Riparian and Upland Afforestation: Improving Success by Excluding Deer from Small Areas with Low Fencing

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ABSTRACT: We propose that small patches of land protected by low (1.2-m tall) fence is a viable approach for restoring and/or conserving forests in riparian or upland areas with high white-tailed deer (*Odocoileus virginianus* Zimmerman) populations. We also propose that this new approach may be advantageous because, unlike tree shelters, fenced areas protect shrubs just as well as trees in afforestation projects. Multi-year field experiments were performed involving deer exclosures where fence height and fenced area were manipulated in upland and lowland pasture and forest settings. Results show that low fencing significantly increased seedling survival and growth relative to unfenced areas when fenced areas were small (i.e., less than or equal to ~100 m²). Moreover, tall fencing (1.8 or 2.3 m) did not provide significantly greater protection than shorter (1.2-m) fencing when the fenced areas were kept small. We propose that creating small patches of deer-free pasture or forest habitat will greatly support new approaches to afforestation such as applied nucleation. Finally, we show that low-stature fencing may also have application for protecting larger areas (≥0.8 ha) if the fencing is deployed around the perimeter as two low fences erected in parallel and with a small (3-m) space between them. We conclude that low fencing can result in levels of survival and growth of both trees and shrubs suitable to meet the success criteria for afforestation projects funded by the US federal government.

Index terms: afforestation, deer exclosures, deer fence, seedling, water quality

INTRODUCTION

Humans have significantly transformed, through both direct and indirect activities, the old-growth forest ecosystem that once dominated the terrestrial habitat of eastern North America (Williams 1989; see also Hanberry et al. 2014, Dobson and Blossey 2015 for reviews). Among other things, forest regeneration and overall forest health continue to be compromised by large numbers of white-tailed deer (*Odocoileus virginianus* Zimmerman; hereafter “deer”), whose herbivory and trunk rubbing cause high mortality of both seedlings and young trees (Augustine and DeCalesta 2003; Rooney and Waller 2003; Kraft et al. 2004; Latham et al. 2005). Although deer are native to North America, their current populations are unprecedented as a result of human land use changes, loss of natural predators, and harvest strategies that enable large population densities, among other factors (Rooney 2001; Shelton et al. 2014; Waller 2014). Côté et al. (2004), Latham et al. (2005), and Averill et al. (2018) have reviewed the major ecological impacts of deer overabundance, and these reviews (and other studies such as Alver son et al. 1988; Anderson 1994; Horsley et al. 2003; Shelton et al. 2014) point to major impacts, such as the consequences of altered ecological succession, lost biodiversity of forest and its understory, reduced forest regeneration, and local plant extinctions. Additional studies have described other impacts of deer on forest ecosystems, including altered nutritional dynamics of forest food webs (Roberson et al. 2016; Landsman and Bowman 2017), unleashing of the negative ecological effects of nonnative plants (Christopher et al. 2014), altered seedbank composition (Gill and Beadall 2001; Chaideftou et al. 2009, 2011), modified soil properties (Wardle et al. 2001; Singer and Schoennecker 2003), and increased invasion by introduced plants (Eschtruth and Battles 2009a, 2009b; DeJager et al. 2013). In addition to these direct effects of deer browse, indirect non-consumptive effects on non-palatable plant species are increasingly reported (Heckel et al. 2010; Kalisz et al. 2014). Furthermore, there is growing evidence that large deer populations lead to increased abundance of introduced species at the expense of native species (Eschtruth and Battles 2009a, 2009b; Fischelli et al. 2013; Kalisz, Spigler and Horvitz 2014; Waller 2014) as well as non-preferred (by deer) native species (Royo and Carson 2006) that can, in turn, alter understory conditions to reduce overall regeneration potential of forest canopy species. Moreover, the significant and profound effects of elevated deer densities on understory vegetation can persist for 20 y and more (Nuttle et al. 2014). Although there have been reports and discussion of plant species gradually evolving increased tolerance to deer browse over time (Martin et al. 2015), there are few data regarding this phenomenon. Therefore, it is likely that forest structure going forward will continue to be greatly affected by deer populations (Russell et al. 2017).
We propose here that, in eastern North America, the abundance and negative impact of deer on forest structure, growth, and reproduction also pose a significant impediment to a previously little appreciated factor—the ability of watersheds to provide a sustainable supply of clean fresh water. We make this case because afforestation has become an important tool for aquatic ecologists to use to improve the quantity and quality of fresh water supplying our aquifers and streams. But, as noted above, deer can be and often are one of the major impediments to reestablishing natural forest on both upland and riparian pieces of watersheds in large geographic regions of North America. However, aquatic and terrestrial ecologists often do not interact or exchange information related to processes such as deforestation or afforestation. So, for example, in terms of water quantity, it is known that a partial loss of forest structure and cover may accelerate water discharge and increase flood risk in the wet season, yet conversely reduce river flow in the dry season (Calder et al. 2007). This is not to say that we believe that deer can cause extensive deforestation (which can be devastating to local hydrology) but rather that alteration of canopy and subcanopy structure (as noted earlier) can certainly alter seasonal stream flow (and water quality—see below) to some extent. In addition to such seasonal impacts, scale is also critical. Thus, even though each tree counts in a watershed, their collective role can differ depending on scale (e.g., trees reduce runoff in small catchments but increase precipitation and water availability in larger ones; Ellison et al. 2012).

