

ADDITIVE AND NONADDITIVE EFFECTS OF HERBIVORY AND COMPETITION ON TREE SEEDLING MORTALITY, GROWTH, AND ALLOCATION¹

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The interaction between simulated cotyledon herbivory and interspecific competition was studied in a greenhouse experiment using two species of trees, *Acer rubrum* and *Quercus palustris*, which commonly invade abandoned agricultural fields. Herbivory treatments were applied as a gradient of cotyledon removal for *A. rubrum* with 0, 25, 50, 75, and 100% of cotyledon tissue removed. Cotyledons from *Q. palustris* were clipped and removed (control, early, and late removal) to create a gradient of seed reserve availability. The competition treatment consisted of plugs of old-field vegetation that filled the pots with perennial cover. Mortality of seedlings was higher with competition. There was a significant interaction between herbivory and competition with the highest mortality occurring with competition at the highest intensity of herbivory in both species. Herbivory reduced biomass for *Q. palustris* only, while competition reduced biomass in both species. Neither species showed an interaction between herbivory and competition for growth. There was a significant interaction between herbivory and competition on allocation patterns for both species, with greater allocation to roots with competition at the highest intensity of herbivory. This study demonstrates the potential for cotyledon herbivory and competition to interact, altering the invasion of tree seedlings into abandoned agricultural land.

Key words: *Acer rubrum*; competition; cotyledon herbivory; *Quercus palustris*; tree seedling establishment.

Biotic factors that affect the establishment of trees in successional habitats are of great importance, as there is the potential to affect the long-term structure and composition of regenerating forests. Many biotic factors are known to affect tree establishment, such as seed predation (De Steven, 1991a; Gill and Marks, 1991; Manson and Stiles, 1998), seedling predation (Ostfeld and Canham, 1993), herbivory (Myster and McCarthy, 1989; Inouye, Allison and Johnson, 1994), and competition (De Steven, 1991b; Burton and Bazzaz, 1995; Hill, Canham, and Wood, 1995; Buckley, Sharik, and Isebrands, 1998). As seedlings are often more susceptible to environmental stresses than well-established plants (Dirzo, 1984; Fenner, 1987), studies that focus on the earliest demographic stages have the greatest potential to reveal the underlying mechanism(s) controlling community structure.

Tree seedling establishment in abandoned agricultural land often occurs in a brief window of invasion (Rankin and Pickett, 1989; Peroni, 1994). The cause of these limited invasions is unclear. While competition with old-field vegetation may be intense (De Steven, 1991b; Burton and Bazzaz, 1995; Hill, Canham, and Wood, 1995), there may also be beneficial effects of an intact vegetation matrix (De Steven, 1991a). Herbivory by meadow voles (*Microtus pennsylvanicus*) and white-tailed deer (*Odocoileus virginianus*) can greatly reduce tree regeneration in old fields (Ostfeld and Canham, 1993; Inouye, Allison, and Johnson, 1994). However, patterns of mammalian herbivory were not sufficient to explain invasion windows in the piedmont of New Jersey (Rankin and Pickett, 1989). Because no single factor is able to explain patterns of invasion,

multiple interacting factors may limit establishment simultaneously.

Partial herbivory, by itself, rarely leads directly to the mortality of a seedling (Fenner, 1987). Once plant tissue has been lost to herbivory, seedlings may suffer from reduced competitive abilities (Hendrix, 1988). This indirect effect of herbivory may subsequently lead to decreased seedling growth or to seedling mortality. The interaction between herbivore damage and competition (hereafter the H × C interaction) has been formalized into the compensatory continuum hypothesis (Maschinski and Whitham, 1989). According to this hypothesis, seedlings growing under favorable conditions, e.g., without competition, will show fewer negative responses to herbivory, while seedlings growing under less favorable conditions will show more dramatic negative responses to herbivore damage (Maschinski and Whitham, 1989). Furthermore, the susceptibility of a seedling to herbivore damage changes with the development of the seedling (Hanley, Fenner, and Edwards, 1995; Karban and Thaler, 1999) with older tissues better defended against insect herbivory.

