WETLANDS, Vol. 19, No. 2, June 1999, pp. 365-371

THE SEED BANKS OF A SOUTHERN APPALACHIAN FEN AND AN ADJACENT DEGRADED WETLAND

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Abstract: Bogs and fens are rare communities in the southern Appalachians of the USA. Many have been degraded, and little ecological information beyond cursory floral inventories is available to help guide conservation and restoration efforts. The seedling emergence technique was used to examine the soil seed banks of open and closed canopy regions of a southern mountain fen in North Carolina. We also examined the seed bank of an adjoining portion of the floodplain, which had been drained and cleared for a golf fairway and is now slated for restoration. A total of 32 taxa emerged, with graminoids (particularly *Juncus* spp.) dominating all three seed banks. Seedlings were assigned to one of five plant types: woody, rush, sedge, grass, or forb. Significantly more woody seedlings emerged in soils from the closed canopy fen than in soils from the other two areas. Most rush seedlings emerged in open canopy fen soils, more sedge and forb seedlings emerged in floodplain soils, and more grass seedlings emerged in floodplain soils than in closed canopy fen soils. A discriminant function analysis separated the open canopy fen from the closed canopy fen and floodplain by seedlings of woody plants and rushes. The floodplain was separated from the open and closed regions of the fen by sedge and grass seedlings. These patterns in seed bank composition bore little similarity to the standing vegetation in the three areas. Restoration activities planned for the floodplain are intended to restore its hydrology and microtopography, which will strongly influence recruitment from the seed bank and surrounding seed sources.

Key Words: southern Appalachians, fen, floodplain, seed bank, wetland restoration

INTRODUCTION

Mountain bogs and fens are rare communities in the southern Appalachians. Fewer than 500 may remain in the Appalachian Highlands (Moorhead and Rossell 1998), and many of these have been degraded by logging, ditching, road construction, grazing, or highway and farm runoff. Interest in restoring and managing the remaining wetlands has increased. However, little is known about the dynamics of plant communities in these systems, as only cursory floral surveys have been conducted at some sites (Weakley and Schafale 1994).

Soil seed banks, which represent the viable reserves of seeds in soil, may provide clues to the vegetational history of a site and may help predict future vegetational communities. Seed banks have been studied in a variety of wetland types, including freshwater marshes (van der Valk and Davis 1976, Poiani and Johnson 1988), swamps (Schneider and Sharitz 1986, Titus 1991), riparian forests (Hanlon et al. 1998), lake shorelines (Wisheu and Keddy 1991), Carolina bays (Poiani and Dixon 1995), and freshwater tidal marshes (Parker and Leck 1985). However, virtually no work has investigated seed banks in bogs or fens. We found only three published studies: one of a Canadian bog (Moore and Wein 1977), one of a quaking fen in the Netherlands (van der Valk and Verhoeven 1988), and one of a southern Appalachian bog (McGraw 1987). Additional studies on the species composition of wetland seed banks are needed to help assess the contribution that seed banks can make to wetland restoration projects (van der Valk et al. 1992).

Typically, the species composition of a seed bank is analyzed by floating or otherwise separating seeds from soil or by allowing seedlings to emerge in a greenhouse. A detailed comparison of these two methods can be found in Brown (1992). Since it is generally easier and more accurate to identify seedlings rather than seeds, the seedling emergence technique is most often the method of choice, particularly if most of the seeds are very small (Brown 1992). Although this method may underestimate species with germination requirements that are not met in the greenhouse, Poiani and Johnson (1988) reported that it accurately estimated the seed composition of semi-permanent prairie wetlands.

In this study, we used the seedling emergence technique to examine the seed banks of two plant communities in a western North Carolina mountain fen, as well as the seed bank in an adjoining portion of the floodplain that had been degraded and is now slated for restoration. We also compared the composition of the seed bank to the composition of the standing vegetation in these three areas.

