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Regeneration of woody plant species within riparian zones of headwater streams whose watersheds vary by dominant land cover

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Abstract

Riparian vegetation, particularly along headwater streams, is important in controlling nutrient and pollutant runoff from terrestrial ecosystems, in maintaining stream bank stability, and in controlling in-stream temperatures. Previous research has indicated that riparian zones containing a high abundance and diversity of native plant species protect the stream ecosystem most effectively. Therefore, regeneration of native and diverse plant communities is vital for the prolonged protection of stream environments. This study was conducted to evaluate the potential impacts that different land covers have on regenerating woody plant communities along headwater streams in two adjacent watersheds of Hunterdon County, New Jersey. Twelve headwater streams and their subwatersheds were selected based on the predominant land covers within the subwatershed. The subwatersheds were divided into three groups (land-cover classes) to reflect a disturbance gradient. Agricultural and urban dominated (Ag_Urban) subwatersheds represented the most disturbed, followed by agriculturally dominated forest/wetland (Ag_Forest_Wetland), and forest/wetland dominated subwatersheds (Forest_Wetland) represented the least disturbed. Overall, there were no significant differences between the seedling communities' species richness, density, and diversity based on the dominant land cover classes. Species-specific responses were more informative compared to community level measures and tended to vary based on the land cover category. There were greater similarities between seedling and mature tree species dominance in the Forest_Wetland class compared to the other two classes where there was greater similarity in the dominance of the seedling and mature components of several shrub species. This and similar studies contribute to our understanding of how riparian vegetation communities potentially react to a diverse landscape.

Introduction

Riparian zones serve as the transition from terrestrial habitats to stream habitats and irrespective of the relatively low percentage of the landscape that is occupied by riparian zones, they provide critical functions for the surrounding landscape. The persistence of the highly diverse and productive plant community within riparian zones is dependent on regeneration of the plant community. However, anthropogenic activities may influence the riparian zone's ability to be self-sustaining. Since the regenerating riparian plant communities indicate the future of the headwater streams and riparian habitat, it is important to better understand how anthropogenic impacts within the landscape can alter the composition of the regenerating vegetation community. Therefore, the objective of this study was to determine if regeneration of woody plant species in riparian zones along headwater streams is influenced by the predominant land cover within the watershed.

Headwater streams potentially have a significant influence on an entire watershed. In the United States, first-order streams comprise nearly fifty percent of the total river systems (Cushing and Allan, 2001). A study conducted on a typical Piedmont stream showed that 88.8% of the total stream length was first and second order streams (Sweeney, 1992). Small streams have the greatest potential for interaction with the terrestrial ecosystem because inputs are primarily limited to lateral flows from the land. In contrast, higher order streams receive input from both the land adjacent to the stream and from the upstream reaches (Lowrance et al., 1995). Therefore, headwater streams potentially bear more of a signature from the land covers within their catchment areas.

It has become increasingly important to understand aquatic-terrestrial interfaces from a water quality perspective. Near-stream vegetation has been shown to reduce nutrient and sediment transport from the terrestrial ecosystem to the aquatic ecosystem; to provide temperature control, which enables stream biota to thrive; and to assist in the maintenance of natural stream morphology by decreasing erosion and sediment deposition (Naiman and Décamps, 1997). The removal of near-stream vegetation has been shown to have many negative effects on stream ecosystems. Karr and Schlosser (1978) have shown that that the removal contributes to increased nutrient and sediment transport from terrestrial to aquatic ecosystems. Increased levels of nutrients and sediments have been shown to decrease the richness of aquatic macroinvertebrates that are usually found in undisturbed streams (Lenat and Crawford, 1994).

Riparian zones as well as other ecotones are unique in the fact that they contain an unusually high richness of species and are usually much more complex and dynamic than other ecosystems (Nilsson and Svedmark, 2002). High plant diversity may contribute to the riparian zones ability to fuction as efficient buffers that filter nutrients and sediments before they reach the stream system (Naimen and Décamps, 1997). For example, in a watershed that drains into the Chesapeake Bay, the most effective buffers for maintaining natural stream temperatures and controlling lateral subsurface and surface flow from terrestrial ecosystems were those with high levels of natural plant structural diversity (Lowrance et al., 1995). In addition to protecting streams, riparian plant communities provide substantial allochthonous (terrestrially derived organic material) inputs that supply critical food resources to aquatic ecosystems (Gregory et al., 1991).

The effects of both natural and anthropogenic disturbances on riparian plant species have been studied case-by-case, but there has been limited study of riparian plant communities positioned along a gradient of anthropogenic disturbance. For the purposes of this paper we consider disturbance as "any relatively discrete event in space and time that disrupts ecosystem, community, or population structure and changes resources, substrate, or the physical environment" (Pickett and White 1985). The intermediate disturbance hypothesis (Connell 1978) is a well-documented theory that describes patterns of species diversity and how they relate to various levels of non-anthropogenic disturbance; disturbance levels are characterized by frequency and severity. The intermediate disturbance hypothesis has provided a framework for studies focusing on disturbance gradients inherent in a stream's natural flow regime and flood frequency (Vervuren et al, 2003; Johansson and Nilsson, 2002; Abernethy and Willby, 1999). This hypothesis has also been applied to account for the longitudinal trends of stream systems where higher levels of species richness are found in the mid reaches than in the headwater and high order reaches (Tabacchi et al., 1996). However, this hypothesis has not been tested rigorously on a gradient of anthropogenic disturbances created by a change in land cover at the scale of the subwatershed.

Disturbances created by fragmenting the landscape have been shown to have considerable impacts on riparian plant communities. Deforestation, which is usually associated with agricultural expansion or increased urban development, has been proven to be one of the largest factors that contribute to declining habitat diversity in riparian ecosystems (Sweeney, 1992). Agricultural practices have also been shown to have detrimental effects on the plant diversity of riparian buffers in Denmark (Hald, 2002). Data from a stream system in Michigan showed that land use had a considerable impact on the habitat quality and biotic integrity of near-stream ecosystems: areas with less farming and more forest and wetlands have the most desirable in-stream habitat qualities (Allan et al., 1997). There has been little research conducted on why and how changing land covers affect riparian plant communities.

In New Jersey and specifically in the Piedmont region, where this study took place, urban sprawl has been a driving force in land cover changes over the last 20 years (Hasse and Lathrop, 2001). Developed land in the Piedmont region increased by 6.8% between 1986 and 1995 while forested and wetlands were reduced by 8.3% (Hasse and Lathrop, 2001).

Although studies have been conducted on the effects of agricultural land use (e.g Hald, 2002), relatively little is known about the impacts of other land cover types such as residential and urban mix regimes. Furthermore, New Jersey there has been little study of plant diversity patterns along small streams and even less study of how diversity is affected by land cover. Understanding what types of species dominate certain areas subjected to different land cover regimes, will be vital to determining the effects that dominant land cover has on species diversity and the regeneration of plant species. With this pressing need to understand how adjacent land cover affects the riparian plant community, hypotheses were formulated and tested based on the intermediate disturbance hypothesis (IDH). Specifically, we hypothesized that land altered to an intermediate degree would have greater diversity in the regenerating community than would catchments dominated by either thoroughly altered or by natural land covers. The results have implications for the ability of riparian communities to be self-sustaining. This study is part of a larger one that examined the influence of both current and historic land cover on the overall riparian plant community (Bakacs 2003).

