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Forest Ecology and Management 192 (2004) 361-373

Forest Ecology and Management

www.elsevier.com/locate/foreco

Riparian forest restoration: why each site needs an ecological prescription

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Received 13 May 2003; received in revised form 19 August 2003; accepted 1 February 2004

Abstract

Although restoration of riparian forests improves water and habitat quality of streams, it can be a slow and difficult process, particularly in landscapes where competition from non-native invasive plants and mammalian herbivores produces high seedling mortality. We experimentally evaluated the short-term (1 year) and long-term (5 years) effects on seedling survival and growth of measures to reduce both herbivory (tree shelters) and plant competition (herbicides, tree mats, and mowing) for five species of deciduous trees in two riparian sites in the coastal plain of eastern Maryland, USA. Study species included: Quercus palustris (pin oak), Quercus rubra (red oak), Quercus alba (white oak), Acer rubrum (red maple), and Liriodendron tulipifera (tulip poplar). Results show that: (1) seedlings protected by tree shelters exhibit on average about 39% higher survival and 300% greater growth after 5 years than seedlings without shelters; (2) tree shelters alter the relative growth relationships among species of seedlings; (3) controlling plant competition may be less important for increasing survival in optimal sites than in marginal sites and more effective when used in conjunction with other measures (e.g. tree shelters) for improving seedling survival and growth; (4) local herbivores preferred certain species of seedlings (tulip poplar and red maple) over others; (5) herbivory can mask the effects of other factors such as site-to-site differences in soil moisture and fertility. Based on these results, we conclude that most prescriptions for restoring a diverse and natural streamside forest need to include a proactive program to enhance the survival and growth of seedlings. This is because local site characteristics (soil moisture and fertility, light and temperature regime, etc.) will not be optimal for all species of seedlings, and herbivores and non-native invasive plants are at, and will continue to be at, historically unprecedented levels. Furthermore, if money and labor are limited, such a plan (especially in the mid-Atlantic region of North America) should give first priority to protecting seedlings from herbivory and assign protection from plant competition a lower priority.

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Keywords: Forest buffer; Riparian; Tree shelter; Weed-abatement; Herbivory; Plant competition; Seedling growth

1. Introduction

Many programs and technical documents related to mitigating non-point source pollution of streams have

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adopted a two-tiered approach, or policy, which includes: (1) the importance and value of upland measures to control soil erosion and nutrient transport (e.g. terracing, grass waterways); (2) riparian measures, especially riparian buffers, to intercept or process sediment and pollutants before they enter a stream or river (US EPA, 1995; Lowrance et al., 1995, 1997a,b). However, it has been known for some

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^{0378-1127/\$ –} see front matter \odot 2004 Elsevier B.V. All rights reserved. doi:10.1016/j.foreco.2004.02.005

time that riparian buffers can play a much larger role than simply "intercepting or preventing" pollutants from entering streams and rivers (Sweeney, 1993). Specifically, buffers can help maintain and/or enhance the overall health of a stream ecosystem, thereby improving its ability to provide important "ecosystem services" (sensu Daily and Ellison, 2002) to humans such as in-stream processing of nutrients, pesticides, etc. Thus, the proper conservation, restoration, and management of riparian zones should play a critical role in maintaining and improving water quality in streams and rivers throughout the world.

One of the main aspects of riparian zones that humans have altered is its vegetation. In eastern North America, where riparian vegetation was historically dominated by forest, significant areas were deforested to facilitate human occupation, activity, or aesthetics (Matlack, 1997). The removal of forest and its replacement with grass or shrub vegetation has had a negative effect on the structure and function of the region's stream and river ecosystems by significantly altering physical and chemical habitat features, trophic dynamics, and life history characteristics of native aquatic plant and animal species (Sweeney, 1992, 1993). However, the rate and degree of restoration of a riparian forest buffer's ability to improve stream ecosystem function and water quality depends on afforestation practices that maximize seedling survival and growth in streamside areas and provide natural diversity in the final canopy.

Afforestation, or the process of restoring forests on cultivated or cleared land, is more difficult than one might think. For riparian areas, it involves: (1) changing societal (landowner) perceptions about what constitutes an aesthetically and functionally acceptable level and type of vegetation for the riparian zone; (2) restoring native vegetation in the face of unnatural levels of exotic invasive plants and herbivorous animals (which has been well documented (Marquis, 1977; Marquis and Brenneman, 1981; Davies, 1987; Harmer, 2001)). During the past decade, several new techniques have been used to increase afforestation success in both upland and riparian areas. Fencing (Opperman and Merenlender, 2000) and tree shelters (Sweeney, 1992, 1993; Buresti and Sestini, 1994; Kjelgren et al., 1994; Lantagne, 1995; West et al., 1999; Dubois et al., 2000; Bendfeldt et al., 2001; Weitkamp et al., 2001; Sweeney et al., 2002) have been the primary techniques used to protect seedlings from herbivory. Mulching, herbicides, and tree mats have been used to reduce competition with invasive plants (Stange and Shea, 1998; Bendfeldt et al., 2001; Sweeney et al., 2002). Although a precise prescription for riparian afforestation will undoubtedly vary from site-to-site, our ability to write the prescription will depend on detailed knowledge of the reforesting "tools" available and the performance of those tools across a variety of landscapes.

