 2%, 5% etc) reflecting different leaf shapes, sizes and types of damage (e.g., chewing, mining; for details see Carson and Root 2000). Plot means were calculated as mean percent leaf area damaged per stem.

In mid-August, I also surveyed 23-34 *S. canadensis* stems and 17-32 non-*S. canadensis* stems per plot for evidence of damage by insect herbivores that attack stems (e.g., stem galling, boring insects). Plots means were calculated as the percentage of stems damaged.

4.2.3.3 Herbivore control

Because herbivores can both increase and decrease mean stem mass (see Strauss and Agrawal 1999), I calculated 'herbivore control' as the percent change in mean stem mass due to herbivory (see also Osenberg and Mittelbach 1996, Chase et al. 2000, Long et al. 2003). I used an herbivore control index where herbivore control = ($\text{control}_i - \text{spray}_i$) / plot_i of maximum mean stem mass; (where i = a paired spray plot and control plot (sensu Wilson and Keddy 1986, Bonser and Reader 1995, Long et al. 2003). Dividing by the plot within a pair that had the greatest mean stem mass constrains this index between 1 and -1, where 1 indicated the 100% increase in mean stem mass in response to herbivory (i.e., overcompensation), 0 indicates herbivores did not change mean stem mass (i.e., compensation), and -1 indicated a 100% decrease in mean stem mass due to herbivory.

4.2.3.4 Statistical analyses

To test for correlations between herbivore abundance, herbivore damage, or herbivore control versus the gradients, I separately analyzed the monoculture, polyculture community-level, S. canadensis in polyculture, and non-S. canadensis stems in polyculture. Analyses are based on year 2, when my experiments were fully established. I constructed mixed models that included both fixed treatment effects and random effects. All treatment effects were considered fixed while all unmanipulated but measured effects were considered random (Table 4.4). A variety of transformations of response variables were used to meet the assumptions of linear mixed models (Sokal and Rohlf 1999; *see Results*). Mixed model regression analysis was performed using JMP's (5.0.1.2) mixed model REML procedure. These analyses produced mean squares estimates for fixed effects and variance components for random effects. Percentages of variance explained (i.e., r^2s) can only be calculated on fixed effects and not on random effects. Therefore, in keeping with mixed model conventions, the ANOVA tables report F-ratios and associated r^2s for fixed effects while Variance Components are reported for random effects (JMP 5.0.1.2). In addition, 'Percents of Total' (where $\% = VC_i / \sum VC_{ij}$) are also reported for random effects (JMP 5.0.1.2). Note that r^2 values, which are calculated using sum of squares, estimate the proportion of the total variance explained by a fixed effect (Sokal and Rohlf 1999). The % value for a random effect, however, is calculated as the ratio of the random effect in question divided by the summed random effects and their residual only (JMP 5.0.1.2). Since % values are not estimates of the proportion of the total variance explained by a random effect, % values should not be compared to r^2 values or considered an estimate of the total variance explained (JMP 5.0.1.2). The % values should only be used to compare the relative magnitude among random effects.

For many random effects, the REML procedure either resulted in a negative variance component estimate or failed to estimate the 95% confidence interval. Both cases are commonly discussed in the statistical literature and are indicative of numerical instabilities that may arise when the true variance component is zero (i.e., when x explains no variation in y and therefore x does not contribute to the fit of the model: Smith and Murray 1984, Searle et al. 1992, Gould and Nichols 1998, JMP 5.0.1.2). A statistically acceptable solution is to remove the offending random effects (justified since the variance component is zero anyway) and re-run the model (Searle et al. 1992). If a random effect is listed in Table 4.4 but is not shown for an analysis reported in an ANOVA table, that random effect was removed from that analysis because its variance component estimate indicated that it did not contribute to the fit of the model. I validated models reduced in this way, however, based on goodness-of-fit tests and likelihood ratio tests (Sokal and Rohlf 1999), which tests for lack of significant reduction in explanatory power of the model when the effect is removed relative to the inclusive model. Correlations among predictor variables (Appendix A), however, indicated caution in deciding what variable to remove in these cases. Therefore I further validated the REML results by re-testing the variance components for the offending random effects using a variety of models. These included models that only contained the offending random effect. I also examined models in which correlated random effects were removed but the offending effect left in the model, in case this would result in variance shifting from the correlated random effect to the offending random effect. Finally, I ran models with only the offending random effect and the full set of fixed treatment effects. The vast majority of models that contained random effects either did not explain any variation in response variables, or explained little variation relative to the fixed effects (*unpublished data* JP Cronin). There were cases where a model that only contained the offending random effect was significant, but the random effect was not significant when fixed effects were also included in the model. In addition, in no cases did removal of correlated effects shift meaningful variance to the offending random effect. This indicates that these offending random effects had no explanatory power beyond their relationship with the fixed treatment effects. Thus, my removal of a random effect from a model with non-convergent MLE or zero-tending variance appears to be fully justified.

4.3 RESULTS

I successfully created substantial variation in the key gradients of interest (Table 4.4). In both experiments, my measure of herbivore control (the herbivore control index) was a direct measure of herbivore control over mean stem mass because it was not confounded with other vegetation differences between spray and control plots (Table 4.5). Similarly, the ability of spray to reduce damage did not change along my gradients in polyculture (Table 4.6). Thus, the herbivore control index in polyculture was not confounded with the ability of spray to reduce herbivore damage. The ability of spray to reduce the % leaf area damaged in monoculture, however, did increase 22% as stem density increased (Table 4.6). Despite this, I show in *Results* that I was able to test each of the hypotheses.

4.3.1 Community-level herbivore control hypotheses

4.3.1.1 NPP

NPP (i.e., total plant mass) was not correlated with herbivore abundance (Table 4.7), herbivore damage (Tables 4.8, 4.9), or herbivore control (Table 4.10) in either monoculture or polyculture. Some community-level NPP-based hypotheses (i.e., resource controlled food chains) do predict that herbivore control will stay constant as NPP increases but they simultaneously require that herbivore abundance increase as NPP increases (Chase et al. 2000). I found no evidence for an increase in herbivore abundance as NPP increased. Other community-level NPP-based models (i.e., consumer controlled food chains) predict that herbivore control should increase as NPP increases (Chase et al. 2000). I also found no evidence for this. Finally, some community-level NPP-based models (i.e., heterogeneous food webs) predict that herbivore control decreases because herbivore abundance increases as NPP increases. This increase in herbivore abundance causes an increase in the relative abundance of inedible plant species. It is this shift to inedible plant species that decreases herbivore control (Chase et al. 2000). Again I found no evidence that herbivore abundance increased with NPP (Table 4.7). Furthermore, herbivore control did not vary with the percent inedible stems (Table 4.10).

4.3.1.2 Total stem density

Total stem density was strongly negatively correlated with herbivore abundance in both monoculture and polyculture (Table 4.7, Fig. 3). Thus, I did not find evidence to support community-level hypotheses based on total stem density.

4.3.2 The host concentration hypothesis

4.3.2.1 Host plant productivity

Did herbivores respond to either absolute or relative *S. canadensis* productivity? In monoculture, total plant mass was not correlated with herbivore abundance (Table 4.7), damage to plants (Table 4.8, 4.9), or herbivore control (Table 4.10). While this demonstrates that herbivores did not respond to absolute *S. canadensis* mass, it leaves open the possibility that herbivores responded to relative host mass because relative host mass did not vary in monoculture (see Fig. 1a). The polyculture results, however, do not support this: percent *S. canadensis* mass was not correlated with herbivore abundance (Table 4.7), leaf damage (Table 4.8), or herbivore control (Table 4.10) on *S. canadensis* in polyculture or at the community-level in polyculture. These results demonstrate that herbivore abundance did not respond to absolute or relative *S. canadensis* mass.

4.3.2.2 Host plant stem density

Did herbivores respond to increases in absolute *S. canadensis* stem density? In monoculture, herbivore abundance strongly declined as *S. canadensis* stem density increased (Table 4.7, Fig. 3). Therefore, herbivores did not prefer patches with high absolute *S. canadensis* stem density. Thus, the monoculture results do not support host concentration hypotheses based on absolute host stem density.

Did herbivores respond to relative *S. canadensis* stem density? In polyculture, herbivore abundance (Table 4.7, Fig. 3) and damage to plants (Tables 4.8, 4.9) declined as total stem density of all plant species increased (i.e., as the percent *S. canadensis* stems declined). These declines were not, however, due to herbivores preferring plots with high relative *S. canadensis* stem density because neither herbivore abundance on *S. canadensis* in polyculture (Table 4.7, Fig. 3) nor damage on *S. canadensis* in polyculture (Tables 4.8, 4.9) declined as total stems increased (i.e., as the percent *S. canadensis* stems declined). Thus, the polyculture results do not support a host concentration hypothesis based on relative *S. canadensis* stem density. In total, I did not find any support for host concentration hypotheses based on either absolute or relative host stem density or host productivity.

4.3.3 The resource availability hypothesis

In monoculture, polyculture, and on *S. canadensis* in polyculture, herbivore abundance increased with fertility (Table 4.7, Fig. 3). Despite this increase in herbivore abundance, the reduction of mean stem mass due to herbivory actually decreased with fertility in monoculture, polyculture, and over *S. canadensis* in polyculture. This means that where herbivores were located and where they had a strong impact did not coincide. I also used light levels to test resource availability hypotheses. In monoculture, herbivore abundance (Fig. 3), stem damage (Table 4.7), and the percent reduction in mean stem mass (Fig. 4) were greatest where understory light availability was low. Light in polyculture, however, was not correlated with herbivore abundance (Table 4.7), damage (Tables 4.8, 4.9), or herbivore control (Table 4.10).

In combination, the fertility and light results do not support the nutrition-based resource availability hypothesis, which predict that herbivore activity (i.e., abundance or damage) and herbivore control will coincide (i.e., respond in the same direction to resource availability, e.g., White 1984). The results also do not support the plant defense-based resource availability hypothesis, which predicts that herbivore damage should peak at intermediate fertility, decline as light availability increases, and decline as stem density increases (see Stamp 2003, Stamp et al. 2004).