Study Area

Research was conducted along two Piedmont streams, the Wickecheoke and Lockatong Creeks, in Hunterdon County, New Jersey (Figure 1). These two streams were selected because of their close proximities and similarities in geology, length, and flow direction. The Wickecheoke is fourteen miles long and drains a 26.57-square-mile watershed into the Delaware River at approximately 040° 24' 37.68"N and 074° 59' 15.97"W. The Lockatong lies directly northwest of the Wickecheoke, is thirteen miles long, and drains a 27.8-square-mile watershed into the Delaware River at approximately 040° 24' 28.35"N and 075° 00' 51.83"W. The upper halves of both watersheds are underlain by poorly drained Lockatong argillite, a lake bottom deposit formed during the Triassic period, while the lower halves are underlain by Stockton sandstone.

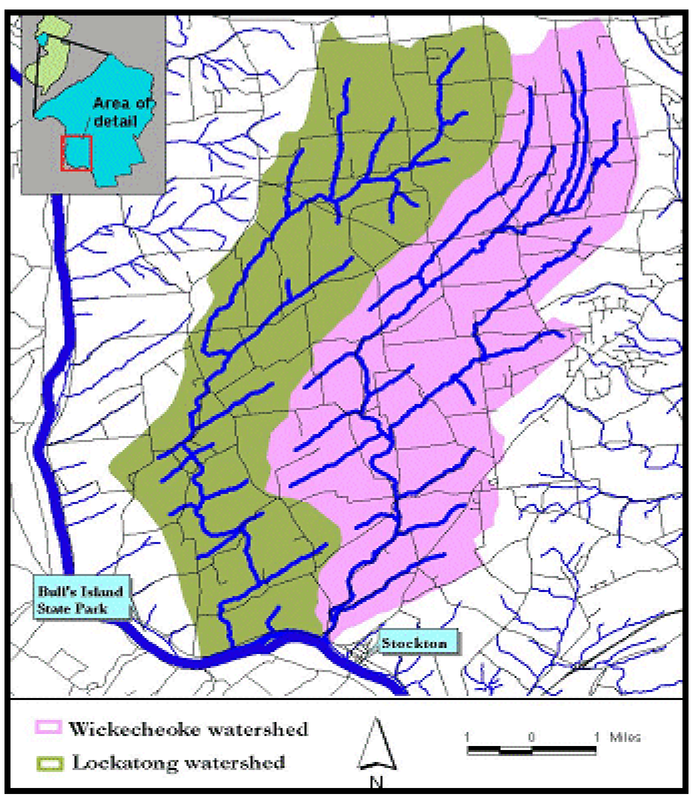


Figure 1. Location of the Wickecheoke and Lockatong Creek watersheds in Hunterdon County, New Jersey. The two watersheds flow into the Delaware River. Each stream has a similar geology, length, flow direction, and predominant land use.

Although these streams have many similarities, they differ in the spatial organization of the predominant land covers in their catchment areas (Figure 2). The upper portion of the Wickecheoke's watershed is dominated by forest and wetlands while agriculture is dominant in the lower portions of the watershed. The Lockatong, on the other hand, displays the reverse pattern. In the upper reaches of the Lockatong's catchment area, agriculture is predominant while forest and wetland are more dominant in the lower portions of the watershed. Commercial and residential land covers are scattered throughout both of the watersheds (NJDEP, 1995).

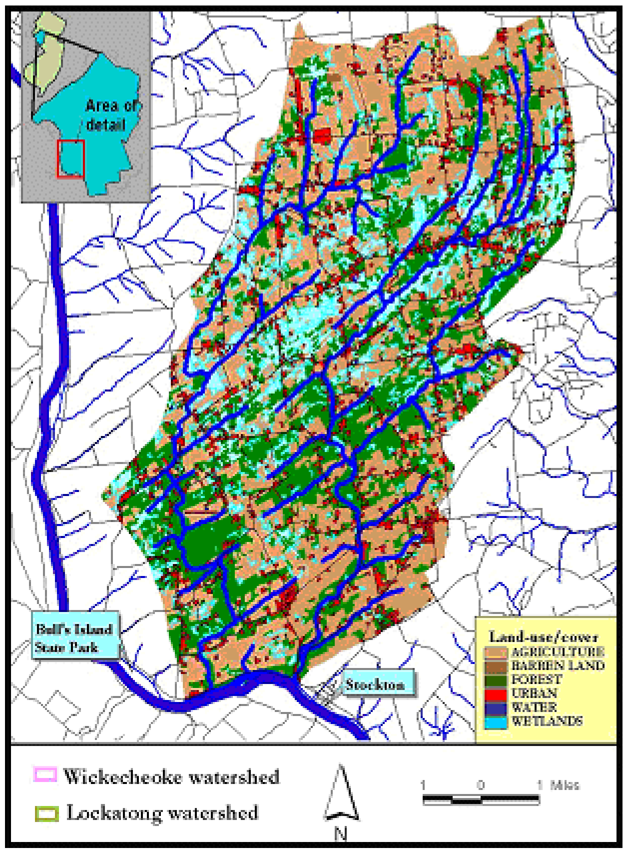


Figure 2. Predominant land covers of the Wickecheoke and Locaktong Creek watersheds in Hunterdon County, New Jersey.

The entire state of New Jersey has been experiencing changes in its land use regime. In Hunterdon County, where the Lockatong and Wickecheoke are located, the primary land use was agriculture in the early part of the twentieth century. Since that time, the amount of agricultural land has decreased as it has been converted to forested land and suburban development. Within the subwatersheds selected for this study, the area covered with upland forests increased from 14% in 1962 to 25% in 1995, cultivated land decreased from 68% to 49%, and developed land increased from 4% to 10% (Bakacs 2003).

Methods

Sixteen subwatersheds of headwater streams within the larger watersheds of the Wickecheoke and Lockatong Creeks were delineated and categorized as being either 1) forest/wetland dominated (Forest_Wetland), 2) agriculturally dominated forest/wetlands (Ag_Forest_Wetland), or 3) agricultural-urban dominated (Ag_Urban). The dominant land cover of each subwatershed was determined using the NJDEP 1995 land use/land cover maps and the Anderson Level 1 description (NJDEP, 1995 and Anderson et al., 1976). The Anderson 1 descriptions coarsely classify land cover into different classes including barren land, wetlands, agriculture, and forest. Four subwatersheds were chosen as replicates for each of the three dominant land cover classes (Table 1). The subwatersheds were given labels based on their positions within the larger watersheds and the stream with which they were associated. Labeling began at the northeastern part of each watershed with the letter 'A' and continued consecutively toward the southwest. After each letter an 'L' or a 'W'was placed to denote either Lockatong or Wickecheoke. The letter and number patterns are not consecutive along each stream because only twelve of sixteen sites originally considered were used in the final study.

