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Restoration of three forest herbs in the Liliaceae family by manipulating deer herbivory and overstorey and understorey vegetation

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Background: Research on herbaceous vegetation restoration in forests characterised by overstorey tree harvests, excessive deer herbivory, and a dominant fern understorey is lacking. Most of the plant diversity found in Eastern hardwood forests in the United States is found in the herbaceous understorey layer. Loss of forest herbaceous species is an indicator of declining forest conditions.
Aims: The combined effects of deer herbivory, competitive understorey vegetation removal, and overstorey tree removal on the abundance and reproductive capacity of three understorey herbs in the Liliaceae family were evaluated.
Methods: A split-plot randomised block design was used with three replicates. Treatments included three harvest intensities, fenced/unfenced, herbicide/no herbicide-treated, prescribed burn/no prescribed burn, and all combinations. A generalised linear model was used to compare treatment effects over 8 years.
Results: Both fruit production and cover increased significantly in fenced areas for all three species. There was a significant 6-year recovery period for cover of the three species in response to herbicide. There was a significant 4-year recovery period of fire-treated plots for fruit production of the three species. The most intensively cut, fenced, and herbicide-treated plots had the greatest increases in sapling and *Rubus* spp. cover. Cover and fruit production of the three herbs were significantly greatest in the moderate-cut treatment.
Conclusions: Restoration of these three liliaceous species is most likely to occur in Eastern deciduous forests and similar forests using a combined fenced and moderate-cut treatment.

Keywords: *Dennstaedtia punctilobula*; deer herbivory; fire; fruit production; herbicide; *Medeola virginiana*; Northern hardwood forests; shelterwood; *Trillium undulatum*; *Uvularia sessilifolia*

Introduction

A decrease in forest understorey plant diversity and productivity of Eastern United States forests has been attributed to increasing populations of white-tailed deer (*Odocoileus virginianus* Zimmermann) over the twentieth century (Russell et al. 2001; Côté et al. 2004). Much of the concern associated with deer herbivory has focused on the loss of tree seedlings that could grow successfully into saplings, ensuring regeneration of the existing closed-canopy forest. Two types of impacts related to tree regeneration due to deer overabundance have been documented: (1) stalled succession after a disturbance (Horsley and Marquis 1983; Hobbs 1996; Stromayer and Warren 1997), and (2) a change in tree species composition (Webb et al. 1956; Ross et al. 1970; Trumbull et al. 1989; Horsley et al. 2003), which may include an increase in dominance of invasive exotics (Eschtruth and Battles 2009; Knight et al. 2009) and weedy native species (Horsley et al. 2003). The negative impacts of deer herbivory on native herbaceous forest understorey species are also well documented, and include both reductions in abundance and fruit production for several species (Augustine and Frelich 1998; Fletcher and McShea et al. 2001). There is also evidence that chronic, high levels of deer herbivory may lead to irreversible changes in herbaceous species composition and associated pollinators and seed dispersers, to such an extent that the removal of herbivory may not be enough to restore the impacted ecosystem (Fletcher et al. 2001a; Ruhren and Handel 2003; Webster et al. 2005). Chronic deer herbivory may be more likely to occur with herbaceous species than tree seedlings because there is no potential of escaping the zone of deer accessibility for most herbaceous plants (Alverson et al. 1988).

Timber harvesting may impact understorey herbaceous species in both negative and positive ways. Negative impacts include forest floor disturbance, resulting in removal of individuals and a switch in species dominance towards more shade-intolerant, ruderal species (Meier et al. 1995; Fredericksen, et al. 1999; Gilliam 2002; Kraft et al. 2004; Huebner and Tobin 2006). With more intensive harvests, such as clear cuts, recovery of the herbaceous understory is relatively slow and the resulting herbaceous understory is unlikely to return to its original species composition within 40–150 years, which are typical logging cycles (Duffy and Meier 1992). Less intense harvesting techniques, such as group selection and shelterwood harvests, show fewer impacts on herbaceous species with recovery approaching the initial conditions (Reader and

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Bricker 1992). Positive impacts associated with harvesting include increases in sexual reproduction and fruit production for many understorey species. This response has been noted in both lower (e.g. single-tree selection and group selection; Perry et al. 1999) and higher (e.g. shelterwood and clear cut) intensity harvesting levels (Hughes and Fahey 1991; Perry et al. 1999). The potential mechanisms behind these positive responses include increases in light, soil moisture (Harpole and Haas 1999; Lindh et al. 2003; Dech et al. 2008), and soil nutrient availability (Vitousek et al. 1982; Coomes and Grubb 2000; Dech et al. 2008), all of which have been attributed to overstorey tree removal and reduced tree root competition.

Removal of dominant weedy species may benefit associated, less-dominant plant species. For instance, the removal of *Kalmia angustifolia* L. (sheep laurel) resulted in increased size of three conifer species, possibly due to an increase in soil fertility after its removal (Moroni et al. 2009). *Erythronium americanum* Ker. Gawler (trout lily) increased in abundance and frequency after removal of surrounding vegetation, with the greatest effect following removal of both overstorey and understorey vegetation (Hughes 1992). Removal of the invasive *Lonicera maackii* (Rupr.) Maxim. (bush honeysuckle) in Ohio forests resulted in increased growth and fecundity of several perennial forest herbs (Miller and Gorchov 2004). *Dennstaedtia punctilobula* (Michx.) Moore (hayscented fern) removal resulted in greater *Betula* L. sp. (birch) growth, though it had no impact on the growth of *Quercus rubra* L. (northern red oak) or *Acer rubrum* L. (red maple). *Dennstaedtia punctilobula* cover can act as a filter for specific tree species regeneration, with *Q. rubra* and *A. rubrum* being examples of species that are capable of growing through the fern layer (George and Bazzaz 1999). Such a filter may be a detriment to the species that are able to grow through the fern in areas of high deer herbivory, because the deer feed on the visible oaks and maples (Buckley et al. 1998). Also, removal of taller, more protective weedy understorey species, such as *Rubus* sp. L., could be detrimental to several understorey species, such as oak seedlings, in areas with high deer herbivory (Gordon et al. 1995). The potential mechanisms behind a positive effect of understorey plant competition removal include increases in light, soil moisture and soil nutrients associated with the removal of dominant plants (Vitousek et al. 1992; Coomes and Grubb 2000; Lindh et al. 2003). Fire may also directly add nutrients (ephemerally) to soil with the formation of ash. However, fire could decrease soil moisture due to increased water repellency (Certini 2005), which is more likely to occur under xeric conditions (Iverson and Hutchinson 2002). Likewise, some herbicides directly increase ammonium in soils after application, but this is usually a very rapid (less than 6 h) release of ammonium (Vitousek et al. 1992).

While the combined effects of deer herbivory, harvesting, and removal of understorey weedy species have been studied in terms of impacts on tree seedlings (Buckley et al. 1998), their effects on common herbaceous understorey species have not been evaluated. Kraft et al. (2004) evaluated the effects of harvesting (thinning) and deer herbivory on several understorey plants. Their results showed that thinning increased the richness and cover of graminoid species as well as one *Rubus* sp., while deer-browse control was linked to increased physical stature and reproductive capacity of several shade-tolerant herbaceous species, including *Smilacina racemosa* (L.) Desf. (false Solomon-seal) and *Trillium grandiflorum* (Michaux) Salisb. (big white trillium) (Kraft et al. 2004).