The results do support the tolerance-based resource availability hypothesis, which predicts that the ability of plants to cope with herbivory increases as resource availability increases. I found that herbivore *control* was always greatest when resource availability is low, regardless of where herbivore activity was highest. Furthermore, the effect of fertility on herbivore control in polyculture was due to herbivore impact on *S. canadensis* because there were no significant correlations between fertility and herbivore abundance, damage, or control over the non-*S. canadensis* stem pool in polyculture (Table 4.7, 4.8, 4.9, 4.10). In total, the best explanation for the strength of herbivore control at the community level in both experiments was that the ability of *S. canadensis* to tolerate herbivory decreased as resource availability decreased.

4.3.4 Other Factors

In polyculture, neither plant species diversity nor relative mean non-*S. canadensis* stem mass were correlated with herbivore abundance (Table 4.7), herbivore damage to plants (Tables 4.8, 4.9), or herbivore control (Table 4.10). While there were significant effects of predator abundance (Table 4.7, 4.9) and final mean stem mass (Table 4.10), these factors explained very little variation in each case (predators r^2 range: 0.004 - 0.007; mean stem mass r^2 range = 0.002 - 0.01). Interestingly, leaf damage on *S. canadensis* in polyculture strongly increased as the % inedible stems increased (Table 4.8) but herbivore control did not vary with the % inedible stems (Table 4.10).

4.4 DISCUSSION

I did not find support for community-level hypotheses, host concentration hypotheses, or resource availability hypotheses based on plant quality. I did, however, find strong support in both experiments for resource availability hypotheses based plant tolerance (e.g., McNaughton 1979, Maschinski and Whitham 1989, Strauss and Agrawal 1999). Resource availability hypotheses based on plant tolerance predict that herbivore control should decline as resource availability increases because plants growing in high resource conditions can better cope with herbivory (e.g., McNaughton 1979, Maschinski and Whitham 1989, Strauss and Agrawal 1999). I found that herbivores caused the greatest reductions in mean stem mass at low fertility and low understory light, regardless of where herbivore abundance or damage was greatest (e.g., compare Fig. 3 and 4). The effect of resource availability on plant tolerance is further supported by the fact that herbivores also caused a greater percent reduction in mean stem mass in high total stem density polycultures (i.e., high resource competition environments; Fig. 4) even though herbivore abundance was lowest at high total stem density (Fig. 3).

I found, however, three patterns that contradict popular perspectives on plant tolerance. First, discussions of plant tolerance focus heavily on overcompensation (e.g., McNaughton 1979, 1983, Maschinski and Whitham 1989, Augustine and McNaughton 1998, Strauss and Agrawal 1999). In contrast, I found that very few monocultures or polycultures fully compensated for insect herbivory (Fig. 4). This result, and results from other field studies (e.g., Brown 1994, Long et al. 2003) and meta-analyses (e.g., Schädler et al. 2003, Coupe and Cahill 2003), suggest that overcompensation does not strongly contribute to patterns of insect herbivore control over plant communities (although indirect effects of herbivores on nutrient cycling might be important, see McNaughton 1979, Pastor and Cohen 1997, Augustine and McNaughton 1998, de Mazancourt and Loreau 2000, Weisser and Siemann 2004). For example, Brown's (1994) field experiment demonstrated that herbivory on *S. missouriensis* reduced total mass, leaf mass, and stem mass. Despite that herbivory also increased per capita resource availability and increased relative growth rate, herbivory still caused strong reductions in *S. missouriensis* mass.

Second, studies of plant tolerance emphasize a need to understand the average plant taxon's tolerance to herbivory (e.g., herbaceous forbs vs. basal meristem monocots vs. woody species: Hawkes and Sullivan 2001). I found, however, that changes in herbivore control over both monocultures and polycultures were determined by the effect of resource availability on a single, dominant plant species' tolerance to herbivory (Fig. 4; also see McNaughton 1979, Uriarte and Schmitz 1998, Carson et al. 2004, and citations therein). Therefore, I caution that understanding the average tolerance across plant taxa in a community may provide little insight to predicting herbivore control over plant communities.

Third, studies of plant tolerance indicate that increasing per capita resource availability has highly variable effects on plant tolerance, and even decreases tolerance on average for herbaceous forbs (Hawkes and Sullivan 2001). For example, Meyer and Root (1993) found that the tolerance *Solidago altissima*'s sexual reproduction to insect herbivory declined as fertility increased. In contrast, my results suggest the tolerance *S. canadensis* increased with per capita resource availability. Tolerance studies such as Meyer and Root (1993), however, typically vary the amount of a resource available to individually potted, greenhouse-raised stems that are then subjected to are herbivory by a single herbivore species or by clipping (see Table 1 in Hawkes and Sullivan 2001). These studies, however, do not determine if the manipulated resource in these studies is actually most limiting to plant growth in the field, or if herbivory directly affects acquisition of the limiting resource in the field (or even the greenhouse; reviewed by Wise and Abrahamson 2003). In addition, most plant species, particularly dominant plant species such as *Solidago altissima* and *S. canadensis*, are typically attacked by numerous herbivore species, not a single herbivore (see *Tolerance of dominant plant species to herbivory* below). Thus, while theory does predict that consumers can have a variety of effects on their prey (reviewed in Chase et al. 2002, Wise and Abrahamson 2003), methodological differences likely explain why the results of Meyers and Root (1993) do not strongly match the results of this field study or other field studies of herbivory on *Solidago* spp: (e.g., Brown 1994, Long et al. 2003). Field studies from other plant community types that have investigated the interactive effect of herbivory and plant competition on plant mass also suggest that insect herbivory will typically cause stronger reductions in host-plant mass as per capita resource availability decreases (Table 4.11). Together, this body of evidence suggests that the vast majority of published tolerance studies are not representative of insect herbivore pressure, plant resource competition, or indirect effects in the field, which prevents them from explaining herbivore control over natural plant populations and communities.

Indeed, a major concern in ecology has been that community-level patterns might not be predicted from patterns at the species-level if complex communities have emergent properties (i.e., higher-order interactions: Fowler 1981, 1982, 2002, Fowler and Rausher 1985, Wilbur and Fauth 1990). Emergent properties are thought to occur when the outcome of the interaction between a subset of species is altered by the presence of other species (Fowler and Rausher 1985, Wilbur and Fauth 1990). My field experiments demonstrate, however, that that strength of herbivore control in monoculture was determined by the effect of resource availability on *S. canadensi*s' tolerance to herbivory and that this mechanism also explained patterns of herbivore control in complex polycultures. Thus, this and other field studies (e.g., Fowler and Rausher 1985, Fowler 2002) support the hypothesis that patterns of insect herbivore control in complex communities can be understood from species-level patterns, namely that species-level cascades (cf. Polis and Strong 1996, Polis 1999) involving abundant plant species will typically determine patterns herbivore control (also see Bach 1994, 2001a,b, Fagan and Bishop 2000, Carson et al. 2004, Bishop 2002, Letourneau et al. 2004, Stiling and Moon 2005).

4.4.1 The relationship between herbivore activity and herbivore control

Field studies that investigate the interaction between herbivory and competition typically manipulate plant competition and herbivory, but researchers then measure either the response of herbivore control over plant mass or the response of herbivore abundance and damage, but not both (reviewed in Hambäck and Beckerman 2003). Here, I measured herbivore control, herbivore abundance, and herbivore damage. Surprisingly, the response of herbivore abundance, herbivore damage, and herbivore control showed opposite responses to fertility and to total stem density (e.g., compare Fig. 3 and 4). This sharply contrasts with the prominent view that vegetation characteristics (e.g., defenses, tissue N, size, productivity, host concentration) alter the strength of herbivore control over plant communities only through the affect of plant traits on herbivore abundance or consumption. For example, the host concentration hypothesis (Carson et al. 2004), nutrition-based resource availability hypothesis (e.g., White 1984), and most NPP hypotheses (see Chase et al. 2000) predict that increases in herbivore abundance will typically lead to relatively stronger herbivore control over plants. I demonstrated experimentally, however, that regardless of where herbivore abundance was greatest or where they caused the most damage, herbivore control was always the strongest under low resource conditions (e.g., compare Fig. 3 and 4). Other studies also found that herbivore abundance or damage were not good predictors of herbivore control (Mitchell and Wass 1996, Carson and Root 1999, Cook and Holt 2002, Schmitz et al. 2000, Halaj and Wise 2001, Hambäck and Beckerman 2003). It is often suggested that the differences between measures of herbivore control and measures of herbivore abundance and damage is due to the ability of plants to compensate for lost tissue (e.g., Schmitz et al. 2000, Halaj and Wise 2001, Hambäck and Beckerman 2003). My results suggest that this also occurs because insect herbivore control is largely determined by per-capita resource availability to dominant plants (not by herbivore abundance or damage) but herbivores respond to aspects of plant tissue quality (see *Resource Availability and Herbivore Activity* below).

4.4.2 Per-capita resource availability, dominant plants, and herbivore control

If my results apply broadly, then the tolerance of dominant plant species will typically decrease as per-capita resource availability decreases. Thus, the direct effect of resource availability on the tolerance of dominant plant species will then subsequently lead to relatively greater herbivore control over entire plant communities under conditions of relatively low resource availability. In this section, I first address why the tolerance of dominant plant species should be more sensitive to changes in resource supply compared to rare plant species. Next, I discuss what processes drive changes in per-capita resource availability. Then, I reinterpret the results of two previous herbivore control studies.

