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Distribution and Dynamics of the Invasive Native Hay-Scented Fern

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The spread and dominance of the invasive native hay-scented fern in the understory is one of the most significant changes that has affected the forest ecosystems in the northeastern United States in the last century. We studied changes in the distribution and dynamics of hay-scented fern at a large scale over a 10-yr period in Pennsylvania. The study included 56 stands covering 1,009 ha in two ecoregions. Hay-scented fern was more widely distributed and occurred at higher densities in the Allegheny Plateau ecoregion vs. the Ridge and Valley. Hay-scented fern abundance was positively associated with overstory red maple abundance in both ecoregions. After overstory removal, the density and distribution of hay-scented fern tended to increase and remain at elevated levels in stands that were not treated with herbicide. Herbicide treatments resulted in temporary reductions in fern densities and created a "window of opportunity" for the establishment of tree regeneration.

Nomenclature: Hay-scented fern, *Dennstaedtia punctilobula* (Michx.) Moore; red maple, *Acer rubrum* L.
Key words: Invasive species dynamics, herbicide, regeneration, harvest.

The spread and dominance of the invasive native hay-scented fern in the understory is one of the most significant changes that has affected the forest ecosystems in the northeastern United States in the last century. Hay-scented fern has been classified as a native invasive species because of its ability to respond aggressively to sudden increases in resource availability by way of vegetation expansion of rhizomes and sexual reproduction through spore dispersal (Hughes and Fahey 1991; Penrod and McCormick 1996). The influence of dense cover of hay-scented fern is a major biological and economic concern because it often interferes with the establishment and growth of desirable tree regeneration (George and Bazzaz 1999; Horsley et al. 1992; Moser et al. 1996). Tree seedling regeneration is adversely affected because of the ability of hay-scented fern to influence the availability of light, nutrients, and water (Horsley 1991; Lyon and Sharpe 1996). The clonal characteristics of hay-scented fern allow dense colonies to develop and hinder the establishment of tree seedlings, which have to penetrate the herbaceous layer (George and Bazzaz 1999). Hay-scented fern is able to intercept most of the light that penetrates through closed-canopy stands, resulting in altered light quality and reduced light quantity beneath the herbaceous layer.

Although the factors responsible for invasion and management practices for controlling hay-scented fern have led a number of studies, the posttreatment large-scale dynamics of this species is still unclear. In light of the regeneration problem facing mixed-oak forests in the northeastern United States, there is a need to better understand the distribution and dynamics of this invasive native species. This paper focuses on the distribution of hay-scented fern at a landscape scale in mixed-oak stands in Pennsylvania and its dynamics after overstory and herbicide treatments over a decade. As Strayer et al. (2006) pointed out, most studies on invasive species have been brief and lack a temporal context. We hope this long-term, large-scale study on a well-established invasive native will help to shed light on the dynamics and management of invasive species in general.

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Methods

Study Area. The study area is spread across two distinct ecoregions, the Allegheny Plateau and the Ridge and Valley (Figure 1) (Bailey et al. 1994; Cuff et al. 1989). Soils in both ecoregions are derived from sandstone, siltstone, and shale and are typically well drained and support moderately productive forests. Stand elevations range from 250 m above mean sea level in the Ridge and Valley province to 700 m on the Allegheny Plateau. Precipitation and frost-free periods vary with elevation and topography. Mean annual precipitation ranges from 960 to 1,070 mm and frost-free periods range from 140 to 160 d (Cuff et al. 1989). Mixed-oak forests are the dominant natural vegetation in the Ridge and Valley region. Mixed-oak forests transition into Allegheny hardwoods moving from south to north on the Allegheny Plateau, though oaks continue to be locally important in the northern part of Pennsylvania (Bailey et al. 1994; Stout 1991).

Data Collection. Field measurements in 56 mixed-oak stands in Pennsylvania were performed on a total area of 1,009 ha during 1996 to 2008. All of the stands were measured 1 yr before treatment, and a subset of stands was remeasured 1, 4, 7, and 10 yr after treatment (Table 1). Depending on stand area, 15 to 30 permanent plots with 8.02-m radii were systematically installed in a square grid to represent the whole stand. Four permanent subplots with 1.13-m radii were established within each plot (Figure 2). On each subplot, the percentage of hay-scented fern cover was estimated. Diameter at breast height (dbh) for all trees over 5.1 cm in dbh were measured on each plot. In addition, slope shape (sum of percentage slope uphill, downhill, and at 90° to aspect), slope percentage, exposure angle (the angle between the visible east horizon and west horizon), and slope aspect were also measured on each plot. In total, we measured 6,080 subplots before treatment, and 4,395, 4,102, 2,875, and 650 subplots at 1, 4, 7, and 10 yr after treatment, respectively. The reason for the decreasing number of measured subplots along stand age is because part of the 56 stands had not reached the subsequent age after treatments were applied.

