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Does Balsam Fir (Abies balsamea) Facilitate the Recruitment of Eastern Hemlock (Tsuga canadensis)?

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ABSTRACT.—Eastern hemlock (*Tsuga canadensis*) was a major component of mesic forests in the Upper Great Lakes region, but presently persists in only a few locations. Many of these stands experience poor regeneration due to herbivory by white-tailed deer (*Odocoileus virginianus*), suggesting that hemlock will become progressively less common in these stands. We tested the hypothesis that balsam fir (*Abies balsamea*) facilitates establishment of eastern hemlock at 11 sites in northern Wisconsin. Hemlock saplings are three times as dense and twice as tall when growing within patches of balsam fir compared to growing outside such patches. Hemlock saplings growing outside balsam fir patches are also four times as likely to exhibit deer browsing damage as those growing inside. These results suggest that patches of balsam fir create a physical or visual barrier to deer and thus provide a refuge for hemlock saplings from white-tailed deer browsing. Because balsam fir saplings are much more abundant than hemlock in northern Wisconsin forests and establish on a wider range of sites, foresters could use patches of balsam fir to facilitate local hemlock establishment and so promote restoration of this important forest type.

INTRODUCTION

Eastern hemlock (*Tsuga canadensis*) is a long-lived, shade-tolerant conifer. In presettlement forests, it was a canopy dominant on mesic sites in the Upper Great Lakes states (Curtis, 1959). It typically formed uneven-aged stands that were maintained by gap-phase dynamics (Hett and Loucks, 1976; Frelich and Lorimer, 1991). The abundance of hemlock trees declined by an estimated 95–98% following extensive logging early in the twentieth century (Eckstein, 1980; Hanson, 1984). Seedling establishment is microsite-limited (Mladenoff and Stearns, 1993; Rooney and Waller, 1998), and the abundance of saplings (30–300 cm tall) is negatively correlated with white-tailed deer (*Odocoileus virginianus*) density (Waller *et al.,* 1996). Because deer use hemlock as winter food and deer populations in the region remain several times higher than they were before European settlement (Swift, 1946; Alverson *et al.,* 1988), some researchers believe mortality induced by deer browsing precludes eastern hemlock recovery in the Upper Great Lakes region (Frelich and Lorimer, 1985; Alverson *et al.,* 1988; Waller *et al.,* 1996; Alverson and Waller, 1997).

Because of its historic decline and persistent low levels of recruitment (Lorimer, 1996), the maintenance and restoration of eastern hemlock has been identified as a regional conservation goal by land management agencies (*e.g.,* Crow *et al.,* 1994). Concurrently, land and wildlife management practices tend to maintain high deer populations to meet social and economic pressures (Diefenbach *et al.,* 1997). Given this socioeconomic context, it is worth pursuing management strategies that might promote hemlock recruitment in areas with high deer populations. One such approach includes identifying locations that contain areas inaccessible to deer browsing (Rooney, 1997; Long *et al.,* 1998), or where the saplings are less apparent to deer. During our 1996 field season, we noticed that sites with the highest hemlock sapling densities often had dense patches of balsam fir (*Abies balsamea*)

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growing beneath canopy gaps. Hemlock saplings were typically found growing in these dense patches of balsam fir, even when deer-browsing intensity was high. Balsam fir is considered a "starvation food" and is seldom browsed by white-tailed deer (Swift, 1946). In this study, we tested the hypothesis that balsam fir facilitates hemlock growth and recruitment by providing a physical barrier against white-tailed deer herbivory.

METHODS AND MATERIALS

We conducted this study in the summer of 1997, in Wisconsin's Northern Highland State Forest and Chequamegon National Forest (Oneida, Price and Vilas counties). This region is transitional between boreal and deciduous forests, containing a combination of conifers and hardwood species (Curtis, 1959; White and Mladenoff, 1994). Deer browsing pressure is high throughout these counties (Waller *et al.,* 1996). Both balsam fir and hemlock occupy mesic sites with sandy loam soils (Kotar *et al.,* 1988). Both species are very shade tolerant and can persist beneath a closed canopy (Curtis, 1959), but saplings are most abundant beneath treefall gaps.

We selected preliminary sites from among the 145 sites established throughout northern Wisconsin and Michigan's Upper Peninsula by Waller *et al.* (1996) for studying hemlock demography. Specifically, we returned to sites where our field notes indicated a balsam fir understory. During roadside surveys in June 1997 we selected additional candidate sites. From these, we chose 11 representative sites with an abundant understory of balsam fir and used a randomization procedure to establish a 50×50 m (0.25 ha) sample plot in each site. Plots contained several dense patches of balsam fir saplings.