The potential for nonadditive effects of herbivory and competition on plant demography and growth has been studied in predominately herbaceous species with varied results. Some studies have found no statistical interaction between herbivory and competition (Duggins and Dethier, 1985; Fowler and Rausher, 1985; Rees and Brown, 1992; Steinger and Müller-Schärer, 1992; Maron, 1997; Reader and Bonser, 1998), while others have found a H × C interaction for plant mortality (Parker and Salzman, 1985; Müller-Schärer, 1991; Reader, 1992), growth (Bentley and Whittaker, 1979; Lee and Bazzaz, 1980; Cottam, Whittaker, and Malloch, 1986; Müller-Schärer, 1991; Swank and Oechel, 1991; Hjältén, Danell, and Ericson, 1993; McEvoy et al., 1993; McPherson, 1993; Ang et al., 1994; Shabel and Peart, 1994; Mutikainen and Walls, 1995; Frost and Rydin, 1997), population size structure (Weiner, 1993; Shabel and Peart, 1994), and reproduction (Lee and

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Bazzaz, 1980; Müller-Schärer, 1991; Ang et al., 1994). These studies have focused on a variety of herbivores, plant functional types, and demographic stages. However, there have been no studies of the $H \times C$ interaction that incorporate tree seedlings of successional habitats competing with old-field herbs. By having access to larger seed reserves, seedlings of woody plants may be less responsive to tissue loss than herbaceous species. In addition, most published studies have focused on the removal of mature tissue rather than tissue from the more sensitive seedling stage (Fenner, 1987).

Understanding the role of herbivory and competition in limiting the establishment of trees in successional systems is crucial to the management of regenerating forests. However, field studies of competition can be complicated by the presence of herbivores within the system (Reader, 1992; Hulme, 1996; Reader and Bonser, 1998). By altering the competitive environment, researchers may also alter the amount of herbivory experienced by a plant (Reader, 1992; Burger and Louda, 1995; Buckley, Sharik, and Isebrands, 1998). Because of these potential field complications, greenhouse studies may be the only way to effectively determine the individual and combined effects of herbivory and competition on plant recruitment and growth where herbivore removal is not practicable.

This study focuses on the seedlings of two tree species that commonly invade abandoned agricultural fields in the Piedmont region of New Jersey, USA. Cotyledon herbivory frequently occurs on tree seedlings in these old fields (Facelli, 1994; Meiners, 1999) and appears to have large effects on tree establishment. In previous field studies, cotyledon herbivory on *Acer rubrum* was high, averaging 33% of cotyledon tissue removed in 1995 ($N = 55$; range 0–100%) and 22% ($N = 214$; range 0–100%) in 1996. Based on insecticide application in this field experiment, insect herbivory also decreased emergence and survival in *Quercus palustris* (Meiners, 1999). This occurred without visible aboveground damage, suggesting that insects were feeding on the cotyledons or emerging roots.

We tested the role of competition and herbivory in determining tree seedling growth and allocation in a greenhouse experiment with simulated invertebrate herbivory on cotyledons and competition with old-field flora. The experiment was designed to test for a statistical interaction between herbivory and interspecific competition for tree seedling mortality, growth, and allocation patterns.

MATERIALS AND METHODS

Acer rubrum L. seed were collected from Busch Campus of Rutgers University, Piscataway, New Jersey in early May 1997. *Quercus palustris* Muenchh. seed were purchased from a commercial supplier (Sheffield Seed Co., Locke, New York, USA). Pregermination treatment for *Quercus* consisted of soaking in water for 48 h to fully hydrate seeds, followed by storage at 5°C for 90 d. *Acer rubrum* seed were stored at 5°C until planting.

The competition treatment consisted of a plug of surface soil collected from an abandoned agricultural field at the Hutcheson Memorial Forest Center near East Millstone, New Jersey, USA (40° 30' N, 74° 34' W). The plug was cut with a post-hole digger and contained the aboveground and rhizome portions of the old-field vegetation. These plugs resulted in a continuous and vigorous perennial vegetation in the competition pots. Each pot contained several species with *Achillea millefolium*, *Fragaria virginiana*, *Trifolium repens*, *Hieracium casepitosum*, and *Solidago canadensis* the most abundant.

Herbivory treatments differed for the two tree species. For *Acer rubrum*, which has epigeal germination, either half or the entire cotyledon was clipped with scissors and removed from the pot. *Acer rubrum* herbivory was applied as a gradient of 0, 25, 50, 75, and 100% of cotyledons removed. This her-

bivory treatment was applied within 2 d of emergence to simulate the timing and extent of cotyledon removal by invertebrate herbivory in field experiments (Meiners, 1999). The 50% removal treatment consisted of all of one cotyledon removed.