4.4.2.1 Tolerance of dominant plant species to herbivory

Compared to rare plant species, abundant plant species typically have higher herbivore loads and are more likely to be hosts to specialist herbivores (Bernays and Chapman 1994, Thompson 1994, 2005). In addition, specialist herbivores are less negatively affected by host-plant defenses (Cornell and Hawkins 2003). In my study, *S. canadensis* in polyculture had a 63% greater herbivore abundance per stem, 54.5% greater leaf damage per stem, and a 60% greater reduction in mean stem mass due to herbivory compared to non-*S. canadensis* plant species. I suggest that dominant plant species growing under natural conditions will typically suffer greater damage and higher specialized herbivore loads (also see Thompson 1994, 2005, Carson et al. 2004). Thus, dominant plant species growing in the presence of their natural herbivore loads will likely be more sensitive to changes in resource availability compared to rare plant species also growing under similar natural conditions. Indeed, Carson and Root (2000) found that only the dominant species showed an increase in abundance following more than 8 years of insect exclusion in a goldenrod dominated old-field in central New York. Others have also found that insect exclusion leads to an increase in the abundance of only dominant plant species (e.g., Brown 1990, Brown and Gange 1989, 1992, Fine et al. 2004). I caution here, however, that some plant species that are highly vulnerable to herbivory may be rare for this reason and low sample sizes would make this difficult to detect (Carson and Root 1999).

4.4.2.2 Variation in per-capita resource availability

Two general processes can lead to differences in per capita resource availability among habitats: the strength of resource competition (e.g., Tilman 1982, 1988, Fowler 2002, Hambäck and Beckerman 2003) and the rate of resource supply / nutrient cycling (e.g., Tilman 1982, 1988, Brown 1994, Pastor and Cohen 1997, de Mazancourt and Loreau 2000, Hawkes and Sullivan 2001). Resource competition can reduce per-capita resource availability regardless of resource supply and regardless if the stand is a monoculture (i.e., intraspecific competition) or polyculture (i.e., interspecific competition). I experimentally demonstrated that, as total stem density increased in polyculture (i.e., as interspecific competition increased), herbivore control increased and this occurred regardless of fertility (i.e., there were no significant density*fertility interactions; Table 4.10). In addition, as understory light availability decreased in monoculture (i.e., as intra-specific competition increased), herbivore control also increased. Second, differences in the supply of resources (e.g., low nitrogen mineralization rates) can determine differences in per-capita resource availability, regardless of plant abundance or plant diversity. I experimentally demonstrated that herbivore control was always strongest at low fertility, regardless of total plant density (i.e., there were no significant fertility*density interactions) and regardless if the stand was a monoculture or polyculture (Table 4.10, Fig. 4).

Reinterpreting previous studies. I suggest that the effects of resource supply and resource competition on per-capita resource availability could explain the results found in previous herbivore control studies. For example, Long et al.'s (2003) experiment found that herbivore control over *S. altissima* increased as the concentration of *S. altissima* increased, which subsequently increased herbivore control over plant mass and species diversity. The authors proposed that this result was caused by greater host concentration. An alternative explanation that is consistent with my results is that as host concentration increased, intraspecific competition reduced per-capita resource availability thereby inhibiting the ability of *S. altissima* to tolerate or compensate for herbivory.

Fraser and Grime (1997) found that herbivore activity and control were greatest at sites of intermediate NPP. They concluded that this supported an NPP-based model. The effect of per-capita resource availability on plant tolerance provides an alternative explanation. For example, per-capita resource availability could have been lowest at intermediate NPP because total stem density is typically higher at intermediate levels of NPP (Stevens and Carson 1999a,b). In addition, Fraser and Grime's (1997) NPP gradient was confounded with a gradient in species diversity, such that intermediate NPP sites had > 20 species but the low and high NPP sites were monocultures. These differences in species composition could have caused lower resource availability at intermediate NPP sites because functionally diverse plant communities can have lower resource availabilities compared to monocultures (e.g., Tilman et al. 1997).

With few exceptions in terrestrial systems (Ritchie 2000, Ovadia and Schmitz 2004, Stiling and Moon 2005), experiments typically test one hypothesis (e.g., NPP, host concentration) but do not control other factors that covary with the gradient of interest. This has been particularly problematic because many studies use fertility or density gradients as a blanket manipulation for 'bottom-up effects' but do not control for the numerous confounding effects of other key gradients (i.e., NPP, plant species diversity, plant species composition, host concentration, plant quality, plant tolerance, the number of trophic levels, etc.). Thus, even meta-analyses (e.g., Schmitz et al. 2000, Halaj and Wise 2001, Schädler et al. 2003, Coupe and Cahill 2003) may either fail to find a general relationship between the strength of herbivore control and key gradients or, alternatively, may incorrectly conclude that there is empirical support a gradient when that gradient in tightly correlated with other key gradients.

4.4.3 Resource availability and herbivore activity

I suggest that the simplest explanation for herbivore abundance in both experiments was the direct effect of resource availability on the tissue quality of *S. canadensis* (vs. more indirect effects of fertility that I ruled out, e.g., NPP, plant growth rates, predators, Fig. 3; see also Stiling and Moon 2005). Herbivore abundance in both the monocultures and polycultures responded to effects of fertility on *S. canadensis* (i.e., there were no significant effects of fertility for non-*S. canadensis* stems, Table 4.7). Nitrogen fertilization universally increases the concentration of nitrogen in plant tissue (reviewed in Ayers 1993, Throop and Lerdau 2004), which repeatedly has provided the best explanation for insect herbivore activity (reviewed in Mattson 1980, Mattson and Scriber 1987, Scriber and Slansky 1981, Stamp and Casey 1993, Awmack and Leather 2002, Throop and Lerdau 2004). Herbivore abundance was also strongly negatively correlated with total stem density and with light in monoculture, both of which can affect tissue N concentrations (see also Pimentel 1961, Kareiva 1983, Karban et al. 1989). These results also provide indirect evidence that greater resource availability directly affected increased *S. canadensis* tissue quality.

Alternatively, herbivore abundance may respond to anti-herbivore defenses. Plant defense theory does predict that allocation to secondary metabolites increases sigmoidally with density (Stamp 2003, Stamp et al. 2004). If so, then herbivore damage might show a decreasing sigmoidal relationship. I did not see any consistent patterns in either experiment, possibly because the vast majority of herbivores in this study feed on *Solidago* spp. (Root and Cappuccino 1992, Table 4.2) and therefore were probably not highly sensitive to *S. canadensis* defenses (also see Dyer and Coley 2001, Cornell and Hawkins 2003). Plant defense theories also predict that plants should allocate more to secondary metabolites at intermediate fertility and high light (Stamp 2003). If so, then herbivore abundance might show a convex relationship with either fertility or mean stem mass. I did not observe any consistent pattern in either experiment. Thus, I suggest that the effects of resource availability on the nutritional quality of *S. canadensis* tissue (i.e., nitrogen concentrations) explained the observed patterns in herbivore activity. My experiments, however, were not designed to distinguish between herbivore responses to nutritional hypotheses vs. herbivore defense hypotheses.

4.4.4 Herbivore traits and herbivore control

There is evidence that the effect of resource availability on plant tolerance explains patterns of herbivore control over plant communities for herbivores that have very different traits (e.g., vertebrates: McNaughton 1979, McNaughton et al. 1983, Augustine and McNaughton 1998; vs. invertebrate herbivores: Moon and Stiling 2005, this study). Herbivore control over plant communities, however, might predictably vary with certain herbivore traits, such as body size, energy demands, and diet specialization (e.g., Strong et al. 1984, Price 1997) or because plants respond differently to different herbivores (e.g., vertebrate vs. invertebrate herbivory: Kotanen and Rosenthal 2000) (also see Chase et al. 2002, Hambäck and Beckerman 2003). For example, Fowler (2002) predicted that the negative impact of generalist herbivores on a target plant might typically decrease as resource competition among plants increases (i.e. herbivory and competition are antagonistic: one process has a smaller impact in the presence of the other process). This occurs because generalist herbivores not only attack the target plant, but they also remove biomass of competitors (Fowler 2002). This indirect, positive effect of grazing on the target plant would increase as resource competition among plants increases. In contrast, the negative impact of specialist herbivores should increase as resource competition among plants increases (i.e., herbivory and competition are synergistic: one process has a stronger negative impact in the presence of the other; Fowler 2002). This occurs because specialists only attack the target host plant; assuming all else is constant (e.g., non-host cues do not mask the host plant) there is no opportunity for a positive, indirect effect of specialist herbivory. Field studies that have investigated how herbivory interacts with competition to determine plant mass support Fowler's (2002) prediction (Table 4.11): the negative impact of insect herbivores, which are relatively specialized, is often greater when the host plant is in the presence of competitors, while studies that found the negative impact of herbivory decreased as competition increased were included mammalian herbivores, which have relatively broader diets compared to insects.

Finally, Chase et al. (2000), using meta-analysis, found that the strength of mammalian herbivore control over plant communities decreased with NPP. Therefore, they concluded that NPP-based models explained mammalian herbivore control. For invertebrates, however, meta-analyses suggest that NPP does not explain the strength of invertebrate herbivore control over plant communities (e.g., Schädler et al. 2003, Couple and Cahill 2003). Though all of these meta-analyses had limited ability to test multiple alternative herbivore control hypotheses (but see Borer et al. 2005), they support Oksanen et al's (1981) original prediction that NPP will only explain patterns of mammalian herbivore control because of the energy required to support mammalian herbivore populations. Future research should determine if there are general, predictable relationships between herbivore traits and the strength of herbivore control.