Our goal was to evaluate how typical Eastern United States forest management strategies used for oak regeneration (e.g. fencing, canopy tree removal, prescribed fire, and herbicide) impact forest understorey herbaceous species. More specifically, our research experimentally compared the relative impact of deer herbivory, timber harvesting, and removal of weedy species (using herbicide and fire) on the abundance and reproductive capacity of *Medeola virginiana* L. (Indian cucumber root), *Uvularia sessilifolia* L. (sessile bellwort), and *Trillium undulatum* Willd. (painted trillium) in an oak-dominated forest of northern Pennsylvania, USA. We hypothesised that: (1) there would be a positive response (increased cover and fruit production) of the three species to increasing harvesting intensities as well as to the removal of both deer herbivory and fern cover; (2) temporary negative impacts caused by non-target species herbicide and fire effects and harvesting-related soil disturbances would reduce the relative positive response of the three liliaceous species to deer and fern removal and a more open canopy; and (3) the increased dominance of other competing understorey species (e.g. *Rubus* spp. and saplings) in response to one or more of the treatments would counter the positive effects of fencing, harvesting, and fern removal on the three liliaceous species.

Methods

Study area

This study was located within the Moshannon State Forest (41° 07′ 30″ N, 78° 30′ 00 W) in the Unglaciated Allegheny Plateau physiographic province in Clearfield County of north-central Pennsylvania, USA. This property, which is currently managed by the Pennsylvania Department of Conservation and Natural Resources, Bureau of Forestry (PA DCNR, BOF) has a relatively flat topography and an elevation of about 650 m. Average annual precipitation and temperature are 1170 mm and 6.4 °C, respectively (National Climate Data Center 2010).

The forest overstorey trees on the study site are about 85 years of age and are currently dominated by *Q. rubra* (PA DCNR, Moshannon State Forest web page 2009). Due to previous single-age harvesting (clear cuts) and relatively high and constant deer herbivory pressure, the understorey of this study site and similar sites has been dominated by *D. punctilobula*, a weedy native fern, since at least the late 1970s (Horsley and Marquis 1983).

Study plants

Trillium undulatum, *Uvularia sessilifolia*, and *Medeola virginiana* are all members of the Liliaceae family and are palatable to deer (Atwood 1941; Balgooyen and Waller 1995; Thompson and Sharpe 2005), with *T. undulatum* possibly ranking as the most preferred species of the three (Augustine and Frelich 1998; Fletcher et al. 2001b; Webster et al. 2005). Liliaceous plants in general appear to be preferred by deer over other plant groups (Miller et al. 1992). All three species are present throughout the understorey at the site, with *M. virginiana* being the most common (C. Huebner, unpublished data). The three species are classified as clonal (McCall and Primack 1987; Cook 1988; Cain and Cook 1988; Moola and Vasseur 2008). *Medeola virginiana* and *U. sessilifolia* are both hermaphroditic but self-incompatible, requiring pollination (McCall and Primack 1987). *Trillium undulatum*, which is also hermaphroditic, is highly autogamous (self-compatible and possibly apomictic), which should indicate no dependency on pollinators (Barrett and Helenurm 1987). *Uvularia sessilifolia* and *T. undulatum* flower in May or late May and *M. virginiana* flowers in late June (Barrett and Helenurm 1987; McCall and Primack 1987).

Trillium undulatum and *U. sessilifolia* are both myrmecochores (having ant-dispersed seed), although the seed of *T. undulatum* is also dispersed by deer (Vellend et al. 2003) and invertebrates (Gunther and Lanza 1989; Kalisz et al. 1999), suggesting relatively long-distance dispersal. Both *U. sessilifolia* and *M. virginiana* seeds are documented to disperse as far as 11 m and 15 m, respectively (Singleton et al. 2001). *Trillium undulatum* and *U. sessilifolia* were both present in the seed bank of a second-growth northern hardwood forest (Hubbard Brook Experimental Forest, New Hampshire), where all three species were present in the existing vegetation, although *M. virginiana* was uncommon (Hughes and Fahey 1991). *Trillium undulatum* and *M. virginiana* were present in the seed bank and current vegetation of a second, possibly third-growth forest, in a northern hardwood forest of the Adirondacks, New York (Smallidge and Leopold 1995). Although present in the existing vegetation, none of the three species was present in the seed bank of an Allegheny Plateau riparian hardwood forest in the Allegheny National Forest, not far from the sites of this study (Hanlon et al. 1998).

These three species were chosen as focal species because (1) they were likely to occur in enough abundance to make treatment comparisons legitimate; (2) their fruits were easy to count accurately; and (3) they shared habitat preferences (mesic and low-light) and reproductive strategies (perennials that can reproduce sexually and asexually) with other closed-canopy, understorey herbaceous plants that also suffer from deer herbivory, but were more rarely found in our research site (C. Huebner, unpublished data). Plant species nomenclature follows the International Taxonomic Integrated System (ITIS 2010) and Rhoades and Block (2000).

Experimental design

Three replicate sites, each approximately 17 ha in size (about 500 m × 340 m, with 10 m buffers around herbicide and fence treatments and 20 m buffers between cut treatments) were selected. Replicates 1 and 2 were approximately 50 m apart, while the third replicate was approximately 7 km away from the two other sites. Within each replicate site, 24 plots, each 0.4 ha in size (50 m × 80 m), were established such that each treatment type combination was represented once. Four treatments were applied: (1) harvesting (control, moderate, intensive); (2) fencing (fence, no fence); (3) prescribed burn (burn, no burn); and (4) herbicide (herbicide, no herbicide). In order to minimise edge effects, the three harvesting treatments were blocked along the long axis of each site. The fencing, herbicide, and prescribed burn treatments were also blocked, and the blocks were randomly located (Figure 1), such that the location varied with each replicate site.

Treatments

The treatment combinations applied in this study represent those recommended by Brose et al. (2008) to regenerate mixed-oak forests in the Mid-Atlantic Region of the US. The key to successful oak regeneration is the presence of competitive seedlings or sprout sources at the time of a harvest or other stand-replacing event (Loftis 1990). Barriers to successful oak regeneration include insufficient micro-site light on the forest floor, heavy seed predation and browsing by deer, and the presence of competing vegetation.

The overstorey tree removal treatments took place in December 2001 to January 2002 and included three levels: (1) the control with no tree removal (76% stocked on average), maintaining a light level of 2–5% of full sunlight in the understorey controls and 5–10% of full sunlight in plots treated with herbicide or fire; (2) a moderate first-stage shelterwood harvest with 10–15% of the total basal area removed (64% stocked on average), resulting in a light level of 10–15% of full sunlight; and (3) an intensive first-stage shelterwood harvest with 20–30% of the total basal area removed (52% stocked on average), resulting in a light level of 20–25% of full sunlight. Our use of 'moderate' vs. 'intensive' is only relative to this study. The intensive cut described in this study is moderate when compared with other timber harvests, including many shelterwood harvests. Trees removed for the moderate harvest included mid-storey trees, about 7.5–25 cm in diameter at breast height (dbh). Trees removed in the intensive harvest treatment included all the trees of the moderate harvest and 20–25% of the dominant and co-dominant trees, creating several canopy gaps. Non-commercial trees marked for harvest were felled between March and April 2002 and left on the plots.