It is known, however, that natural forests also make a significant impact on the ability of a watershed to produce high water quality for both humans and wildlife (e.g., many studies have confirmed that upstream forest cover assures delivery of high-quality water; see Bruijnzeel 2004, Calder 2007, Van Dijk and Keenan 2007 for summaries). For drinking-water-supply watersheds, natural forest is clearly the best ground cover because forest activities generally do not involve the application of fertilizers and pesticides, nor do they generally suffer from the sewage and industrial pollutants associated with high human population levels (Herrera et al. 2017). It is well known that the strategic placement of natural forest in streamside areas of the watershed actually prevents many pollutants from entering their waters and thus enhances the quality and quantity of in-stream ecosystem services, such as processing, degrading, or otherwise sequestering pollutants that do enter them (see Sweeney et al. 2004, Sweeney and Newbold 2014 for reviews). Specifically, these reviews showed that (1) the wider the forest buffer, the greater the removal of surface sediment and subsurface nitrogen prior to getting to the stream; (2) stream channel meandering and stream bank erosion was significantly lower in reaches buffered by forest; and (3) water temperatures remained within 2 °C of natural levels and macroinvertebrate and fish communities remained near natural or semi-natural states when the stream was bordered by >30 m of forest. In fact, it has been known for a long time that the more forest cover in a watershed, the higher the water quality and hence the lower the treatment costs for water purveyors (Ernst 2004). Finally, two studies of drinking-water watersheds in the Delaware River watershed in eastern North America have shown convincingly that the level of water quality for a stream or river is closely correlated with the amount of forest cover in its watershed (Kratzer et al. 2006; Jackson et al. in prep). Thus, overall, forests are considered the best land cover to maximize water yield, moderate seasonal flows, and assure high water quality (Calder et al. 2007).

Indeed, the conservation and restoration of natural upstream and riparian forests is considered an important part of any overall strategy for improving the water quality of streams, rivers, and estuaries (Hassett et al. 2005). However, as noted above, the impact of deer makes conserving existing streamside forests and quickly and efficiently restoring previously destroyed forests difficult, if not impossible, in many areas of eastern North America. Consequently, there has been a large experimental effort to develop methods to increase the survival and growth of seedlings and young trees and to facilitate afforestation and/or forest regeneration in watersheds with high deer populations (Sweeney et al. 2002; Sweeney and Czapka 2004; Dobson and Blossey 2015). Although deer hunting has been consistent and widespread enough to allow recovery of degraded vegetation communities (Jenkins et al. 2014) in some landscapes, proactive conservation and restoration has been the most common method of maintaining or restoring forest cover in our watersheds.

So, for conservation and afforestation of upland and streamside areas, state and federal programs have endorsed planting small seedlings protected by tree shelters of various types and sizes as the preferred afforestation approach (see USDA NRCS 2007 for review). And, for improving the regeneration of existing forests, the method of choice has been to exclude deer from the forest stand by completely surrounding it with tall “deer fence” (Kangas et al. 2014). Although complete exclusion of deer creates an artificial condition in most forests, it seems to work. Thus, a few long-term studies (10–18 y) have shown that deer exclusion and controlling deer densities can lead to a significant increase in the density of tree stems, a decline in small herbaceous species, and an increase in abundance of larger herbaceous understory species (Horsley et al. 2003; White 2012; Webster et al. 2017). Short-term deer exclusion studies (<4 y) have shown reduced mortality in browse-sensitive species, such as white cedar (Thuja occidentalis L.; Palik et al. 2015) and a fourfold decrease in herb cover (Bugalho et al. 2013) compared to unfenced areas. Deer exclosures operated by Sabo et al. (2017) for 10–20 y showed that, beyond decreasing direct mortality and tissue removal, the exclusion of deer increased tree abundance, decreased the amount of light available to ground-level plants, and reduced soil compaction and thickness of the soil E horizon, all of which resulted in significant positive effects on understory community structure. In a 23-year-old exclusion study involving paired plots, deer reduced phylogenetic diversity by 63% due to the selective nature of their browsing (Begley-Miller et al. 2014). After studying the effects of deer exclusion on paired plots at 12 sites, Dabalos et al. (2014) concluded that, to maintain populations of important plant species, they needed to change their...
management approach from invasive plant removal to white-tailed deer control. In addition, Faison et al. (2016) demonstrated that deer eat native and nonnative plant species, as their 15-y study found a decline in both categories in unfenced plots relative to fenced plots.

As noted earlier, although tree shelters and tall fencing are the most popular approaches to afforestation and forest conservation where deer are a limiting factor, they are labor intensive, expensive to install, and often difficult and expensive to maintain. Moreover, success using these two approaches has been highly variable and not without side effects and issues. From our experience, for example, tree shelters require proactive planting of seedlings and are more laborious and expensive than natural or direct seeding methods and shelters do not work well with shrubs. Also, tall fences are expensive and difficult to install and maintain, and neighboring landowners often do not like them because they impede human and wildlife use of the fenced areas. So, we tested a novel approach to creating deer exclosures by using low fencing in small areas to exclude deer and improve plant establishment and reproduction in both new and existing forest. We say “novel” because using low fence to exclude deer is counterintuitive. Deer can jump 2–3 m high from a standstill and one would expect a priori that low-stature fences would not exclude them. However, our approach grew out of local personal observations in the mid-Atlantic region that small areas (<0.1 ha) protected by low fencing seemed to remain deer free, whereas larger areas (>0.5 ha) protected by low fencing seemed to be readily invaded by deer. In other words, the ability of low fencing to keep deer out of an area seemed to be related in some way to the size of the area being protected.

In the experiments described here, our overarching hypothesis was that 1.2-m high fencing (hereafter low fencing) can be as effective as taller fencing (i.e., >1.8 m) for increasing seedling survival and growth relative to areas unprotected from deer by fence—if the area being protected is sufficiently small in size. We tested this hypothesis using data from multi-year field experiments in both abandoned agricultural fields and standing mature forest. We also established and tested three separate but related field experiments and sub-hypotheses, which addressed the “sufficiently small-in-size” aspect of our overarching hypothesis as well as the “low-fencing” versus “taller-fencing” aspect of it. All experiments involved planting native seedlings and following their growth and survival in various experimental deer exclosure areas for several years, as well as evaluating over time the community structure of the vegetation in the experimental areas where the seedlings were planted.