4.4.5 Other factors and issues of scale

In addition to the experimental gradients that I created, I also used statistical techniques to evaluate whether other factors explained herbivore control. These other factors, however, explained virtually no variation in herbivore control (Table 4.10). Nonetheless, previous research suggests that these and other factors are important. For example, there is ample evidence that predators can have strong indirect effects on plant mass and species composition (Schmitz et al. 2000, Halaj and Wise 2001, Schmitz 2003). In addition, herbivory that shifts plant species composition will likely affect herbivore control by altering limiting nutrient cycles, which can feedback onto plant mass (e.g., McNaughton 1979, de Mazancourt and Loreau 2000, Weisser and Siemann 2004). Recent studies have also found that fluxuations in abiotic factors can temporarily swamp trophic interactions (Ritchie 2000, Ovadia and Schmitz 2004). Although my experiments were conducted on longer spatial scales and larger temporal scales compared to the vast majority of experimental studies on trophic interactions (e.g., see Schmitz et al. 2000, Hambäck and Beckerman 2003, Englund and Moen 2003), these factors are often expected to become important over longer temporal scales or larger spatial scales (Hunter and Price 1992, Schmitz et al. 2000, Halaj and Wise 2001, Carson et al. 2004, Borer et al. 2005). The effect of per capita resource availability on plant tolerance should operate independent of spatial or temporal scales, provided that resource availability varies on a scale that plants can perceive and respond too (also see Fargione and Tilman 2002, Hambäck and Beckerman 2003). Thus, other factors will operate by modifying the relationship between per-capita resource availability and the tolerance of dominant plants to herbivory. The challenge is to model and to experimentally determine when these other factors will likely come into play.

Compared to plant tolerance, however, the factors that control herbivore abundance and damage are much more sensitive to temporal and spatial scales (reviewed in Karieva 1983, Hambäck and Beckerman 2003, McGeoch and Price 2005). For example, literature reviews by Carson and Root (2000) and Carson et al. (2004) demonstrate that short-term studies fail to observe insect herbivore outbreaks, even though these outbreaks repeatedly occur during the lifetime of abundant, widespread plant species. In addition, at small spatial scales (e.g., among stems) and at intermediate spatial scales (e.g., among patches), patterns of herbivore abundance and damage are influenced by olfactory cues and visual cues from both the host plant and non-host-plants, host plant encounter rates, predation risk, etc. because these factors strongly influence herbivore foraging decisions (reviewed in Hambäck and Beckerman 2003). Increasing the spatial scale, however, often shifts foodweb dynamics from being relatively open (i.e., foraging behavior is the critical demographic parameter) to relatively closed (i.e., herbivore reproduction, growth, and mortality demographic parameters become more important; also see Wootton and Power 1993, Oksanen et al. 1995, Hambäck and Beckerman 2003). For example, Price and colleagues have provided strong evidence that the distribution and abundance of the sawfly, *Euura lasiolepis*, at small spatial scales (clonal area of host-plant) are determined by the response of female oviposition foraging behavior and larval survival to host plant quality (see McGeoch and Price 2005). At the landscape scale, however, dispersal among sites is limited, preventing foraging behavior from heavily influencing sawfly distribution and abundance (though the survival-host quality relationship was scale invariant; McGeogh and Price 2005). Although I did not directly observe herbivore foraging behavior, field observations suggested that my food webs were open, at least for the dominant insect herbivores. Thus, patterns in the distribution and abundance of insects observed in this study may have been strongly influenced by herbivore foraging behavior. Therefore, increasing the spatial or temporal scale might increase the relative importance of other herbivore demographic parameters (e.g., birth, growth, and death rates) that are sensitive to factors other than host tissue quality (e.g., NPP).

The potential for scale dependent relationships between vegetation characteristics and herbivore demographic parameters is often used to argue that empiricists incorrectly test NPP-based models (e.g., see Englund and Moen 2003). On one hand, empiricists are criticized for concluding that NPP models based on herbivore birth, growth, and death rates (e.g., Oksanen et al. 1981) explain the results of their small-scale (i.e., open) experiments. On the other hand, empiricists are criticized for rejecting NPP models because they didn't conduct the experiment at a large enough spatial or temporal scale. Recent NPP models have addressed open systems and suggest that foraging behavior responses to NPP in open food chains generate the same predictions as NPP-based closed food chains (e.g., Wootton and Power 1993, Oksanan et al. 1995). Thus, NPP-models are expected to apply across spatial and temporal scales. Despite this theoretical result, it is difficult to imagine that herbivores make foraging decisions by actually perceiving a rate of plant production. It might be more appropriate to consider that NPP has historically been expected to provide such predictive power because rates of plant productivity are correlated with other key vegetation characteristics, such as plant tissue quality or total plant mass (see Fretwell 1987, Power 1992). Irrespective, my results (also see Stiling and Moon 2005) and those of meta-analyses (i.e., patterns across large spatial scales: Schädler et al. 2003, Couple and Cahill 2003) suggest that NPP-based models do not provide a good explanation for patterns of insect herbivore abundance, herbivore damage, and herbivore control regardless of spatial scale.

4.5 CONCLUSIONS

To my knowledge, this is the first study to convincingly demonstrate that a specific factor, per capita resource availability, determined herbivore control over plant communities. The experiments demonstrated that herbivores caused the greatest reductions in community-level mean stem mass when the dominant plant species (*S. canadensis*) could not tolerate herbivory, which occurred under low resource availability conditions, regardless of where herbivore abundance and damage was greatest. In contrast to widely cited herbivore control hypotheses (i.e., predation, NPP, food web complexity), this result provides a very parsimonious and potentially very general explanation for variation in the strength of herbivore control. I suggest that future herbivore control hypotheses use effects of resource availability on the tolerance of dominant plants as their foundation and then investigate how other processes (e.g., abiotic factors, predators, shifts in species composition) modify the outcome of this relationship.

Table 4.1 Plant species composition and species-specific allometric regressions

Relative stem density was calculated for non-*S. canadensis* species pool in polyculture plots over two years. For species that lack allometric regressions, the number of stems per species recorded during the mass census is indicated in () under 'Regression' (27 stems over 2 years).

Species (Gleason & Cronquist 1991)	% Stems	R^2	Regression*
Ambrosia artemisiifolia	0.02	-	(1)
Apocynum cannabinum†	0.29	0.713	ln(y) = -2.128972+0.036814*x
Arctium lappa	0.05	-	(2)
Aster lanceolatus	21.9	0.811	ln(y) = -0.786634 + 0.0232804 * x-0.0000432 * (x-105.486)^2
Aster lateriflorus	18.9	0.848	ln(y) = -2.198723 + 0.0409084 * x-0.000244 * (x-73.7349)^2
Aster novae-angliae†	1.0	0.873	y = -1.307077 + 0.0670814 * x + 0.0009038 * (x-47.2097)^2
Aster pilosus	8.7	0.839	ln(y) = -1.493424 + 0.032735 * x-0.000102 * (x-91.9333) ^ 2
Aster prenanthoides†	0.18	0.734	y= -0.388134 + 0.0370978 * x + 0.0007961 * (x-26.612)^2
Calystegia sepium†	0.64	0.576	y = ln(-5.81950204610813 + 1.47483685803348 * x)
Carex annectens (inedible)	0.04	-	(2)
Carex spp b (inedible)	0.02	-	(1)
Cirsium discolor	0.13	-	(6)
Dipsacus sylvestris	0.07	-	(4)

Table 4.1 (continued)

Euthamia graminifolia	12.4	0.771	ln(y) = -0.846092 + 0.0333567 * x-0.0003145 * (x-94.6578)^2
Hieracium aurantiacum	0.02	-	(1)
Juncus tenuis (inedible)	18.9	0.786	ln(y) = -0.443645 + 0.0747702 * x-0.0006031 * (x-24.902)^2
Sisyrinchium angustifolia	0.22	-	(10)
Solanum carolinensis†	4.9	0.560	y = -0.094014 + 0.0223518 * x + 0.00024 * (x-21.425)^2
Solidago canadensis	-	0.803	ln(y) = 0.0760538 + 0.0197548 * x - 0.0000735 * (x - 143.113)^2
Solidago gigantea	7.5	0.793	ln(y) = -0.792124 + 0.0246924 * x - 0.0000373 * (x - 124.785)^2
Solidago rugosa	3.9	0.866	ln(y) = -0.974031 + 0.0262044 * x - 0.0001235 * (x- 105.692)^2

* y = total aboveground dry mass (g stem, leaf and flowers). x = height (cm), except for J. tenuis (x = diameter; mm) and C. sepium (x = length of longest leaf; cm). n ≈100 individuals per species. Stem were harvested on site, dried and weighed. *Apocynum cannabinum* and *Calystegia sepium* data were obtained from JC Cahill and H. Schumacher, respectively.

† y = above ground stem and leaf dry mass (g).

Table 4.2 Insect herbivore species composition

Described are the insect herbivores observed on all plant species in this study. Species #1-18 were identified as a single species in the field while insects #40-46 could not identified as a single species in the field. Also described are the insect herbivores observed in a 6-year survey of *S. altissima* stems in 16 old-fields in New York, USA (Root and Cappuccino 1992). For insects observed in the current study, the feeding guild, diet, abundance (# sampled), and host association are described. Species #1-18 are ranked according to their abundance in year two of the current study. Species with * were used to test the herbivore diet breadth hypothesis. To compare species composition and species dominance rankings in this experimental study to those of natural field conditions, Root and Cappuccino's (1992) rankings for the abundance, temporal variability, and spatial variability among old-fields are described (except #33-46, which Root and Cappuccino 1992 could not identify to species in the field). Of the herbivores identified to species in my experiments, 9 were found in the current study and in Root and Cappuccino (1992). Some of the differences in species composition are due to the inability to either study to identify individuals to species (e.g., I did not identify most leaf chewing and tip-boring Lepidoptera to species in the field because this would have damaged plants, but Root & Cappuccino 1992 did for many Lepidoptera). In addition, Root and Cappuccino (1992) only sampled *S. altissima*. Both studies had similar dominant herbivore species (e.g., *A. carbonifera and M. vittata*). Differences in the rankings of 11 other dominant old-field herbivores are likely explained by either high variability of specific insect species in space in time (*T. virgatta, E. canadensis, G. solidaginis*), present but low abundance in the current study (*C. solidaginis, E. solidaginis*), not present or not identified to species (*C. magna/vulgaris, A. gothica, Emposaca spp., Dichomeris spp, and O. conferta*), or because the species was present at my field site, but peaked prior to my herbivore census (*P. spumarius*). *P. spumarius* was predominantly observed by JP Cronin feeding on non-*Solidago* spp., namely *Trifolium pratense*, in the buffer zones among the experimental plots.