METHODS

Study Site

Our study site included three adjoining areas in the floodplain of Tulula Creek in Graham County, North Carolina, USA (elevation 800 m). Although this site is known locally as Tulula Bog, the term "bog" is a misnomer for this and many other southern mountain wetlands, as they have less peat accumulation than northern systems, receive ground-water inputs from surrounding mineral soils, and support vegetation more characteristic of minerotrophic than ombrotrophic conditions (Moorhead and Rossell 1998). Nevertheless, the North Carolina Natural Heritage Project has classified the site as a forest-gap bog complex (Schafale and Weakley 1990), a rare community type characterized by small "boggy" openings interspersed in a forested floodplain. The site was owned by the U.S. Forest Service until the mid 1980s, when it was traded to a private corporation for development into a commercial golf course. Subsequently, portions of the floodplain were drained, cleared, and graded for golf fairways. The golf course was never completed, and in 1994, the site was purchased by the North Carolina Department of Transportation for restoration and use as a wetland mitigation bank. Restoration activities, which will commence in 1999, include removing spoil, filling drainage ditches, reconstructing the original creek channel, and restoring portions of the forest canopy.

At the present time, only one fen (approximately one ha in size) remains intact in the floodplain. It is a depressional fen, divided roughly in half into distinct closed and open canopy regions. The closed canopy region has an overstory of mature red maple (*Acer rubrum* L.) and is also characterized by black gum (*Nyssa sylvatica* Marsh.), winterberry (*Ilex verticillata* (L.) Gray), swamp dewberry (*Rubus hispidus* L.), cinnamon fern (*Osmunda cinnamomea* L.), tussock sedge (*Carex stricta* Lam.), and peat mosses (*Sphagnum* spp.). The open canopy region is dominated by sapling red maple, elderberry (*Sambucus canadensis* L.), swamp rose (*Rosa palustris* Marsh.), red chokeberry (*Sorbus arbutifolia* (L.) Heynold), black chokeberry (*S. melanocarpa* (Michx.) Schneid.), soft rush (*Juncus effusus* L.), tussock sedge, and peat mosses.

Adjoining the fen is a portion of the floodplain that was drained, cleared, and graded for a golf fairway. This area is now dominated by sedges (*Carex* spp.), soft rush, grasses (*Calamagrostis cinnoides* (Muhl.) Barton, *Panicum dichotomum* L.), forbs such as goldenrods (*Solidago* spp.) and asters (*Aster* spp.), and scattered peat moss. Soils in all three areas are classified as Nikwasi loam (Typic Fluvaquents) (United States Department of Agriculture 1995). A more detailed description of the soils, hydrology, flora, and fauna across the site is available in Rossell et al. (in press).

Field and Lab Methods

We collected seed bank samples 2–4 June 1994 from the open and closed canopy regions of the fen and from the adjoining degraded portion of the floodplain. Although the fen and the degraded wetland area are both situated within the floodplain of Tulula Creek, for ease of distinguishing the sites here, we will refer to the degraded area as the "floodplain" area. To facilitate sampling, a grid of twenty-five 10 × 10m plots was established across each fen region, and 20 plots were chosen at random for the seed bank analysis. In the floodplain, where the vegetation and hydrology were more uniform than in the fen, a smaller area was sampled (twelve 10x10m plots). In each plot, a soil probe was used to collect 45 soil cores (2.5-cm diameter × 5.0-cm depth). Loose surface litter was brushed aside before sampling to ensure that samples were collected from a uniform depth, and the soil probe was wiped clean between plots. The 45 soil cores from each plot were composited, placed on ice in a cooler in the field, then refrigerated in the lab.

Samples from each plot were potted in triplicate between 16 and 18 June 1994. Each sample was thoroughly mixed and divided into three equal portions. One-third of each sample was placed on top of sterile potting soil in square plastic pots (10.5 cm-wide × 9.5-cm deep). The depth of the seed bank soil was approximately 2.5 cm. Pots were arranged randomly on a shelf in a greenhouse with no supplemental light, heat, or air-conditioning, kept moist, and monitored daily for seedling emergence As seedlings emerged, they were identified (nomenclature follows Radford et al. 1968) and removed from the pots. On 14 October 1994, pots were moved to a greenhouse with supple-

Table 1. ANOVA results comparing the number of emerged seedlings of five plant types in three study areas (alpha = 0.0067).