Because *Quercus* has hypogeal germination, it is not possible to remove cotyledons singly. To simulate herbivory, entire cotyledons were removed from the seedling axis below the soil surface (Sonesson, 1994; Frost and Rydin, 1997). A range of *Quercus palustris* herbivory treatments was created by altering the time that the cotyledons remained on the seedling. Treatments were: early—cotyledons removed when the first whorl of leaves began to expand; late—cotyledons removed when the second whorl of leaves was expanded; and control—cotyledons never removed. Scissors were sterilized in 70% isopropyl alcohol between clippings to minimize pathogen spread for both species.

Soil for the experiment was collected from the Hutcheson Memorial Forest Center, at the same site and time of competition plug collection. The 15-cm pots were filled with either all soil or soil topped with a vegetation plug. The experiment was set up as a complete factorial design with competition and herbivory treatments in all combinations for each species. Replicates, consisting of one pot for each herbivory \times competition combination, were arranged as blocks across the greenhouse bench. Five blocks were set up for *A. rubrum* and eight blocks for *Q. palustris* for a total of 50 and 48 pots, respectively. Pot position was randomized within each block, and the two species were placed on separate ends of the same greenhouse bench. Pots received ambient light and photoperiod and were watered daily. On very hot and sunny days at the beginning of the experiment, pots were watered twice a day to increase *Acer* seedling emergence. On 19–20 May 1997, 15 seeds of *Acer rubrum* or eight seeds of *Quercus palustris* were planted into each pot. *Quercus palustris* acorns were planted with the seed axis parallel to the soil surface to facilitate later removal of the cotyledons.

Pots were monitored daily to record emergence and mortality and to apply herbivory treatments. Seedlings were marked with plastic toothpicks upon emergence to allow mortality to be determined. After 49 d for *A. rubrum* and 72 d for *Q. palustris*, above- and belowground biomass were harvested for determination of growth and allocation patterns. Seedlings were dried for 3 d at 70°C, separated into root and shoot portions, and weighed. The aboveground biomass of competing vegetation was also harvested, dried, and weighed.

Emergence in competition and control pots was compared with a chi-square test of independence. Mortality of seedlings was analyzed with log-linear analysis (Proc CATMOD; SAS, 1989) including competition, herbivory, and the $H \times C$ interaction. Growth and allocation patterns were analyzed with ANOVA (Proc GLM; SAS, 1989). Total growth of *Q. palustris* and root:shoot ratio data for both species were log transformed to conform to normality assumptions of ANOVA. Total seedling biomass was included in analyses of root:shoot ratio to account for developmental changes in allocation patterns (Gedroc, McConnaughay, and Coleman, 1996). Because seedling density was low (<4 seedlings per pot on average) and seedling size was small, intraspecific competition did not appear to be important. The biomass of competing vegetation was much less important than the presence of competition and was dropped from the analyses.

RESULTS

A total of 180 (24.0%) *Acer rubrum* and 192 (50.0%) *Quercus palustris* seedlings emerged. Emergence did not differ between the competition treatment and control for both *A. rubrum* ($\chi^2 = 1.42$, 1 df, $P > 0.05$) and *Q. palustris* ($\chi^2 = 0.78$, 1 df, $P > 0.05$) seedlings. Dry biomass of competing vegetation at harvest averaged 6.32 ± 0.29 g for *Acer rubrum* and 7.96 ± 0.57 g for *Quercus palustris* (mean \pm 1 SE).

Mortality of emerged seedlings was 21.7% for *A. rubrum* and 8.9% for *Q. palustris* seedlings. Seedling mortality varied with competition and herbivory (Table 1). Seedling mortality was significantly higher in competition pots for both species (log-linear analysis; *A. rubrum*: $\chi^2 = 6.89$, 1 df, $P = 0.0087$;

TABLE 1. Effect of cotyledon herbivory and competition on the percentage mortality of *Acer rubrum* and *Quercus palustris* seedlings. Numbers in parentheses are number dead/number emerging.

Herbivory treatment	Mortality (%)	
	Control	Competition
<i>Acer rubrum</i>		
0% ^a	8.3 (2/24)	33.3 (6/18)
25%	33.3 (5/15)	9.1 (2/22)
50%	5.3 (1/19)	42.9 (6/14)
75%	5.3 (1/19)	36.4 (4/11)
100%	23.8 (5/21)	41.2 (7/17)
<i>Quercus palustris</i>		
Control	2.7 (1/37)	0.0 (0/31)
Late removal ^b	6.3 (2/32)	0.0 (0/25)
Early removal	15.2 (5/33)	29.0 (9/34)

^a Percentages refer to amount of cotyledons removed.