In this paper, we evaluate both the short-term (1 year) and long-term (5 years) effects of specific tools (tree shelters, herbicides, tree mats, and mowing) to improve seedling survival and growth of five species of deciduous trees in the coastal plain of eastern Maryland, USA. We propose that this type of ecological information can and should provide the basis for site-specific prescriptions to increase the success of proactive afforestation programs in streamside areas, given the widespread problem of slow growth and high mortality of seedlings due to competition from invasive plants and herbivory by mammals.

2. Study sites

The study was conducted at Chino Farms Inc. on the eastern shore of Maryland, USA. Treatments were applied in a split-plot design with the following variables: site location, species, tree shelter use, and weed treatment. Sixteen replicate plots, in four blocks (i.e. a randomized combination of each of the four weed treatment plots) were established at site A (39°13'35"N; 76°00'50"W), and eight replicate plots in two blocks were established at site R3 (39°11'12"N; $75^{\circ}55'44''W$). Weed treatments, applied at the plot level, consisted of mowing (weed eater), tree mats (VisPore[®], Tredegar Corporation, Richmond, VA, USA), herbicide application (Roundup[®], Monsanto Co., St. Louis, MO, USA), or control (no treatment). Soil types for site A ranged from Galestown loamy sand, clayey substratum with 0-5% slopes (GAB) to Galestown loamy sand, clayey substratum with 5-10% slopes (GAC), while site R3 ranged from Sassafras sandy loam with 5-10% slopes (SFC2) to Sassafras sandy loam with 15-30% slopes (SFE). The corners of each experimental plot had labeled fence posts to facilitate weed treatments and the subsequent location of seedlings.

Both study sites were plowed and disked about 1 month before planting, making them initially weed free. The sites revegetated quickly (within months). A variety of native and non-native annual grasses and the non-native, perennial Johnsongrass (*Sorghum halepense*) were the first plants to become established in the disked area. In addition to Johnsongrass, the other common non-native, invasive plants colonizing the study sites were: Multiflora Rose (*Rosa multiflora*), Japanese Honeysuckle (*Lonicera japonica*), Oriental Bittersweet (*Celastrus orbiculatus*), Canadian Thistle (*Cirsium vulgare*), and Tree of Heaven (*Ailanthus altissima*).

3. Methods

Seedlings were obtained from Natural Landscapes Nursery in Chester County, PA, USA. All seedlings were hand planted on 26 and 29 April 1996 at Sites A and R3, respectively, using a dibble bar on a 3 m \times 3 m spacing. One Right Start[®] Fertilizer Packet (Treessentials Inc., Mendota Heights, MN, USA) was placed in each hole before planting. Each plot at site A was planted in four rows of 10 seedlings each, for a total of 640 seedlings in the 16 plots. Each plot at site R3 was planted in two rows of 10 seedlings each, for a total of 160 seedlings in the eight plots. At both sites, each row contained two individuals of each test species, planted in a random order, with one individual of each species randomly selected to have a tree shelter placed over it.

Five tree species were tested in each plot: Quercus palustris (pin oak), Quercus rubra (red oak), Quercus alba (white oak), Acer rubrum (red maple), and Liriodendron tulipifera (tulip poplar). All plants were 1-year-old, bare-root seedlings. The seedlings were not culled prior to planting to eliminate small, large, or damaged plants. Seedlings with large roots (e.g. oaks) were not root pruned prior to planting. The species chosen are native to the region, with good potential for improving the stream or providing a crop (marketable timber) for a landowner. Specifically, red maple is adapted to wet conditions, and its broad root system will provide stream bank stabilization. The oak species benefit wildlife through mast production, the stream through their leaves, fruits, and shade, and also represent a potential cash crop for the landowner. This cropping aspect is important because most

riparian areas are on private lands, and landowners, especially farmers, may be unable or unwilling to reforest these areas due to financial or other constraints. Consequently, oaks were included because they could eventually provide landowners with a source of income, albeit not annually. The three oak species represent an adaptation gradient for wet conditions, with pin oak being the most tolerant and white oak the least.

Tubex[®] (Aberaman Park, Aberaman, South Wales, UK) tree shelters (1.2 m tall and tan) were placed over half the seedlings at planting (one individual of each species per row). Shelters were pushed into the soil approximately 3–4 cm and fastened with plastic ties to 1.2 m tall by 2 cm diameter plastic stakes driven into the ground approximately 0.3 m. Coarse (\sim 2 cm mesh) plastic netting was placed over the top of the shelters to prevent birds from entering and becoming trapped inside.

