Evaluation of Tree Seedling Mortality and Protective Strategies in Riparian Forest Restoration

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ABSTRACT

Riparian forest restoration can be severely constrained by tree seedling mortality. I evaluated the effects of tree shelters and planting density on herbivory and seedling mortality at a restoration site in the Lake Champlain Basin of Vermont. Eighteen experimental units were established along a 5th-order stream and planted with bare-root seedlings of seven species associated with northern hardwood floodplain forests. Two treatments were applied in a factorial design: shelters versus no shelters and high versus low planting density. Mortality and herbivory data were collected over three growing seasons. Survivorship declined to 56.4% after three growing seasons and varied significantly by species. Planting density, presence/absence of shelters, and their interaction had significant effects on survival, browse, or girdling intensity when tested for all species combined. Browse rates were high (44%), whereas girdling rates were low (3.4%). Both browse ($P < 0.001$) and girdling ($P = 0.022$) contributed to seedling mortality. High rates of deer browse on seedlings in shelters were due, in part, to the short height (60 cm) of the shelters, suggesting a need for taller shelters. A large portion (39%) of dead seedlings were neither browsed nor girdled, signaling the importance of other mortality agents. An adaptive approach is recommended to compensate for high seedling mortality and the limited effectiveness of protective devices.

Keywords: riparian restoration, seedling mortality, herbivory, tree shelters, northern hardwoods

Restoration of riparian forests is a central element of riverine and watershed management in many ecosystems globally (Jungwirth et al. 2002, Sweeney et al. 2004). Foresters are increasingly called on to apply their knowledge of forest establishment, growth, and development to this endeavor. Riparian restoration is of particular interest in agricultural and developed watersheds where streamside forest cover has been lost (Sweeney and Czapka 2004). In this context, restoration can improve important ecological functions provided by riparian forests, such as habitat for terrestrial and aquatic species, stream bank stabilization, and regulation of water, sediment, and pollutant movement into streams (Peterjohn and Correll 1984, Naiman et al. 1998, Brinson and Verhoeven 1999, Endreny 2002). Riparian forest restoration is now a primary emphasis of stream and river restoration projects throughout the United States; these receive an average of $1 billion or more in annual funding (Bernhardt et al. 2005). However, the ability of riparian reforestation to achieve streambank stabilization objectives has been variable, sometimes failing to establish self-maintaining vegetative cover in the desired time period (Jungwirth et al. 2002, Sweeney et al. 2002). Determining the factors that constrain riparian restoration must be a priority, both to make restoration more cost-effective and to ensure that ecological objectives are achieved.

Despite the potential for poor or limited attainment of restoration objectives, only 10% of stream and river restoration projects include effectiveness assessment or monitoring (Bernhardt et al. 2005). Failure to incorporate experimental design principles (e.g., treatment replication) limits the utility of observational data gained from restoration projects (Opperman and Merenlender 2000). Restoration conducted as experimentation, where feasible, would help inform adaptive approaches, wherein restorationists learn from successes and failures. This article reports on one such experiment, which was incorporated into a community-based watershed restoration project. The experiment evaluates tree seedling mortality and survivorship as limiting factors for riparian restoration in forested floodplain/hardwood swamp ecosystems in northern Vermont.

Tree seedling and plant propagule mortality rates are an important limitation on restoration and reforestation and have been widely investigated in forest systems around the world (Hammond 1995, Chapman and Chapman 1999, Robinson and Handel 2000, Sweeney et al. 2002, Alvarez-Aquino et al. 2004, Lai and Wong 2005). Although these studies include work on a limited number of tree species in southern New England (Ward et al. 2000) and the mid-Atlantic States (Sweeney and Czapka 2004), mortality constraints on riparian forest restoration have not been investigated in northern New England ecosystems. Mortality levels can be severe in the degraded conditions often encountered at restoration sites, such as moisture stress and poor soil conditions, competition with herbaceous species, and herbivory from rodents, rabbits, and deer (Stange and Shea 1998, Harmer 2001, Opperman and Merenlender 2000). Because of the anticipated high levels of mortality, survival rates as low as 50% are sometimes deemed acceptable (Sweeney et al. 2002).