The fencing treatment divided the overstorey blocks in half (Figure 1). The fence used was a 2-m tall woven wire

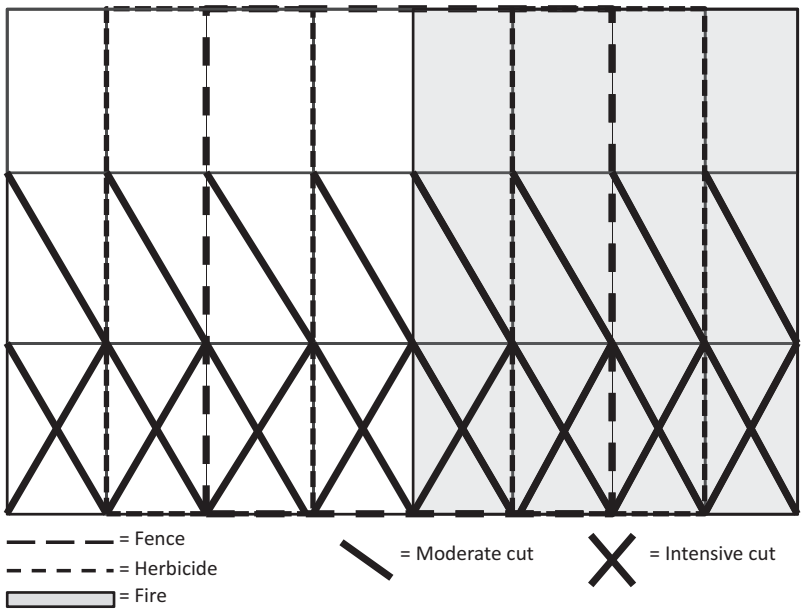

Figure 1. Experimental design showing an example replicate site with 24 plots. The upper row contains all the plots in the uncut treatment.

fence with approximate 10 × 10 cm square openings, and was installed in February to March 2002.

The herbicide treatment was a broadcast foliar application with a sprayer. Approximately 0.370 kg per 0.4 ha glyphosate (Accord®) mixed with 43 g per 0.4 ha of sulfometuron-methyl (Oust®) was applied on 28 and 29 June 2001. This application removed all herbaceous and small woody understorey vegetation. On 2 July 2001 a second herbicide application, using only triclopyr (10–20% solution) sprayed directly onto individual stems, was used to treat stems taller than 3 m (the maximum height of the initial sprayer treatment).

The prescribed fires were conducted on 6 May (Replicate 3) and 20 May (Replicates 1 and 2) 2004. Weather conditions were recorded on site during each burn with a belt weather kit every 30 min (Table 1). Moisture of dead and downed woody debris between 0.64 and 2.54 cm in diameter was measured shortly before each burn using a wood moisture probe. All prescribed fires were ignited with drip torches in a strip-head fire pattern. Flame length was estimated by observing the flaming front passing by overstorey trees (two per plot) whose lower boles were marked with paint in 0.3-m intervals to a height of 2 m (Rothermel and Deeming 1980). Rate-of-spread was calculated by marking, timing, and measuring one 2-min run per plot with a stopwatch. Fire temperature was measured in each plot with nine metal tiles marked with heat-sensitive paint (40–300 °C in 20 °C intervals) and one thermocouple/data logger unit. In general, all were low-intensity fires because 2004 was a wet year in Pennsylvania (Palmer Drought Severity Index was +3.53, National Climate Data Center 2010) and burning opportunities were few and of poor quality. Replicate 3 displayed the most intense fire behaviour of the three burn units. Weather conditions were less

Table 1. Environmental conditions and behaviour of the three prescribed fires.

Conditions	Replicate 1	Replicate 2	Replicate 3
Date	20 May 2004	20 May 2004	06 May 2004
Time of burn	11:00–12:30	12:30–14:00	13:00–15:00
Air temperature (°C)	18–20	20–21	21–24
Relative humidity (%)	42–46	40–42	27–30
Wind direction	South-west	South-west	West
Wind speed (km/h)	< 1	1–3	1–3
Cloud cover (%)	50	75	0
Fuel moisture (%)*	18	19	15
Flame length (m)	0.1–0.2	0.1–0.3	0.1–0.7
Rate of spread (m/min)	1–2	1–3	1–4
Thermocouple temperature (°C)	Not recorded	Not recorded	47–180
Painted tile temperature (°C)	Not recorded	Not recorded	60–300
Area burned (%)	83	65	98

*Moisture of downed woody debris between 0.64 and 2.54 cm diameter.

favourable for burning in Replicates 1 and 2, which was evident in the reduction of area burned. A miscommunication resulted in the data loggers and painted tiles not being deployed in Replicates 1 and 2, so no maximum fire temperature data were recorded for these two burn units (Table 1).

Reproductive capacity and abundance

Fruits were tallied over a 3-day period in mid-July of 2006, 2007, 2008, and 2009 both in 20 1-m^2 circular quadrats and along two 1-m wide belt transects bifurcating the plots in both directions. The transects were off-set slightly from centre in order to avoid dissecting a quadrat (Figure 2). All fruits were tallied as a total count per species for the entire plot (summing all quadrats and transect tallies). As the fruits of *M. virginiana* mature slightly later than those of *U. sessilifolia* and *T. undulatum*, its fruit counts are likely to be lower than the total possible fruit count for this species. Nonetheless, this species also produces 10–20 times more fruit in general per individual compared with the other two species. Absolute cover of all herbaceous species was determined in each quadrat and averaged per 1-m^2 quadrat (Figure 2) for each plot since 2001 (pre-treatments) through 2008, and for the three liliaceous species also in 2009. Fruit counts and cover estimates for all three species were combined for the statistical analyses to improve statistical robustness; trends in both variables for the separate species were similar.

Competing species

The abundance (estimated using cover or density) of potentially competing species that were also likely to be affected by the three treatments was determined. These measurements included the total cover of all *Rubus* spp., total density of all tree saplings over 1 m in height and less than 3 cm in diameter, and the cover of *D. punctilobula*. All values were determined from the average of 20 1-m^2 quadrats. Sapling quadrats were located in separate quadrats from the herb, fern, and shrub quadrats (Figure 2). Sapling data were only collected in full for years 2001, 2002, 2004, 2006, and 2008.

Seed bank

In late July of 2001 and 2006, five soil samples, 15 × 15 cm^2 in area and 10 cm deep were taken from randomly located points (that excluded existing vegetation quadrats) within each of the 0.4-ha plots (Figure 2). The five samples per plot were mixed, removing rocks, roots, and rhizomes, and spread over a 3-cm layer of sterile potting soil at a 1 cm depth, resulting in 11,250 cm^3 of soil per plot. The 72 trays were placed in a greenhouse, watered as needed, and emerging seedlings recorded until late November of each year. Germinants were identified and tallied every 14 days. The seed bank results presented in this paper only focus on the three lilaceous species.

Statistical analyses

We used generalised linear models (Proc GenMod, SAS v. 9.1) to test for the effects of fencing, harvesting, fire, and herbicide treatments on (1) the fruit production of the liliaceous species; (2) the cover of the liliaceous species; and (3) the cover of the competing species (*Rubus* spp., saplings, and *D. punctilobula*). Fruit counts and cover of the three liliaceous species were compared for each treatment and their interactions by using a gamma distribution (best fit due to the skewed distribution) and a log link function (nonlinear transformation of the predicted variables). *Rubus* spp. cover, sapling density, and *D. punctilobula* cover were also analysed using a gamma distribution and log link function. Years were analysed separately because

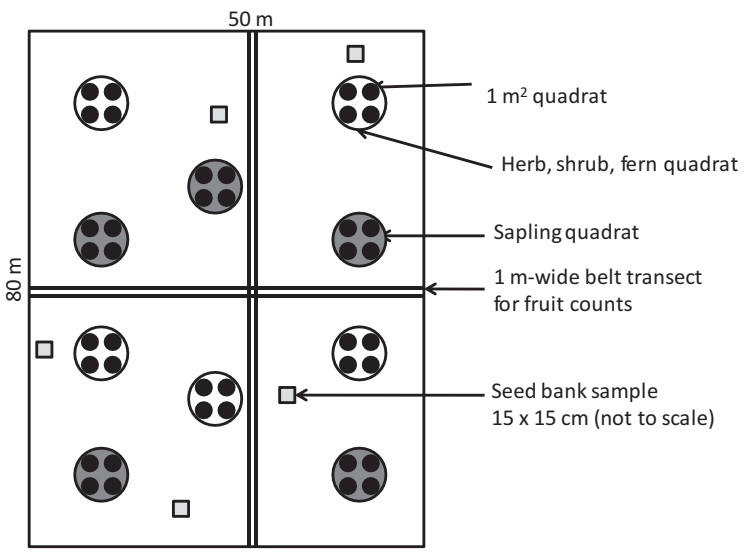

Figure 2. Example individual plot showing the 20 1-m^2 quadrats, the two transects, and the random seed bank samples.

the number of replicates (three) did not produce a stable model after inclusion of a repeated measure (time covariate). Generalised linear models are best suited for data where it is not reasonable to expect normal distributions or constant variances. Selected distributions were chosen using univariate and residual analyses. Goodness of fit for each model was assessed by determining (1) whether or not the deviance divided by the degrees of freedom was close to one, and (2) whether or not the log likelihood values differed significantly from the model with the intercept only, as well as with models using Poisson, negative binomial (which are often better suited for count data), and normal distributions (with and without data transformations).