To examine the effects of weed competition on seedling survival and growth, one of the four weed treatments was applied to each plot. Plot treatment locations were randomly determined within each block. At sites A and R3 there were four and two plots of each weed treatment, respectively. Treatment application took place in an area between 0.8 and 1.0 m² around the seedling base. Black VisPore[®] tree mats $(0.9 \text{ m} \times 0.9 \text{ m})$ were in place at planting, with seedlings located at the center. Mowing and herbicide treatments were applied twice each growing season for the 5 years of the study. The vegetation within 0.9 m of each seedling was mowed with a weed eater on 3 July and 5 August 1996, 9 June and 22 July 1997, 4 June and 10 August 1998, 2 June and 9 August 1999, and 5 June and 3 August 2000 at site A, and 9 July and 7 August 1996, 16 June and 28 July 1997, 9 June and 14 August 1998, 7 June and 13 August 1999, and 6 June and 14 August 2000 at site R3. In herbicide-treated plots, Roundup[®] (1% solution of glyphosate) was applied to the vegetation within 0.9 m of each seedling. Roundup[®] was used because the habitat was classified as non-wetland. In wetland sites, other herbicides (e.g. Rodeo[®]) should be substituted for Roundup[®]. Unsheltered seedlings were protected from overspray by a flexible plastic pipe which had part of its side removed to facilitate wrapping it around the seedling. Herbicide treatments were applied on 9 July and 7 August 1996, 17 June and 29 July 1997, 9 June and 14 August 1998, 7 June and 13 August 1999,

and 6 June and 17 August 2000 at site A, and 3 July and 4 August 1996, 9 June and 22 July 1997, 4 June and 10 August 1998, 2 June and 9 August 1999, and 5 June and 14 August 2000 at site R3. The vegetation located between the rows of each plot and greater than 0.9 m from each seedling was mowed three times a year with a rotary mower (\sim 2 m diameter; tractor operated) to keep shade from confounding the experiment.

Mean (S.E.) seedling height (cm) at planting, which was determined by measuring 20 randomly selected individuals of each species, was as follows: pin oak (45.1 (1.28)), red oak (43.1 (1.9)), white oak (21.8 (0.9)), red maple (41.8 (1.8)), tulip poplar (19.7 (0.9)). All seedlings were measured at the end of each growing season, when survival rates were also determined. Here we only report results after the first and fifth growing seasons (i.e. for monitoring dates 25 July 1996 and 31 August 2000 at site A, and 1 August 1996 and 11 September 2000 at site R3).

3.1. Survival analysis

Trees were scored as alive or dead, with dead meaning that there was no indication that any part of the tree was still alive. Survival data were analyzed with repeated measures logistic regression models (Proc GENMOD; SAS Institute Inc., 1989). The models included all main effects and two-way interactions, with survival as the dependent variable and site location, species, tree shelter use, and weed treatment as independent variables. For first-year survival, the site location by species, site location by weed treatment, and species by weed treatment interactions were removed from the model to achieve convergence due to complete separation of the data. Specifically, after 1 year, all red oaks had survived at site R3, all seedlings in herbicide plots had survived at site R3, all pin oaks had survived in mow plots and all white oaks had survived in tree mat plots. Probabilities of seedling survival were calculated by back transformation of the least squares mean (LSM) from the logistic models $(e^{\text{LSM}}/(1+e^{\text{LSM}}))$.

3.2. Growth analysis

Seedling growth was estimated by subtracting the mean initial height (at planting) from the height at the

end of the first and fifth growing seasons. Height was taken as the highest vertical extent of either the stem or leaves. Growth measures were analyzed with linear regression models (Proc MIXED; SAS Institute Inc., 1989). The models included all main effects and two-way interactions, with seedling growth as the dependent variable, and site location, species, tree shelter use, and weed treatment as independent variables. Results of seedling growth are presented as LSM \pm S.E.

4. Results

4.1. First-year survival

Significant main effects after 1 year included species and site (Table 1), reflecting that: (1) pin oak, white oak, red oak, and red maple (averaged across treatments and sites) had significantly higher survival than tulip poplar, and pin oak had significantly higher survival than red maple (Table 2, Fig. 1); (2) seedlings at site R3 (averaged across species and treatments) had significantly higher survival than those at site A (98.4% (CI: 96.0, 99.4) versus 91.3% (CI: 87.4, 94.1), respectively).