METHODS

Hypotheses and Study Design

As noted above, we subdivided the test of the main hypothesis of the study into three field experiments, each with its own sub-hypothesis (H1, H2, H3) for testing. Specifically, H1: that low (1.2-m) fencing can significantly increase seedling survival and growth relative to unfenced areas when fenced areas are relatively small; H2: that low fencing can provide the same level of protection for seedling growth and survival as taller (1.8-m or 2.6-m) deer fencing under certain circumstances; and H3: that low fencing can also provide sufficient protection for seedlings planted on large areas (≥0.8 ha) if the perimeter is protected by two fences with a relatively small (3 m) space between them.

Field Tests of H1 and H2

To test hypotheses H1 and H2, we chose seven experimental plots at five geographic locations in southeastern Pennsylvania and northern Delaware (Figure 1). The abbreviated name (landowner) combinations for the five geographic locations were ELKN (Elkins), PTLK (Point Lookout Preserve), SPRV (Stroud Preserve), SWRC (Stroud Water Research Center), and WEYG (Weygandt). Locations ranged from riparian (SPRV, SWRC) to semi-riparian (ELKN, PTLK, WEYG) in character. For both sets of field experiments, replicate sites were located in a standing forest and a deforested pasture area, in more or less balanced fashion. Tree seedlings were planted in all seven plots, with three sites (PTLK pasture, PTLK forest, WEYG forest; Table 1) used for testing the exclosure area hypothesis (H1) and four sites (ELKN forest, PTLK forest, SPRV pasture, SWRC pasture; Table 2) used for testing the fence height hypothesis (H2). At the start of the experiments, the pasture sites were completely deforested (having been active pasture areas) and the forest sites were mature deciduous forest (with many trees >75–100 y old). The forested sites were closed canopy and heavily shaded with low light levels (although we did not quantify the light). The understory was generally sparse at most of the forested sites, with deer browse being fairly intense throughout and with only low densities of shrubs or herbaceous plants not preferred by deer. The exception was the WEYG forest site where the understory was much better developed, and deer pressure seemed less intense. All seedlings planted for both sets of experiments were native to the region.

Exclosure Area Experiment for Testing H1

For the exclosure area experiment to test H1, we constructed three different-sized exclosures (small [3 m × 3 m], medium [4.6 m × 4.6 m], large [6 m × 6 m]) in both forested and pasture areas. All areas involved the same type of fence (1.2-m high metal fence; 0.05 m × 0.1 m mesh). Each H1 study plot (PTLK pasture, PTLK forest, WEYG forest) had 56 individual exclosure areas, which were separated into 4 test blocks of 14 exclosure areas each (Table 1). Each individual block contained 8 small, 4 medium, and 2 large exclosure areas. By varying the number of the different-sized areas per block, we were able to achieve more or less the same amount of experimental area (range 74–83 m2) devoted to each of the different-sized treatment areas across the experiment. We fenced half of each group of exclosure areas within each block on all four sides (hereafter referred to as “closed”) and fenced the other half of the exclosure areas only on three sides (hereafter referred to as “open”). The purpose of the “open” exclosures was to control for the possibility that deer might not choose to enter an exclosure area sim-
Figure 1. Geographic location of study sites in southeastern Pennsylvania and northern Delaware with symbols differentiating the sites used to test $H_1$ (fenced exclosure area and open/closed extent of fencing), $H_2$ (height of fencing), and $H_3$ (use of double fencing with small space). Forest cover is from the National Land Cover Data 2006 Land Cover product (http://www.mrlc.gov).
ply because they were “psychologically” avoiding the fence or fence post structures. The orientation of the opening on the open exclosure areas was randomized among four possibilities (north, east, south, west). We planted two seedling species in each plot’s three exclosure areas, with the number of seedlings varying with test area size (specifically, 4, 8, and 16 seedlings planted in the small, medium, and large exclosures, respectively), but we kept the spacing of seedlings more or less constant. The goal was to have the same number of seedlings planted in each size of exclosure area for each block (Table 1). However, minor mistakes made by helpers during planting and differences in the availability of some seedling species resulted in slightly unequal numbers across the areas for some blocks. In general, however, the planters were experienced and well supervised and so these kinds of mistakes were minimal.

We varied the species of seedlings from site to site depending on local light and moisture conditions to avoid undue stress on the test species. For the exclosure area experiment we planted red maple (Acer rubrum L.) and green ash (Fraxinus pennsylvanica Marshall) seedlings in the single pasture plot (PTLK), and white oak (Quercus alba L.) and scarlet oak (Q. coccinea Muenchh.) at both forested sites (WEYG and PTLK). These decisions were based more on soil moisture conditions than other factors (e.g., light levels). All seedlings for the exclosure area experiment were planted during the fall and all seedlings throughout the study were 2 y old (ranging ~25–75 cm tall) and potted rather than bare root. In the rare case where we could not positively identify seedling

<table>
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<th>Exclosure extent</th>
<th>Species</th>
<th>Exclosure treatment size (area)</th>
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<td>S. Oak</td>
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species post-planting, due to damage or deer browse, we did not include them in the analysis. Seedling survival and growth were determined following two growing seasons. Tree height was measured as the distance from the base of the stem to the terminal bud. We did not attempt to determine the cause of death when we encountered a dead seedling.

**Fence Height Experiment for Testing H$_2$**

For the fence height experiment, we kept the exclosure area constant at 9.75 m $\times$ 9.75 m and tested five different fencing configurations at each site (forested sites: ELKN, PTLK; pasture sites: SPRV, SWRC): (1) single 1.2-m tall fence; (2) single 1.8-m tall fence; (3) single 2.3-m tall fence; (4) double 1.2-m tall fence with 3-m spacing between the two fences; and (5) no fence (i.e., just four metal posts marking the corners of the seedling planting area). At three of the four study sites, each exclosure area/fence height combination was replicated twice for a total of 10 exclosure areas. At the fourth site (SWRC), each exclosure type was replicated three times for a total of 15 total exclosure areas. Within each experimental block of five different exclosure area/fence height configurations, the location of the various configurations was assigned at random, and each exclosure area was planted with 16 seedlings split evenly between two species (Table 1). Scarlet oak and white oak seedlings were planted at the SPRV site in late fall and at the ELKN and PTLK sites in early fall and spring, respectively. Scarlet oak and silky dogwood (*Cornus amomum* Mill.) seedlings were planted at the SWRC site in the spring. We used white oak seedlings to replace any dead scarlet oak or silky dogwood seedlings the following spring to avoid any future confusion over the exact date of planting of each seedling. We sampled all study sites in the fifth year. Tree height for the oaks was measured as above but for silky dogwood, a multi-stem shrub, we measured the length of the longest stem.