Stand Management. Stand management activities were based on management objectives developed by the Pennsylvania Department of Conservation and Natural Resources Bureau of Forestry for each stand and were not experimentally controlled.

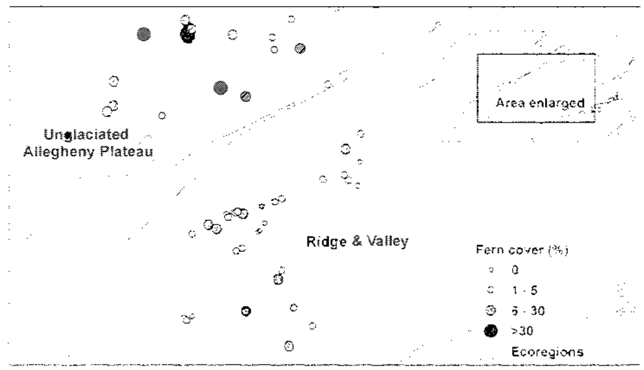

Figure 1. Distribution of average hay-scented fern cover in 56 mixed-oak stands in Pennsylvania.

The primary objective of these silvicultural practices was to establish or release desirable tree regeneration. Overstory harvest ranged from 20 to 80% basal area reduction at the stand level. Stands were treated with herbicide if hay-scented fern densities appeared likely to inhibit regeneration. Sulfometuron-methyl or a glyphosate/sulfometuron-methyl mix was applied to dense hay-scented fern at various rates depending on fern density. Herbicide was applied before the first remeasurement in 11 of the 18 Allegheny Plateau stands and 3 of the 38 Ridge and Valley stands.

Data Analyses. For each stand, average hay-scented fern cover, frequency of occurrence (percentage of subplots with some level of fern cover), and problematic hay-scented fern cover frequency (percentage of subplots with $>$ 30% fern cover) were calculated. The problematic hay-scented fern cover ($>$ 30%) reflects the level of competing vegetation that is considered detrimental for forest regeneration in a portion of the region of study (Marquis 1994). Percentage cover by hay-scented fern was also reclassified into four classes—none, low (1 to 5% cover), moderate (5 to 30%), and problematic (over 30%).

Statistical tests were carried out at the plot level (the mean percentage cover of the four subplots) to find potential associations between fern cover and environmental factors and overstory composition. Because subplots within each plot and plots within each stand are potentially autocorrelated, special attention is needed to deal with possible pseudoreplication. To avoid this, we used the mean percentage of all subplots within a plot as the basic data element, and stand effects were included as a random effect in a mixed-model analysis (GLIMMIX; SAS 2009) of fern cover percentage as a function of other measured variables. Slope aspect, θ, is a circular variable, and attention must be given to its periodic nature during model building. In this analysis, heat load index ($[1 - \cos\{\theta - 45\}]/2$; McCune and Grace 2002), a more biologically meaningful index, was used to assess aspect-

Table 1. Number of stands surveyed and resurveyed by ecoregion, herbicide treatment, and time of assessment.

		Time of assessment				
Ecoregion	Herbicide	Pretreatment	1 yr	4 yr	7 yr	10 yr
Allegheny Plateau	No	7	4	4	3	0
	Yes	11	10	9	5	1
Ridge and Valley	No	35	27	25	19	4
	Yes	3	3	3	2	2

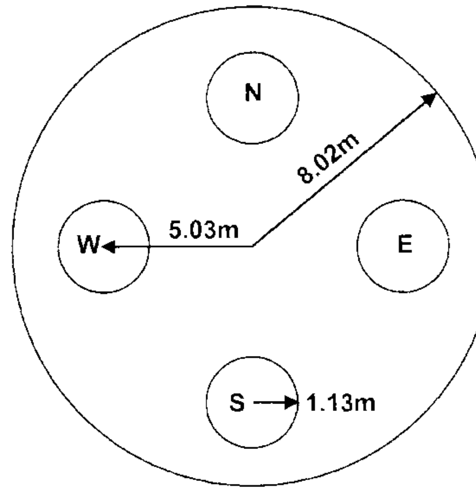

Figure 2. Diagram of the layout of plot and subplots within each plot.

related effects. Average fern cover was set as the response variable, whereas stand, heat load index, exposure angle, slope shape, slope percentage, total overstory basal area before harvest, percentage of oak basal area, and percentage of red maple basal area were the independent variables. Because fern abundance differed greatly between the two ecoregions, the association between fern cover and biotic and abiotic factors before treatment was analyzed for each ecoregion individually.