4.2. Fifth-year survival

Significant main effects after 5 years included tree shelter use and site (Table 1). Also, a tendency towards significance was observed for species (P = 0.07). More detailed analyses showed that: (1) survival for seedlings with shelters (averaged across species, treatments, and sites) was significantly higher than those without shelters (Table 2); (2) overall survival declined between the first and fifth year at each site, with the largest decline observed for unsheltered trees (95.2–68.9%; Table 2, Fig. 1); (3) seedlings at site R3 (averaged across species and treatments) had significantly higher survival than those at site A (94.4% (CI: 87.4, 97.6) versus 74.3% (CI: 68.2, 79.6), respectively); (4) the relative pattern of survival among species after 5 years was similar to that after 1 year for sheltered trees but fifth-year survival for unsheltered tulip poplar and red maple was substantially lower than might have been predicted from the firstyear data (Fig. 1); (5) pin oak, white oak, red oak, and

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Source			Survivorship				Growth			
	d.f.	First year		Fifth year		First year		Fifth year		
		F	Р	F	Р	F	Р	F	Р	
Site	1	7.61	0.006	9.85	0.002	1.69	0.212	0.88	0.362	
Species	4	11.40	0.022	8.65	0.070	65.88	< 0.001	27.85	< 0.001	
Tree shelter	1	0.92	0.339	8.76	0.003	52.88	< 0.001	472.90	< 0.001	
Weed treatment	4	0.97	0.808	3.38	0.336	0.65	0.592	7.11	0.003	
Site \times species	4	_	_	5.89	0.208	12.32	< 0.001	1.23	0.299	
Site \times tree shelter	1	0.56	0.454	6.16	0.013	5.87	0.016	9.80	0.002	
Site \times weed treatment	3	_	_	1.42	0.701	0.15	0.926	0.72	0.556	
Species \times weed treatment	12	_	_	12.34	0.419	0.51	0.911	2.02	0.021	
Tree shelter \times species	4	1.11	0.892	8.73	0.068	0.92	0.450	5.19	< 0.001	
Tree shelter \times weed treatment	3	2.76	0.430	1.96	0.580	1.69	0.168	3.54	0.015	

Results from regression models analyzing seedling survival and seedling growth for first and fifth growing seasons

Models included all main effects and two-way interactions.

red maple (averaged across treatments and sites) had significantly higher survival than tulip poplar, and white oak had significantly higher survival than red maple (Table 2).

One significant interaction and one tendency towards significance were observed for survival after 5 years (Table 1). First, the significant tree shelter use by site interaction resulted because survival at site R3 was significantly higher than site A for both sheltered and unsheltered seedlings (98.8% (CI: 95.4, 99.7) versus 85.7% (CI: 81.4, 89.2) and 77.9% (CI: 62.8, 88.1) versus 58.13% (CI: 48.4, 67.3), respectively). Second, the tendency towards significance (P = 0.068) between tree shelter use and species resulted because pin oak, white oak, and red oak had significantly higher survival than tulip poplar when seedlings were unsheltered. Meanwhile, only white oak had significantly higher survival than tulip poplar when

Table 2

Table 1

Comparison of seedling survivorship (mean % (confidence limits)) and growth (mean cm (±S.E.)) after the first and fifth growing season

	Survi	vorship	Growth		
	First year	Fifth year	First year	Fifth year	
Shelter					
Unsheltered	95.2 A (91.8, 97.3)	68.9 A (59.2, 77.2)	-3.3 A (±1.0)	52.5 A (±4.7)	
Sheltered	97.0 A (92.8, 98.8)	95.6 B (91.3, 97.9)	5.6 B (±1.0)	156.7 B (±4.2)	
Species					
Red maple	95.0 B (90.7, 97.3)	78.6 AB (69.5, 85.5)	-5.6 A (±1.4)	69.6 A (±6.3)	
White oak	98.8 BC (96.9, 99.5)	93.1 C (87.9, 96.2)	5.1 B (±1.4)	84.7 AB (±5.7)	
Red oak	95.8 BC (92.1, 97.8)	92.7 BC (81.8, 97.3)	-4.6 A (±1.5)	101.1 BC (±5.8)	
Pin oak	98.8 C (96.3, 99.6)	94.8 BC (80.8, 98.7)	-8.6 A (±1.4)	118.8 C (±5.7)	
Tulip poplar	79.0 A (68.0, 87.0)	59.1 A (40.1, 75.6)	19.5 C (±1.5)	148.8 D (±7.0)	
Weed treatment					
Control	96.7 A (91.9, 98.7)	86.5 A (74.1, 93.4)	0.9 A (±1.5)	86.6 A (±7.4)	
Mow	96.6 A (91.5, 98.7)	83.3 A (75.5, 88.9)	-0.4 A (±1.5)	89.5 A (±7.5)	
Tree mat	96.7 A (92.5, 98.6)	91.6 A (82.4, 96.2)	2.1 A (±1.5)	114.0 AB (±7.3)	
Herbicide	94.5 A (88.7, 97.4)	87.1 A (78.7, 92.6)	2.1 A (±1.5)	128.4 B (±7.6)	

Values in a given column followed by the same letter are not significantly different within the grouping variables shelter, species, and weed treatment.