Table 4.2 (continued)

						Current Study		Root & Cappuccino (1992) rankings §		
#	Insect herbivore species	Order	Family	Guild †	Diet ‡	# sampled (% on non-*S. canadensis*)	Primary Hosts (secondary hosts)	# (load)	Temporal variation	Spatial variation
1	*Asteromyia carbonifera**	Diptera	Cecidomyiidae	LG		2186 (7)	*S. canadensis* (*S. gigantea, S. rugosa, A. lanceolatus, A. pilosus, E. graminifolia, A. lateriflorus*)	1	9	2
2	Miscellaneous (Unknown D)*	Diptera	?	LG		667 (12)	*S. canadensis* (*E. graminifolia, S. gigantea, A. lanceolatus, S. rugosa, A. pilosus*)	-	-	-
3	*Asphondylia bifolia**	Diptera	Cecidomyiidae	LG		621 (<1)	*S. canadensis* (*A. lanceolatus, S. gigantea, A. lateriflorus, A. pilosus*)	3	13	3
4	*Rhopalomyia solidaginis**	Diptera	Cecidomyiidae	SG		429 (7)	*S. canadensis* (*S. gigantea, E. graminifolia*)	2	16	3
5	*Microrhopala vittata**	Coleoptera	Chrysomelidae	LM		361 (11)	*S. canadensis* (*E. graminifolia, S. gigantea, S. rugosa*)	8 (3)	6	10
6	*Corimelaena pulicaria (sp)*	Hemiptera	Thyreocoridae	SF		322 (20)	*S. canadensis* (*A. lateriflorus, A. pilosus, A. lanceolatus*)	-	-	-
7	Miscellaneous (Unknown C)*	Diptera	?	LG		272 (100)	*E. graminifolia* (*S. gigantea, A. lateriflorus, A. pilosus*)	-	-	-

Table 4.2 (continued).

8	*Paria thoracica* (sp)	Coleoptera	Chrysomelidae	LC	?	266 (46)	*S. canadensis* (*A. lanceolatus, A. lateriflorus, A. pilosus, E. graminifolia, S. gigantea, S. rugosa, J. tenuis, A. novae-angliae*)	-	-
9	Miscellaneous (Unknown B)*	Diptera	?	LG	O	172 (5)	*S. canadensis* (*S. rugosa, S. gigantea*)	-	-
10	*Eurosta solidaginis**	Diptera	Tephritidae	SG	M	161 (<1)	*S. canadensis* (*A. lateriflorus*)	7 (4)	17
11	Miscellaneous (Unknown E)*	Homoptera	Psyllidae sp.	LG	P	136 (99)	*E. graminifolia* (*A. lanceolatus, S. gigantea, S. canadensis*)	-	-
12	*Cremastobombycia solidaginis**	Lepidoptera	Gracillariidae	LM	M	79 (2)	*S. canadensis* (*E. graminifolia, S. gigantea*)	5	10
13	*Melanagromyza* spp. B*	Diptera	Agromyzidae	LM	P	38 (16)	*S. canadensis* (*A. pilosus, A. lanceolatus, S. gigantea, E. graminifolia*)	-	-
14	*Gnorimoschema gallaesolidagis**	Lepidoptera	Gelechiidae	SG	M	32 (0)	*S. canadensis*	21 (7)	21
15	Miscellaneous (Unknown F)*	Diptera	?	LG	P	22 (77)	*S. gigantea* (*A. lanceolatus, S. canadensis*)	-	-
16	Miscellaneous (Unknown A)*	Orthoptera	?	LC	O	14 (7)	*S. canadensis* (*S. gigantea*)	-	-
17	*Exema canadensis**	Coleoptera	Chrysomelidae	LC	M	2 (0)	*S. canadensis*	9	5

Table 4.2 (continued).

18	*Trirhabda virgata**	Coleoptera	Chrysomelidae	LC	*M*	2 (0)	*S. canadensis*	3 (1)	2	11
19	*Adaina montana*	Lepidoptera	Pterophoridae	LC	*P*	--	--	19	23	5
20	*Agonopteryx pulvipennella*	Lepidoptera	Oecophoridae	LC	*P*	--	--	20	22	3
21	*Amphiigonalia gothica*	Hemiptera	Cicadellidae	SF	*O*	--	--	6	19	4
22	*Calycomyza solidaginis*	Diptera	Agromyzidae	LM	*O*	--	--	15	8	4
23	*Corythucha marmorata*	Hemiptera	Tingidae	SF	*P*	--	--	16	7	12
24	*Craspedolepta magna/vulgaris*	Hemiptera	Psylidae	SF	*M*	--	--	4	14	3
25	*Empoasca* spp.	Hemiptera	Cicadellidae	SF	*P*	--	--	10	1	4
26	*Epiblema scudderiana*	Lepidoptera	Tortricidae	SG	*O*	--	--	18	18	3
27	*Lygus lineolaris*	Hemiptera	Miridae	SF	*P*	--	--	14	4	6
28	*Oidaematophorus homodactylus*	Lepidoptera	Pterophoridae	LC	*O*	--	--	23	20	8
29	*Phaneta formosana*	Lepidoptera	Tortricidae	SG	*O*	--	--	11	11	5
30	*Philaenus spumarius*	Hemiptera	Cero-pidae	SF	*P*	--	--	2 (2)	12	5

Table 4.2 (continued).

31	*Publilia concava*	Hemiptera	Membracidae	SF	*M*	--	--	22	15	20
32	*Scrobipalpula sacculicola*	Lepidoptera	Gelechiidae	LM	*?*	--	--	17	3	8
33	Miscellaneous	Hemiptera	Membracidae	SF	?	--	--	--	--	--
34	Miscellaneous	Hemiptera	Homptera	SF	?	--	--	--	--	--
35	Miscellaneous	Hemiptera	Miridae	SF	?	--	--	--	--	--
36	Miscellaneous	Hemiptera	Heteroptera	SF	?	--	--	--	--	--
37	*Ophraella conferta*	Coleoptera	Chrysomelidae	LC	?	--	--	-- (6)	--	--
38	Miscellaneous	Coleoptera	-	LC	?	--	--	--	--	--
39	*Dichomeris* spp	Lepidoptera	Gelechiidae	LC	?	--	--	-- (5)	--	--
40	*Uroleucon spp**	Hemiptera	Aphididae	SF	P	290 (11)	*S. canadensis* (*A. lanceolatus*, *S. rugosa, S. gigantea*, *A. pilosus*, *E. graminifolia*, *A. lateriflorus*, *A. novae-angliae*)	---	---	---
41	Miscellaneous	Lepidoptera	?	TB	?	1343 (9)	*S. canadensis* (*A. lanceolatus, E. graminifolia, A pilosus, A. lateriflorus, S. gigantea, S. rugosa*)	---	---	---
42	Miscellaneous	Lepidoptera	?	LC	?	185 (18)	*S. canadensis* (*A. lanceolatus, E. graminifolia, S. gigantea, A. lateriflorus, A pilosus*)	---	---	---

Table 4.2 (continued).

43	Miscellaneous	Diptera	Agromyzidae	LM	?	2850 (10)	*S. canadensis* (*A. lanceolatus, A pilosus, S. gigantea, A. lateriflorus, E. graminifolia, A. novae-angliae, S. rugosa)*	---	---	---
44	*Melanagromyza* spp. A & *Cerodontha* spp. A	Diptera	Agromyzidae	LM	?	283 (12)	*S. canadensis* (*A. lanceolatus, S. gigantea, A. pilosus, A. lateriflorus, A. novae-angliae, E. graminifolia*)	-	-	-
45	*Bucculatrix* spp.	Lepidoptera	Lyonetiidae	LM	?	34 (100)	*A. lanceolatus* (*A. pilosus, A. lateriflorus, A. novae angliae*)	-	-	-
46	Miscellaneous	?	?	?	?	109 (25)	*S. canadensis* (*E. graminifolia, A. lanceolatus, S. gigantea, A. lateriflorus, A. pilosus, J. tenuis*)	-	-	-

† LG = leaf galler; SG = stem galler; LM = leaf miner; SF = sap feeder; LC = leaf chewer; TB = tip borer

‡ P = polyphagous on *Solidago* spp & *Aster* spp, more than 1 family, or on Composites; O = Oligophagous on *Solidago* spp.; M = monophagous on *S. canadensis*. Determined from field observations, Root & Cappuccino 1992, or published literature.

§ Abundance rankings: 1 = highest median mean abundance vs. 23 = lowest abundance: see Fig 2 in Root and Cappuccino 1992; Temporal variability: 1 = highest variability over time vs. 23 = lowest variability over time: see Fig 4 in Root and Cappuccino 1992; Spatial variability: 1 = greatest randomness in distribution among field sites vs. 20 = more clumped, see Fig. 6 in Root and Cappuccino 1992.

- = not sampled/identified in Root and Cappuccino (1992); -- = not sampled/identified in current study; --- sampled in both Root and Cappuccino (1992) and in current study, but information was not provided by Root & Cappuccino (1992).

Table 4.3 Insect herbivore guild composition

Described are the relative abundances (# sampled) of the feeding guilds from the insects sampled in the current study (see #1-18 & #40-46 in Table 4.2). Also described are the abundance rankings of feeding guilds from Root and Cappuccino's (1992) 6-year survey of 16 old-fields in New York, USA. This table demonstrates that the herbivore community in the current study was similar in guild structure compared to other old-field communities. This study, however, was more strongly dominated by gallers and leaf miners compared to Root and Cappuccino's (1992), who observed dominance of leaf chewers and miners (June) or gallers and sap feeders (September). This suggests that my census was conducted during species compositional turnover between June and September.