The locations of the sampling sites were selected prior to the start of field collection by using United States Geological Survey (USGS) maps (1:24,000) and ArcView 3.3 (ESRI 2002). The expectation was that some of these locations might have to be changed based on conditions in the field. To capture the potential influence of land cover over an entire subwatershed, the sampling sites were chosen to be as close as possible to the downstream end. Further, to limit the influence of variables other than land cover, each study site was chosen to be at least 250 meters upstream from any major confluences or anthropogenic disturbance such as roads or dams. The selected sites were located in the field using a Global Positioning System (Trimble GeoExplorer3). After inspection in the field, the site locations were either accepted or changed slightly, depending on local disturbance, the existence of a riparian plant community, and accessibility. The data collection at each site was conducted during the plants' growing season, June-August, of 2002.

Field Procedures

The side of the stream sampled at each site was chosen randomly. Downstream aspect was determined, and the riparian aspect was then taken to be perpendicular (±90 degrees) to the downstream aspect. It was normally easy to determine the boundaries of the riparian plant community by observing sharp topographic shifts and/or marked increases in the prevalence of upland plants.

Two line transects were randomly located within the riparian zone at each sample site; they extended perpendicularly from the stream bank to the edge of the riparian zone.

Site Name	Land Cover				Total Dominant Land Cover Percentage (%)	Average % of Dominant Land Cover and Classification
	Developed	**Cultivated/ Grassland**	**Upland Forest**	**Palustrine Wetland**		
AW	**12**	**66**	13	7	78	79% **Ag_Urban**
DL	**7**	**66**	13	11	73	
EL	**6**	**80**	6	7	86	
HL	**16**	**65**	9	10	81	
BW	10	**42**	**18**	30	60	67% **Ag_Forest_Wetland**
FW	16	**40**	**29**	15	69	
IW	11	**42**	**23**	23	65	
JL	9	**48**	**26**	16	74	
CL	2	46	**42**	**10**	51	57% **Forest_Wetland**
DW	17	20	**31**	**32**	63	
FL	4	46	**31**	**19**	50	
IL	9	28	**45**	**19**	63	

Table 1: Total percent of each land cover and the resulting classification of either Ag_Urban dominated, Ag_Forest_Wetland dominated, or Forest_Wetland dominated for each subwatershed. The percentages in bold were used to obtain the average percent of the dominant land cover in each subwatershed and the final classification.

The first transect was always placed in the most downstream position possible within the subwatershed and the second transect was located fifty to one hundred meters in the upstream direction.

On each transect, one vegetation sampling plot (10 m x10 m) was placed at the edge of the stream (near-stream plot) and one at the edge of the riparian buffer (far-stream plot). For transects longer than 40 m, a third plot was placed in between. Within each of the vegetation plots, six one-meter-square seedling quadrats were placed randomly using a random number counter and a grid system. Within these quadrats, all tree and shrub seedlings were identified, measured, and recorded. Any tree shorter than the height of 1.3 m was considered a seedling; a shrub was considered to be a seedling if it did not exceed 0.33 m in height.

All mature, woody plants within each 10 m x 10 m plot were identified by species and the abundance of each species was recorded. Land use directly adjacent to the riparian zone was also classified as being a cultivated field, a fallow field, a low-density housing development, a mature upland forest, or a mid-successional forest.

Data Analysis

The sampling regime allowed the examination of patterns of vegetation regeneration at different scales. At the broadest scale, the data were analyzed by land cover to determine whether there were regeneration differences associated with the three different dominant land cover delineations. The vegetation plots were also analyzed at a near-stream and far- stream scale, to examine variation within the site. The vegetation sampling plot was the smallest scale at which the data were analyzed; these data were used to study species-specific patterns within the riparian zone based on site and land cover classes.

Means and standard errors were calculated for seedling species richness and seedling density for each site. One-way Analysis of Variance (SAS Ver 8.02, 2002) was used to determine if there were significant differences in seedling measures among the different land covers. Importance values were calculated for each seedling species using the formula: Importance Value = (Relative Frequency + Relative Density) x 100 (Smith and Smith, 2001), where the frequency of species A is determined by:

$$\text{Frequency (A)} = \frac{\text{Number of Plots in which 'A' Occurs}}{\text{Total Number of Plots}}$$

Relative Frequency and Relative Density are determined by:

$$\text{Relative Frequency} = \frac{\text{Frequency of Species 'A'}}{\text{Total Frequency of All Species}}$$

$$\text{Relative Density} = \frac{\text{Total Individuals of Species 'A'}}{\text{Total Individuals of All Species}}$$

The total importance value cannot exceed 200 for each seedling species within a site. The relative importance values for seedlings were also adjusted in order to compare them with importance values for mature shrub and tree species using the following formulas:

$$\text{Relative Seedling Importance Value} = \frac{(\text{Relative Density} + \text{Relative Frequency}) \times 100}{2}$$

$$\text{Relative Tree Importance Value} = \frac{(\text{Relative Density} + \text{Relative Frequency} + \text{Relative Cover}) \times 100}{3}$$

$$\text{Relative Shrub Importance Value} = \frac{(\text{Relative Density} + \text{Relative Frequency} + \text{Relative Volume}) \times 100}{3}$$

Relative Density and Relative Frequency were determined for trees and shrubs in the same manner as for seedlings above. For Tree Importance Values, Relative Cover for the mature tree species was calculated by converting measures of diameter at breast height (dbh) to basal area using the formula: Basal Area of Species 'A' $= \pi(\text{dbh Species 'A'} \div 2)^2$, where dbh = diameter at breast height of species 'A.' For Shrub Importance Values, Relative Volume was determined by multiplying shrub height by shrub width and depth to derive an approximate shrub volume measurement.

Finally, to compare variation in seedling measures within the riparian zone, a one-way Analysis of Variance (ANOVA) was used to test for differences between the plots adjacent to the stream versus plots at the outer edge of the riparian zone. The ANOVA was used to examine seedling community measures including species richness, species density, and species diversity.

The seedling data were also compared with the tree canopy and the shrub layer (overstory) at the species-specific level to determine if the regeneration plant species were similar to those already dominating the riparian plant community. This comparison was conducted using importance values of the dominant seedling species in each land cover, i.e. the species occurring in at least two out of the four replicate sites within a land cover category (Table 2). Site importance values of the dominant seedling species were summed across the multiple sites within a land cover to get a total importance value for a particular species based on dominant land cover. The respective importance values of the mature species were summed within a land cover in a similar manner.

Results

Land Cover

The total number of regenerating woody seedling species recorded within all the land cover classes was 48. Within each of the specific land covers, however, the species richness varied. Species richness was highest at the Ag_Forest_Wetland sites with a total of 30 different species, followed closely by Forest_Wetland with 28 species. Ag_Urban sites were lowest with a total of 19 species. However, total species richness did not significantly vary by land cover ($F=21.0$, $p= 0.18$).