Models containing the different interaction levels (two-way, three-way, and four-way) were also compared in terms of goodness of fit. Because all four treatments were executed on each plot, using the four-way interaction term in the models was the most ecologically sound. Moreover, using the two-way and three-way interaction models resulted in more independent variables (six additional terms for the two-way interaction, and four additional terms for the three-way interaction) in each of the models; model overfitting is more likely to occur when there are several independent variables relative to the sample size (72). Nonetheless, significant two-way and three-way interactions are also described in the text.

Results

Reproductive capacity

Fencing and fire were the only two variables that showed a significant effect on fruit production of the three liliaceous species (Table 2). Fencing had a positive effect while the effect of fire was a negative non-target species response lasting for 4 years. Total fruit counts of the three species were higher in the fenced compared with the unfenced plots for all 4 years (Figure 3). The fenced plus fire plots showed the lowest fruit production of all the fenced plots in each cut type; this three-way interaction was only significant in 2006 ($X^2 = 5.87$, $P = 0.015$). The fenced and herbicide plots showed the highest significant fruit production, but this two-way interaction was only significant in 2008 ($X^2 = 5.41$, $P = 0.020$). There was a trend for fruit counts to decrease over the 4-year period in the fenced plots with the intensive-cut treatment; the fenced and intensive-cut plots also had approximately half as many fruit as the fenced uncut and moderate-cut plots (Figure 3). The unfenced plots had very low fruit counts, with an overall average for all years and treatments of 0.93 fruit per plot, and showed no differentiation across time, harvest type, or whether or not the plots were treated with fire or herbicide. The decrease in fruit counts in 2009 for all treatments may be explained in part by weather, if we assume the relatively low rainfall in May of 2009 (37.8 mm) compared with May of 2008 (97.0 mm) for the Dubois, Pennsylvania area could impact the three species well into early July (National Climate Data Center 2010). However, June rainfall in 2009 averaged 175.5 mm, which was higher than that of June 2008 (125.2 mm).

The main effects model for fruit production explained 56% of the deviance on average (2006–2009). Adding all two-way interactions explained an additional 9% of the deviance on average; adding the four-way interaction explained an additional 32% of the deviance on average. Models that included four-way interactions were stable and had the best fit compared with the two-way and three-way interaction models, and the significant main effects remained the same. Thus, only the four-way interaction models are presented in Table 2.

Abundance

The effect of the fencing treatment on cover of these three species was significant for every post-treatment year (Table 3). For every cut, herbicide, and fire treatment, the fenced plots showed greater cover than the unfenced plots (Figure 4). The effect of harvesting on cover was significant in the first post-treatment year and then again in 2004 (when the fire treatment was first applied). The harvesting treatment was not significant from 2005 to 2007, but became

Table 2. Comparison of total fruit counts of the three liliaceous species (*M. virginiana*, *T. undulatum*, and *U. sessilifolia*) across treatments using a generalised linear model with a gamma distribution and log link function.

	X^2 (Deviance/DF, scaled Pearson X^2)			
Treatment	2006 (1.17, 29.14)	2007 (1.41, 28.91)	2008 (0.96, 44.68)	2009 (1.44, 24.60)
Fence	68.09***	37.40***	87.14***	20.55***
Cut	3.19	0.8145	2.70	4.68
Herbicide	0.02	2.32	2.06	1.06
Fire	7.42**	4.54*	3.84*	1.07
Interaction	20.84	10.99	23.61	14.68

The four-way interaction is shown. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Both deviance/DF (closer to 1 being stronger) and scaled Pearson X^2 (smaller being better) are indicators of model strength.

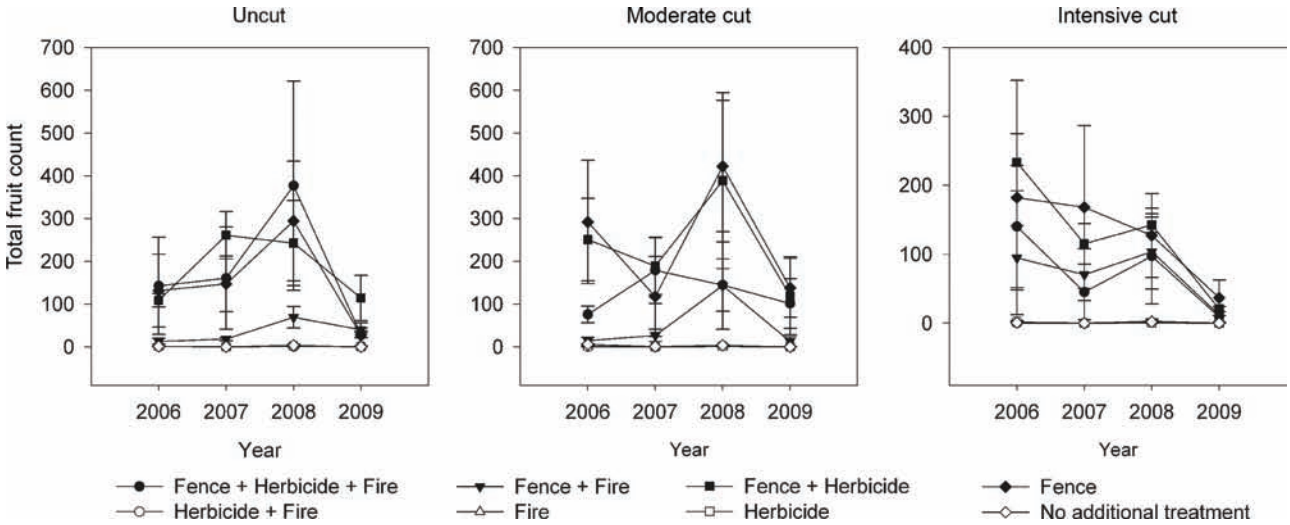

Figure 3. Comparison of fruit counts per plot of the three liliaceous species across treatments by year. Error bars are the standard error. Fencing, herbicide and cut treatments started in 2002; the fire treatment started in 2004. Significant differences between treatments were analysed by using a generalised linear model with a gamma distribution and log link function (see Table 2).

Table 3. Comparison of total percent cover of the three liliaceous species (*M. virginiana*, *T. undulatum*, and *U. sessilifolia*) across treatments using a generalised linear model with a gamma distribution and log link function.