^b Entire cotyledons were removed from seedling axis below the soil.

Q. palustris: $\chi^2 = 49.17$, 1 df, $P < 0.0001$). Herbivory significantly increased mortality in *Q. palustris* ($\chi^2 = 206.14$, 2 df, $P < 0.0001$) but was insignificant for *A. rubrum*. The H \times C interaction was significant for both species (*A. rubrum*: $\chi^2 = 11.81$, 4 df, $P = 0.0189$; *Q. palustris*: $\chi^2 = 57.43$, 2 df, $P < 0.0001$) with the highest mortality occurring with competition at the highest level of herbivory.

Competition reduced the growth of *A. rubrum* (Fig. 1A, Table 2) with no effect of herbivory and an insignificant H \times C interaction term. *Quercus palustris* had reduced growth in both herbivory and competition treatments (Fig. 2A, Table 3) with an insignificant H \times C interaction term. For both of these species, growth decreased as the intensity of herbivory increased.

Allocation patterns were not significantly related to seedling development (i.e., total mass) in either species (Tables 2 and 3). Competition was the only significant main effect for allocation in *A. rubrum* while there were no significant main effects for *Q. palustris*. There was a significant H \times C interaction for allocation in both species. Allocation to roots was consistently greater with competition in *Acer rubrum* (Fig. 1B). *Quercus palustris* had greater allocation to roots with competition, in the control and early removal herbivory treatments, but greater root allocation in control plots with late cotyledon removal (Fig. 2B). The greatest differences between competition and control plots in root allocation occurred at the highest levels of simulated herbivory for both species.

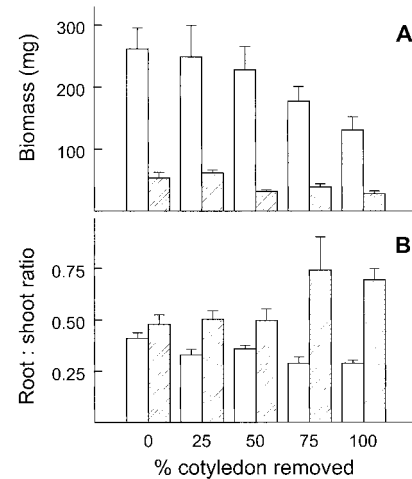


Fig. 1. Effects of competition and simulated herbivory on growth and allocation of *Acer rubrum* seedlings. Open bars represent control treatment, and hatched bars represent competition treatment. Data plotted are mean \pm 1 SE.

DISCUSSION

The two species studied differed in which main effect had the greatest impact on seedling performance. *Acer rubrum* survival and growth were reduced more by the competition treatment than by the removal of cotyledon tissue. In contrast, *Q. palustris* performance was reduced more by the herbivory treatment. This may reflect the relative impacts of the two methods of simulated herbivory. The removal of cotyledon reserves within the acorn may have been a relatively greater loss to *Q. palustris* seedlings than the clipping of photosynthetic cotyledons in *A. rubrum*. In a study of *Quercus robur*, removal of cotyledon reserves had no effects on seedling growth or survival (Sonesson, 1994) while in two Mexican *Quercus* species, cotyledon removal had strong negative effects on both growth and survival (Bonfil, 1998). It is possible that any initial cotyledon removal effects for *Q. robur* would not be detectable after two years of growth in the absence of competition, or that cotyledon reserves are much larger than needed for establishment (Sonesson, 1994).

The differential responses of *A. rubrum* and *Q. palustris* may also be explained by differences in the competitive abilities of the two species. *Quercus palustris* competes well with

TABLE 2. Analysis of variance of the effects of competition and herbivory on *Acer rubrum* growth and allocation. Total seedling biomass included in root:shoot (R/S) ratio analysis to account for developmental changes in allocation patterns. Total growth and ratio data were log transformed to conform to normality assumptions of ANOVA. Significance values: * $P < 0.05$; *** $P < 0.001$.