Species density showed a trend similar to that of species richness. The sites located within the Ag_Forest_Wetland land cover class exhibit the highest density of species with 4.00 ±1.03(standard error) seedlings/m2. The next highest density was within the Forest_Wetland sites where there were 3.00 ±1.20 seedlings/m^2, and the lowest species density was found in the Ag_Urban land class with a density measure of 2.00 ±0.83 seedlings/m^2. However, differences in species density werenot statistically significant at the land cover scale ($F=0.72$, $p=0.51$).

Species diversity was measured using the Shannon-Weiner Index (Krebs, 1999), Sites located within the Forest_Wetland classification exhibited the highest diversity index followed by sites in the Ag_Forest_Wetland category and the Ag_Urban classes, respectively (Figure 3). A Forest_Wetland site displayed the highest diversity index, 2.59, while the lowest score, 0.796, was displayed by a Ag_Forest_Wetland site. As with species richness and density, differences in species diversity data at the land cover scale were not statistically significant ($F=1.40$, $p=0.39$)

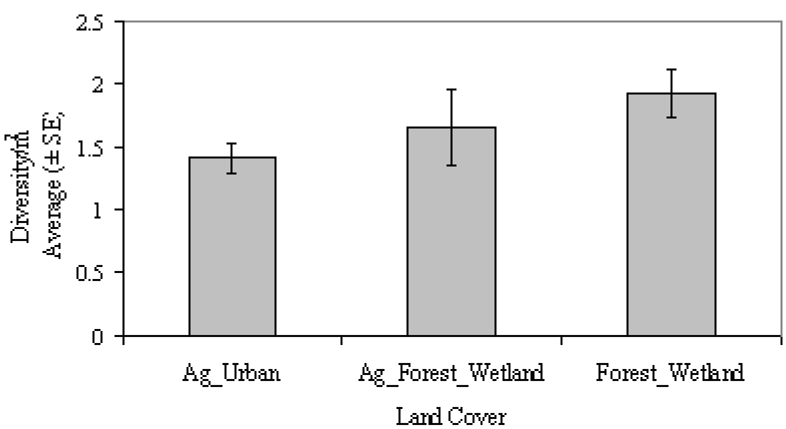


Figure 3. Seedling species diversity (Average ± Std Error)for each of the land cover classes.

Species-specific analysis

Seedling Species Dominance in each Land Cover. To examine which regenerating species were important in the different land covers, the five seedling species in each land cover classification with the highest average importance values, were identified (Table 2). No one seedling dominated across all land covers. For example, the tree seedlings *P. serotina* (black cherry) and *Nyssa sylvatica* (black gum) were more dominant in the Ag_Urban subwatersheds. *P. serotina* was also present in Forest_Wetland sites but was of less importance. *N. sylvatica*, on the other hand, was dominant only in the Ag_Urban subwatersheds. In Ag_Forest_Wetland subwatersheds, *Carpinus caroliniana* (ironwood) and *Q. palustris* (pin oak) were the dominant tree seedling species. However, these species displayed differences between their dominance in the other two land cover classes. *C. caroliniana* was a dominant seedling species primarily in the Ag_Forest_Wetland subwatersheds and, to a lesser extent, a dominant species in the Forest_Wetland subwatersheds. In contrast, *Q. palustris* was an important dominant in both Ag_Forest_Wetland subwatersheds and Forest_Wetland subwatersheds.

Within the Forest_Wetland subwatersheds, *Fraxinus americana* (white ash) and *Ostrya virginiana* (eastern hophornbeam) were among the most dominant woody seedling species (Table 2), but they varied markedly in other land cover classes. *F. americana* was a dominant species in the communities with an Ag_Forest_Wetland land cover, but was limited in communities in Ag_Urban subwatersheds. *O. virginiana* was the only seedling species that was found in just one land cover classification.

Lindera benzoin (spice bush) and *Vibernum prunifolium* (black haw viburnum) were the two dominant shrub seedling species (Table 2). Like the tree seedlings, these species had different trends in relation to dominant land cover. *V. prunifolium* was a dominant within Ag_Forest_Wetland subwatersheds and had much lower importance values in the other two land cover classes. In contrast, *L. benzoin* displayed a decreasing gradient in dominance from Ag_Urban to Forest_Wetland land covers. Within the Ag_Urban subwatersheds, *L. benzoin* had the second highest importance value being superseded only by *P. serotina* indicating that this shrub species is an important component of the regenerating community in this particular land cover. In the Ag_Forest_Wetlandland subwatersheds, both *L. benzoin* and *V. prunifolium* were important while in the Forest_Wetland land cover, no shrub species were consistently important.

Species	Species Abbreviation	Land Cover		
		Ag_Urban	**Ag_Forest_ Wetland**	**Forest_ Wetland**
Trees:				
Acer rubrum	ACERUB	**19.39**	17.50	**24.26**
Carya ovata	CAROVA	**20.38**	15.59	20.04
Carpinus caroliniana	CARCAR	2.47	**46.39**	15.41
Prunus serotina	PRUSER	**53.21**	2.93	**24.39**
Fraxinus americana	FRAAME	2.85	**19.41**	**22.58**
Nyssa sylvatica	NYSSYL	**23.16**		4.29
Ostrya virginiana	OSTVIR			**47.81**
Quercus palustris	QUEPAL	2.00	**38.23**	**31.83**
Shrubs:				
Viburnum prunifolium	VIBPRU	7.21	**23.33**	1.35
Lindera benzoin	LINBEN	**43.16**	**27.07**	6.30

Table 2. Importance values for the dominant seedling species in each land cover classification. The five largest values in each category are bolded.

Comparison of Seedling Species Dominance and Mature Species Dominance. To determine if the regenerating communities were similar to the existing mature plant communities, the dominant seedlings' importance values (Table 2) were compared with the respective relative importance values of their mature counterparts. In general, the patterns varied among the different land covers as well as among the different species. For example, within the Forest_Wetland subwatersheds the importance values were consistently higher for seedlings compared to mature importance values (Figure 4) indicating that dominant tree seedling species were more dominant in the regenerating communities than in the mature communities. This trend was especially obvious with *P. serotina* and *O. virginiana*. It is also interesting to note that all eight seedling species that exhibited dominance in at least one land cover category and all eight were present in this particular category with varying degrees of dominance.