Plant Type	F	P > F
Woody	15.5	0.0001
Grasses	8.6	0.0014
Sedges	10.6	0.0003
Rushes	17.2	0.0001
Forbs	8.4	0.0052

Table 2. Mean (± S.E.) number of emerged seedlings per plot of five plant types in three study areas. Across rows, values followed by the same letter are not significantly different at P > 0.0067.

Plant Type	Closed Canopy	Open Canopy	Floodplain
Woody	1.9 ± 0.4a	0 ± 0b	0.4 ± 0.2b
Grasses	7.9 ± 1.7b	12.4 ± 1.2ab	18.9 ± 2.3a
Sedges	19.4 ± 1.2b	21.3 ± 1.8b	35.6 ± 3.7a
Rushes	5.9 ± 1.4b	39.0 ± 5.4a	11.8 ± 2.8b
Forbs	11.3 ± 1.5b	12.4 ± 1.2b	21.0 ± 2.9a

mental heat (mean temperature = 21°C) but no supplemental light. Some seedlings never matured or flowered but were identified to family, when possible. The study was terminated after 7 months, when emergence of new seedlings had ceased.

The composition of the standing vegetation in the herbaceous layer of each of the three study areas was documented in July 1994 by randomly locating a 1.0-m^2 quadrat within each 10 × 10m plot. The quadrat frame was held at knee height, and the percent cover of all species occurring within the quadrat was visually estimated. Species were subsequently classified as woody plants, forbs, grasses, sedges, or rushes.

Data Analysis

For the seed bank study, the numbers of seedlings of each taxon in the triplicate samples were summed for each plot. Because seedling numbers were low for some taxa, plants were grouped as woody plants, grasses, sedges, rushes, or forbs.

Analysis of variance (ANOVA) was used for the seed bank study to determine whether the total number of seedlings of each of the five plant types differed among the three areas (open canopy fen, closed canopy fen, floodplain). ANOVAs were also used to determine whether the mean cover of each of the five plant types in the standing vegetation differed among the three areas. In each case, Bonferroni-type adjustments of the alpha level were used because multiple comparisons were made (Tabachnik and Fidell 1989). The experimentwise error rates were set at 0.1, with comparisonwise error rates (alpha levels) of 0.0067. Differences among areas within each plant type were tested with Tukey's multiple comparison procedure. Statistical Analysis System programs (SAS Institute, Inc. 1990) were used for all analyses.

A discriminant function analysis was used for the seed bank study to determine which plant type best distinguished the floodplain, open canopy fen, and closed canopy fen. Discriminant function analysis identifies linear combinations of observation variables (canonical variables) that differentiate among groups (Williams 1983). Because discriminant function analysis is sensitive to the inclusion of outliers (Tabachnick and Fidell 1989), eight outliers (one forb, one grass, one woody, three sedge, and two rush entries) were eliminated from the data set prior to conducting the analyses. Boxplots and stem-and-leaf plots generated with the PROC UNIVARIATE procedure were used to identify outliers.

RESULTS

Thirty-two taxa of seedlings emerged in the seed bank study (Appendix): 26 in closed canopy fen soils, 19 in open canopy fen soils, and 22 in floodplain soils. Graminoids represented 85%, 77%, and 69% of the total number of seedlings in open canopy fen, floodplain, and closed canopy fen soils, respectively.

The number of seedlings of each of the five plant types differed significantly between the three areas (Table 1). Most of the woody seedlings emerged in closed canopy fen soils, most rushes emerged in open canopy fen soils, and significantly more sedges and forbs emerged in floodplain soils than in soils from either of the other sites (Table 2). More grasses emerged in floodplain soils than closed canopy fen soils, but grass emergence did not differ between the floodplain and the open canopy region of the fen.

Two canonical variables resulted from the linear discriminant function analysis. These accounted for 59.1% (Can1) and 40.9% (Can2) of the total variability. Can1 had a high positive loading for woody taxa and a high negative loading for rushes. Can2 had high positive loadings for sedges and grasses (Table 3). In a plot of these two variables, Can1 separated the open canopy fen from the closed canopy fen and the floodplain along the x-axis, and Can2 separated the floodplain from the fen along the y-axis (Figure 1).