Early reports of the potential for tree shelters (mesh or translucent tubes) to improve seedling survival rates (Marquis 1977, Kelty and Kittredge 1986) led to experimental evaluations of effectiveness in many forest systems (e.g., Ward et al. 2000, Sweeney and Czapka

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2004). These studies have shown that tree shelters have the potential to (1) significantly increase survival rates; (2) accelerate growth rates; and (3) improve growth form (e.g., reduced taper). Survival and growth rates are enhanced both through protection from herbivory and, in some cases, ameliorated microclimate conditions inside tubes. Sweeney and Czapka (2004) found survival and growth of central hardwood species in the US mid-Atlantic region to be 39% and 300% higher, respectively, after 5 years of growth in shelters. Similar effectiveness has been demonstrated in many different regions of the world (e.g., Ward et al. 2000, Hau and Corlett 2003, Lai and Wong 2005), although effects on within-tube microclimate are not consistently advantageous, depending on tube material and color (Ward et al. 2000).

Although a number of previous researchers have found tree shelters to be effective, reports from field practitioners of seedling mortality, stem girdling, and top browse affecting seedlings inside shelters has been of concern in the Lake Champlain Basin of Vermont, New York, and Quebec, which is currently the focus of a major international watershed restoration and management effort (Lake Champlain Basin Program 2005). My objective, therefore, was to test the hypothesis that tree shelters reduce mortality and herbivory (basal girdling and top browse) given (1) plantings of native species endemic to floodplain forests in the Lake Champlain Basin (LCB), and (2) the types and sizes of seedling protection typically used in the region.

An additional study objective was to examine the effect of stocking density on mortality and herbivory over several growing seasons postplanting. Density can affect competitive dynamics and plant community development on restoration sites (Jefferson 2004). The objective in this study was to determine whether there is an interaction between planting density and browse-induced mortality through a hypothesized attraction of herbivores to higher-density areas. Preferential browsing by deer is influenced by tree species selection (Vangilder et al. 1982, Canham et al. 1994, Waller and Alverson 1997) and choice of planting strategy (Stange and Shea 1998, Opperman and Merenlender 2000) but has not been evaluated with respect to browse density on restoration sites.

Brush mats (perforated plastic or fabric sheets, see Figure 1) are widely used in riparian restoration to control competition with herbaceous plants and exotic shrubs. However, studies have shown mats to have only a limited effect on survival rates (Sweeney et al. 2002, Lai and Wong 2005); in some cases, brush mats actually increase herbivory by attracting deer to exposed seedlings (Stange and Shea 1998). Despite this mixed track record, brush mats are commonly used as best management practices in northern New England. For this reason and to hold this source of variability constant, I used standard brush matting practices. Herbicides are not commonly used to control competing vegetation on hardwood sites in New England and are virtually never used in riparian restoration in the region. Consequently, this study did not use herbicides.

Figure 1. Photographs of the Lewis Creek restoration site after planting. Note the alternating pattern of square treatment units, with half of each unit using tree shelters. Shown are nonoverlapping perspectives along two different sections of the 0.5-km stream reach.

Methods

Study Site

The project was conducted for the Lewis Creek Association, a community-based watershed organization that works cooperatively with private landowners to restore riparian buffers. Restoration sites are identified annually from a pool of candidate sites on the basis of restoration need, ecological significance, watershed context, and landowner needs and disposition. The project site was selected in this way, and is representative of cleared, agricultural floodplains in the LCB.

The study was conducted along Lewis Creek, a 5th-order stream in the LCB, located in northwestern Vermont (44°16′24.49″N, 73°11′24.15″W). Lewis Creek has its headwaters in the northern Green Mountains and flows in a westerly direction into Lake Champlain. The site is located on the first floodplain terrace immediately adjacent to the stream channel and is surrounded by moderate to steep hill slopes. Soils on the floodplain terrace are Winooski very fine sandy loams. The site's geophysical characteristics are representative of the silver maple (*Acer saccharinum*)–sensitive fern (*Onoclea sensibilis*) riverine floodplain forests and red maple (*Acer rubrum*)– green ash (*Fraxinus pennsylvanica*) swamps described in Thompson and Sorenson (2000). Land use is wet pastureland, fenced from the stream but no longer used for livestock grazing. Vegetation is currently dominated by a dense cover of goldenrod (*Solidago* spp.) with scattered, isolated patches of exotic honeysuckles (*Lonicera* spp.) and common buckthorn (*Rhamnus cathartica*).