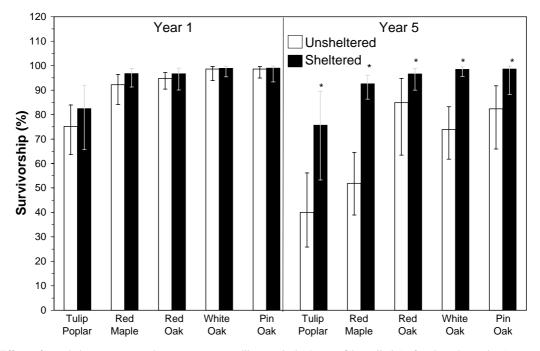


Fig. 1. Effects of tree shelter presence or absence on mean seedling survival ($\% \pm$ confidence limits) of each study species (averaged across weed treatments) through one and five growing seasons. Asterisks indicate significant differences between sheltered and unsheltered pairings.

seedlings were sheltered (due to high variability in the data), but there was a tendency for pin oak and red oak to have higher survival than tulip poplar (Fig. 1).

4.3. First-year growth

Significant main effects after 1 year included tree shelter use and species (Table 1), showing that: (1) there was a slight but significant increase in height for seedlings with tree shelters (averaged across species, treatments, and sites), whereas seedlings without shelters actually lost significant height (Table 2, Fig. 2); (2) only tulip poplar and white oak (averaged across treatments and sites) increased in height (Table 2, Fig. 2); (3) height change for tulip poplar was significantly greater than all other species; (4) height change for white oak was significantly greater than red oak, red maple, and pin oak (Table 2).

Two significant interactions were observed for growth after 1 year (Table 1). First, the tree shelter use by site interaction resulted because seedlings at site R3 suffered a significantly smaller decrease in height than at site A when unsheltered (-0.8 ± 1.7 cm versus -5.7 ± 1.0 cm, respectively), while there was no difference between sites for sheltered seedlings (5.1 ± 1.7 cm versus 6.1 ± 0.9 cm, respectively). Second, the species by site interaction resulted because tulip poplar had significantly greater growth at site R3 than at site A (28.4 ± 2.5 cm versus 10.6 ± 1.6 cm, respectively), while white oak had significantly greater growth at site A (9.3 ± 1.3 cm versus 1.0 ± 2.4 cm, respectively). No significant differences between sites were observed for the remaining three species (red oak: -5.5 ± 2.6 cm versus -3.7 ± 1.3 cm; red maple: -6.4 ± 2.5 cm versus -4.9 ± 1.3 cm; pin oak: -6.9 ± 2.5 cm versus -10.2 ± 1.3 cm).

4.4. Fifth-year growth

Significant main effects after 5 years included tree shelter use, species, and weed treatment (Table 1), showing that: (1) seedlings with tree shelters (averaged across species, treatments, and sites) grew three times faster than seedlings without shelters (Table 2, Fig. 2); (2) tulip poplar (averaged across treatments

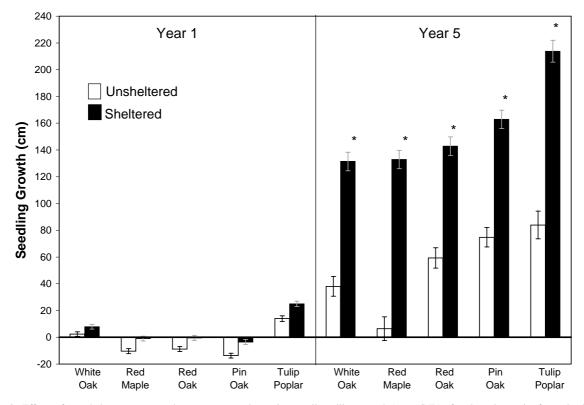


Fig. 2. Effects of tree shelter presence or absence on mean change in overall seedling growth (cm \pm S.E.) of each study species from planting (averaged across weed treatments) through one and five growing seasons. Asterisks indicate significant differences between sheltered and unsheltered pairings.

and sites) grew significantly faster than all other species, while pin oak grew significantly faster than white oak and red maple, and red oak grew significantly faster than red maple (Table 2, Fig. 2); (3) seedlings in herbicide plots (averaged across tree shelter use, species, and sites) grew significantly faster than those in mow or control plots (Table 2, Fig. 3); (4) the relative effects of the various weed–abatement treatments was fairly consistent across all species (i.e. herbicide > mat > mow > control; Fig. 4).

Four significant interactions were observed for growth after 5 years (Table 1). First, the tree shelter use by weed treatment interaction resulted because seedlings with shelters grew significantly faster in herbicide plots than in mow or control plots, while no differences were observed between weed treatment plots for unsheltered seedlings (Fig. 3). Second, the tree shelter use by species interaction resulted because: (1) tulip poplar grew significantly faster than all other species, and pin oak grew significantly faster than red maple and white oak when seedlings were sheltered (Fig. 2); while (2) unsheltered tulip poplar and pin oak grew significantly faster than white oak and red maple, and unsheltered red oak and white oak grew significantly faster than red maple (Fig. 2). Third, the tree shelter use by site interaction resulted because sheltered seedlings at site R3 grew significantly faster than sheltered seedlings at site A (167.6 \pm 7.1 cm versus 145.8 ± 4.5 cm, respectively), while there was no significant difference between the two sites for unsheltered seedlings (48.6 \pm 7.8 cm versus 56.4 \pm 5.1 cm, respectively). Finally, the weed treatment by species interaction resulted because tulip poplar grew significantly faster in herbicide plots than in mow or control plots and red oak grew significantly faster in herbicide plots than in mow plots, while no significant differences were observed between the four weed treatment plots for the remaining three species (Fig. 4).