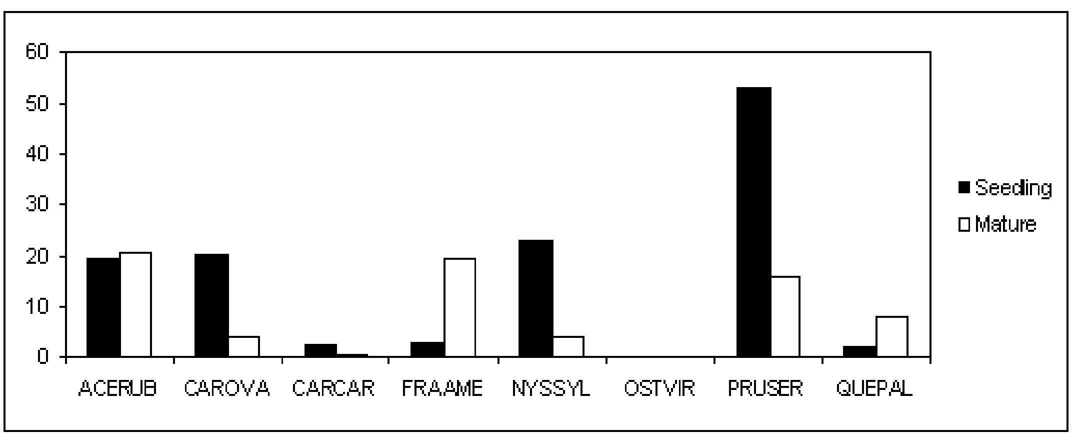
In the Ag_Forest_Wetland dominated subwatersheds, two species, *N. sylvatica*, and *O. virginiana* had no seedlings present and very few mature individuals while the opposite was true for *P. serotina* where there were no mature individuals but some seedlings. Generally, the mature dominance was less for each of the species in the Ag_Forest_Wetland compared to the Forest_Wetland.

Patterns were notably different in the Ag_Urban subwatersheds compared to the other two classes of land cover. *F. americana* was one of the dominant species within the canopy, but had quite low importance values within the seedling layer. The other species that was more dominant as a mature species than as a seedling species was *Q. palustris*, but its dominance in both of the layers was low compared to those of the other species in this particular land cover category.

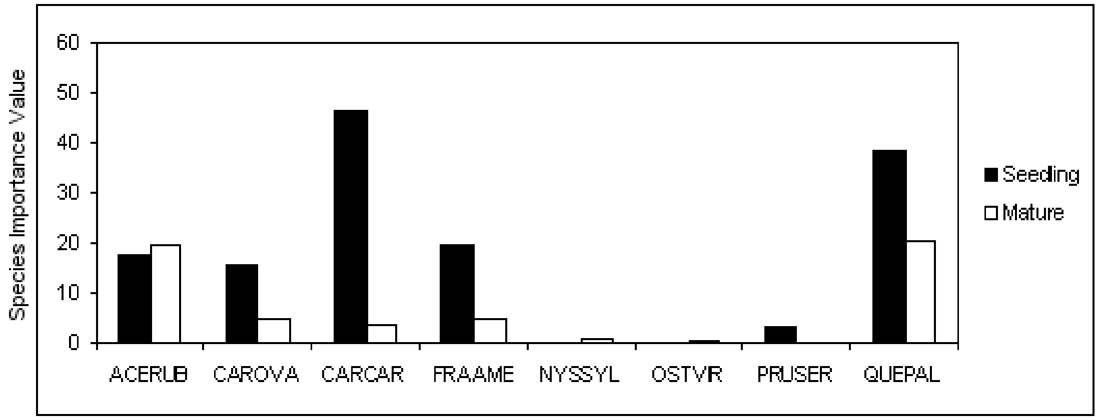
None of the tree species exhibited a similar pattern across the three different land cover classes. The closest was *C. ovata* where dominance values were similar for seedlings across the land cover classes. Seedling dominance was higher than mature dominance but mature dominance was over two times greater in the Forest_Wetland subwatersheds compared to the other two watersheds.

For the two dominant seedling shrub species, the importance values for both the seedling and mature components of *L. benzoin* decreased from Ag_Urban to Forest_Wetland subwatersheds (Figure 5). However the decrease was markedly greater for the seedlings than for the mature component and in fact, in the Forest-Wetland category, mature dominance was almost twice as large as seedling dominance. *V. prunifolium* was a more dominant component of the community in the Ag_Forest_Wetland category. Similar to that of *L. benzoin*, *V. prunifolium* seedling dominance was lower than mature dominance in the Forest_Wetland subwatersheds. Within each land cover, *L. benzoin* had a higher dominance in both the seedling and mature layers than did *V. prunifolium*.

Ag_Urban



Ag_Forest_Wetland



Forest_Wetland

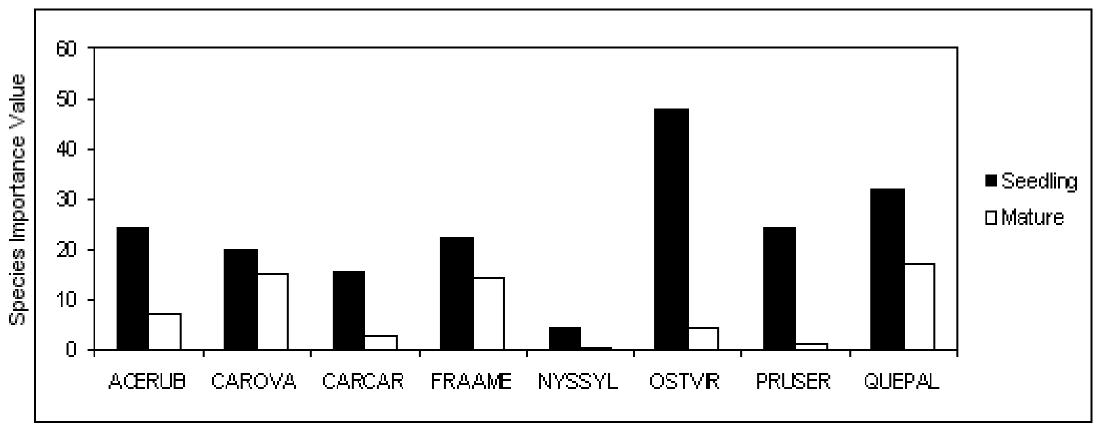
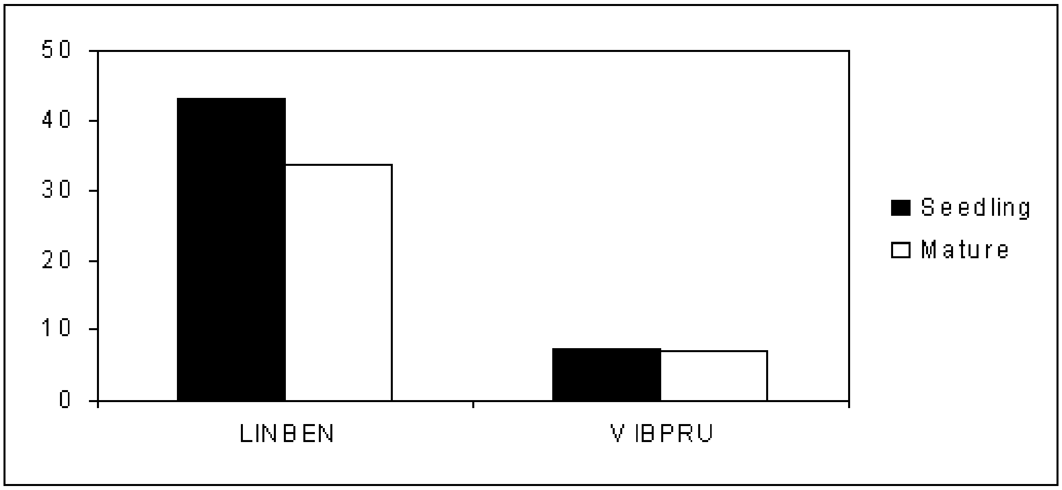
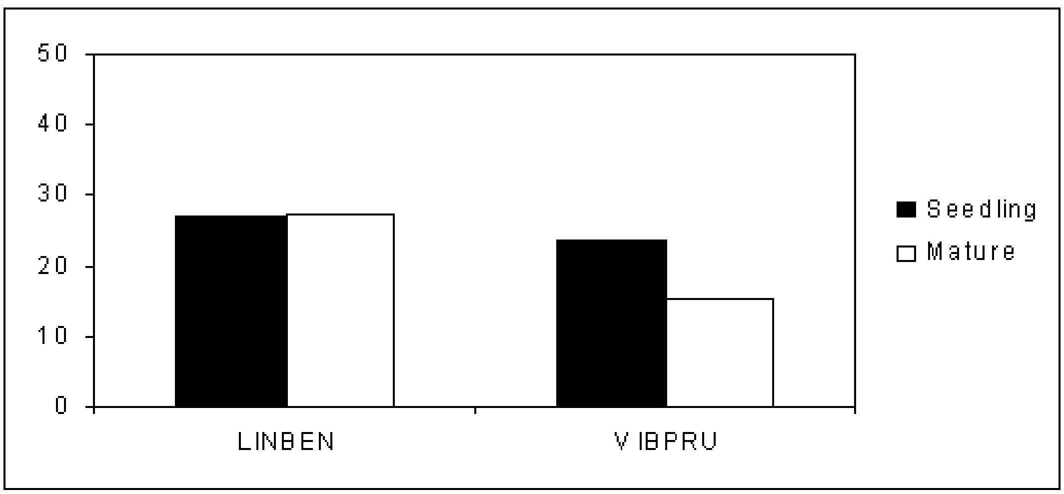