	Current Study		**Ranking of guilds (see Fig 8 in Root and Cappuccino 1992)**	
Guild†	**# sampled (% on non-*S. canadensis*)**	**% of total abundance**	**June Abundance**	**September Abundance**
Leaf chewers	469 (33.4)	4.3	1	3
Leaf miners	3645 (11)	33.5	2	4
Sap feeders	612 (15.7)	5.6	3	2
Gall makers	5217 (13.6)	55.5	4	1
Leaf gallers	4076 (16.4)	37.5	?	?
Stem gallers	622 (5.1)	5.7	?	?
Tip borers	1343 (9)	12.3	?	?
Miscellaneous	109 (25)	1	?	?

Table 4.4 Descriptive statistics for the predictor variables used to construct mixed models Using these predictor variables, mixed models were constructed for each response variable. Monoculture mixed models initially included the first six predictor variables listed and an interaction between fertility and density. Polyculture mixed models (either at the community, *S. canadensis,* or non-*S. canadensis* levels) initially included all of the predictor variables listed and an interaction between fertility and density. Random effects (†) were removed from models when JMP's (5.0.1.2) REML procedure estimated the variance component as zero, which is indicated by negative variance estimates or failure to estimate 95% confidence interval. Note that which random effects were removed differed among response variables. The final model for a response variable can be determined by looking at the effects that are reported in the ANOVA table for that response variable. For example, the final model for the monoculture analysis of monophagous herbivore abundance (Table 3.6) included fertility, density, fertility*density, and predators. The final model for polyculture community-level analysis of monophagous herbivore abundance (Table 3.6) included fertility, density, fertility*density, predators, and mass^{-2}.

	Monoculture		**Polyculture**	
Predictor Variable	**mean +/- stdev**	**range**	**mean +/- stdev**	**range**
Mass m^{-2} (g) †	491.7 +/- 234.7	154.3 - 1119.9	346.7 +/- 108.5	154.3 – 644.5
Plant tems m^{-2}	-	8 - 32	-	8 - 32
Fertility (g N m^{2} yr^{-1})	-	0 - 16	-	0 - 16
Light (DIFN) †	0.32 +/- 14	0.12 – 0.72	0.42 +/- 0.14	0.15 - 0.72
Mean stem mass (g) †	24.7 +/- 7.1	8.5 - 45.7	20.3 +/- 7.4	8.2 – 42.5
# predators per plot†	2.05 +/- 1.8	0 - 8	1.46 +/- 1.46	0 - 8
Plant diversity (H') †	0	0	1.04 +/- 0.65	0 – 1.89
% *S. canadensis* mass m^{-2} (g)†	1	1	0.69 +/- 0.21	0.22 - 1
% inedible stems m^{-2}†	0	0	0.066 +/- 0.07	0 – 0.31
Relative non-*S. canadensis* stem mass†	0	0	0.35 +/- 0.24	0 – 0.99

Table 4.5 ANCOVA results for stem density and diversity m^{-2}

Analysis (F-ratios, R^2 and r^2s) only included fixed treatment effects (i.e. no random effects were used). These analyses demonstrate that the spray treatment did not have an unintended effect of changing stem density, percent S. canadensis mass, percent inedible stems, or plant species diversity. Therefore, I obtained a direct measure of herbivore control over mean stem mass because it was not confounded with differences between spray and control plots. Though several other polyculture effects were significant, in all cases they explained <0.1% of the variation.

	Polyculture				Mono-culture
Source	Stems m^{-2} (df= 1,160)	% *S. canadensis* stems m^{-2} (df= 1,160)	% inedible stems m^{-2} (df= 1,118)	Diversity (df= 1,118)	Stems m^{-2} (df= 1,160)
Full Model	1170.2*** (0.98)	4710.2*** (0.99)	1.5	0.28	1196.1*** (0.98)
Spray	9.3** (0.001)	3.11			2.86
Fertility	0.0016	0.92			0.02* (0.001)
Stems m^{-2}	8160.6*** (0.98)	32948*** (0.99)			8364.5*** (0.98)
Spray*Fertility	0.007** (0.001)	11.8** (0.0004)			0.13
Spray*Stems m^{-2}	5.5* (0.001)	0.26			0.09
Fertility*Density	0.20	1.4			0.07
Spray*Fertility* Stems m^{-2}	8.7** (0.001)	5.8* 0.0002			0.11

* $0.01 \leq P < 0.05$; ** $0.001 \leq P < 0.01$, *** $P \leq 0.001$.

n=84 for each analysis, except % inedible and diversity (n = 63) because 8 stem monocultures were excluded.

Table 4.6 Descriptive statistics and mixed model results for the % reduction in herbivore damage

If the effect of spray varied along gradients, then changes in herbivore control along gradients could be due to changes in the ability of our spray treatment to reduce damage, not due to an actual change in herbivore control. Spray only varied with stems m^{-2} in monoculture, such that the % reduction in the % leaf area damaged increased by 22% as stem density increased.

	Source and type of damage	**Mean % reduction +/- stdev**	**Full model**	**Fertility**	**Stems m^{-2}**	**Fertility* Stems m^{-2}**
Mono-culture (df = 1, 80)	Leaf	0.73 +/- 0.24	**2.6***	0.07	**7.6**** (0.07)	2.7
	Stem	0.7 +/- 0.29	1			
Polyculture	*Community-level* (df = 1, 80)					
	Leaf	0.66 +/- 0.25	1.4			
	Stem	0.59 +/- 0.45	1.2			
	S. canadensis (df = 1, 80)					
	Leaf	0.71 +/- 0.25	0.4			
	Stem	0.7 +/- 0.25	0.69			
	All Non-S. canadensis leaves (df = 1, 58)	0.6 +/- 0.37	1.9			
	Edible non- S. canadensis (df = 1, 58)					
	Leaf	0.69+/- 0.24	1.4			
	Stem	0.47 +/- 0.72	1.2			
	A. lanceolatus leaves (df = 1, 53; n= 54)	0.67 +/- 0.4	1.5			
	A. lateriflorus leaves (df = 1, 53; n= 54)	0.69 +/- 0.6	1.5			

* $0.01 \leq P < 0.05$; ** $0.001 \leq P < 0.01$, *** $P \leq 0.001$.

Table 4.7 REML results for total # herbivores per control plot

Random effects without statistics (or not shown) were removed from a model because they did not contribute to the fit of the model (see *Statistical Analyses* for model selection criteria; e.g. mass m^{-2} was excluded from all five analyses; # predators was included in the monoculture and *S. canadensis* in polyculture analyses). Values in () indicate the % increase (+) or decrease (-) in y as x increases.

			Predictor Variables						
Analysis		**Statistic**	**Full Model**	**Fertility**	**Stems m^{-2}**	**Fertility* Stems m^{-2}**	**Light†**	**# Predators†**	**% inedible stems m^{-2}†**
	Mono-culture (n = 84)	*F* or *VC*†	**11.1***	**14.1***	**29.2***	0.22	**0.45***	**0.002***	
		r^2 or %	0.41	0.1 (+28)	0.22 (-49)	-	0.8 (-29)	0.004 (+)	
Polyculture	Community (n = 84)	*F* or *VC*†	**16.5***	**10***	**55.1***	0.12	0.33		
		r^2 or %	0.45	0.07 (+27)	0.38 (-57)	-	-		
	S. canadensis (n = 84)	*F* or *VC*†	**5.5***	**15.5***	2.6	0.6	0.14	**0.003***	0.2
		r^2 or %	0.29	0.14 (+27)	-	-	-	0.007 (+)	-

Table 4.7 (continued)

Polyculture	Non-*S. canadensis* (n = 63)	*F* or *VC*†	1.7	3.8	1.7	0.02	0.32
		r^2 or %	-	-	-	-	-
	Edible non-*S. canadensis* (n = 63)	*F* or *VC*†	1.7	3.8	1.8	0.009	0.33
		r^2 or %	-	-	-	-	-

† Variance Components (*VC*) and Percent of Total (%) are reported for random effects (vs. *F* ratios and r^2 for fixed effects)

\- r^2 not reported because effect was non-significant

* $0.01 \leq P < 0.05$; ** $0.001 \leq P < 0.01$, *** $P \leq 0.001$.

Data were ln(y) transformed for monoculture (df: 1, 78), polyculture community-level (df: 1, 79) and *S. canadensis* in polyculture (df: 1, 77). Data were ln(y+1) transformed for non-*S. canadensis* (df: 1, 58).

Table 4.8 REML results for mean percent leaf area damaged per stem in control plots

Analysis		Statistic	Full Model	Fertility	Stems m^{-2}	Fertility* Stems m^{-2}	% inedible stems m^{-2}†	Relative non-*S. canadensis* stem mass†	Plant mass m^{-2} †	Mean stem mass†	Light†
	Monoculture	*F* or *VC*	1.2	0.82	0.004	2.8					
		r^2 or %	-	-	-	-					
Polyculture	Community	*F* or *VC*	**4.7****	2.2	**11.3*****	**4.5***	1.5				
		r^2 or %	0.19	-	0.11 (-37)	0.045	-				
	S. canadensis	*F* or *VC*	**2.1***	2	1.2	0.66	**4.6***	0.21	8.18e^{-7}	0.00007	
		r^2 or %	0.16	-	-	-	0.9 (+42)	-	-	-	
	Non-*S. canadensis*	*F* or *VC*	1.9	0.47	3.2	2.4					0.25
		r^2 or %	-	-	-	-					-
	Edibles (n = 63)	*F* or *VC*	1.4	0.63	0.39	1.2	0.7				0.3
		r^2 or %	-	-	-	-					-

Symbols as in Table 4.7. Data were SQRT(y) transformed for Monoculture (df = 1, 80) and *S. canadensis* in polyculture (df = 1, 76). Data were ln(y) transformed for Polyculture community-level (df = 1, 79) and non-*S. canadensis* (df = 1, 57).