To understand the effects of overstory removal and herbicide treatment, a mixed-model analysis (GLIMMIX) was used. Change in hay-scented fern cover percentage at the plot level before treatment to 1 yr after treatment was used as the response variable. Residual basal area, total basal area removed, percentage of basal area removed, herbicide treatment, and the interaction terms between overstory removal and herbicide treatment were used in the model. Again, stand was included in the model as a random effect to avoid pseudoreplication arising from the potential autocorrelation among plots within stands.

Average stand-level hay-scented fern cover, frequency of occurrence, and problematic fern cover frequency were summarized by herbicide treatment group in each ecoregion before treatment to 1, 4, 7, and 10 yr after treatment. To minimize sampling bias, subgroups at each measurement period with fewer than three surveyed stands were not summarized. Fern cover class transition rates from before harvest to each remeasurement were calculated at the plot level. Transition rates were calculated as the percentage of plot in a given pretreatment cover class that fell in each cover class at the time of reassessment. Consequently, transition rates sum to 100% for each pretreatment cover class. Again, subgroups with fewer than three stands surveyed were not summarized. Transition rates were calculated separately for herbicide-treated and nontreated stands in each ecoregion.

Results

Pretreatment Distribution and Association. Average stand-level hay-scented fern cover, frequency of occurrence, and problematic fern cover frequency were higher on stands on the Allegheny Plateau than those in the Ridge and Valley ecoregion (Figures 1 and 3). Before treatment, average hay-

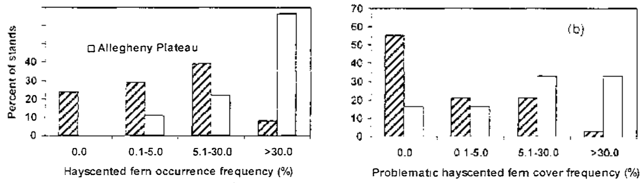

Figure 3. Percentage of stands by hay-scented fern occurrence frequency class (a) and problematic cover frequency class (b) in the Allegheny Plateau and Ridge and Valley ecoregions. Occurrence frequency is defined as percentage of subplots infested by hay-scented fern in each stand, and problematic cover frequency is defined as percentage of subplots with over 30% hay-scented fern cover. Both frequencies were divided into four classes (0, 0.1–5.0, 5.1–30.0, and > 30.0%).

scented fern cover was 17% for stands on the Allegheny Plateau and 3% for stands in the Ridge and Valley. Average hay-scented fern occurrence frequency was 48% for the Allegheny Plateau stands and only 11% for the Ridge and Valley stands. All 18 stands on the Allegheny Plateau had some level of hay-scented fern cover, among which 67% stands had over 30% of their subplots infested with hay-scented fern and only 11% stands had less than 5% of their subplots infested (Figure 3a). For the 38 stands in the Ridge and Valley, nearly a quarter of the stands had no hay-scented fern before treatment and only 8% of the stands had over 30% of their plots infested with hay-scented fern (Figure 3a). Similarly, more subplots within each stand reached the problematic fern level on the Allegheny Plateau than in the Valley

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Table 2. Model coefficients for factors that influence the abundance of pretreatment hay-scented fern cover.

Physiographic region	Model coefficient (standard error)*			
	Intercept	Red maple %[a]	Total_BA[b]	HLI[c]
Ridge and Valley	3.22 (1.12)	0.1 (0.02)	—	−3.59 (1.25)
Allegheny Plateau	23.5 (4.6)	0.1 (0.03)	−0.09 (0.02)	—

[a] Fern cover with percentage of basal area (BA) contributed by red maple.
[b] Fern cover with total BA.
[c] Fern cover with heat load index (HLI).
* $P < 0.01$.