Figure 4. Comparison of importance values for the dominant tree seedlings (Table 2) and their mature counterparts in each of the land cover classes. (Refer to Table 2 for species abbreviations.)

Ag_Urban



Ag_Forest_Wetland



Forest_Wetland

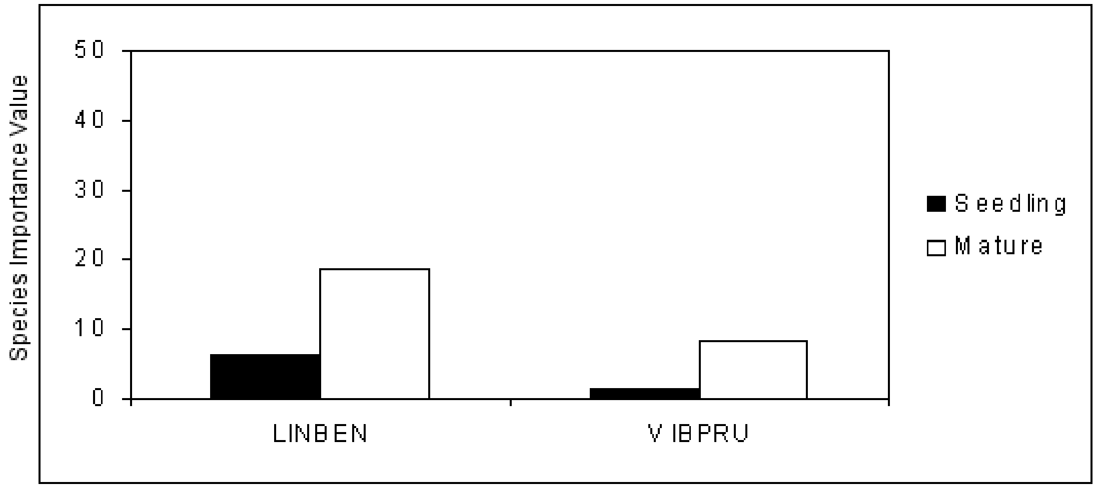


Figure 5. Comparison of importance values for the dominant shrub seedlings (Table 2) and their mature counterparts in each of the land cover classes. (Refer to Table 2 for species abbreviations.)

Discussion

Riparian zones are subjected to many different influences that may affect the plants that grow there. There are regional factors such as land cover and climate; local factors such as sunlight, soil type and pH, nutrient availability, micro-topography; and moisture, biotic factors such as competition, and both natural and anthropogenic disturbance factors. All of these factors can affect a plant species' ability to persist. The hypothesis tested in this study concerns the local anthropogenic disturbance created from different land cover types. The regeneration of natural plant communities within riparian zones is vital to the protection of entire stream systems. Because different disturbances associated with land cover might affect plant communities and individual species differentially, it is important to study community level responses as well as species-specific responses to a land cover disturbance gradient. The responses of the vegetation community and the individual species to external land cover disturbances will potentially determine the future structure and composition of the riparian communities.

The intermediate disturbance hypothesis (IDH) predicts the behavior of species diversity under differing levels of disturbance (Connell, 1978). This hypothesis predicts that moderately disturbed areas will contain the most species diversity because the magnitude and frequency of disturbances are not great enough to destroy entire plant communities. Therefore, there is available space for colonization of new species while a portion of the pre-disturbance community still exists. In contrast, areas that are disturbed more frequently and intensely will contain less species diversity because only those species that have the capability to regenerate quickly between disturbance events will prevail. On the other hand, areas where disturbances are infrequent and lesser in magnitude will also contain low species diversity because there, the species that are superior long-term competitors will have displaced their rivals. IDH has been used as a framework to study patterns in riparian systems that experience different levels of natural disturbance from flooding (Bendix, 1997). However these patterns have not been examined in the context of anthropogenic disturbances that are associated with different types of land covers.

IDH also suggests how patterns of plant regeneration might be related to the mature plant community in areas with different amounts of disturbance (Connell, 1978). Areas that have a moderate disturbance signature should contain mixed communities that are very diverse in both the mature canopy and in the regenerating layer. More frequently and intensely disturbed areas will be expected to have a regenerating community that is similar to the plant community that persisted through the disturbance as these species are within the closest dispersal range. These areas should also contain relatively high levels of regeneration among the species that persisted as interspecific competition will be less due to the lack of species diversity. Conversely, more stable areas that experience decreased disturbance levels are expected to contain similar species within their regenerating and canopy communities. This inferred pattern is based on the assumption that once an ecosystem has reached its mature, stable condition, the species effectively retard invasions from other species. Though both high and low levels of disturbance predict low diversity, species composition would not be similar. In frequently disturbed sites, species composition would comprise early successional species while infrequently disturbed sites would comprise of superior competitor species. The predictions afforded by IBH for the regenerating community were examined within the subwatersheds to determine if differences in dominant land cover had a differential impact on the regenerating community.