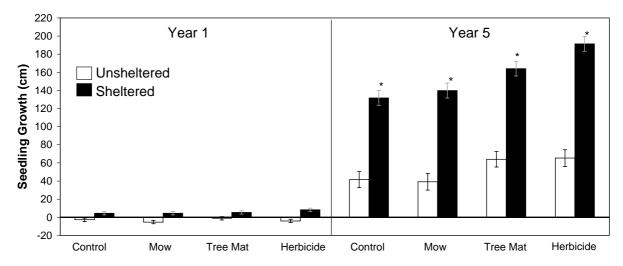


Fig. 3. Effects of tree shelter presence or absence on mean change in overall seedling growth ($cm \pm S.E.$) for each weed treatment from planting (averaged across species) through one and five growing seasons. Asterisks indicate significant differences between sheltered and unsheltered pairings.

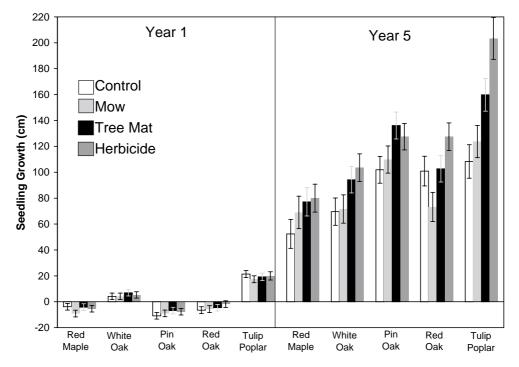


Fig. 4. Effects of each weed-abatement treatment on mean change in overall seedling growth ($cm \pm S.E.$) of each species from planting (averaged across all sheltered and unsheltered seedlings) through one and five growing seasons.

5. Discussion

It has been known for some time that maintaining a buffer between a stream and the human activities occurring in the stream's watershed can greatly help intercept and process contaminants associated with those activities and prevent them from polluting the habitat and water quality of the stream (Welsch, 1991; Sweeney, 1993; US EPA, 1995). It is now becoming clear that the kind of vegetation growing in the riparian buffer can affect the stream's ability to process and/or sequester contaminants in situ, hence keeping them from moving downstream into large rivers and estuaries (Sweeney et al., unpublished data).

In stream ecosystems, there is a close relationship between structure and function (viz. the more intact the ecosystem, the better it is able to process materials entering from the landscape; Allan, 1995). This means that in landscapes where riparian areas were historically forested, trees are the vegetation of choice for the buffer space. A close match between historic and contemporary vegetation in the buffer is needed because the native species comprising the ecosystem (microbes, plants and animals) have evolved morphological, physiological, and behavioral adaptations to stream conditions that are closely aligned with the long-term conditions associated with having forest cover on their banks (i.e. food, temperature, light). These adaptations are fundamental to stream ecosystem function and hence the stream's ability to deliver the "ecosystem services" that are needed by humans to provide sufficient quantity and quality of water for sustaining human life and wildlife biodiversity. Thus, natural streamside forests help provide services such as bank stability, flood and erosion control, in-stream root habitat, wildlife habitat/corridors (Manci, 1989; Rhodes and Hubert, 1991; Welsch, 1991), channel shading and optimal temperatures (Johnson and Jones, 2000), as well as sufficient quality and quantity of food in the form of in-stream algal production, wood/leaf litter inputs (Smock et al., 1989; Angradi, 1996), and dissolved organic matter to the stream. In addition, forest cover minimizes ultraviolet light damage to stream communities (Bothwell et al., 1994), helps degrade and sequester pesticides (Lowrance et al., 1997a), and reduces nutrient inputs to streams from groundwater and overland flow (Peterjohn and Correll, 1984; Pinay and Decamps, 1988; Lowrance et al., 1995, 1997b). All this leads to enhanced macroinvertebrate and fish community structure and productivity (Barton et al., 1985; Bilby and Bisson, 1992).

Given this context, it is critical that we restore natural forest cover to streams that were historically forested as quickly and efficiently as possible. Our results suggest that each streamside area has unique environmental and ecological characteristics that can affect seedling survival and growth. In practice, this means that for afforestation to be successful both ecologically and economically (for the landowner), each streamside area will likely require a site-specific prescription. This prescription needs to include the species of seedlings to plant, why they were chosen, where and how to plant them, and how and to what degree they need to be managed after planting. This study further confirms that, for many potential riparian restoration sites in eastern North America, the prescription must also include a proactive program to enhance the survival and growth of seedlings because local site characteristics (soil moisture and fertility, light and temperature regime, etc.) will not be optimal for all species of seedlings and because herbivores and non-native invasive plants are at, and will continue to be at, historically unprecedented levels.