Experimental Design

In this study, I planted 40–50 cm tall, 2-year-old bareroot seedlings of tree and shrub species endemic to floodplain/swamp forested plant associations in the LCB (Thompson and Sorenson 2000). These were silver maple, red maple, green ash, red-osier dogwood (*Cornus amomum*), common elderberry (*Sambucus canadensis*), and high bush cranberry (*Viburnum trilobum*). I also planted eastern white pine (*Pinus strobus*) for several reasons. First, white pine formed a minor, although ecologically important, component of lowland riverine systems in the LCB pre-European settlement (Cogbill et al. 2002). Second, white pine is long-lived and grows to a height, girth, and volume not achieved by other species in the region, and it thus provides riparian functions not provided by other species, such as very large downed logs (Keeton et al. 2007). Third, there is interest in testing the utility of white pine in riparian restoration because this species has (1) low appeal as deer browse and (2) high tolerance of open-canopied, drought-prone conditions.

Treatments were applied to square 0.023-ha (15.2×15.2 m) experimental plots. There were 18 plots distributed along a 0.5-km stream reach (Figure 1). Plots were separated by 15-m-wide no-treatment buffers and placed 2–5 m from the channel bank. The total area planted was 0.4 ha; total size of the restoration area (plots plus buffers) was approximately 1.5 ha. Two aspects of seedling planting were manipulated: planting density and tree shelter use. Manipulations were applied using a split plot, factorial design combining two levels of each factor. This resulted in four treatments: (1) high density with tree shelters, (2) low density with tree shelters, (3) high density without tree shelters, and (4) low density without tree shelters. High-density treatments consisted of plantings at 1.8×1.8 m spacing (68 seedlings per plot, or 2,964 per ha), whereas low-density plots were planted at 3×3 m spacing (26 seedlings per plot, or 1,130 per ha), the later being representative of recommended tree-planting densities for northern hardwoods.

High- and low-density treatments were replicated in nine experimental plots (18 total). Each plot was divided perpendicular to the stream in two subplots (so that both were equidistant from the stream), one of which was planted using tree shelters and one without. In the high-density (versus low-density) treatment, each subplot was planted with eight (three for low-density) shrub seedlings (approximately equal proportions by species), seven (three) seedlings of white pine, seven (three) seedlings of silver maple, six (two) seedlings of red maple, and six (two) seedlings of green ash planted in completely random, mixed-species arrangement. Thus, a subplot in the high-density treatment contained 34 seedlings and a subplot in the low-density treatment contained 13 seedlings, for a total of 846 seedlings in the entire study. This resulted in a sample size of $n = 9$ per factorial treatment, or $n = 18$ for evaluations of shelter versus no shelter independent of density. Treatments were assigned systematically in an alternating pattern because of landowner preference for a uniform distribution of planting densities. Although treatments were not applied randomly, there was no evidence of periodicity in pretreatment site conditions. Vegetation and topography were distinctly homogeneous across treatment units. Treatment effects were thus not likely to vary according to specific location. To validate this assumption, single factor analysis of variance (ANOVA) was used to test for differences in response variables among blocks of units. The units were blocked into three groups of six. Blocking was performed three ways: (1) random selection, (2) selection by reach subsection, and (3) selection by every third unit. In all cases, there were no significant ($P > 0.05$) differences among groups.

Whereas previous research in other regions has evaluated comparatively tall (1 to 1.5 m) tree shelters, for this study I used 60 cm tall because that is the height most commonly used in the LCB. These were BLUE-X polyurethane tree shelters (manufactured by McKnew Enterprises, Inc.) of a make and design similar to those used widely throughout the LCB. When assembled, they were 8.5 cm in diameter, translucent, and designed to transmit photosynthetically active radiation. Shelters were set at least 5 cm into the soil, with dirt packed carefully around the base. Each shelter was tied with a wire to a 1.0-m-tall wooden stake. All seedlings were planted within 90×90 cm perforated brush mats made from photoselective polyethylene film and manufactured by Arbortec Industries Ltd. Brush mats were fixed to the ground using five 10-cm-long metal staples (placed at the four corners and center).