Influence of Land Cover on Aggregate Vegetation Patterns

Species composition measures, including species richness, density, and diversity exhibited different patterns between the different dominant land covers (though many were not statistically significant). The Ag_Urban sites consistently exhibited lower measures of species richness, density, and diversity in the regenerating community compared to the other land cover classes. Similar patterns were also observed in the tree canopy of these sites (Bakacs 2003). These consistent results potentially suggest that the Ag_Urban land cover, which we considered had the most intense and frequent disturbance signature, reflects patterns expected in IDH with a less diverse plant community, dominated by a few similar species.

The Forest_Wetland and Ag_Forest_Wetland subwatersheds were more similar to one another than eiterh one of them was to the Ag_Urban subwatersheds. The Forest_Wetland and Ag_Forest_Wetland subwatersheds had relatively high species density and richness in the seedling layer, but the Ag_Forest_Wetland subwatersheds had higher measures in each case. However, the Forest_Wetland subwatersheds had higher levels of seedling species diversity. These are trends that would not be expected under IDH. Forest_Wetland sites hypothetically represented the least disturbed land cover classification, and thus, would be expected to have lower species diversity.

Species-Specific Trends

Because many species have particular growth habits and can be easily affected by different levels of disturbance, it was important to examine the trends exhibited by individual species as well as by the aggregate plant communities. When seedlings of species were examined from a land cover perspective, certain trends became apparent for different species. Importance values for *A. rubrum* and *C. ovata* seedlings did not vary markedly across the dominant subwatershed land covers. These species may be insensitive to the influence of land cover and may reflect tolerance for a wide range of conditions and disturbance regimes. This finding is somewhat counterintuitive for *C. ovata* inasmuch as it is slow growing, has intermediate shade tolerance, and normally requires up to 40 years before an individual tree reaches seed- bearing age (Tirmenstein 1991). The prevalence of *A. rubrum* and *C. ovata* across all land cover classes suggests that these two species may be generally important in determining overall seedling community composition and future community structure of the riparian zone irrespective of the predominant surrounding land cover.

N. sylvatica and *P. serotina*, both early successional species frequently associated with disturbance, were among the dominant species in the Ag_Urban subwatersheds. *P. serotina* had the highest importance values of all of the seedling species in this particular subwatershed class. This species regenerates in canopy gaps where sunlight reaches the forest floor (Curtis 1959). It is common to find the highest regeneration of *P. serotina* seedlings in areas where the species is dominant in the canopy (Uchytil 1991), a pattern observed in the Ag_Urban sites (Figure 4). However, *P. serotina* was also one of the dominant seedling species in the Forest_Wetland subwatersheds, though not a dominant component of the canopy. Evidently, the Forest_Wetland sites have both adequate light in the understory and a seed source to facilitate this species' seedling dominance. In a true climax habitat, early to mid-succession species such as *P. serotina* would not be expected to be an important component of the seedling community. Its presence, therefore suggests that these particular Forest_Wetland sites are not fully developed climax habitats.

In the Ag_Forest_Wetland subwatersheds, *C. caroliniana* and *Q. palustris* were the dominant seedlings. Both, and in particular, *Q. palustris*, were also important components in the Forest_Wetland subwatersheds. Both species are mid- successional species and the seedlings are somewhat shade tolerant. However, the high density and dominance of C. caroliniana in the Ag_Forest_Wetland subwatersheds suggests that conditions are particularly favorable for seedlings of this species. The seeds of this species are primarily bird dispersed and seedlings can tolerate deep shade. However, it is not clear what was so favorable for the Ag_Forest_Wetland sites over the other sites.

The dominance of *O. virginiana* in Forest_Wetland subwatersheds may indicate that these subwatersheds are in later stages of succession than the other subwatershed classes. *O. virginiana* is a later succession sub-canopy species (Coladonato, 1992, Metzger 1990) and seedlings and adults are shade tolerant. Birds and wind disperse the seeds of this species and adult plants begin to produce seeds at approximately 25 years of age depending on site conditions.

Two shrub species, *L. benzoin* and *V. prunifolium*, and three tree species were found to be dominant in the seedling community in Ag_Forest_Wetland subwatersheds . In contrast, in the Forest_Wetland subwatersheds, all five of the dominant seedling species were tree species. Both *L. benzoin* and *V. prunifolium* are shade tolerant and are found in association with a number of different tree species. The reason for the high dominance of *L. benzoin* in the Ag_Urban subwatersheds is not clear. This species is one of the most common species found within the understory communities of mid-successional and mature moist forest systems in New Jersey (Martine, 2002) and so to observe its predominance in the Ag_Urban land cover sites is counter-intuitive. In contrast, *V. prunifolium* is common along edges and in drier areas of thin forest patches (Martine, 2002).

Comparison of Seedling Importance and Mature Importance Measures

According to the IDH, in areas where there are intermediate levels of disturbance, the composition of the regenerating and the mature communities should differ due to increased species diversity in both vegetation layers. For example, as space becomes available via disturbance, while there is the chance that a seedling from the local mature community might become established, there is also the chance that a species not present in the canopy could become established, thus contributing to greater differences in the species composition in the two vegetation layers. Conversely, the expectation would be greater similarity in less or more disturbed areas. The Forest_Wetland sites exhibited the trends that might be expected in less disturbed areas in that there was greater consistency between the two vegetation layers (i.e. what was dominant in the mature layer was also important in the seedling layer, Figure 5). However, the Forest_Wetland subwatersheds contained a very high diversity of mature and seedling species, which might indicate they resemble moderately disturbed patterns more closely than minimally disturbed patterns. In addition, the Forest_Wetland sites and Ag_Forest_Wetland sites were also very similar to one another with respect to seedling diversity, seedling species richness, and seedling species density, which might further support the assertion that the Forest_Wetland communities might be better described as moderately disturbed areas than as stable areas.

For the Ag_Forest_Wetland sites where the expectation would be for greater discrepancies in dominance between the seedling and mature vegetation layers, six of the eight tree species and both shrub species were dominant in both layers though less so in the mature layer. The two missing species are of note since one (*N. sylvatica*) is an early successional species and the other (*O. virginiana*) is a later successional species. Moderately disturbed areas should comprise both early successional species and later successional species and the combination of both types of species in an area has been shown to facilitate the regeneration of faster-growing species while slow-growing species are still present in the canopy (Smith and Smith, 2001). Based on IDH, it would be expected that all the seedling species that were dominant across the land covers would be regenerating in Ag_Forest_Wetland (Tabacchi et al. 1996; Connell, 1978).

The Ag_Urban dominated subwatersheds exhibited patterns that differed from what might be expected in communities that are subjected to high levels of disturbance. The dominant species in the mature community were *A. rubrum*, *F. americana*, *P. serotina*, and *Q. palustris*.