Our results, along with others (West et al., 1999; Ponder, 2000), show that there are significant local differences in overall survival and growth among seedling species and that each species seems to respond differently to devices designed to counteract the negative effects of herbivores and competing plants. For example, overall survival of seedlings at the sites reported here was generally much higher than for other sites nearby (within 20 km) (e.g. 68.9% (after 5 years) versus 12.1% (after 4 years; Sweeney et al., 2002) for unsheltered seedlings). However, the geographic scale of this differentiation may be much finer than 20 km because, in this study, average seedling performance at site R3 was significantly better than at site A for 5-year survival of both sheltered and unsheltered seedlings and for 1- and 5-year growth of unsheltered seedlings. In addition, 5-year growth of sheltered trees was greater at site R3, which suggests that factors such as soil type and moisture were better at site R3 than at site A (i.e. soils SFC2 and SFE were better than GAB and GAC) for the species studied, even though the two sites were only 7.5 km apart.

Such site-to-site variability notwithstanding, the focus at each riparian restoration site should be the rapid re-establishment of a diverse, natural canopy because of its immediate positive effects on the habitat and water quality of small streams (see above). Thus, each prescription for riparian afforestation should include an array of species, even though local site conditions for some of them will be sub-optimal. Our data and that of others suggest that two viable methods are currently available for improving survival and growth for such species-use of tree shelters (Sweeney, 1992, 1993; Buresti and Sestini, 1994; Kjelgren et al., 1994; Lantagne, 1995; West et al., 1999; Dubois et al., 2000; Bendfeldt et al., 2001; Weitkamp et al., 2001; Sweeney et al., 2002) and control of plant competition (Stange and Shea, 1998; Bendfeldt et al., 2001; Sweeney et al., 2002). In this study, shelters had a significant positive effect on average seedling survival after 5 years. In terms of growth, seedlings without shelters actually lost significant height after 1 year for three of the five species. After 5 years, however, seedlings with shelters were on average three times taller than seedlings without shelters. Recent, longer-term studies (Ward et al., 2000; Heitzman, 2001) have shown that this height advantage persists beyond 5 years. Our study also demonstrates that the impact of tree shelters on growth varies significantly among species. Thus, tulip poplar grew significantly faster than pin oak with shelters but not without; and, red maple grew significantly slower than white oak and red oak without shelters but all had the same growth rate with shelters. These results and others (Ward et al., 2000; Jacobs and Steinbeck, 2001) suggest that tree shelters alter the relative growth relationships among species of seedlings (i.e. how fast or slow a species grows relative to another species under the same conditions). This observed positive effect of tree shelters on seedling survival and growth is consistent with previous studies and is likely related to one or more of the following: defense against herbivory, reduced damage from mowing, protection from herbicide overspray, lateral branch suppression, reduced trunk tapering, and lower water stress (Potter, 1991; Sweeney, 1992, 1993; Buresti and Sestini, 1994; Dunn et al., 1994; Kjelgren et al., 1994; Peterson et al., 1994; Lantagne, 1995; Ward and Stephens, 1995; Schuler and Miller, 1996; Ward, 1996; Stange and Shea, 1998; West et al., 1999; Dubois et al., 2000; Ponder, 2000; Ward et al., 2000; Weitkamp et al., 2001; Sweeney et al., 2002).

In contrast to the significant and positive response of seedlings to tree shelters, control of plant competition was not observed to be a significant factor affecting survival in this study, even though it has been reported as such at other sites in the region (Sweeney et al., 2002) and elsewhere (Bendfeldt et al., 2001). It is important to note, however, that overall survival on control plots at other sites in the region were substantially lower than for control plots in this study. This indicates that conditions for survival at the study sites reported here were more optimal for our study species than for the same species at other sites in the region, even though site preparation (plowing and disking) and maintenance were similar. Hence, based on this study, it appears that controlling plant competition to increase survival may be more important for marginal sites where soil fertility, moisture, and temperature are limiting.

This observation regarding seedling survival may not apply to seedling growth. Thus, we show that growth was significantly faster for seedlings in the herbicided plots (i.e. herbicide control of vegetation within 0.9 m of the seedling) than in mat, mow, or control plots. The relative response pattern of growth to the various weed-abatement treatments in this study was fairly consistent across all species, with greatest growth in herbicide plots, followed by mat plots, then mow plots, and finally control plots. However, the increased growth due to tree mats or mowing did not differ significantly from controls for any of the species, and the effect of using herbicides to reduce plant competition appears to be species dependent, as growth increased significantly only for tulip poplar and red oak. Our study also indicated that controlling plant competition might be more effective when used in conjunction with other measures for improving plant survival and growth. For example, a significant tree shelter by weed-abatement interaction in our analysis of 5-year growth patterns suggests that weed-abatement (especially herbicide) is significantly more effective when used in conjunction with tree shelters. The positive effect of the tree shelterherbicide treatment is most likely related to a combination of increased availability of moisture for the seedling (due to herbicide removal of competing vegetation) and decreased moisture requirements of the seedling (due to the shelter). It is unlikely that the effect is related to shelters affording seedlings protection from herbicide overspray because unsheltered trees were protected from overspray during application.