We operationally defined balsam fir patches as areas containing only balsam fir and hemlock saplings, covering at least 12 m^2 of forest floor with a mean density of at least 1.5 stems m^{-2} if saplings were >4-m tall or at least 2 stems m^{-2} if saplings were between 0.3 and 4-m tall. We used a randomization procedure to select two balsam fir patches in each plot for detailed investigation. At each balsam fir patch, we laid out a 4-m wide and 12–16-m long belt transect beginning inside the balsam fir patch. The transect extended out of the patch in a randomly chosen direction, and we established the midpoint of the transect at the "edge" of the balsam fir patch. Because borders of balsam fir patches are not exact, we used our best judgment to locate the midpoint of the transect. Once the transect was established, we measured the height of and counted all hemlock and balsam fir saplings >30-cm-tall inside and outside the balsam fir patch along the transect. We sampled in contiguous 2×2 m quadrats along each side of the transect. We also noted if hemlock saplings had deer-browsing damage. Deer typically consume hemlock leaves and new shoots, but not woody stems, so they leave a fairly characteristic signature which allows for easy interpretation.

To test whether hemlock attains higher densities inside patches of balsam fir vs. outside these patches, we used a nonparametric G-test for heterogeneity (Sokal and Rohlf, 1981). This test examines both the overall goodness of fit across all sites while accounting for the heterogeneity introduced by individual sites. Specifically, we tested the null hypothesis that hemlock sapling density does not differ inside and outsidse of balsam fir patches. We pooled data from the two balsam fir patches at each site for this analysis ($n = 11$) to increase sample sizes and because such pairs can not be assumed to be independent. Next, we compared the height of hemlock saplings inside and outside balsam fir patches across all sites using a t-test with separate variances. Our null hypothesis was that there was no difference in hemlock sapling heights inside and outside balsam fir patches. We examined deer-browsing damage to hemlock saplings by testing the null hypothesis that the proportion of hemlock saplings exhibiting deer-browsing damage is the same inside and outside

TABLE 1.—G-test for heterogeneity, testing the null hypothesis that the number of hemlock saplings inside balsam fir patches is not different from the number outside patches

Site	Inside patches	Outside patches	df	G	P
1	1	1	1	0	1.000
2	9	4	1	0.97	0.325
3	10	3	1	1.99	0.158
4	11	3	1	2.54	0.111
5	30	3	1	14.08	<0.001
6	94	33	1	15.69	<0.001
7	24	20	1	0.18	0.669
8	63	19	1	12.95	<0.001
9	44	36	1	0.40	0.526
10	24	3	1	10.04	0.002
11	24	11	1	2.48	<0.001
Total	334	135	11	61.23	0.010
		Pooled	1	43.78	
		Heterogeneity	10	17.54	

balsam fir patches. We again used a G-test for heterogeneity, pooling data from the two balsam fir patches at each site. Lastly, we asked whether or not balsam fir facilitates hemlock growth when there is no observed browsing damage on hemlock. We did this by removing browsed hemlocks from the analysis to simulate deer-induced mortality. We then constructed a 2×2 contingency table in which all hemlock trees were pooled and classified by site (browsing on hemlock, no browsing on hemlock) and position along transect (inside balsam fir patch, outside patch). We tested significance using a G-test for independence (Sokal and Rohlf, 1981), and determined the power of this test using a one-tailed test for two proportions, and the minimum sample size needed with this power (Zar, 1984).

RESULTS

The mean density of hemlock saplings is almost three times greater within balsam fir patches (1.97 ± 0.28 SE m^{-2}) than outside such patches (0.69 ± 0.12 SE m^{-2}). This difference is highly significant (G-test, df = 1; $P < 0.001$; Table 1). The association between hemlock saplings and balsam fir patches is not consistent across all sites, however, resulting in significant heterogeneity among sites (G-test, df = 10; $P = 0.01$). However, there are consistently more hemlock saplings inside balsam fir patches than outside at 10 of the 11 sites (G-test, df = 11; $P < 0.01$). Additionally, hemlocks growing within balsam fir patches are almost twice as tall as those growing outside patches (189.7 cm $\pm$ 5.6 SE vs. 97.5 cm $\pm$ 6.0 SE, respectively, $t = 11.22$, $P \ll 0.001$).

A total of 54 hemlocks (11.5% of all hemlocks in the study) show browsing damage. Of these, 41.8% are inside balsam fir patches and 58.2% are outside. When the data are pooled across all four of the sites that experienced browsing and adjusted to expected frequencies, hemlocks outside patches are significantly more likely to be browsed than those inside patches (G-test, $P = 0.003$; Table 2). Because browsing damage was only observed at these four sites, the statistical significance of $G_{heterogeneity}$ and G_{total} depends on whether or not we use only sites where browsing damage occurred or all sites examined. The lack of fit to the null model for G_{total} is significant if we include only the four browsed sites (df = 4; $P < 0.01$), but not significant if we include all 11 sites (df = 11; $P > 0.10$). Heterogeneity is not significant in either case, which indicates browsing was consistently higher outside patches.

TABLE 2.—G-test for heterogeneity, testing the null hypothesis that the proportion of hemlock saplings with deer-browsing damage does not differ between hemlocks growing inside balsam fir patches from those growing outside. Browsing damage to hemlock saplings was observed at only four of the 11 study sites

Site	% hemlock browsed inside patches	% hemlock browsed outside patches	df	G	P
2	33	100	1	0.34	0.558
3	30	100	1	1.10	0.295
6	3	45	1	13.49	<0.001
7	58	50	1	0.08	0.770
Total	16.8	53.3	4	15.01	<0.005
		Pooled	1	8.60	0.003
		Heterogeneity	3	6.41	<0.100

When browsed individuals are removed from the analysis to simulate mortality, the difference between hemlock density inside vs. outside balsam fir patches becomes larger, although not significantly so ($G = 3.16$, $df = 1$; $P = 0.08$). The power of this test was 0.74, so the number of hemlock saplings sampled in browsed sites would need to be increased by 188% to demonstrate statistical significance.