In addition to measurements on planted seedlings at the various study sites, we took a census of unplanted, woody “volunteer” species growing within each experimental area for the fence height experiment (but not for the exclosure area experiment). Although this “volunteer seedling” census had not been part of the original study design, it became apparent as the study progressed that differences were developing between fenced and unfenced areas with regard to the relative abundance and species composition of shrubs and trees. The tally of volunteer shrub and tree species took place in year five, at the same time that we assessed the survival and growth of the planted seedlings. We recorded the total number of individuals for each species in each exclosure, with species identification based on Rhodes and Block (2007). Given the ad hoc nature of this census, data are presented without any statistical rigor. Results are provided only to show the potential for such passive regeneration as an ancillary effect of fencing small exclosure areas to eliminate deer herbivory.

**Double Fence Experiment for Testing H$_3$**

To begin testing H$_3$, we planted seedlings in two relatively large (0.8 ha) treeless pastures located within 500 m of one another in the riparian zone of Brandywine and Taylor Run Creeks in Chester County, Pennsylvania (<1 km from test site SPRV for H$_3$). We planted 920 seedlings in each of the two pastures representing six species of trees (*American sycamore* [*Platanus occidentalis* L.], *silver maple* [*Acer saccharinum* L.], *green ash* [*Fraxinus pennsylvanica* Marshall], *swamp white oak* [*Quercus alba* Mill.], *black willow* [*Salix nigra* Marshall]), and seven species of shrubs (*serviceberry* [*Amelanchier canadensis* (L.) Medik.], *red chokeberry* [*Aronia arbutifolia* L.], *buttonbush* [*Cephalanthus occidentalis* L.], *silk dogwood* [*Cornus amomum* Mill.], *winterberry* [*Ilex verticillata* L.], *smooth alder* [*Alnus serrulata* (Aiton) Willd.], and *southern arrowwood* [*Viburnum dentatum* L.]). Protection from deer for the seedlings in the Taylor Run pasture consisted of two low fences (1.2-m high metal fence; 0.05 m $\times$ 0.1 m mesh) placed around the perimeter of the field, with the outer fence exactly 3 m from the inner fence (sensu the double-fence treatment of small reforestation areas that was part of testing H$_3$). Protection of tree seedlings from deer in the Brandywine Creek pasture consisted of 1.2-m Tubex tree shelters (Treessentials, Duluth, MN) but shrubs were unprotected from deer. Tree and shrub heights were measured to the nearest 1 cm and survival assessed on all planted seedlings after 6 y.

**Statistical Analysis**

Due to differences in field design for testing the three hypotheses, different statistical analyses were applied to the separate datasets for testing H$_1$, H$_2$, and H$_3$. However, all statistical analyses were performed at an $\alpha = 0.05$ and were run using SAS/STAT 9.3 (SAS Institute, Cary, NC).

**Seedling Survival: Exclosure Area Experiment for Testing Seedling Survival Associated with H$_1$**

In this experiment we used logistic regression to analyze survival, with the probability of survival as the dependent variable. We assessed the effects of exclosure type (open vs. closed) and exclosure size (large vs. medium vs. small areas) across all sites and locations within sites, and our model also included an interaction term between exclosure type and size. Survival within exclosure type and size was also assessed within each site/location pair. We examined specific location effects by comparing pasture and forest at PTLK and our model also included location type and size plus all possible two-way interactions. Site effects were analyzed by considering only forest locations for the two study sites. This model also included location type and size as main effects along with all possible two-way interaction terms. Contrasts were constructed within each model for each main effect in order to compare each level to every other level within each of these main effects.

**Seedling Survival: Fence Height Experiment for Testing Seedling Survival Associated with H$_2$**

Seedling survival was assessed using contingency table analysis. To this end, a single table was analyzed for each main
effect (e.g., survival among exclosure area treatments within a single location) followed by separate 2 × 2 tables to assess differences between variable pairs (such as survival between the control and each separate exclosure within a single site). We assessed survival between replicate exclosure treatments, between exclosure treatments within a site, and between sites for each exclosure treatment. Regardless of any statistical differences among replicate treatments, we combined replicate data for each subsequent set of analyses due to the low level of replication (only two or three treatment replicates for each exclosure area type). While the chi-square statistic was the primary test procedure for analyzing these contingency tables, there were many cases where 20% or more of the cells within a table had individual cell frequencies less than five, which leads to questionable validity of the chi-square test result (SAS/STAT FREQ procedure). In these cases, we used the Fisher’s exact test to analyze the contingency table.

Seedling Growth: Exclosure Area Experiment for Testing Seedling Growth Associated with $H_1$

Seedling growth within the exclosure area experiment was assessed using ANOVA. Growth was calculated as the difference between seedling height at planting and after the fifth year of the study. We measured the initial height of each seedling planted at the PTLK site. At the WEYG site, we calculated the initial seedling height as the average of 20 randomly selected seedlings of each species we measured prior to planting. All models for the survival analysis described above, and including the assessment of replicate variability, were analyzed for differences in growth. To minimize the impact of outlier values, data were log$_{10}$ transformed with 1 added to avoid taking the log of 0. Tukey’s posthoc tests were used to determine significant differences between mean values within each main effect. Growth data were ranked from smallest to largest and analyzed via ANOVA models as previously described as a means to assess whether data nonnormality was having any effect on ANOVA results based on log-transformed values. Significant results were only reported if there was agreement between the ranked and log-transformed ANOVA analyses.