Table 4.9 REML results for percentage of stems damaged by stem feeding insects

Analysis		Statistic	Full Model	Fertility	Stems m^{-2}	Fertility* Stems m^{-2}	Light†	Plant mass m^{-2} †	# Preda-tors†	% *S. canadensis* mass m^{-2}†	Mean stem mass†
Mono-culture		*F* or *VC*	**3.1*****	0.18	3.7	0.01	**767***	0.0004	4.8*		
		r^2 or %	0.19	-	-	-	0.78 (-28)	-	0.005		
Polyculture	Comm-unity	*F* or *VC*	**25.4*****	0.6	**5.9***	3.7				**6.5****	0.002
		r^2 or %	0.61	-	0.03 (-35)	-				0.9 (+55)	-
	S. cana-densis	*F* or *VC*	0.78	0.01	1.6	0.42					
		r^2 or %	-	-	-	-					
	Non-*S. canadensis*	*F* or *VC*	0.87	0.09	0.33	2.2					
		r^2 or %	-	-	-	-					
		r^2 or %									

Symbols as in Table 4.7. Data were not transformed for Monoculture (df = 1, 77), SQRT(y) transformed for *S. canadensis* in polyculture (df = 1, 80) and Polyculture community-level (df = 1, 78), and SQRT(y)+3/8 for non-*S. canadensis* (df = 1, 59).

Table 4.10 REML results for herbivore control index on mean stem mass

Note that positive correlations between herbivore control and an effect indicates that the impact of herbivory decreased (see Fig. 4.3).

Analysis		**Statistic**	**Full Model**	**Fertility**	**Stems m^{-2}**	**Fertility * Stems m^{-2}**	**Light†**	**Mean stem mass†**	**% inedible stems m^{-2}†**	**Relative non-*S. canadensis* stem mass†**	**Diversity†**
Monoculture		*F* or *VC*	**16.3*****	**31.5*****	0.6	0	**0.22*****	**0.0005*****			
		r^2 or %	0.5	0.2 (+66)	-	-	0.92 (+74)	0.002 (-)			
Polyculture	Community	*F* or *VC*	**6.8*****	**19.1*****	**14*****	1.8	0.01	**0.0006*****	0.12	0.03	
		r^2 or %	0.37	0.15 (+54)	0.11 (-65)	-	-	0.003 (-)	-	-	
	S. canadensis	*F* or *VC*	**4.3****	**9****	**6.5****	3.5		**0.0005*****			0.009
		r^2 or %	0.21	0.09 (+41)	0.06 (-50)	-		0.01 (-)			-
	Non-*S. canadensis*	*F* or *VC*	1.13	0.03	0.07	3.3					
		r^2 or %	-	-	-	-					
	Edibles (n = 63)	*F* or *VC*	2.0	0.02	0.01	0.43				0.36	
		r^2 or %	-	-	-	-				-	

Symbols as in Table 4.7. Data were not transformed for Monoculture (df = 1, 78); *S. canadensis* in polyculture (df = 1, 78), Polyculture community-level (df = 1, 76), and non-*S. canadensis* (df = 1, 59) were Arcsine transformed.

Table 4.11 Empirical field studies of the interaction between competition and herbivory on plant mass

Competition and herbivory were simultaneously manipulated to determine their individual and interactive impacts on the performance (e.g., mass) of a target plant species. Fowler (2002)* and Hambäck and Beckerman (2003)** classified the interactions as synergistic (S: competition reinforces the negative impact of herbivory), antagonistic (A: competition or herbivory weakens the effect of the other process), or independent (I: neither process changes the effect of the other process on plant mass). A '–' means citation not reviewed.

Citation	Target plant species	Competitors	Herbivores	*	**
Parker and Salzman 1985	*Gutierrezia microcephala*	Community	Insect	S	I
McEvoy et al. 1993	*Senecia jacobaea*	Community	Insect	S	I
Friedli and Bacher 2001	*Cirsium arvense*	Grass	Insect	-	S
Gurevitch et al. 2000	meta-analysis†		Insects, Gastropods	S†	-
Rachich and Reader 1999	*Verbena hastata*	Community	Insects	S	-
Bonser and Reader 1995	*Poa compressa*	Community	Mammals	S	-
Dyer and Rice 1997	*Nassella pulchra*	Community	Mammals	S	-
Fowler 2002	Average of 6 grass spp	Community	Mammals	A	-
van der Wal et al. 2000	*Triglochin maritima*	Community	Mammals, Birds	A	-
Dormann et al. 2000	*Atriplex portulacoides*	Community	Mammals	-	A
	2 herbaceous plant spp			-	I
Erneberg 1999	*Anthemis cotula*	Community	Insect	-	I
Rees and Brown 1992	4 annual crucifer spp	Community	Insects, Molluscs	I	-
Reader and Bonser 1998	6 herbaceous spp	Community	Mammals, Molluscs	I	I
Sheppard et al. 2001	*Echium plantagineum*	Community	Insect	-	I
Taylor et al. 1997	*Panicum virgatum*	Grass	Mammals	-	I
	2 *Spartina spp.*			-	I
Steinger & Müller-Schärer 1992	*Centaurea maculosa*	Grass	Insects	-	I

†20% studies were on herbivory; three were gastropods and one was on insects. Fowler classified Gurevitch et al. as antagonistic, which is correct when predation or predation and herbivory are considered. Herbivory alone, however, was synergistic.

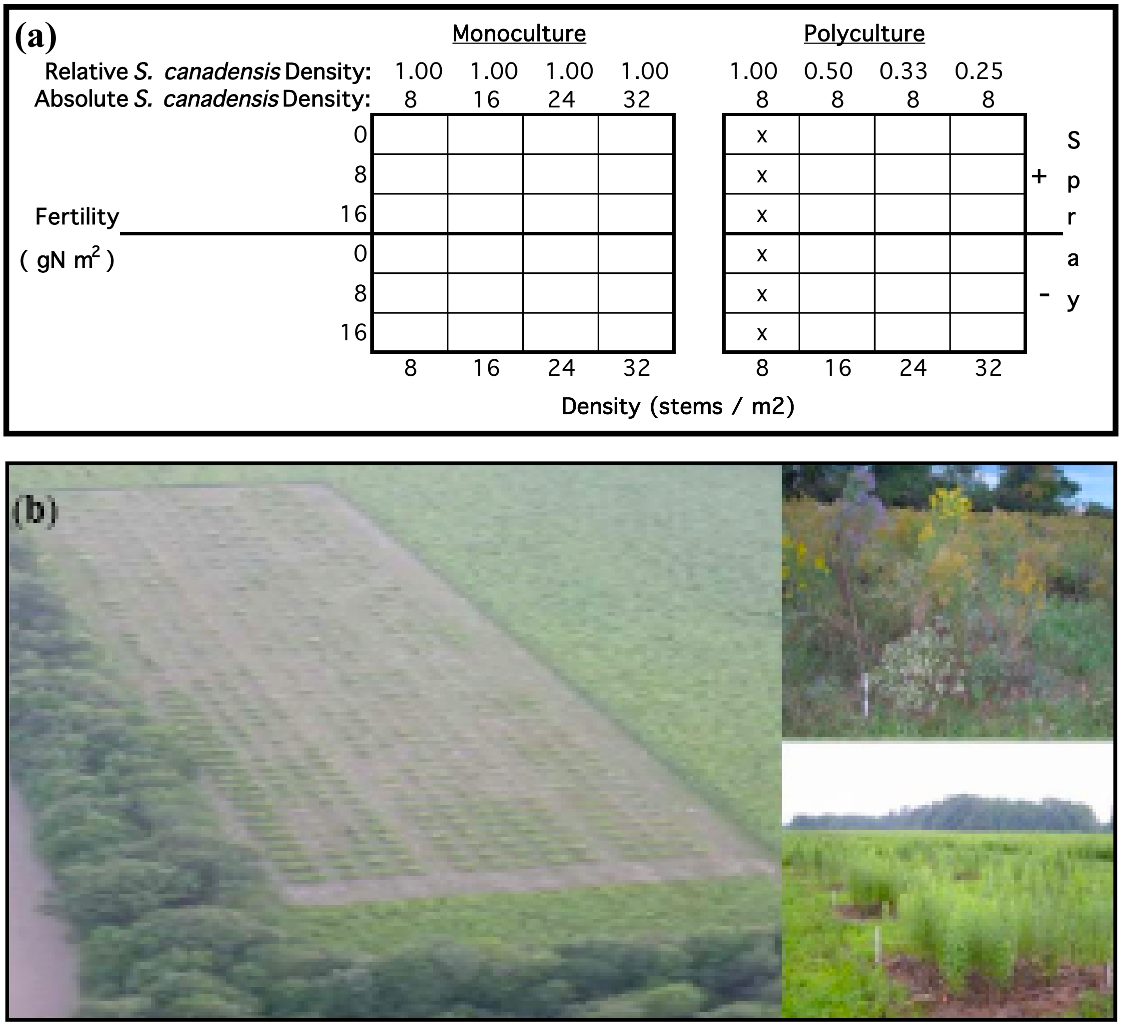

Figure 4.1. Experimental design and study site

(a) Design for the Monoculture and Polyculture Experiments. The 8 stem density polyculture treatments (represented with an 'x') were monocultures and were not replicated in the field. Instead, the data from the 42, 8 stem monoculture plots were used for both the monoculture and polyculture analyses. (b) Aerial photo of the common garden containing 600 4m^2 plots, 294 of which were used in the experiment (photo: A. Turner). Plots were separated by 2-5m mowed-buffers. The right-top and right-bottom photos show examples of a 24-stem density polyculture and monoculture, respectively.