	X^2 (Deviance/DF, scaled Pearson X^2)							
Treatment	2002 (0.55, 68.42)	2003 (0.96, 59.87)	2004 (1.15, 45.56)	2005 (0.96, 51.20)	2006 (1.22, 45.80)	2007 (0.88, 49.83)	2008 (0.82, 49.21)	2009 (0.99, 47.07)
Fence	7.60**	14.15***	14.36***	26.48***	33.42***	56.80***	52.20***	31.34***
Cut	16.09***	3.53		8.40**		3.30		4.66
	4.89	13.27**	17.28***					
Herbicide	53.68***	30.17***	16.05***	17.26***	7.13**		5.21*	0.50
0.46								
Fire	–	–	20.90***	7.75**	0.69	2.47	0.00	1.69
Interaction	8.72	4.83	22.95	22.41	13.25	17.61	22.68	23.41

The interaction shown for 2002–2003 is Fence × Cut × Herbicide, while it is Fence × Cut × Herbicide × Fire for 2001 and 2004–2008. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. The results for 2001 (pre-treatment year) were Fence ($X^2 = 2.33$, $P = 0.127$), Cut ($X^2 = 5.50$, $P = 0.064$), Herbicide ($X^2 = 2.25$, $P = 0.134$), Fire ($X^2 = 0.19$, $P = 0.665$), and four-way interaction ($X^2 = 15.24$, $P = 0.646$), confirming no pre-existing significant differences (though the cut plots were marginally significantly different); deviance/DF and scaled Pearson X^2 were 0.67 and 44.65, respectively. Fencing treatment began in 2002 and lasted the duration of the study; herbicide and cut treatments took place in 2002; fire treatment took place in 2004. Both deviance/DF (closer to 1 being stronger) and scaled Pearson X^2 (smaller being better) are indicators of model strength.

significant once again in 2008 and 2009. In general, the effect of harvesting on liliaceous species cover was positive for the moderate-cut plots (about twice as much cover) and negative for the intensive-cut plots (about half as much cover) in comparison with the uncut plots. Cover of the three species was variable in the uncut plots, while it continued to increase in the moderate-cut plots, and it levelled off in the intensive-cut plots (Figure 4). The herbicide treatment affected cover significantly and negatively in every post-treatment year until 2008. In 2008, there appeared to be a switch in importance from herbicide to harvesting. The non-target, negative herbicide effects on cover of these three species, therefore, appears to last 6 years, which is slightly longer than its 4-year effect on fruit production. The effects of fire were only significant for 1 year after the first year of treatment in spring of 2004 (Table 3). The two-way interaction fence × herbicide was significant in 2008 ($X^2 = 4.98$, $P = 0.026$). This combined treatment manifested the lowest cover values of all the fenced plots except in the moderate-cut type. Likewise, the three-way interaction fence × herbicide × fire was significant in 2004 ($X^2 = 7.40$, $P = 0.0065$), 2005 ($X^2 = 7.99$, $P = 0.0057$), and 2007 ($X^2 = 4.65$, $P = 0.031$). In each of these years, this combined treatment showed lower cover values than the other fenced plots except fenced plus fire plots (Figure 4). These significant interactions support the fact that herbicide and, to a lesser extent, fire had a negative non-target species impact on the three liliaceous species.

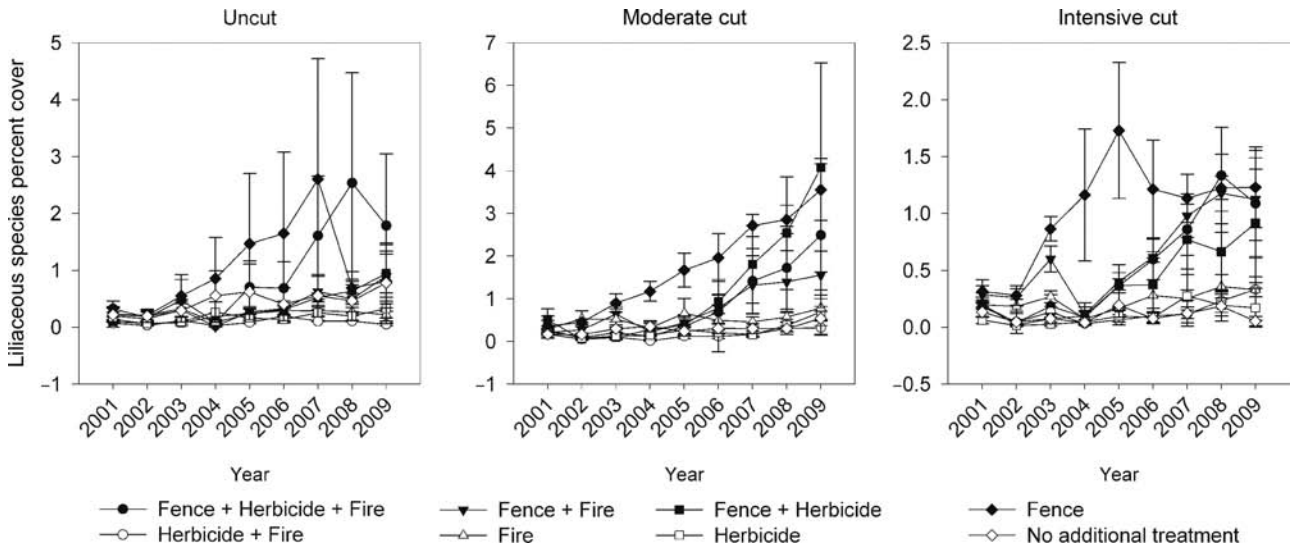

Figure 4. Comparison of mean percent cover per 1 m^2 quadrat of the three liliaceous species across treatments by year. Error bars are the standard error. Fencing, herbicide and cut treatments started in 2002; the fire treatment started in 2004. Significant differences between treatments were analysed using a generalised linear model with a gamma distribution and log link function (see Table 3).

The main effects model for abundance explained 44% of the deviance on average (2002–2009). Adding all two-way interactions explained an additional 9% of the deviance on average, adding the four-way interaction explained an additional 25% of the deviance on average. Models that included four-way interactions were stable and had the best fit compared with the two-way and three-way interaction models, and the significant main effects remained the same. Thus, only the four-way interaction models are presented in Table 3.

Response of potentially competitive species

Fencing, harvesting, and herbicide treatments had a significant effect on *Rubus* spp. cover, with the most intensively cut plots showing a 10-fold increase compared with the uncut plots (Table 4, Figure 5). However, *Rubus* spp. cover increases in fenced plots were only significant if the plots were also treated with herbicide. The positive response to the fencing and herbicide did not start, consistently, until 2004. This response was further confirmed by a significant two-way fence × herbicide interaction in the years 2004 ($X^2 = 4.53$, $P = 0.033$), 2005 ($X^2 = 9.11$, $P = 0.0025$), 2006 ($X^2 = 11.29$, $P = 0.0008$), 2007 ($X^2 = 5.85$, $P = 0.016$), and 2008 ($X^2 = 7.28$, $P = 0.007$). *Rubus* spp. cover increased in response to intensive harvesting beginning in 2002 (Table 4). There was a significant fence × cut interaction ($X^2 = 6.80$, $P = 0.033$) and herbicide × cut interaction ($X^2 = 7.59$, $P = 0.023$) in 2005. Likewise, the fence × cut × herbicide three-way interaction was significant in 2004 ($X^2 = 7.21$, $P = 0.027$) and 2005 ($X^2 = 15.30$, $P = 0.0005$). These interactions support the positive impact of fencing, harvesting, and herbicide treatments on *Rubus* spp. cover. In contrast, fire appears to have had no significant effect on *Rubus* spp. cover, though it is possible that its response is delayed beyond our sample period or its effect is downweighted by harvesting or fencing due to interaction effects. The fire × fence × cut three-way interaction was significant in 2007 ($X^2 = 6.29$, $P = 0.043$), and the four-way interaction was significant in 2005 (Table 4), suggesting that the importance of fire may have increased slightly, but with little or no impact on the effect of fencing and herbicide on *Rubus* spp. cover.