Table 3. Model coefficients for change in fern cover percentage with stand conditions and herbicide 1 yr after treatments were applied.

Model coefficient (standard error)*			
Intercept	BA_Post[a]	BA_diff_percent[b]	Herbicide[c]
−30.7 (4.3)	0.11 (0.03)	−0.14 (0.04)	18.8 (4.1)

[a] Change in fern cover with basal area (BA) postharvest.
[b] Change in fern cover with percentage of change in BA ([BA_Post − BA_Pre]/BA_Pre × 100).
[c] Change in fern cover with herbicide treatment (coefficient multiply by 0 for herbicide stand and by 1 for no herbicide stand).
* $P < 0.05$.

percentage of overstory removed. At the plot level, as more basal area remained after harvest, both in absolute terms and as a percentage of original, there was less reduction in fern cover immediately after harvest. Although initial fern abundance was different between ecoregions, no significant difference was observed in treatment effects.

Posttreatment Dynamics. Development patterns of hay-scented fern after herbicide treatment were similar for both ecoregions. On the Allegheny Plateau, hay-scented fern cover and problematic fern cover frequency were typically reduced 1 yr after herbicide treatment (Figures 4a and 4e) and fern cover frequency also decreased (Figure 4c). Hay-scented fern abundance by all three measures was gradually recovering 4 yr after treatment. Seven years after treatment, all three measures

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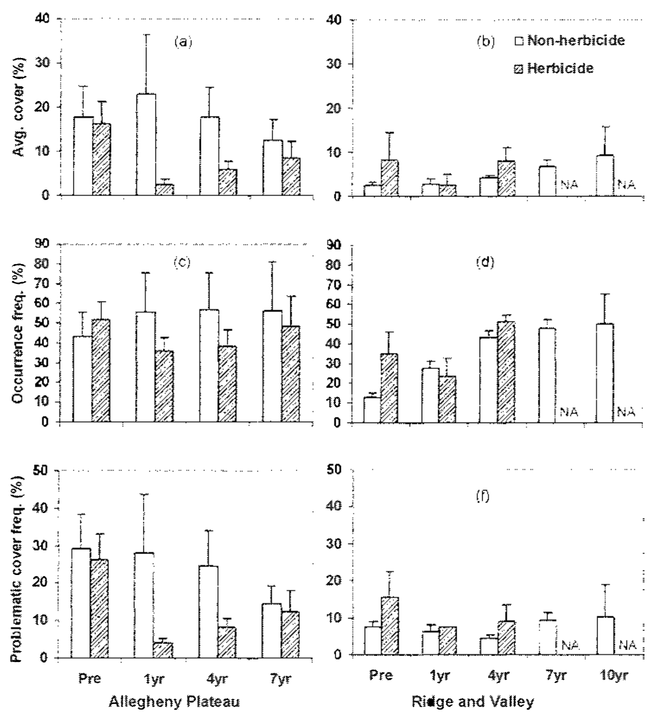

Figure 4. Average hay-scented fern cover (top), occurrence frequency (middle), and problematic cover frequency (bottom) for stands located on the Allegheny Plateau region (left column) and in the Ridge and Valley ecoregion (right column) by assessment period and herbicide treatment.