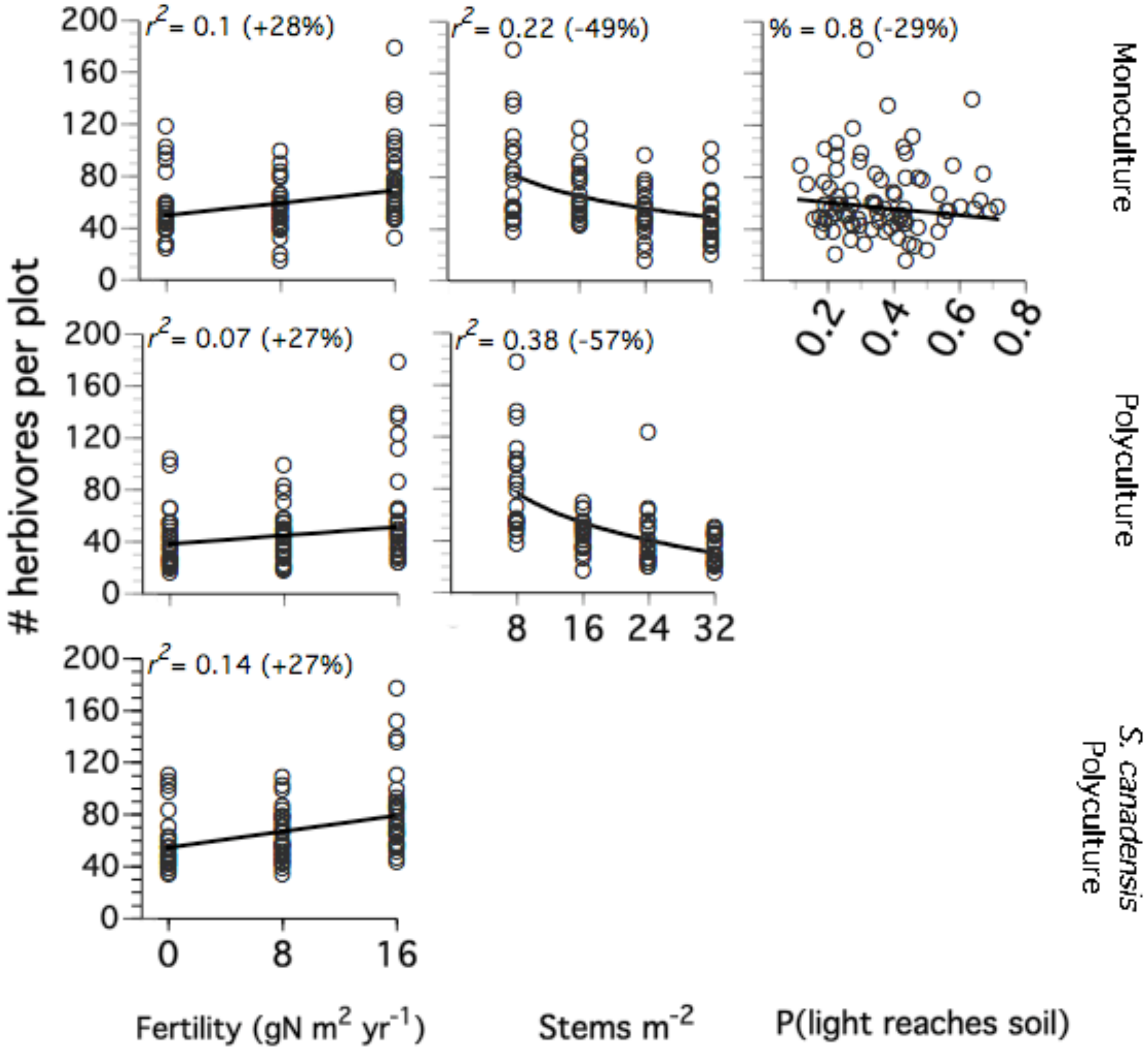

Figure 4.2 Total number of herbivores per plot

Total herbivore abundance was best explained by direct effects of resource availability on *S. canadensis* tissue quality in monoculture (top panels), polyculture (middle panels), and S. canadensis in polyculture (bottom panels). The () show the percent increase (+) or decrease (-) in herbivore abundance per plot across the entire range of that predictor variable.

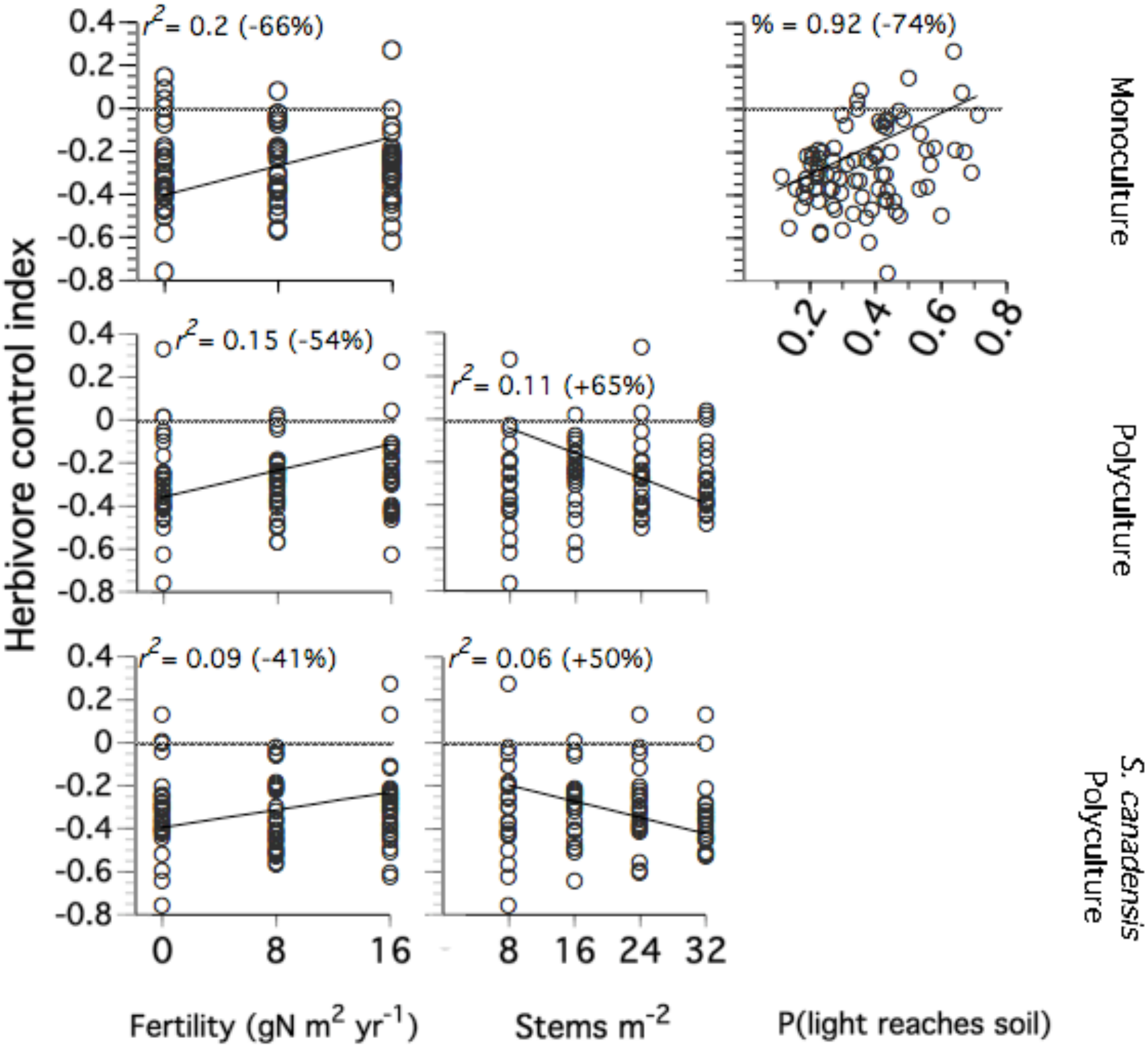

Figure 4.3 Herbivore control index for mean stem mass

Herbivore control was determined by herbivory on *S. canadensis* in both experiments and was always greatest in low resource availability environments for monocultures (top panels), polycultures (middle panels), and for S. canadensis in polyculture (bottom panels). () indicate the percent increase (+) or decrease (-) in herbivore control across the entire range of that predictor variable. ---- lines represent an herbivore control index value of 0; above this line plants overcompensated for herbivory, below this line herbivores caused a % reduction mean stem mass. 6% of monocultures and 8.3% of polycultures tolerated or over-compensated for herbivory.

APPENDIX A

PAIRWISE CORRELATIONS COEFFICIENTS (R^2) AMONG THE PREDICTOR VARIABLES.

MONOCULTURE	**Fertility**	**Stems m^{-2}**	**Light**	**#Predators per plot**	**Mean stem mass**	**Mass m^{-2}**			
Fertility	1.00								
Stems m^{-2}	0.00	1.00							
Light	-0.12	**-0.56**	1.00						
# Predators per plot	0.00	-0.04	**-0.22**	1.00					
Mean *S. canadensis* stem mass (g)	**0.63**	**-0.31**	0.02	0.10	1.00				
***S. canadensis* mass m^{-2}**	**0.41**	**0.76**	**-0.54**	0.03	0.29	1.00			
POLYCULTURE	**Fertility**	**Stems m^{-2}**	**Diversity**	**Mass m^{-2}**	**% *S. canadensis* mass m^{-2}**	**Light**	**%inedible stems m^{-2}**	**Mean stem mass**	**Relative non-*S. canadensis* stem mass**
Fertility	1.00								
Stems m^{-2}	0.00	1.00							
Diversity	-0.03	**0.81**	1.00						
Mass m^{-2}	**0.45**	**0.612**	**0.53**	1.00					
% *S. canadensis* mass m^{-2}	0.06	**-0.83**	**-0.91**	**-0.6**	1.00				
Light	-0.09	**-0.31**	**-0.25**	**-0.23**	**0.26**	1.00			
% less-edible stems m^{-2}	-0.14	**0.49**	**0.54**	0.16	**-0.51**	0.05	1.00		
Mean stem mass	**0.39**	**-0.7**	**-0.79**	-0.16	**0.78**	0.11	**-0.48**	1.00	
Relative non-*S. canadensis* stem mass (g)	-0.04	**0.54**	**0.75**	**0.38**	**-0.77**	**-0.24**	**0.46**	**-0.51**	1.00
# Predators per plot	0.00	**-0.24**	**-0.33**	-0.13	**0.31**	-0.20	**-0.28**	**0.3**	**-0.32**

Bolded R^2s are significant.

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