Seedling Growth: Fence Height Experiment for Testing Seedling Growth Associated with $H_2$

Differences in seedling growth for the fence height experiment were assessed using ANOVA on both log$_{10}$ transformed values (adding 0.25 to avoid log transforming 0 values) and ranked values. Growth was calculated as for $H_1$. Replicate variability was assessed, but as with survival, replicate data were combined for all subsequent analyses, regardless of any statistically significant differences we found among replicates.

RESULTS

Closure Area Experiment for Testing $H_1$

Seedling Growth

Averaged across all sites and locations, significant differences in the survival of planted seedlings were observed in response to exclosure type (i.e., open vs. closed fence areas; Table 3, Figure 2; $P < 0.001$) but not for exclosure size (i.e., small, medium, large). Survival ranged from 65% to 74% for closed enclosures but only 14–23% for open enclosures at the PTLK sites whereas survival was high for both open and closed enclosures at the WEYG site. The significant interaction between exclosure type and size ($P = 0.015$; Table 3) indicates that survival for open-versus-closed enclosures was not consistent among the three exclosure sizes.

Seedling Survival

Averaged across all sites and locations, significant differences in survival of planted seedlings were generally observed in response to different exclosure treatments (i.e., three fence heights, double fence, no fence) and study sites (ELKN, PTLK, SPRV, SWRC) but not for seedling species (white oak vs. scarlet oak; $P < 0.001$; Table 4, Figure 4). Only one site (SPRV) deviated from this pattern with differences among fence height/configurations only approaching the significance cutoff of 0.05 ($P = 0.079$). The SWRC site had the highest overall survival, followed by PTLK (Figure 4). We observed significant site differences in survival response to open or closed exclosure treatments across the sites ($P < 0.001$). The control treatment of no fencing had significantly lower survival than the other treatments across all sites and also within the PTLK and SWRC sites (Figure 4). At the SWRC site, all fenced treatments had nearly 75% survival, in contrast to the PTLK site where survival varied from ~30% to 75%, with the 1.8-m and 1.2-m fences having significantly greater survival than the remaining treatments. Also, at the ELKN site, only the 2.3-m fenced areas had greater than 30% survival (and it was the only treatment found to be significantly different from the no-fence control). The SPRV site had no significant differences in survival among the five fence heights because there was very little seedling survival at this site overall (Figure 4).
Table 3. Results of planted seedling survival and growth analyses examining exclosure extent (open vs. closed fencing) and area for testing H2. Analysis of survival after two growing seasons was performed using logistic regression with the Wald chi-square statistic \( \chi^2 \) providing the evaluation of model effect significance. Growth (total increase in height [cm] through two growing seasons) was log10-transformed for the analyses, which was based on ANOVA models with the \( F \) statistic \( F \) providing the evaluation of model effect significance. Each model effect heading represents a separate analysis.

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Seedling Growth

Averaged across all sites and locations, significant differences in the growth of planted seedlings were generally observed in response to different exclosure treatments (i.e., three fence heights, double fence, no fence) and study sites (ELKN, PTLK, SPRV, SWRC) but not for seedling species (white oak vs. scarlet oak; \( P < 0.001 \); Table 4, Figure 4). Only one site (SPRV) deviated from this pattern, with differences among fence height/configurations only approaching significance (\( P = 0.1 \)). The SWRC site had the highest overall growth followed by PTLK (Figure 4). We observed significant site differences in growth in response to exclosure treatments across the sites (\( P < 0.001 \)), with ELKN and SPRV having significantly lower seedling growth compared to PTLK and SWRC (Figure 4). The control treatment of no fencing exhibited significantly lower growth than most other treatments at SWRC and PTLK but not at ELKN and SPRV where, as noted above, growth was generally poor across all treatments (Figure 4).

Volunteer Seedling Recruitment

The level of volunteer seedling recruitment varied across the four study sites. At the PTLK and SWRC study sites, there were substantially fewer species (Table 5) and numbers (Figure 5) of volunteer seedlings in the unfenced control exclosure areas than in any of the fenced exclosure areas. At ELKN, the unfenced areas had slightly fewer volunteer species than the fenced areas (5 vs. 7), but both the unfenced and 1.2-m single fenced areas had substantially more volunteer species than areas protected by either a double 1.2-m fence or taller single (1.8-m or 2.6-m) fencing. At the SPRV site, only a single volunteer species (autumn-olive [Elaeagnus umbel-lata Thunb.]) occurred in the unfenced control exclosures, versus nine species in the fenced exclosures. It should be noted that the riparian area containing the SPRV site was an abandoned agriculture field that had been cleared of a dense stand of autumn-olive trees (suggesting it is unpalatable to deer) 6 months prior to the start of the experiments, and so a substantial seed base was present for this species.

Double Low Fencing for Testing H3

Figure 6 shows the gradual transition of the treeless riparian pasture along Taylor Run protected from deer by a double low stature fence from the time of tree planting (Figure 6A) to 2 y (Figure 6B) and 8 y later (Figure 6C). We observed 45% overall survival after 6 y, when averaged across the entire 0.8-ha planting and 13 species of seedlings involved in testing H3. Average survival was 33% for the six tree species and 54% for the seven species of shrubs. However, survival varied widely among the tree species (American sycamore [21%], silver maple [24%], green ash [70%], swamp white oak [47%], pin oak [13%], black willow [25%]) and the shrubs (service berry [40%], red chokeberry [13%], buttonbush [57%], silky dogwood [80%], winterberry [56%], smooth alder [51%], arrowwood [83%]). After 6 y, there was a standing density of 519 live-planted woody stems per hectare. In contrast, overall survival of trees and shrubs protected by tree shelters in the nearby Brandywine Creek...
pasture was 25.6%, with survival being 33.1% for the tree species and 19.4% for the shrubs.