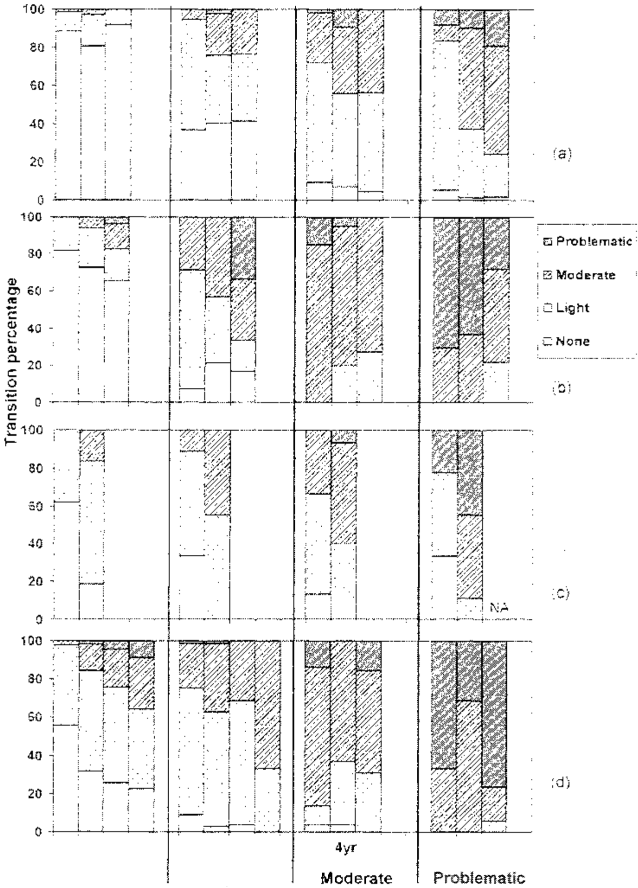

Figure 5. Plot-level hay-scented fern cover class transition percentages from 1 yr before treatment to 1, 4, 7, and 10 yr after treatment for each fern cover class; (a) plots in the Allegheny Plateau region that received herbicide treatment, (b) plots in the Allegheny Plateau region without herbicide treatment, (c) plots in the Ridge and Valley region that received herbicide treatment, and (d) plots in the Ridge and Valley region without herbicide treatment. For example, all plots in the first column in (d) have no fern cover before treatment, 56% remained fern free 1 yr after treatment, 42% transitioned to the light fern cover class, and 2% to the moderate fern cover class.

nearly recovered (Figure 4b) and fern cover frequency exceeded its original level (Figure 4d).

Postharvest patterns of hay-scented fern development in stands that were not treated with herbicide were different between the two ecoregions. On the Allegheny Plateau, average fern cover percentage increased 1 yr after treatment, then gradually decreased with time through year 7 after harvest (Figure 4a); fern cover frequency increased immediately after treatment and maintained that level throughout the rest of the study period (Figure 4c), while problematic fern cover frequency gradually decreased over the study period (Figure 4e). In the Ridge and Valley region, hay-scented fern cover density maintained the same level 1 yr after harvest as before harvest, and gradually increased thereafter (Figure 4b); frequency of occurrence increased more than twofold 1 yr after, more than tripled 4 yr after, and maintained that level 7 and 10 yr after overstory removal (Figure 4d); problematic fern cover frequency was slightly reduced 1 and 4 yr after harvest, but recovered by the seventh year (Figure 4f).

Analysis of fern cover class transition rates further demonstrated that herbicide application effectively reduced fern cover, at least initially (Figures 5a and 5c). On the Allegheny Plateau region, the majority of the plots that had no fern cover before treatment remained fern free throughout the study period (Figure 5a, left column). A result of the herbicide treatment was a conversion of 40% of plots classified in the light fern cover category to fern-free plots after treatment was applied. However, over 20% of plots then transitioned into the moderate cover class 4 and 7 yr after treatment (Figure 5a, mid-left column). Of plots categorized as moderate cover before treatment, over 70% transitioned into the light or no fern cover class 1 yr after treatment, but over 40% were classified back into the moderate or problematic cover class 4 and 7 yr after treatment (Figure 5a, mid-right column). Herbicide also successfully reduced fern cover on plots classified as the problematic fern cover class. Over 80% problematic fern cover plots transitioned into light or no fern cover class 1 yr after treatment. However, the fern recovery process was fast, because 62 and 75% of the plots returned to the moderate or problematic fern cover class 4 and 7 yr posttreatment, respectively (Figure 5a, right column). Patterns were similar in the Ridge and Valley region, but the recovery process was much faster (Figure 5c). Nearly 90% of the plots classified as problematic fern cover class before treatment returned to the moderate or problematic fern classes 4 yr posttreatment (Figure 5c, right column).

Plot-level fern dynamics were similar on the Allegheny Plateau (Figure 5b) and in the Ridge and Valley region (Figure 5d) for stands not treated with herbicide. The number of plots devoid of fern cover before harvest decreased after overstory removal, transitioning into the light, moderate, or problematic fern cover classes (Figures 5b and 5d, left column). Plots classified as light fern cover before harvest also transitioned into the moderate or problematic fern cover classes after harvest. About 67% of plots transitioned from light to the moderate fern cover class 10 yr after harvest in the Ridge and Valley ecoregion. Plots with moderate or problematic fern cover before harvest showed some fern cover reduction but most remained in their original classes after harvest (Figures 5b and 5d, mid-right and right columns).