Determining the correct site prescription for afforestation is further complicated because our study suggests that local herbivores feed selectively. We observed that herbivores preferred tulip poplar and red maple seedlings to other species. For example, 5year survival of unsheltered tulip poplar and red maple seedlings was significantly lower than that for unsheltered red oak, white oak or pin oak seedlings. This was unexpected since seedlings were planted randomly in each experimental block. The growth data provide additional evidence of herbivore preference for tulip poplar and red maple. Although tulip poplar was the fastest growing species at both of our sites (with or without protection from herbivory), it had the lowest overall survival after 5 years, especially for unsheltered trees. Moreover, unsheltered red maple seedlings were significantly smaller after 5 years than red oak and white oak seedlings, whereas red maple, red oak, and white oak were the same size after 5 years when sheltered from herbivory. Since these patterns of selective herbivory only emerged over 5 years, it is clear that studies designed to evaluate selective herbivory need to be long-term in nature. We propose that knowledge of selective herbivory in a region could improve the cost effectiveness and efficiency of a given restoration effort by enabling landowners to restrict the use of shelters to those species preferred by local herbivores.

The importance of herbivory to afforestation lies not only in its impact on seedling mortality and growth, but in the fact that it can actually mask the effects of other factors, such as site-to-site differences in soil moisture and fertility and the effects of certain weed–abatement measures. For example, when, and only when, seedlings were protected from herbivory, did it become obvious that conditions for growth at site R3 were better than at site A for all seedlings and that seedlings grew significantly faster when freed from plant competition. Thus, it appears that herbivory must be an important consideration in site prescriptions and needs to be included in research projects designed to provide information about improving site prescriptions.

6. Conclusions

Restoring a diverse, natural forest along streams flowing through landscapes that were historically forested is now considered best management practice. It can help: (1) intercept and/or process anthropogenic pollutants before they enter the streams; (2) restore the natural stream ecosystem, enabling it to process pollutants in situ, thus preventing them from moving downstream into large rivers and estuaries (i.e. providing important ecosystem services to humans). Unfortunately, natural regeneration of forests in riparian areas can be a slow and difficult process, particularly in landscapes where high levels of competition from non-native species of invasive plants and herbivory associated with large populations of mammals produces high seedling mortality. Thus, proactive restoration (afforestation) is needed to improve habitat and water quality in an effective and timely fashion.

Our study shows that: (1) site-to-site variability in factors relevant to seedling survival and growth can be high, necessitating a careful prescription for afforestation regarding which species to plant, where and how to plant them, and how to maximize their survival and growth; (2) seedlings protected by tree shelters exhibit on average about 39% higher survival and 300% better growth after 5 years than seedlings without shelters; (3) tree shelters alter the relative growth relationships among species of seedlings (i.e. how fast or slow a species grows relative to another species under the same conditions); (4) controlling plant competition to increase survival may be less important for optimal sites than marginal sites (i.e. sites where soil fertility, moisture, and temperature are limiting) and more effective when used in conjunction with other measures (e.g. tree shelters) for improving plant survival and growth; (5) local herbivores prefer certain species of seedlings over others; (6) herbivory can mask the effects of other factors such as site-to-site differences in soil moisture and fertility.

We conclude that most prescriptions for streamside reforestation should include a proactive program to enhance the survival and growth of seedlings because local site characteristics (soil moisture and fertility, light and temperature regime, etc.) will not be optimal for all species of seedlings and because herbivores and non-native invasive plants are at, and will continue to be at, historically unprecedented levels. Furthermore, if money and labor are limited when prescribing such a plan (especially in the mid-Atlantic region of North America), first priority should be given to protecting seedlings from herbivory, and a lower priority should be assigned to protecting against plant competition.

Acknowledgements

The Stroud Foundation, Pennswood No. 2 Research Endowment, Stroud Endowment for Environmental Research, and Chino Farms Inc. supported the research. We thank Dr. Harry Sears for providing the land, personnel, equipment, and supplies needed to establish and maintain the field experiments. We also thank Evan Miles, Salamon Romero, Jabier Tinoco, Henry Davis, Williard Kemp, Bob Spray, Jack Thomas, Ryan Abey, Tim Elbourn, Nick Huffer, John Kling, Evan Miles Jr., and Kevin Sweeney for invaluable assistance in the field during the project. Llwellyn Armstrong, Ducks Unlimited Canada, provided statistical assistance and James G. Blaine edited the manuscript.

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