As expected, the height of the plants in meters (avg [SD]) after six growing seasons varied by species: trees—American sycamore (3.9 [1.2]), silver maple (0.9 [0.6]), green ash (2.7 [0.8]), swamp white oak (2.4 [0.8]), pin oak (2.1 [0.8]), black willow (2.9 [0.7]); shrubs—serviceberry (1.5 [0.5]), red chokeberry (1.2 [0.3]), buttonbush (1.3 [0.3]), silky dogwood (1.9 [0.3]), winterberry (1.1 [0.2]), smooth alder (2.0 [0.5]), arrowwood (1.7 [0.4]).

**DISCUSSION**

**Is Low Fencing Effective for Excluding Deer?**

We hypothesized that low (1.2-m) fencing can significantly increase seedling survival
and growth relative to unfenced areas when fenced areas are relatively small (H₁). We tested H₁ by comparing survival and growth of seedlings for three small areas differing in size (9, 21, 36 m²). The results support this hypothesis, as survival of planted seedlings was significantly higher in small areas completely protected from deer (i.e., fenced on all four sides; range 65–74%) than it was in small areas where deer could access the seedlings without jumping (i.e., fenced on only three sides; 14–23%). Moreover, although seedling growth did not differ significantly among the three treatment areas, growth was always greater within the four-sided exclosures than in the three-sided exclosures (regardless of location or size of the exclosed area). The only inconsistency in this pattern was for the WEYG forested site where survival was almost identically high (65–75%) for both

Figure 3. Total mean (± 1 SE) growth (cm) of seedlings used to test H₁ (fenced exclosure area and open/closed extent of fencing) summarized separately by exclosure size (closed fencing only) and extent (open vs. closed fencing) across all sites/locations and within each site/location pair. Different letters above each bar within a single plot indicate significant (α = 0.05) statistical differences between associated values. A lack of statistically significant results is indicated by “ns.” Growth (log₁₀-transformed) was analyzed using ANOVA with both exclosure size and extent included as independent variables.
the closed and open exclosures but growth was significantly lower in the open relative to the closed exclosure. This suggests that the deer herbarvory pressure at the WEGY forested site was substantial enough to reduce growth, yet not as intense as at the other sites where herbarvory appears to have led to higher mortality. Regardless, the general pattern of lower survival and growth for three-sided exclosures relative to four-sided exclosures strongly suggests greater deer intrusion and herbarvory for the former. Our data suggests that the deer are clearly making a choice not to jump into the exclosure areas because of the combined presence of the fence and small size of the fenced area. Unfortunately, the three different areas chosen to test the effects of exclosure area were all sufficiently small to enable the low stature fence to be effective. Even though we know that low stature fences do not work to keep deer out of extremely large areas (this is why there is a market for tall “deer fence”), based on our experiment with three different size areas, we can only say with certainty that a single low stature fence works well on areas ≤36 m². Thus, our study clearly suggests that the combination of fence height and exclosure size impacts the decisions and behavior of white-tailed deer.

Although the exclosure area experiments confirmed that low fencing greatly increased seedling survival and growth over those without complete fence protection, it did not address the degree of protection afforded by low fencing relative to taller fencing. We hypothesized that low fencing affords the same level of protection for seedling growth and survival as taller fencing for small deer exclusion areas (H₂). Our experiments also showed convincingly that, for seedling survival and growth, (1) the presence of fencing afforded significantly greater protection than no fencing, and (2) tall fencing (1.8 m or 2.6 m) did not provide significantly greater protection than short (1.2-m) fencing. The experiments also showed that, for small areas (less than or equal to ~100 m²), there was no significant difference in growth or survival for seedlings protected by a single or double 1.2-m tall fence, an important point for interpreting the double-fence testing related to testing H₁ below. Finally, these experiments also showed that excluding deer with fencing (low or otherwise) appears to increase the establishment of additional species of plants in both forest and pasture settings.

The utility of using low fencing to protect larger areas also has promise. We know from personal and practical experience that low fencing does not exclude deer. This is why commercial deer fences are ≥2.3-m tall. However, we hypothesized that low fencing can provide sufficient protection for seedlings planted on large areas (≥0.8 ha) if the perimeter is protected from deer by two low fences with a small (3 m) space between them (H₃). This hypothesis was based on results from our tests of H₁, which failed to show any evidence that deer entered any of the 32 small (3 m × 3 m) treatment areas spread over the four experimental blocks. The idea, therefore, was that the small (3-m) space between fences was a psychological rather than a physical barrier because deer can easily jump over a 1.2-m fence from a standstill. Specifically, that deer are evaluating both the difficulty of jumping and landing in the very small areas as well as the reward for doing so. It is unfortunate that, in the definitive experiments (Figures 2, 3), our largest exclosures were always small enough (i.e., always less than or equal to ~100 m²) to enable single low-stature fencing to be effective. Regardless, in the large experimental area (0.8 ha) protected by double low fencing, we observed 45% survival after 6 y, leaving a standing density of 519 live planted woody stems per hectare. To put this in perspective, a typical riparian forest buffer project funded by the US Department of Agriculture’s Conservation Reserve Enhanced Program (USDA CREP) requires a minimum starting density of 296 stems per hectare and a 5-y survival of about 222 stems per hectare. So, using the double low fence method, we could have started with about half the seedlings we used for our H₃ experiment (i.e., about 525 seedlings per hectare).

### Table 4. Statistical analyses of survival and growth of planted seedlings associated with fencing height/configuration experiments for testing H₂. Measurements were made in the fifth year of the experiment. Survival analysis was performed using contingency table analysis where either the chi-square statistic ($\chi^2$) or Fisher’s exact test (chi-square statistic is shown below) and associated $P$ value ($P$) provide statistical significance. Growth analyses were based on ANOVA models with the $F$ statistic ($F$) and associated $P$ value providing the evaluation of model effect significance.