Discussion

Hay-scented fern has been classified as an invasive native species in areas of the northeastern United States because of its low palatability to insects and other animals, suspected allelopathic effects, high propagule mobility, wide climatic and edaphic tolerance, and relatively high fire tolerance due to buried rhizomes and spore banks (Engelman and Nyland 2006). As our results show, this problem tends to be more acute on the Allegheny Plateau than in the Ridge and Valley ecoregion. Stands on the Allegheny Plateau had higher percentages of fern cover, frequency of fern occurrence, and more areas reaching problematic levels of fern cover. In both ecoregions, heavy fern cover was associated with high proportions of red maple basal area, suggesting perhaps that heavy fern cover favors the establishment of red maple over oak (George and Bazzaz 1999) rather than that red maple favors the establishment of fern. The combination of a high proportion of red maple in the overstory and dense fern cover in the understory suggests that regenerating oak species in these areas will be particularly challenging.

Herbicide application and overstory removal both had a significant negative effect on hay-scented fern abundance.

There was less reduction in fern cover immediately after harvest, as more basal area remained after harvest, both in absolute terms and as a percentage of original. Higher proportions of overstory removal could reflect the higher levels of harvest-induced ground disturbance, which could physically reduce hay-scented fern density.

The pattern of hay-scented fern cover in the understory on stands not treated with herbicide was slightly different between the two ecoregions and is likely due to the different initial hay-scented fern densities. Nearly all stands in the Ridge and Valley were not treated with herbicide because hay-scented fern was either absent or present in low levels before harvest. After harvest, both the hay-scented fern cover distribution and density increased as a result of stand disturbance associated with overstory removal (Groninger and McCormick 1991). Overall, the percentage of plots reaching the problematic fern cover class after overstory removal was low. In contrast, frequency of fern occurrence in this region increased dramatically and steadily throughout the 10-yr study period. It is uncertain whether this increase in distribution is a precursor to a greater fern problem in the future, or a short-lived phenomenon associated with overstory disturbance. But certainly it is true that fern is most likely to become a problem in stands that fail to regenerate quickly to trees.

Herbicide treatments created a window of opportunity for the establishment of seedlings after partial overstory removals. One year after treatment, fern cover was reduced to nonproblematic levels on most of the plots with initially problematic fern cover. After 4 yr, fern cover had partially recovered from the herbicide treatments, but stand-level problematic fern frequency was less than one-third of the initial level in the Allegheny Plateau region and one-half in the Ridge and Valley region. However, the recovery rate accelerated 7 yr after treatment. Given that oaks are expected to produce large acorn crops every 4 to 6 yr, the window of opportunity provides a chance to capture a regeneration cohort. A heavy mast year shortly after the herbicide treatment can increase the probability of successfully establishing oak regeneration (Johnson et al. 1989). The rate of fern recovery accelerated 4 yr after treatment, likely resulting in complete recovery of fern cover, thereby closing the window of opportunity for oak establishment if a mast year does not occur in the 4 yr after the herbicide treatment (Horsley et al. 1992). What's more, the 4-yr window of opportunity may be long enough for some tree species but not others. Further studies are needed to look at species-specific response to this window of opportunity. Because not all stands were measured up to 10 yr after treatment, some caution is needed in interpreting the results of this study, but there is no reason to suppose that the relatively unbalanced inventories are biased with respect to hay-scented fern dynamics.

It is believed that the presence of white-tailed deer (*Odocoileus virginianus* Boddaert) has significant impact on the establishment and dynamics of hay-scented fern (de la Cretaz and Kelty 1999; Tilghman 1989; Waller and Alverson 1997). Deer browse tree seedlings and other vegetations but not hay-scented fern. In addition, overstory thinning in combination with high levels of deer browsing can exacerbate the hay-scented fern problem because of the increased availability of light level and assistance of the spread of wind-dispersed, fertile hay-scented fern spores during the harvesting process (de la Cretaz and Kelty 1999; Horsley and Marquis 1983). In this study, the impact of deer on posttreatment hay-scented fern dynamics was minimal because all stands with known deer browsing problems were fenced. To fully understand the impacts of deer browsing, overstory removal, and herbicide treatment on fern dynamics, further experimental studies are needed.

In conclusion, it is nearly impossible to eradicate a well-established invasive species as long as there are adequate propagule supplies. Removal or reduction treatment such as the herbicide treatment in this study can reduce the level of invasive abundance to allow the establishment of desired native species. However, the window of opportunity to reestablish desired native species quickly diminishes as the invasive species recolonizes.

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