DISCUSSION

Multiple ecological factors lead to the establishment of hemlock within balsam fir patches. First, both species reach their highest abundance on the same kinds of sites with respect to soil moisture and nutrient levels (Curtis, 1959; Kotar *et al.,* 1988). Within such sites, hemlock and balsam fir have similar regeneration niches: both prefer mosses or rotten wood for germination (Goder, 1961; Bakuzis and Hansen, 1965; McLaren and Janke, 1996). During this stage of seedling development, balsam fir and hemlock seedlings may compete. In response to canopy gaps, seedlings undergo rapid growth and enter the sapling stage. Once patches of balsam fir form, hemlock saplings growing within patches become better protected from deer browsing. Deer tend to avoid balsam fir because of its bitter taste (Swift, 1946; Muller-Schwarze, 1994). Balsam fir patches are typically quite dense, hard to maneuver through, and difficult to visually inspect, thus creating a physical barrier for white-tailed deer. While we observed browse damage on some hemlock saplings inside balsam fir patches, these hemlock saplings were in every case on the periphery of the balsam fir patch. In the center of the patch, hemlock saplings were always unbrowsed.

Inside balsam fir patches, hemlock saplings are twice as tall and three times more dense than those outside patches, suggesting that at this stage in its life cycle, hemlock benefits from its association with balsam fir. When growing in high density mono- or multispecific patches, plants often allocate more energy towards vertical growth than horizontal branch extension (Schmitt and Wulff, 1993; Givnish, 1995). This could partially explain the observation of taller hemlock saplings inside than outside patches. Because saplings outside balsam fir patches are four times more likely to be browsed than those inside patches, we believe that browse-induced hemlock mortality is higher outside balsam fir patches than inside. While the patterns were not significant at all sites examined, these findings parallel those reported by Long *et al.* (1998) in their study of hemlock saplings growing in deer-browsing refugia. They found that when protected from browsing over a period of 9 y hemlock saplings were on average three times taller, six times as dense, and four times less likely to exhibit browse damage than those in browse-accessible areas.

There was no significant association between the abundance of unbrowsed hemlock inside and outside of balsam fir patches and sites with and without observed browsing on hemlock. This lack of association should indicate that hemlock is facilitated by balsam fir even without deer browsing. However, the browsing-no browsing categories are misleading. All of our sites experience high levels of deer browsing (Waller *et al.,* 1996). Browsing at any given site is temporally variable, and a few deer browsing episodes often kill hemlock saplings (Alverson *et al.,* 1988). We strongly suspect that sites with significant differences between hemlock densities inside vs. outside balsam fir patches reflect the impacts of prior deer browsing. However, without controlled experiments, we can not categorically ascribe these lower densities outside balsam fir patches to deer browsing.

In plant communities, facilitation is commonly reported in relatively stressful environments (Callaway and Walker, 1997; Hacker and Gaines, 1997), yet few examples of herbivore-mediated facilitation are reported in the literature. Pfister and Hay (1988) found that a red alga is protected from sea urchin browsing when it is associated with an unpalatable brown alga in coastal North Carolina. Hacker and Bertness (1996) investigated a salt marsh community, and reported that when black rush (*Juncus gerardi*) and marsh elder (*Iva frutescens*) co-occur, marsh elder plants were less likely to be colonized by aphids (*Uroleucon ambroisae*) than when marsh elder grew alone. Our data demonstrate that eastern hemlock saplings sustain less deer-browsing damage when growing inside patches of balsam fir. While balsam fir patches reduce herbivory and increase the density of hemlock saplings, some questions remain. First, is facilitation dependent on browse intensity, or might balsam fir facilitate hemlock through other mechanisms as well? For example, if balsam fir and hemlock share mycorrhizal symbionts, dense patches of balsam fir may also harbor dense networks of mycorrhizae. Also, do hemlock saplings growing among balsam fir eventually experience higher mortality rates which nullify the early advantage gained by escaping herbivory? Finally, how do competition and facilitation between hemlock and balsam fir change over time?

The facilitation of hemlock saplings by balsam fir suggests that foresters who manage forests with high deer densities should maintain the balsam fir component of stands where they wish to restore eastern hemlock. Presently, balsam fir is more abundant than eastern hemlock in mesic forest stands throughout the Great Lakes region. The retention of balsam fir in logged stands could provide a noninvasive way to preserve and locally restore hemlock communities. The use of balsam fir is a more attractive option than traditional methods of protecting hemlock saplings, which include capital- and labor-intensive site preparations, chemical deer repellents and electrical fencing. Unlike active management, the retention of balsam fir would be more cost-effective and will not require routine maintenance.

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