Based on the intermediate disturbance hypothesis, it might be expected that these species would dominate in the regenerating community because they are closest to the disturbed land area. However, only *P. serotina* and, to some extent, *A. rubrum* followed this trend, while two species, *F. americana* and *Q. palustris*, opposed it. (Meiners et al., 2002) found that *A. rubrum*, *A. saccharum*, and *Q. palustris* regenerate differently in areas of forest versus old field, Specifically, they found found that *Q. palustris* emerged in areas further from the forest edge because the species is highly shade intolerant. This pattern differs from results of our study because the Ag_Urban sites, areas with the most amount of light and where shade intolerant species should thrive, displayed the lowest dominance of *Q. palustris* seedlings of the three land cover classes. It is notable that light levels in our study sites, even in the Ag_Urban sites, were consistently lower than that of the old-field portion of the Meiners et al. (2002) study. Comparatively across the three land cover categories, however, light levels were greater in the Ag_Urban sites yet the other two land categories had higher dominance of *Q. palustris*. Factors other than light availability may be contributing to low regeneration of these particular species, but if the pattern continues, *F. americana* and *Q. palustris* may decline in the Ag_Urban subwatersheds.

Conversely, species that are not dominant in the canopy in Ag_Urban subwateesheds would be expected to have lower importance in the seedling community due to lack of seed source and lack of persistence between frequent disturbance events. This trend was best illustrated by the species *C. caroliniana* and *O. virginiana*, mid and late successional species respectively. They displayed very low relative importance values for both the seedling and mature individuals. However, this pattern is contradicted by *F. americana* and *Q. palustris*, both of which exhibited canopy dominance but very low seedling dominance. In fact, *F. americana* is one of the most dominant species in the mature canopy. Both species are early to intermediate successional species and should have a strong representation in the seedling layer. Our results indicate a general lack of regeneration of these two particular species in Ag_Urban subwatersheds. The mixed results in this particular land cover class suggest that our hypothesized disturbance gradient in land cover does not closely follow the predictions of IDH.

For the two shrub species, patterns in the Ag_Urban and Forest_Wetland subwatesheds are consistent with the predicted trends for different levels of disturbance. In the Forest_Wetland subwatersheds, the presence of mature shrubs assures a source of seeds, which implies that the low regeneration of the shrubs might reflect the relative inability of the shrub seedlings to compete in less disturbed environments. In lesser-disturbed areas, the canopy trees exclude other species by blocking out substantial amounts of light or by using resources more efficiently (Connell, 1978). The regeneration of *L. benzoin* and *V. prunifolium*, two understory shrub species, may be affected by low light levels. Unless regenerating species are adapted to shade tolerance, understory trees and shrubs would have a harder time regenerating in areas that are less frequently disturbed even though they might be dominant within the mature community. However, *L. benzoin*, as mentioned previously, is shade tolerant and is usually found to dominate understory areas of moist forests (Martine, 2002). Conversely, in the Ag_Urban subwatersheds, high dominance values in both the regenerating layer and the mature layer for *L. benzoin* could indicate that this species does well with high levels of disturbance, persisting through the disturbance. *V. prunifolium* is present but perhaps less disturbance tolerant. For the Ag_Forest_Wetland subwatersheds, comparable regeneration in both vegetation layers for both species indicates comparable persistence.

Conclusion

The initial hypothesis was that varying amounts of human-altered land cover within a watershed represented a disturbance gradient that would influence seedling regeneration. The IDH was used as a framework by which to compare different regeneration patterns. Studies that draw upon IDH to test predictions usually include a wide array of disturbance levels. This study included three different levels, which might not be enough to characterize the full scope of the disturbance gradient, but instead captured just a portion of the predicted IDH patterns. For example, the Ag_Forest_Wetland and Forest_Wetland land classes were similar in both their aggregate regenerating communities and their species-specific trends. These results might indicate that the Forest_Wetland sites were not functioning as the relatively undisturbed stable areas and that their disturbance regime may have been more similar to the Ag_Forest_Wetland sites. In the last fifteen to thirty years, an increasing percentage of agricultural land within the subwatersheds has reverted to forest. Historical analysis (Bakacs 2003) revealed that some of the sites were formerly agricultural land which likely shaped the plant communities to a greater extent than current dominant land cover at the subwatershed scale. The general classification of existing dominant land cover as the primary disturbance gradient did not capture this successional timeline. A more detailed study of the relationship between current and historic land cover may help further elucidate the observed patterns.

This study only focused on the potential influence of dominant land cover within a subwatershed on the riparian vegetation regeneration. Many factors influence the regeneration of the riparian community (Bendix, 1997, Spink et al., 1998 and Tabacchi et al., 1996), and to truly understand the future potential of these riparian communities to persist and maintain their current character, more detailed study is required. A better understanding of how the physical environment influences regeneration patterns is necessary. In addition, within the watersheds of the Wickecheoke and Lockatong, there is an abnormally high density of white-tailed deer (*Odocoileus virginianus*) when compared with other regions in New Jersey (NJ Division of Fish and Wildlife Online, 2003). Previous research has indicated that when deer were excluded from riparian vegetation, there was a higher rate of regeneration of plant species (Opperman and Merenlender, 2000). Within the subwatersheds sampled along the Wickecheoke and Lockatong streams, many of the woody seedling species were substantially less than one meter high. This may indicate that many of the seedlings sampled were in early stages of development and that the seedlings are not able to reach maturity. Additional study would help determine whether the high occurrence of deer in the area might be one factor contributing to the low stature of the woody seedling species within the riparian zone. As previously mentioned, the role of historical land cover in the subwatersheds on the regenerating plant community is essential to understand how abandoned farm land conversion to forest land influences successional and regeneration patterns. Finally, the role of invasive species in the regenerating riparian communities in this study requires further attention.

The seedling regeneration patterns did not follow the intermediate disturbance hypothesis as we had predicted. In fact, two of the land cover classes, Ag_Forest_Wetland and

Forest_Wetland, responded similarly in terms of their community level measures of regeneration patterns. This finding may indicate that at least for these two classes, *any* disturbance associated with land cover affected the overall seedling community in similar ways.

Specific species provide a better indicator of land cover impacts within the subwatersheds examined. In the Forest_Wetland subwatersheds, the lack of dominance of two shrub seedling species may indicate low persistence of these native species in the future forested community. *Q. palustris* and *F. americana* may become more minor members or be lost from the Ag_Urban subwatersheds. More generally, there was a difference in the regeneration dominance of particular species that varied with the land cover disturbance gradient. Forest_Wetland and Ag_Forest_Wetland dominated subwatersheds displayed regeneration patterns that typify moderately disturbed areas with a wide variety of species regenerating within these land covers including fast and slow growers and shade tolerant and intolerant species. In contrast, the Ag_Urban sites do not display similar diversity in their regenerating layer, but rather were dominated by fewer species that include both early and mid-succession species. Other factors not considered here are also likely be important, among them local and historic conditions dynamics. A long-term study may provide additional insight. While we cannot identify the causal mechanisms associated with dominant land cover that contributed to the patterns observed, the fact that they are present demonstrates the importance of better understanding the role of land cover on persistence of the riparian plant community.

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