Data Collection

Treatment units were inventoried over three growing seasons following planting. Data collection was conducted in late August 2003 and early August 2004 and 2005. At each reinventory, individual seedlings were inspected and tallied by species and treatment as live or dead, browsed (at top), and/or girdled (at base). Confirmation that browse was caused by deer (as opposed to moose [*Alces alces*], for instance) was performed by checking for the ragged bite/tear mark typical of deer browse. Additional information on tree shelter condition was recorded describing (1) herbaceous plant invasion of tubes and mats, and (2) physical displacement or damage to tubes.

Data Analysis

Data were assembled in a Microsoft Excel database. Statistical analyses were run in SPSS software. Normality of dependent variables was assessed using the Wilks-Shapiro test and histogram plots. No significant departures from normality were detected. Treatment effects were evaluated using two-way ANOVA. General linear models were generated for final tallies after three seasons for each tree species and for all seedlings as a total. Shrub species were analyzed as one group because of the low number of shrub seedlings planted per unit. For each model, density (high or low) and tree shelter use (tubes or no tubes) were the independent variables. Percentage dead, percentage browsed, and percentage girdled were the dependent variables.

Single-factor ANOVA and Bonferroni post hoc multiple comparisons were used to compare general mortality rates among species. Tukey-tests assuming unequal variance were used to compare browse and girdling rates for live versus dead seedlings. Survivorship trends were evaluated over the three growing seasons, and trends were examined using linear regression analysis. Curve fitting techniques (transformations of the dependent variable) were used to evaluate cumulative survivorship trends; linear, exponential, logarithmic, and polynomial curves were fit in this way. All tests were considered significant at the $\alpha = 0.05$ level.

Results

Survivorship Trends

By the end of the first growing season, 88.7% of the seedlings remained alive. Survivorship declined to 80.0% and 56.4% by the end of the 2nd and 3rd growing seasons, respectively. Cumulative

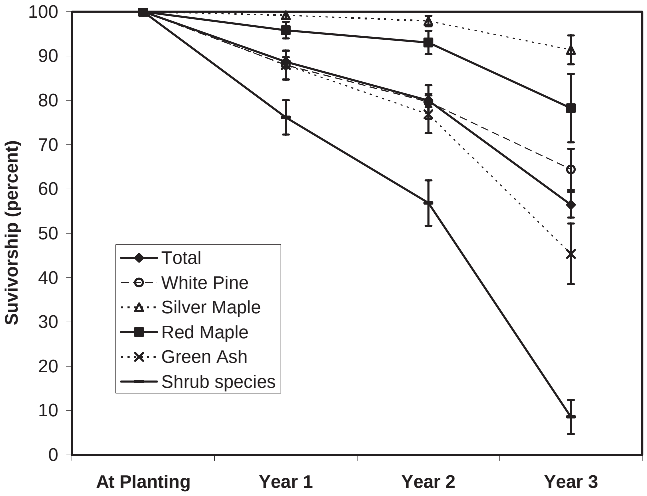

Figure 2. Survivorship trends by species over three growing seasons following planting. Survivorship differed significantly (α = 0.05) among all the species evaluated. Error bars are ± 1 SEM.

survivorship trends were best explained by an inverse negative exponential curve fit to the survivorship data ($n = 18$), and this relationship was statistically significant ($r^2 = 0.95$; $P < 0.001$). Survivorship rates differed significantly among species ($P < 0.001$) based on single-factor ANOVA and post hoc comparisons results. After the 3rd growing season, survivorship had fallen to 8.6% for shrubs (elderberry, cranberry, and dogwood), 43.6% for green ash, 64.4% for eastern white pine, 78.2% for red maple, and 91.1% for silver maple. The magnitude of difference in survival rates between species remained constant over the three seasons of observation (Figure 2).