Each row represents a separate analysis. 1.2-m double = a double fence surrounding the perimeter of the planting area involving two 1.2-m metal fences positioned 3 m apart.

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*Cross-site comparisons among species only include white oak and scarlet oak because other species were not present at all sites.
Figure 4. Mean (± 1 SE) survival (%) and growth (cm) of seedlings used to test $H_2$ (height of fencing) summarized for all treatments across all sites (all values) and within each site. Different letters above each bar within a single plot indicate significant ($\alpha = 0.05$) statistical differences between associated values. A lack of statistically significant results is indicated by “ns.” Survival was analyzed using contingency table analysis; growth was analyzed using ANOVA with Tukey’s post hoc tests. Growth analyses were conducted using log$_{10}$-transformed data. 1.2d = a double fence surrounding the perimeter of the planting area involving two 1.2-m metal fences positioned 3 m apart.

and met the success criteria for USDA CREP. Moreover, the overall survival of seedlings in the 0.8-ha area protected by a double low-stature fence was substantially higher than overall survival in the 0.8-ha area where tree seedlings were protected by shelters and shrub seedlings were unprotected by deer (45% vs. 25%). And, although protection against deer browse by double low-stature fencing versus tree shelters resulted in identical survival (33%) in the two 0.8-ha areas, there was a clear advantage in survival for shrub seedlings (i.e., 54% for double fence versus 19% if shrubs were unprotected). Thus, this experiment also nicely demonstrated an additional advantage of the low fencing approach—specifically, that understory
shrub species can be included in the initial planting and will be well protected and well represented in the restored forest.

What our experiments failed to do, however, was to establish the point at which the area becomes large enough that single low-stature fencing fails to protect the seedlings and requires double low fencing. We can only say, based on the above, that a single low fence is sufficient for areas less than or equal to ~100 m$^2$ while protection of larger areas (i.e., up to ~8000 m$^2$) may be achieved with low fencing if two fences are placed around the perimeter with a small space (e.g., 3 m) separating them. Future experimentation is needed to explore the effectiveness of low-stature fencing for areas in between.

### How Can Small Areas Protected by Low Fencing Help Improve Water Quality and Quantity?

Two of the most widespread environmental conservation practices aimed at improving the quality and quantity of fresh water in our streams, rivers, and aquifers are the restoration of streamside forests as buffers against human land use and the preservation of existing forest stands (upland and riparian) through conservation easements. Tree shelters have enabled us to quickly establish canopy trees as buffers against human land use in streamside and upland areas. However, we currently have no viable method for including smaller trees, shrubs, and herbaceous plants in restoring watersheds with significant herbivory by white-tailed deer (e.g., much of the mid-Atlantic region of North America). While replacing pasture with forest is a key step toward protecting water quality, all forests are not created equal. A standing forest next to a mid-Atlantic stream is better than grass (even if the grass is not being grazed by farm animals; Sweeney et al. 2004; Sweeney and Blaine 2007), but the absence of certain forest characteristics—no structure beneath the canopy level, overall diversity a fraction of what it could be, a reduced ability to infiltrate water and convey dissolved and particulate organic materials to aquifers and nearby streams, and so on—produces non-optimal conditions. This is especially true if the forest imperfections are due largely to our inability to properly establish a new

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<td>x</td>
<td>x</td>
<td></td>
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<tr>
<td>box-elder</td>
<td>Acer negundo L.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>x</td>
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<tr>
<td>cherry sp.</td>
<td>Prunus sp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>x</td>
<td>x</td>
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<tr>
<td>crabapple</td>
<td>Malus coronaria (L.) Mill.</td>
<td></td>
<td></td>
<td></td>
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<td>x</td>
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<tr>
<td>empress-tree</td>
<td>Paulownia tomentosa (Thunb.) Steud.</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>flowering dogwood</td>
<td>Cornus florida L.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>x</td>
<td></td>
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<tr>
<td>mapleleaf viburnum</td>
<td>Viburnum acerifolium L.</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<tr>
<td>mockernut hickory</td>
<td>Carya tomentosa Sarg.</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<tr>
<td>Norway maple</td>
<td>Acer platanoides L.</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>pin cherry</td>
<td>Prunus pensylvanica L.f.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>x</td>
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<tr>
<td>quaking aspen</td>
<td>Populus tremuloides Michx.</td>
<td></td>
<td></td>
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<td></td>
<td>x</td>
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<tr>
<td>red maple</td>
<td>Acer rubrum L.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>x</td>
<td></td>
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<tr>
<td>red mulberry</td>
<td>Morus rubra L.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>x</td>
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<tr>
<td>autumn-olive</td>
<td>Elaeagnus umbellata Thunb.</td>
<td></td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>sassafras</td>
<td>Sassafras albidum (Nutt.) Nees</td>
<td></td>
<td></td>
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<tr>
<td>scarlet oak</td>
<td>Quercus coccinea Muenchh.</td>
<td></td>
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<td></td>
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<tr>
<td>silky dogwood</td>
<td>Cornus amomum Mill.</td>
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<tr>
<td>silver maple</td>
<td>Acer saccharinum L.</td>
<td></td>
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<tr>
<td>spicebush</td>
<td>Lindera benzoin L.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<tr>
<td>sugar maple</td>
<td>Acer saccharum Marshall</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>x</td>
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<tr>
<td>tuliptree</td>
<td>Liriodendron tulipifera L.</td>
<td></td>
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<tr>
<td>white oak</td>
<td>Quercus alba L.</td>
<td></td>
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<td></td>
<td></td>
<td>x</td>
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<tr>
<td><strong>Total Species</strong></td>
<td><strong>75</strong></td>
<td><strong>5</strong></td>
<td><strong>9</strong></td>
<td><strong>2</strong></td>
<td><strong>8</strong></td>
<td><strong>1</strong></td>
<td><strong>18</strong></td>
<td><strong>5</strong></td>
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</table>
forest and jump-start it to a natural or quasi-natural state.