Source	df	Total growth		Root : shoot ratio	
		MS	F	MS	F
Total growth (R/S ratio only)	1			<0.01	0.18
Competition	1	8.00	74.19***	0.54	36.18***
Herbivory	4	0.21	1.94	0.03	1.69
Competition \times herbivory	4	0.17	1.55	0.08	5.05***
Block	4	0.21	1.93	0.02	1.59
Block \times competition	4	0.25	2.29	0.01	0.65
Block \times herbivory	16	0.16	1.51	0.03	2.18*
Block \times competition \times herbivory	11	0.16	1.50	0.02	1.27
Error	96	0.11			
	95			0.02	

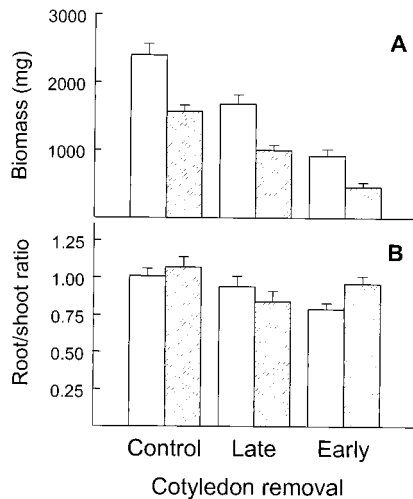


Fig. 2. Effects of competition and simulated herbivory on growth and allocation of *Quercus palustris* seedlings. Open bars represent control treatment, and hatched bars represent competition treatment. Herbivory treatments are: control—no removal; late—cotyledons removed after leaf expansion; early—cotyledons removed at emergence. Data plotted are mean \pm 1 SE.

old-field vegetation, while *Acer rubrum* has depressed growth and survival in these communities (Meiners, 1999). Davis, Wrage, and Reich (1998) found that competition between herbaceous vegetation and tree seedling was largely for water. Water was limiting at times during this experiment, as some wilting of herbaceous vegetation was observed between daily waterings. In this experiment, the deep-rooted *Q. palustris* seedlings would have had access to deeper reserves of water beneath the roots of the competing vegetation. In contrast, *A. rubrum* roots were much shallower and were restricted to depths with high densities of competing roots.

The relative intensity of competitive and herbivore effects does not seem to determine the presence of an interaction in the seedlings attributes tested. Despite the differential responses of these two species, both had the same significant $H \times C$ interactions. In the five terrestrial studies that found no interaction between competition and herbivory, four found competition to be more important (Fowler and Rausher, 1985; Steinger and Müller-Schärer, 1992; Rees and Brown, 1992; Reader and Bonser, 1998) and the other found herbivory to be more important (Maron, 1997). Similarly, of the studies that found an interaction between competition and herbivory for growth, herbivory was more important for one (Bentley and

Whittaker, 1979) and competition more important for others (Müller-Schärer, 1991; Swank and Oechel, 1991; Steinger and Müller-Schärer, 1992; Frost and Rydin, 1997). This relationship may be further complicated as the relative strength of herbivory and competition may change temporally with environmental conditions (Ang et al., 1994). The intensity of herbivory may also affect the $H \times C$ interaction. Bentley and Whittaker (1979) only found an $H \times C$ interaction at high levels of herbivory, while no interaction existed at lower levels.

Both species had a significant $H \times C$ interaction for mortality in this study. This interaction has been found in several other studies (Parker and Salzman, 1985; Müller-Schärer, 1991; Reader, 1992) but was not present in others (Swank and Oechel, 1991; Steinger and Müller-Schärer, 1992; McEvoy et al., 1993; Ang et al., 1994; Maron, 1997). The presence of an $H \times C$ interaction in this study may result from the use of seedlings during the establishment phase. Seedlings are often the demographic stage that is the most susceptible to mortality from environmental stresses (Dirzo, 1984; Fenner, 1987). Studies that do not include this, the most sensitive stage, may be unable to detect an $H \times C$ interaction for plant mortality.

Many studies have found an $H \times C$ interaction for plant growth. This effect can result from competition preventing compensatory growth following herbivory (Maschinski and Whitham, 1989; Shabel and Peart, 1994) or by herbivory affecting the competitive abilities of affected plants (Bentley and Whittaker, 1979; Clay, Marks, and Cheplick, 1993). Rees and Brown (1992) and Reader and Bonser (1998) have suggested that logarithmically transformed growth data should be the basis for assessing an $H \times C$ interaction in growth, as herbivory and competition should be expected to have multiplicative rather than additive effects on growth. As many studies have reported an $H \times C$ interaction for growth based on log-transformed data (Cottam, Whittaker, and Malloch, 1986; Müller-Schärer, 1991; Swank and Oechel, 1991; Ang et al., 1994; Shabel and Peart, 1994; Frost and Rydin, 1997) the presence of this interaction is supported in some species. In this study, neither tree species had a significant $H \times C$ interaction for growth with either untransformed or log-transformed data. It is possible that seedlings with very low growth rates caused by the combination of herbivory and competition died before harvest, increasing the average seedling mass.