Treatment Effects

Interaction Effects

There were no statistically significant interactions between levels of the two treatments (planting density × tree shelter use). This held true for all dependent variables (percentage dead, percentage browsed, and percentage girdled), assessed individually by species and for all species in aggregate.

Seedling Survival

The experimental treatments, in general, also had no statistically significant effects on seedling survival, although there were a few exceptions. White pine survival after 3 seasons was significantly lower ($P = 0.007$) in tree shelters compared with unprotected seedlings (Table 1). Green ash survival was significantly higher ($P = 0.002$) in tree shelters compared with unprotected seedlings. Shelter versus no-shelter differences were not statistically significant for the other species. Looking at all species collectively, 59.9% of the seedlings in shelters and 53.0% not in shelters were still alive at the end of the third growing season.

Planting density had no statistically significant effect on seedling survival. This held for all the species evaluated. In total, 56.0% of seedlings planted in high density and 56.8% planted in low density were alive after three seasons (Figure 3).

Deer Browse

The treatments also had little effect on deer browse for most species. Exceptions included silver maple, for which browse intensity after three growing seasons was significantly ($P = 0.011$) higher on seedlings in tree shelters compared with unprotected seedlings (Table 1). Browse on green ash was significantly ($P = 0.024$) more intense in high-density units (38.9% of seedlings) relative to low-density units (13.9%). Browse on white pine (7.9%) was significantly less ($P < 0.05$) than for other species based on multiple comparisons. Tree shelter effects on browse intensity for other species were not statistically significant. In total (all species), 47.5% of seedlings in shelters and 40.3% not in shelters had been browsed at the top after three seasons. Browse affected 42.3% of seedlings in high-density units and 45.7% in low-density units.

Girdling

Stem girdling rates caused by rodents were low (Table 1) for all species tested. On average, less than 4.0% of the seedlings were girdled after 3 years, and differences between sheltered and unsheltered seedlings or high versus low planting density were minimal. There were no cases of significant correlations between treatment and girdling rate. Red maple and shrub species had girdling rates that were twice as high or more for unprotected seedling in comparison with seedlings in shelters (Table 1). White pine and green ash had girdling rates that were somewhat lower for unprotected seedlings. After 3 years, 3.0% of the seedlings (in total) in shelters were girdled and 3.9% of unprotected seedlings were girdled. These numbers were 1.3% and 5.6% for high- and low-density units, respectively. However, none of these results were statistically significant.

Causes of Mortality

Seedling mortality after three seasons was related to both browse and girdling intensities. Of the dead seedlings, 56.2% had been browsed, whereas 33.5% of living seedlings had been browsed. This difference was statistically significant ($P < 0.001$). Similarly, a significantly ($P = 0.022$) greater number of dead seedlings had been girdled (7.5%), compared with the number of living seedlings with evidence of girdling (1.1%). Of dead seedlings, 2.7% had been both browsed and girdled. There were a large number of dead seedlings (39.0%) that showed evidence of neither browse nor girdling. With the exceptions previously noted, these showed no statistically significant associations with use of shelters or planting density.

Damage-mortality relationships were variable among the individual species assessed. Browse was observed on a significantly greater percentage of dead white pine ($P < 0.001$), silver maple ($P = 0.004$), and shrubs ($P = 0.019$) compared with living seedlings. There were no statistically significant differences in browse intensities when comparing dead with live red maple. For green ash, more living than dead seedlings had been browsed ($P < 0.001$). Girdling was found on more dead than live white pine ($P = 0.026$) and silver maple ($P = 0.019$). The same was true of green ash, but this difference was not statistically significant. More living than dead red maple and shrubs were girdled, but these relationships also were not significant.

Brush Mat Invasion and Shelter Displacement

Invasion of brush mats and tree shelters by herbaceous plants (primarily grasses and *Solidago* spp.) was observed at the study site. After the first growing season, 3.4% of tubes and mats had ingrowth of competing vegetation either through the perforated center of the mat or growing up through the tree shelter. By the second and third

Table 1. Mean percentage of seedlings by species dead, browsed, or girdled after three growing seasons either in tree shelters or unprotected. One SEM (n = 18) is shown in parentheses.