Our experiments here have shown that low (1.2-m) fencing applied to relatively small areas (no larger than ~100 m²) can effectively keep deer out of areas being reforested, promote survival of seedlings, and facilitate the establishment of other tree species that may be part of the regional seed bank. Moreover, unlike tree shelters, which do not work for either shrubs or herbaceous plants, fenced areas afford protection for all plants. Equally important, the creative combination of tree shelters and small fenced areas could greatly enhance the establishment of a riparian forest buffer, which would benefit the overall structure and function of the forest, especially as it relates to better water infiltration, subsurface processing of

Figure 5. Total number of volunteer seedlings, by species, across all the various fence height configurations (i.e., across 400 m² of area) used to test H₂ (height of fencing). Only the five dominant species (by total count) are listed separately for each site; see Table 5 for complete species list. “Other” provides the count for all remaining species found within a site. 1.2d = a double fence surrounding the perimeter of the planting area involving two 1.2-m metal fences positioned 3 m apart.

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Figure 6. A: The 0.8-ha riparian pasture area where 920 seedlings were planted in 2009 and protected with a low (1.2-m high) double fence. Flags indicate planting sites. B: Same site 2 y later in September 2011. C: Same site 8 y later in October 2017.
substances such as nitrogen in the ground water, and transferring food and energy to the nearby stream, to mention a few. In our experience, the cost of installing low fencing in small areas is about the same as protecting all the seedlings planted in the same area with tree shelters (assuming an initial planting density of ~1000 seedlings per hectare and use of 1.5-m tall shelters and stakes). This may make low stature fencing in combination with small size to be an ideal approach to use in conjunction with the latest strategies for reforestation (e.g., applied nucleation—which involves planting small patches of trees as focal areas for recovery; Corbin and Holl 2012).

We do not know how and to what extent the functionality of a riparian forest buffer—or for that matter a patch of upland forest—is improved by the inclusion of a diverse and intact understory of native plants. This has not been an active area of our research because we could not experimentally address it. In our experiment testing 3 here, however, we did include serviceberry, red chokeberry, buttonbush, silky dogwood, winterberry, smooth alder, and arrowwood seedlings. We did this not because the species are major components of the eastern North American forest, but because they are native shrubs, representing a class of plants that has been omitted from most riparian buffer restoration projects where white-tailed deer are abundant in the mid-Atlantic region. Our experimental data suggest that low fencing could play an important role in mitigating the destruction of these shrubs by deer in restoration projects, but we need long-term experiments on how low fencing can improve the diversity of plants in upland and riparian forests, which would in turn improve the functionality and ecosystem services they deliver, especially with regard to watershed hydrology.

Low fencing can and should also play a role in forest preservation, which is a key component in the overall effort to conserve the quality and quantity of fresh water in eastern North America. Here the focus is not on afforestation, but on the long-term sustainability of standing forests and their plant diversity as permanent sources of clean fresh water. We need to borrow a lesson from farm preservation, where the first big step is to get a landowner to adopt a conservation easement that will assure that his/her farm will remain in agriculture forever. Because this step is so important, landowners are often paid for giving up their development rights. However, without a good conservation plan and a commitment to execute it as part of the agreement, preservation can backfire, especially with regard to protecting the quality and quantity of fresh water in our streams and rivers (see Sweeney and Blaine 2016 for discussion). Thus, preserving a polluting farm without a commitment to mitigate the pollution simply perpetuates the pollution, because any incentive to do otherwise is lost when the easement payment is made. For forest preservation, the first big step is a conservation easement that rewards the landowner for giving up all land uses that a forest precludes and thereby assures that the parcel of land remains forever forested. As with farming, if there is no forest stewardship plan and no commitment to execute one, the long-term integrity of the forest (and its ability to produce clean fresh water) is seriously compromised. For example, if the trees do not reproduce, diversity and functionality are lost. Currently, many standing forests in the mid-Atlantic region have little or no reproduction of many canopy and understory species because of excessive deer herbivory. To us, these forests are green cemeteries of standing trees. They demonstrate that the preservation of forest without a viable stewardship plan significantly diminishes the net return on the conservation investment.

To be clear, once a landowner has agreed to a forest preservation plan, the principal challenge is not simply to get trees to reproduce but to ensure that the seedlings survive to sustain the ecosystem services provided by the forest. For the many reasons outlined earlier, the pervasiveness of deer can limit the ability of forest cover to provide and sustain some of those ecosystem services in upland and riparian areas of the mid-Atlantic region. Here we suggest that low stature fencing can help address a few of the key issues that are limiting our ability to create and sustain healthy forest in watersheds containing large populations of deer. For example, tree shelters that work well for creating new forest in a pasture with high sunlight do not work well in a heavily shaded forest. A 2.6-m high perimeter fence that can effectively preclude deer from a small (<5-ha) arborotum or private home does not work well in a large state park or national forest that must accommodate the movement of humans and wildlife. If conservation, like life, is a compromise, then perhaps we do not need trees reproducing in every square meter of a forest to sustain the forest in the long term. In some situations, it may make more sense to establish small patches of reproducing forest at strategic locations throughout the forest interior, effectively creating “hot spots” of reproducing trees and biological diversity. Thus, create hotspots of forest ecosystem function, rain and surface water infiltration and processing, subsurface denitrification, etc., and then move those hot spots around over time. Our results show that low fencing applied to small forest patches can accomplish much of the above while not jeopardizing the needs of either humans or wildlife. And just as USDA CREP and various state agencies reimburse landowners for creating buffers along streams to protect their fresh water, why not create programs to reimburse landowners for creating small patches of sustainable forest (sensu applied nucleation; Corbin and Holl 2012) for the same purpose? Incentivizing forest stewardship as above to protect clean water may be novel, but given that the overall water quality score for about half of the streams and rivers in the United States is poor (USEPA 2016), it may be necessary.

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Charles L. Dow is an Assistant Research Scientist and Director of Information Services at the Stroud Water Research Center.

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