Both of the species used in this study were found to have an $H \times C$ interaction in biomass allocation patterns, with greater allocation to roots with competition and at the highest level of herbivory. *Quercus palustris* had a more complicated

TABLE 3. Analysis of variance of the effects of competition and herbivory on *Quercus palustris* growth and allocation. Total seedling biomass included in root : shoot (R/S) ratio analysis to account for developmental changes in allocation patterns. Ratio data were log transformed to conform to normality assumptions of ANOVA. Significance values: * $P < 0.05$; *** $P < 0.001$.

Source	df	Total growth		Root : shoot ratio	
		MS	F	MS	F
Total growth (R/S ratio only)	1			0.07	3.66
Competition	1	18608239	42.48***	0.06	3.39
Herbivory	2	19795824	45.19***	0.02	1.05
Competition \times herbivory	2	550765	1.26	0.07	3.90*
Block	7	352921	0.81	0.02	0.99
Block \times competition	7	305874	0.70	0.02	0.83
Block \times herbivory	14	315738	0.72	0.02	0.88
Block \times competition \times herbivory	14	550967	1.26	0.03	1.85*
Error	124/123	438052		2.29	

response with decreased allocation to roots in the low herbivory (late removal) treatment. Because allocation patterns change with seedling development (Gedroc, McConnaughay, and Coleman, 1996), the late removal treatment may have interrupted allocation to roots that occurs later in seedling development. *Quercus* seedlings initially develop a large taproot (Young and Young, 1992), which may explain the greater allocation to root in the early removal treatment.

The H \times C interaction for allocation patterns has only been tested in a few species, with no study finding a significant interaction (Fowler and Rausher, 1985; Steinger and Müller-Schärer, 1992; Mutikainen and Walls, 1995). As development patterns may be plastic (Gedroc, McConnaughay, and Coleman, 1996), seedlings may be most useful to assess allocation responses, while studies using established plants may be less sensitive because plants are locked into a specific allocation pattern. The shifts in root:shoot ratio observed in this study may affect future growth, survival, and development of the seedling by altering competitive interactions for both above- and belowground resources.

By reducing tree seedling survival, the H \times C interaction can have direct effects on the establishment of trees in successional systems. Microsites and periods where seedlings are exposed to both competition and herbivory should be characterized by high seedling mortality, making successful establishment unlikely. When competition and herbivore pressure are both low, establishment rates should be high, resulting in the establishment of a cohort of seedlings. A brief period of low competition and herbivory can result in a window of invasion in successional time (Rankin and Pickett, 1989; Peroni, 1994).

The effects of the allocation response to the H \times C interaction are more complicated. By increasing allocation to roots, seedlings exposed to both herbivory and competition may be at a competitive disadvantage for light. However, their ability to compete for belowground resources will be increased. It has been proposed that tree seedlings mainly compete with herbaceous vegetation for water (Davis, Wrage, and Reich, 1998). If competition for water is limiting to tree establishment in this system, then the increased root biomass of seedlings experiencing both herbivory and competition may lead to greater competitive ability in the future. The infrequent seedling that does establish despite herbivory and competition may then be physiologically better able to survive and become a part of the developing forest community.

The ability of competition and herbivory to determine plant community structure is well established, but one must consider the potential for widespread interactions between these two basic organizing forces in shaping the structure of plant communities. This study illustrates the effects of the interaction between herbivory and competition on woody plant attributes, which may alter regeneration in natural communities. Studies that focus on herbivory or competition in isolation can result in incorrect predictions of community or population trajectories. Such studies may grossly underestimate the importance of herbivory and competition in structuring plant communities, leading to inappropriate management recommendations. Furthermore, studies that focus on seedling events may be necessary to determine the strengths of the interactions that drive community composition, where studies of established plants may be unable to detect effects. Finally, different species appear to have different responses to the combined effects of herbivory and competition. Functional classifications of the

interaction between herbivory and competition are not possible yet, particularly for tree species. Additional species will need to be studied before realistic predictions can be made.

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