	Mortality		Browsed		Girdled	
	Shelters	No shelters	Shelters	No shelters	Shelters	No shelters
	(%)					
All Species	40.1 (3.0)	47.0 (3.7)	47.8 (1.1)	40.3 (2.6)	3.0 (3.8)	3.9
White pine	49.2 (6.1)	22.0 (6.9)	6.1 (2.7)	13.8 (3.8)	5.8 (2.8)	3.7 (2.5)
Silver maple	8.7 (7.4)	8.5 (4.4)	74.9 (8.3)	44.7 (8.2)	1.9 (1.9)	0.0 (0.0)
Red maple	12.0 (7.4)	31.4 (9.6)	49.1 (10.5)	36.1 (10.4)	0.0 (0.0)	5.6 (5.6)
Green ash	35.2 (8.4)	74.1 (7.3)	33.3 (8.7)	25.0 (7.4)	2.9 (2.9)	0.0 (0.0)
Shrub species	84.7 (7.6)	98.2 (1.8)	71.8 (8.1)	75.7 (8.7)	3.9 (2.1)	9.3 (5.9)

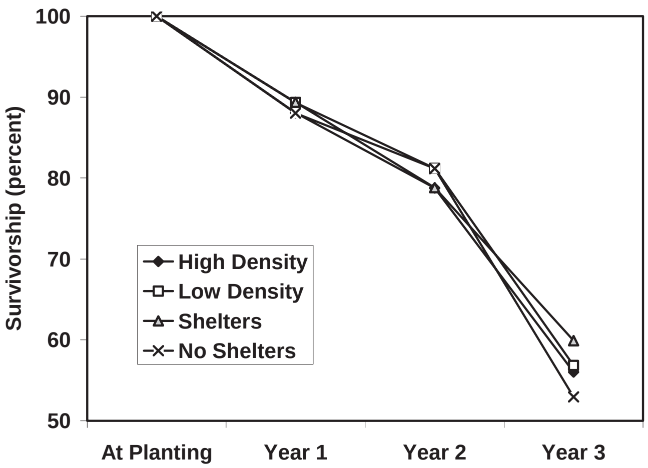

Figure 3. Percentage survivorship as an average for all species over three growing seasons following planting. Data represent survivorship by treatment: shelter versus no shelter and high versus low planting density. There were no significant (α = 0.05) differences by treatment. SEM values for high density were as follows: 1.4 (year 1), 1.7 (year 2), and 2.9 (year 3). SEM values for low density were as follows: 1.7 (year 1), 2.6 (year 2), and 5.4 (year 3). SEM values for shelters were as follows: 1.7 (year 1), 2.1 (year 2), and 3.0 (year 3). SEM values for no shelters were as follows: 1.9 (year 1), 2.7 (year 2), and 3.7 (year 3).

growing seasons this number had grown to 7.7 and 14.4%, respectively. These numbers did not differ significantly by planted species. Competing vegetation invading in this way was often dense and of equal or greater height than planted seedlings. Shelters were displaced from their original positions in the ground at rates of 1.1, 1.9, and 3.7% by the end of the first, second, and third growing seasons, respectively.

Discussion

Seedling Mortality as a Constraint on Restoration Success

Seedling mortality is a critical constraint on the ability of watershed managers to achieve riparian forest restoration objectives, such as reestablishment of self-maintaining forest cover. That high levels of mortality, approaching 40–50%, can be expected within the first few years of planting, even with significant investment in protective devices, is supported by the results reported here and by other studies (Hammond 1995, Chapman and Chapman 1999, Robinson and Handel 2000, Sweeney et al. 2002, Sweeney and Czapka 2004, Alvarez-Aquino et al. 2004, Lai and Wong 2005). The mortality observed in this study (44% after 3 years) is likely to continue to rise over the coming years. This exceeds acceptable levels necessary for adequate long-term stocking leading to establishment of a self-maintaining forested stream buffer. Some degree of self-thinning during the first 10–50 years following planting is intrinsic to stand development and competitive allocation of growing space (Oliver and Larson 1996, Franklin et al. 2002). At the planting densities used in the region, however, mortality exceeding 50% within the first decade will reduce stocking below required minimum levels for development of proper growth form and canopy closure (Smith et al. 1996). Although natural regeneration may supplement plantings over time, competition with herbaceous species can delay or limit this potential (Harmer 2001). For instance, no natural regeneration was observed at the Lewis Creek restoration site. Thus, effective mitigation strategies are essential to ensure restoration success.