Saplings in the fenced plots were significantly denser than saplings in the unfenced plots in 2006 and 2008 (Table 4). Saplings were also significantly denser in the fenced, herbicide-treated, and intensive-cut plots compared with all treatments in both the moderate-cut and uncut plots in 2006 and 2008 (Table 4, Figure 6). The herbicide treatment had no significant impact in any year except 2002, but the negative impact of the fire treatment on sapling abundance began in 2004 and presumably continued through 2005 and into 2006. The two-way interaction cut × herbicide was significant in 2004 ($X^2 = 8.41$, $P = 0.0037$), 2006 ($X^2 = 10.29$, $P = 0.0058$), and 2008 ($X^2 = 13.52$, $P = 0.0012$), as was the three-way interaction fence × cut × herbicide in 2004 ($X^2 = 8.41$, $P = 0.0037$), 2006 ($X^2 = 10.44$, $P = 0.015$), and 2008 ($X^2 = 19.02$, $P = 0.0008$), suggesting that herbicide may have an additive and positive influence on the cut and fencing treatments. The significant fire × herbicide interaction in 2006 ($X^2 = 8.56$, $P = 0.0034$), the significant three-way interaction fire × fence × herbicide in 2006 ($X^2 = 6.06$, $P = 0.013$), and the significant four-way interaction in 2006 and 2008 (Table 4) may indicate that the main effects of fencing and herbicide were strong enough to counter the negative effects of fire on sapling density (Table 4, Figure 6). The negative effect of fire was only strong enough to counter the opposite effects of fencing herbicide, and cutting in 2006 but not 2008.

Table 4. Comparison of the abundance of competing species (*Rubus* spp., tree saplings, and *Dennstaedtia punctilobula*) in response to the treatments for 2001 (pre-treatment) through 2008.

	X^2 (Deviance/DF, scaled Pearson X^2)							
***Rubus* spp.**	2001 (0.24, 0.94)	2002 (0.20, 13.61)	2003 (1.90, 42.37)	2004 (1.48, 25.96)	2005 (1.13, 31.86)	2006 (1.63, 30.35)	2007 (1.82, 25.25)	2008 (1.54, 26.11)
Fence	0.00	3.54	2.74	11.06***	34.74***	39.11***	46.81***	47.77***
Cut	2.25	9.67**	9.13**	26.83***	34.58***	21.61***	23.33***	22.75***
Herbicide	0.12	9.52**	1.72	11.78***	22.43***	23.19***	20.06***	23.60***
Fire	0.58	–	–	3.60	1.00	1.10	0.34	0.00
Interaction	4.00**	9.16	6.41	27.27*	52.58***	25.70	25.73	19.38
Saplings	2001 (0.78, 38.88)	2002 (0.58, 16.87)	2003 –	2004 (0.32, 17.71)	2005 –	2006 (0.82, 20.44)	2007 –	2008 (0.67, 30.69)
Fence	0.08	1.54	–	0.77	–	7.93**	–	4.13*
Cut	8.96*	1.89	–	13.90***	–	10.58**	–	16.28***
Herbicide	0.21	5.89*	–	0.03	–	0.28	–	0.06
Fire	3.47	–	–	20.56***	–	7.92**	–	0.08
Interaction	31.40*	7.20	–	12.27	–	25.76*	–	39.25**
Dennstaedtia punctilobula	2001 (0.60, 52.10)	2002 (0.83, 57.59)	2003 (1.01, 51.25)	2004 (0.86, 47.38)	2005 (1.01, 51.72)	2006 (0.88, 54.75)	2007 (0.82, 54.76)	2008 (0.77, 56.16)
Fence	0.00	3.65	4.77*	2.34	0.85	0.01	0.80	1.36
Cut	8.02*	4.17	1.92	16.04**	22.17***	21.07***	20.87***	20.94***
Herbicide	0.50	150.22***	113.54***	123.43***	91.02***	83.53***	74.72***	76.65***
Fire	0.24	–	–	0.05	0.16	0.62	1.62	1.34
Interaction	8.34	7.90	15.51*	33.74*	21.54	27.39	19.21	20.93

Measurements for cover of these three groups of species were not taken in 2009. In addition, measurements for the saplings were not taken in 2003 or 2005. Fencing began in 2002 and continued throughout the study; herbicide and cut treatments took place in 2002; fire treatment took place in 2004. Statistical comparisons were made using a generalised linear model with a gamma distribution and log link function. The interaction shown in the table is Fence × Cut × Herbicide in 2002–2003, while it is Fence × Cut × Herbicide × Fire for 2001 and 2004–2008. $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$. Both deviance/DF (closer to 1 being stronger) and scaled Pearson X^2 (smaller being better) are indicators of model strength.

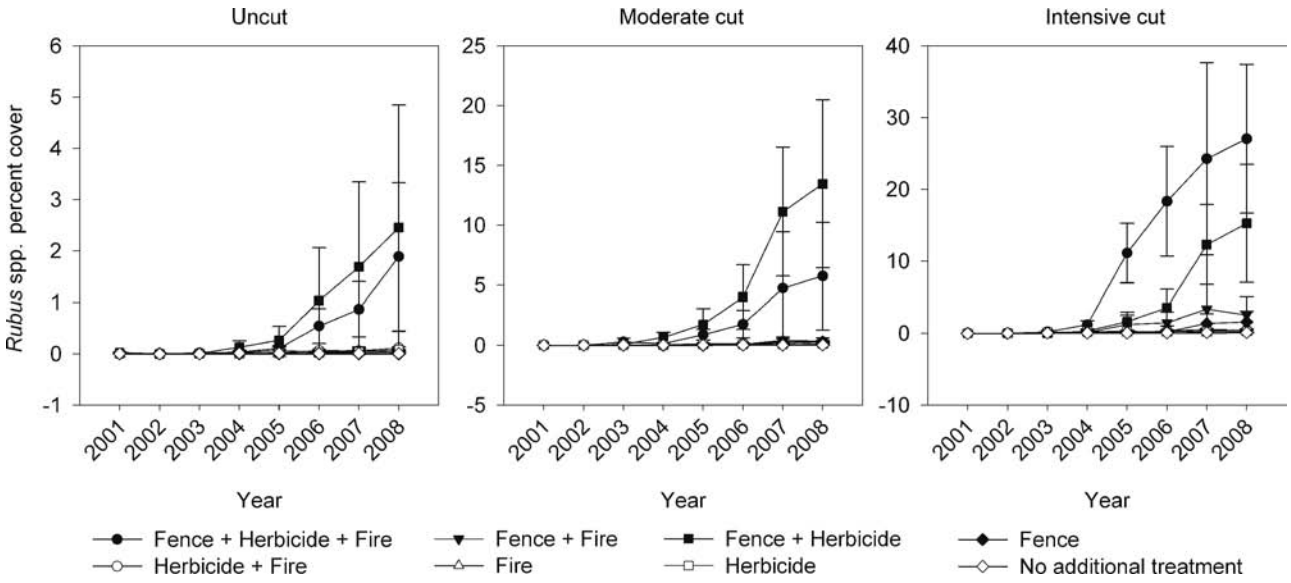

Figure 5. Comparison of *Rubus* spp. cover per 1 m^2 quadrat across treatments by year. Error bars are the standard error. Fencing, herbicide and cut treatments started in 2002; the fire treatment started in 2004. Significant differences between treatments were analysed using a generalised linear model with a gamma distribution and log link function (see Table 4).

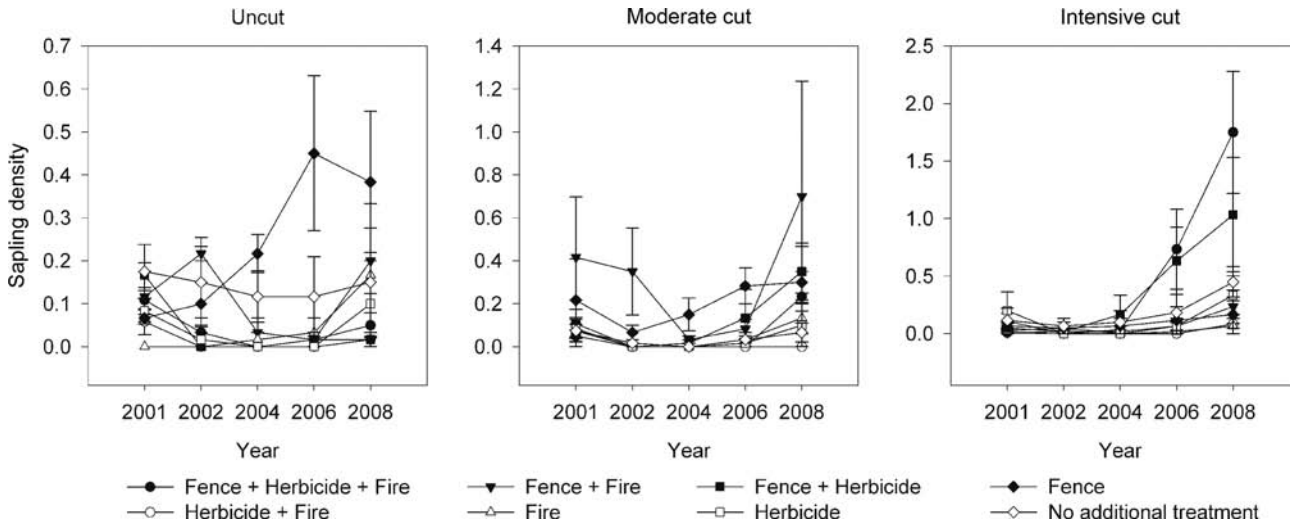

Figure 6. Comparison of sapling density per 1 m^2 quadrat across treatments by year. Error bars are the standard error. Fencing, herbicide and cut treatments started in 2002; the fire treatment started in 2004. Significant differences between treatments were analysed using a generalised linear model with a gamma distribution and log link function (see Table 4).

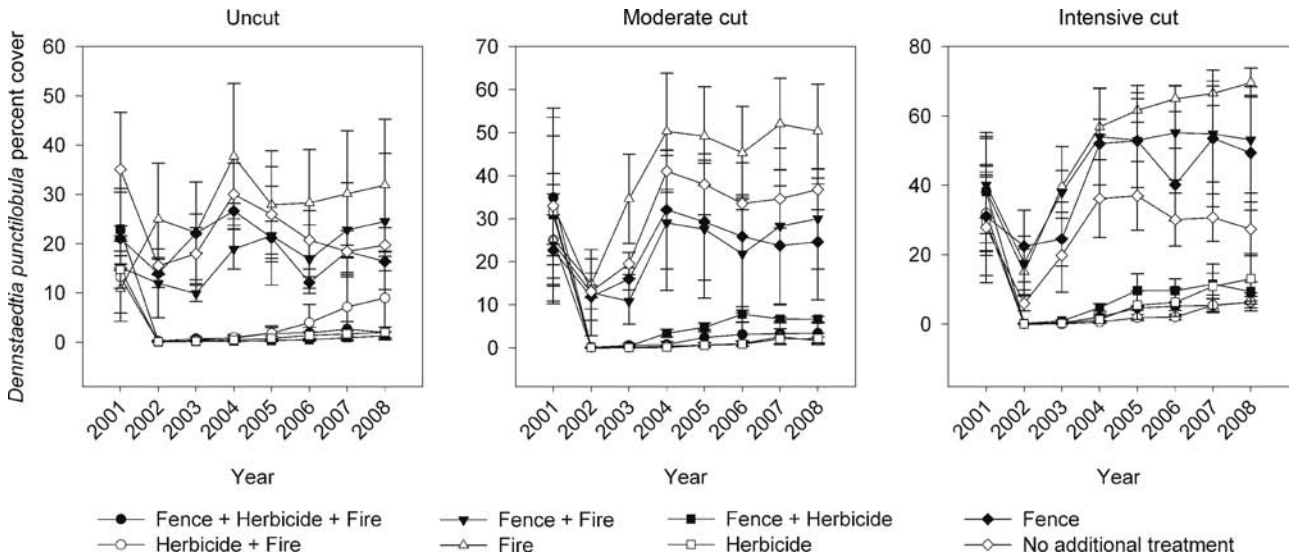

Figure 7. Comparison of *Dennstaedtia punctilobula* cover per 1 m^2 quadrat across treatments by year. Error bars are the standard error. Fencing, herbicide and cut treatments started in 2002; the fire treatment started in 2004. Significant differences between treatments were analysed using a generalised linear model with a gamma distribution and log link function (see Table 4).

Dennstaedtia punctilobula cover remained high in all plots that were not treated with herbicide and increased over time in all plots, with the highest increase in the intensive-cut plots. Fencing had no significant impact on fern cover over this time period, except in 2002 (Table 4, Figure 7). Despite a lack of main effect of fencing, the two-way interaction fence × herbicide was significant in 2003 ($X^2 = 11.19$, $P = 0.0008$) and 2004 ($X^2 = 6.40$, $P = 0.011$), which suggests that fencing may have negatively impacted fern cover (Figure 7) indirectly due to increased cover of other species. Fire, in the absence of the herbicide treatment, increased the cover of *D. punctilobula* (Figure 7). However, fire was never a significant main effect, which may be explained in part by significant three-way interactions of fire × cut × herbicide in 2004 ($X^2 = 6.69$, $P = 0.035$), 2005 ($X^2 = 6.45$, $P = 0.040$), 2006 ($X^2 = 6.89$, $P = 0.032$), and 2007 ($X^2 = 6.13$, $P = 0.047$) as well as significant four-way interactions in 2004 (Table 4). The negative effects of herbicide and the positive effects of harvesting may have countered the positive effects of fire on fern cover.

The main effects model for the competing species explained 61% (*Rubus* spp.), 42% (saplings), and 66% (*Dennstaedtia punctilobula*) of the deviance on average (2002–2008). Adding all two-way interactions explained an additional 20% (*Rubus* spp.), 35% (saplings), and 11%

(*D. punctilobula)* of the deviance on average; adding the four-way interaction explained an additional 34% (*Rubus* spp.), 56% (saplings), and 27% (*D. punctilobula*) of the deviance on average. Models that included four-way interactions were stable and had the best fit compared with models containing two-way and three-way interactions, and the significant main effects remained the same. Thus, only four-way interactions are presented in Table 4.

Seed bank

None of the three liliaceous species were found in the seed bank in 2001 (pre-treatment). While overall seed bank abundance and species richness was higher in 2006 (5 years post-treatment), the three liliaceous species were not among the new germinants.

Discussion

Fencing clearly had the most impact, compared with herbicide application, burning, and harvesting, on increasing the abundance and reproductive capacity of *M. virginiana*, *T. undulatum*, and *U. sessilifolia*. A more rapid understorey re-growth in response to fencing was apparent in the more heavily cut areas. However, intensive cutting also increased the cover of several competing species (fern, saplings, and *Rubus* spp.), resulting in a reduction of cover and fruit production of the three liliaceous species. Thus, if one were to manage solely for these three species, fenced, moderately cut (64% stocked) stands without herbicide or fire application would be the combined treatment choice, at least over an 8-year period.