Are Tree Shelters and Seedling Protection Cost-Effective?

Proper selection of protective devices for tree seedlings is imperative for optimizing effectiveness. Previous studies have shown that tree shelters reduce mortality rates (Sweeney et al. 2002, Sweeney and Czapka 2004, Lai and Wong 2005). The data presented in this study suggest this is not always the case and that shelters may not always meet cost-benefit criteria. The tree shelter heights (60 cm) used in the Lake Champlain Basin and elsewhere in northern New England appear to be too short to prevent browse from white-tailed deer (*Odocoileus virginianus*) based on the results. Browse rates were actually higher on silver maple seedlings planted in shelters, possibly due to an herbivory attraction phenomena similar to that previously documented for brush mats (Stange and Shea 1998). White-tailed deer are able to extend their snout and tongue up to 15 cm into shelters of 8–10 cm in diameter based on anatomical assessments. Thus, as soon as seedlings grow to within this distance from the top of the shelter, they become susceptible to deer browse. To avoid this problem and to allow sufficient time for growth and establishment, shelters should be at least 0.5 m taller than the height of the seedlings at planting. The results clearly show that restorationists should be using taller shelters than are typically used in the northeastern United States. Invasion of mats and shelters by competing vegetation will be a concern regardless, given that 14% of mats and shelters had been densely invaded after only 3 years.

Investment in protection from herbivory must be worth the tradeoff in terms of the associated reduction of investment in planting stock. It will be important to consider site-specific information, such as ungulate population density and different susceptibilities associated with deer versus moose browse. If protective devices yield only limited benefits, a more cost-effective strategy may be to plant at higher densities and then assume that high mortality rates will ensue. Tree shelters of 1 m or greater height cost approximately \$1.50 (\$1.00 per tube plus \$0.50 per wooden stake), compared with an average cost of approximately $1.50 per bare-root seedling, depending on species, time spent in nursery beds, and height. Forgoing shelters would provide enough funds to double initial planting densities. This strategy is not likely to increase damage from herbivory, as the results showed no relationship for most species between seedling damage and planting density. Initial mortality following planting associated with browse and girdling was not density-dependent; seedlings are still too small and separated by sufficient distances such that interstem competition is not likely. Based on the mortality results, a reasonable prediction is that approximately half the seedlings will need to be replaced after several years under a "low density with shelters" planting scheme. Holding prices constant, net costs thus would be 25% higher than a "doubled density with no shelters" scenario, yet the latter would achieve the same stocking density assuming a consistent (50%) mortality rate as evidenced in the results.

Effects of and Protection against Herbivory

The results also showed a strong relationship between herbivory—primarily browse rather than girdling—and seedling mortality over the first three growing seasons in an abandoned pasture setting. Browse had an especially strong association with mortality in white pine, silver maple, and shrubs, suggesting a particular sensitivity in young seedlings of these species. The opposite was true of green ash, for which the majority of browsed stems were still alive. The density of Vermont's deer herd is approximately 40 per km^2. In this example, there were significant losses from browse even with a deer population of only moderate density compared with other northeastern states. Thus, the results suggest that deer populations of greater density would have a severely deleterious effect on restoration success without proper seedling protection.

There was evidence of preferential species selection by deer at the study site, a finding consistent with previous research (Vangilder et al. 1982, Waller and Alverson 1997). Shrubs and silver maple were selected at significantly higher rates, whereas white pine was browsed at much lower rates compared with the other species planted. Choosing species less favored by deer, such as white pine, may be an effective strategy for reducing browse and associated mortality, but this approach clearly limits opportunities for restoring endemic natural community composition. However, it may provide a short-term strategy designed to more rapidly establish forest cover. Additional species could be added over time through natural regeneration and supplemental plantings, conducted, for instance, in conjunction with silvicultural thinning to reduce densities of species initially planted at higher than desirable densities.

At the site investigated in this study, basal girdling can be attributed primarily to meadow voles (*Microtus pennsylvanicus*), the most abundant rodent inhabiting field habitats in the LCB. Meadow voles feed on the cambium of stems and roots and are known to excavate tunnel systems under snow, which provide access to stems throughout the winter (DeGraaf and Yamasaki 2001). Although girdling rates were relatively low, the results show girdling to have been a contributing cause of mortality (i.e., affecting about 8% of dead stems), particularly for white pine and silver maple. Although tree shelters proved ineffective at significantly reducing girdling levels, there were modest (though statistically insignificant) improvements for some species.

Alternative Causes of Mortality

The results do not provide a basis for direct identification of other mortality agents, although these were clearly operative given that almost 40% of dead seedlings had neither browse nor girdling damage. Mortality agents unrelated to herbivory are likely to affect both protected and unprotected seedlings based on the results. The data showed no reduction in mortality from unidentified agents for seedlings in shelters. This contrasted with previous studies (Ward et al. 2000, Sweeney et al. 2004). The results do not necessarily refute those findings, but they do suggest that stressors of sufficient intensity have the potential to overwhelm beneficial effects of tubes. As noted by Sweeney et al. (2004), the effects of tree shelters on seedling growth and survival can be highly variable from site to site. Physiological stress caused by transplanting is another potential contributor to mortality not related to seedling protection. It is possible that even with the use of brush mats there may be some degree of belowground competition with herbaceous vegetation, although that was not evaluated in this study.

Drought stress is likely to be a contributing cause of mortality in seedlings both affected and unaffected by herbivory (Harmer 2001, Hau and Corlett 2003). Previous research has shown that nonmesh shelters can reduce wind speed and increase air temperature adjacent to stems (Ward et al. 2000). Reduced wind speed is often associated with elevated relative humidity (Chen et al. 1999); this might improve moisture status to some degree. Increased temperature, on the other hand, could be advantageous in colder climates but might be deleterious during the summer growth period on warm sites (Neilson and Drapek 1998). The summers of 2003–2005 were not anomalous in terms of drought in Vermont. June–August precipitation was close to the 20-year average (National Climatic Data Center 2005). However, summer drought stress in the hot, open, exposed conditions encountered at the restoration site is highly likely (Chen et al. 1999, Hau and Corlett 2003), even if we assume some degree of increased relative humidity inside tubes. During dry periods especially, warmer temperatures inside tubes have the potential to increase desiccation rates. In drier years, mortality associated with this factor alone could be severe. Since this study did not evaluate these factors directly, this is recommended as a topic for further research. The results of this study suggest that it would be cost-effective to invest in reducing other potential sources of mortality, such as drought stress. This might include choice of planting stock (e.g., use of drought-resistant species), watering programs, etc.

Compensating for Anticipated Mortality

Multiple strategies are needed to reduce or compensate for seedling mortality given the limited effectiveness of protective devices tested in this study. There is always the option to invest more heavily in denser initial plantings or larger planting stock if the latter is deemed to have higher survival rates. Another possibility is to encourage natural regeneration, for instance through soil scarification and removal of competing vegetation. This would help compensate for seedling mortality, providing there is a proximate seed source for the desired species. Use of live stakes and fascines made from willow (*Salix* sp.) and other vegetatively reproducing species provides another effective approach for supplementing plantings of bare-root seedlings or container stock. The objective would be to rapidly establish a closed canopy forest buffer and stabilize stream banks, with the long-term goal of gradually restoring a given natural community composition. Subsequent treatments, such as thinning and underplanting of shade-tolerant species, could be used to encourage successional transitions, for instance in this case to a mature northern-hardwood floodplain community.

Ultimately, where seedling mortality levels are high and seedling protection strategies are of limited effectiveness, it will be necessary to take an adaptive approach to riparian restoration. Central to this approach will be planning for multiple replantings, silvicultural manipulations, and other activities as needed over the first few decades of stand development until a self-maintaining system is restored. This will necessitate incorporation of forestry expertise and practitioners in riparian restoration projects. As demonstrated in this study, riparian restoration conducted as experimentation, including incorporation of robust experimental design principles, would help inform adaptive strategies.

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