The cover of the three liliaceous species recovered from the negative effects of the herbicide treatment within 6 years. The herbicide application provided some benefit for other species, such as *Rubus* spp. and, consequently, oak (Gordon et al. 1995). Including herbicide control of fern may be considered a reasonable management strategy as long as there is no re-application, or re-application intervals are longer than 6 years. Optimal re-application intervals remain undetermined. Other studies support a similar (5 years) recovery period from herbicide application (Sullivan and Sullivan 2003). However, Horsley (1994) showed no significant effect of herbicide treatment on non-target species in terms of species richness and an increase in species diversity in all 7 years after application of glyphosate to an Allegheny hardwood stand in northern Pennsylvania, also dominated by *D. punctilobula* in the understorey. Data on the understorey species richness and diversity of our plots also confirm Horsley's (1994) findings (C. Huebner, unpublished data). Unfortunately, species richness and diversity tell us little about compositional effects. While herbicide treatment appears to show no lasting harm to the three liliaceous species, its effect on other mid- or late-successional understorey species remains undetermined. Most of the herbaceous species that respond positively to herbicide treatment within 5 years are ruderal, early successional species (Sullivan and Sullivan 2003; C. Huebner, unpublished data).

The negative effect of fire on fruit production lasted 4 years post-treatment and 1 year beyond its impact on the cover of the three liliaceous species. This may be due in part to timing of the prescribed burn, which coincided with increases in size and fruiting of the three liliaceous species in the fenced plots (C. Huebner, pers. obs.). While herbicide killed the three species (both shoot and root systems), fire likely only top-killed the shoots of many or most of the ramets. The fact that combined fire and herbicide treatments within fenced areas also showed lower fruit production than fenced plus herbicide-treated plots makes it clear that fire had a direct, though temporary, negative impact on the three liliaceous species. Moreover, the increase in cover of the dominant fern layer in the burned plots provided an additional indirect, negative effect on the three focus species. Nonetheless, the prescribed fire was somewhat effective in reducing sapling density over a 4-year period. Unfortunately, this time interval is likely to have been too short to benefit the liliaceous species, which appear to require a 4-year recovery period from fire. Most research on the effects of fire on herbaceous vegetation fruit production has focused on species that are dependent on fire to maintain an open environment. Fire intervals shorter than 2–3 years are often detrimental to such species (Kesler et al. 2008). However, there are a few studies that support a 5-year or longer recovery period after a fire, because plant reproduction is limited by plant size (Ostertag and Menges 1994; Hamer 1996), which may also be true of our three focal species (Cook 1988, Hanzawa and Kalisz 1993; Kudoh et al. 1999; Knight 2003).

The increase in fruit of the three liliaceous species in the fenced areas may eventually result in seed bank recovery of these species. However, our results show that 5 years post-treatment was not enough time for seed bank recovery. It is currently rare to find these three species in most seed banks, and this fact is likely to be indicative of the deteriorated understorey conditions of many forested sites, because all three of these species have been documented as being able to form seed banks (Hughes and Fahey 1991; Smallidge and Leopold 1995). Delays in recovery, as caused by the herbicide or fire treatments, could also delay the restoration of any potential seed bank. We will need to follow these species and the seed bank for several more years in order to confirm that seed bank recovery is possible using these methods.

Intensive harvesting could also delay complete forest recovery because positive growth and reproductive response of our three focal species levelled off after 6 years post-treatment. Overall cover and fruit production for every year in the intensive-cut plots were less than the corresponding years for the uncut and moderate-cut treatments (though still greater than the unfenced plots). Thus, *M. virginiana*, *T. undulatum*, and *U. sessilifolia* may be less likely to form seed banks under long-term 20–30% canopy removal conditions. However, our results do confirm that

fruit production is still possible at these sites despite many years of disturbance and management leading to the dominant fern understorey. This suggests, at least for the outcrossing *M. virginiana* and *U. sessilifolia*, that the pollinator systems have not broken down and recovery of both plant and their pollinators is possible (Fletcher and McShea et al. 2001). The corm, bulb, and rhizome banks of these perennials and their ability to produce flowering individuals were likely to have sustained the pollinators, though possibly at lower levels than found in forests less impacted by deer and with a more diverse understorey. It is unknown how long a site would have to remain under moderate-cut and fenced conditions for seed bank recovery to be detectable. Also, it is conceivable for *M. virginiana* and *U. sessilifolia*, which both can be dispersed relatively large distances (Singleton et al. 2001), that adjacent untreated areas could indirectly benefit from the successful understorey restoration of the fenced, moderate-cut sites if the seed dispersal vectors are still active.

The second cut (removal of the remaining canopy trees) of the moderate-cut shelterwood will result in conditions more similar to the intensive cut with even more interference from dominant understorey species. Timing of this second cut to coincide with the formation of a seed bank is, therefore, critical. This may be considered analogous with the need for advanced regeneration of oak saplings before performing a second cut for successful oak regeneration (Schlesinger et al. 1993).

Realistically, of course, few land managers are going to manage their forests solely for optimal liliaceous species growth and reproduction. Merchantable tree species, such as *Q. rubra,* are the more likely target species. However, the relatively high sapling density found in our study within the intensive-cut treatments may incorrectly suggest that this treatment is optimal for tree regeneration. Most of the saplings within all cut types are fast growing, shade intolerant (*Prunus pennsylvanica*), moderately shade tolerant (*Betula nigra*), or plastic in terms of shade tolerance (*Acer rubrum*), and not the slower-growing, moderately shade-tolerant *Q. rubra*. In fact, the largest percentage of oak saplings per 1 m^2 quadrat found in fenced, intensively cut plots was 25% (SE = 35%) of the total sapling density in 2008. The next largest percentage of all the treatment combinations was found in the fenced, herbicide-treated, and moderately cut plots with 4.2% (SE = 7.2%) of the saplings being oak. Given the large variation, our study does not yet support one treatment over another for successful advanced oak regeneration during this time period. Schlesinger et al. (1993) found no significant difference in advanced oak sapling abundance when comparing uncut, 40%, 50%, or 60% residual stocking levels, but they did find that on relatively rich sites, heavy understorey treatments (killing all woody vegetation less than 4 cm in diameter, except oaks) were required to achieve significant levels of advanced oak regeneration. The most effective advanced oak regeneration was found with 60% residual stocking (roughly equivalent to our moderate-cut treatment) and a heavy understorey treatment. Similarly, Spetich et al. (2009) found that two woody competition control treatments (using glyphosate) resulted in the most cost-effective red oak regeneration. Even with these conditions, development of adequate oak regeneration took longer than 10 years (Schlesinger et al. 1993), and our study has only run for 7 years post-treatment. Nonetheless, these findings show that successful oak regeneration and restoration of understorey herbs may be achieved using similar management strategies – fencing with herbicide under a stand with approximately 60% residual stocking. An additional understorey treatment (herbicide or fire) to remove the now dominant, faster-growing saplings may be necessary to achieve oak regeneration on our study sites. However, our results suggest that repeating understorey treatments could delay or prevent restoration of the herbaceous understorey, which leads to a potential conflict between management goals.

Conclusions and recommendations

Our study supports the use of a moderate cut (about 60% residual stocking) and fencing as the first-stage management strategy of a shelterwood. Doing so should increase the size and maintain the populations of *M. virginiana*, *T. undulatum*, and *U. sessilifolia* and, hopefully, other understorey species that have decreased in abundance due to historic deer herbivory and timber harvests. Adding herbicide to the moderate-cut and fenced treatments may ensure oak regeneration, without doing harm to the abundance and reproductive capacity of the three liliaceous herbs. However, recovery of the herbaceous species will be delayed by about 6 years and multiple applications may impede their restoration altogether. While the surviving oaks will grow beyond the reach of deer within a few years of the final (second) harvest, retaining the fence indefinitely will likely be necessary to sustain fruiting populations of *M. virginiana*, *T. undulatum*, and *U. sessilifolia* as long as deer densities remain high.

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