In the standing vegetation, coverage by rushes and woody plants did not differ among the three study areas (Table 4). Sedge cover was significantly greater in the open canopy fen, while grass and forb cover were greater in the floodplain than in the closed canopy fen.

Table 3. Canonical coefficients for number of emerged seedlings of five plant types in three study areas.

Plant Type	Can1	Can2
Woody	0.710	−0.214
Grasses	0.009	0.531
Sedges	0.160	0.621
Rushes	−0.744	−0.272
Forbs	0.308	0.377

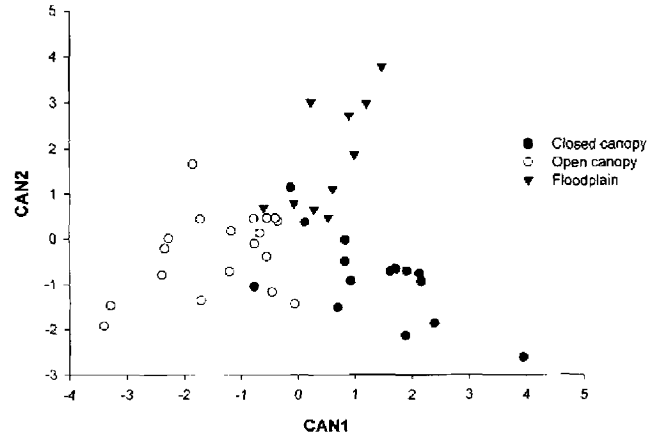

Figure 1. Discriminant function analysis of three study areas, based on the number of emerged seedlings of five plant types (woody plants, grasses, sedges, rushes, and forbs).

DISCUSSION

To our knowledge, only one published study (McGraw 1987) has examined the seed bank of a southern Appalachian bog or fen. In that study, 13 taxa emerged in soils collected from four plant communities at Big Run Bog in West Virginia. We found greater taxonomic richness at our site: 19 taxa of seedlings emerged in open canopy fen soils, and 26 emerged in closed canopy soils. It is difficult to make direct comparisons between our study and McGraw's, as his study focused on plant communities dominated by sedges and mosses growing in peat soils, while ours sampled a wider diversity of plant communities occurring on soils with less organic matter (a comparison of the soil characteristics in each of these wetlands can be found in Moorhead and Rossell (1998)). In addition, we sampled to a depth of 5 cm, while McGraw sampled to 45 cm, and McGraw inverted his samples after 7 weeks. If anything, our study underestimated the contents and composition of the seed bank relative to McGraw's study because we took shallower samples and likely overcame the dormancy requirements of fewer species. Although we sampled soils early in the growing season (the first week of June), our samples may still have contained seeds shed that spring, some of which may have been dormant at the time of sampling. Since we did not manipulate conditions in the greenhouse to stimulate the germination of dormant species, our data should be interpreted as a relative comparison of the three study areas at a point in time, not as a complete inventory of all species in the seed banks.

Leck (1989) noted that the dominant species in wetland seed banks are usually monocots and often graminoids. This held true in our study, where graminoids constituted up to 85% of emerged seedlings. McGraw (1987) reported that *Juncus effusus* L. contributed 81–95% of the total emerged seedlings at Big Run Bog, leading him to suggest that the overall size of seed banks in Appalachian bogs might depend on the abundance of *J. effusus* seeds. The contribution by *Juncus* in our study was less dramatic: 46% of seedlings in open canopy fen soils, 14% in floodplain soils, and 13% in closed canopy fen soils. The high number of *Juncus* seedlings in the open canopy region of the fen may indicate that this area is most similar to the sedge- and moss-dominated communities that McGraw sampled at Big Run Bog.

Only five woody taxa emerged in our study: *Acer rubrum*, *Rosa palustris*, *Rubus hispidus*, *Vitis aestivalis*, and one unknown taxon. In each case except *R. hispidus* (which was represented by 31 seedlings), fewer than four seedlings of each taxon emerged. In McGraw's (1987) study at Big Run Bog, only three woody taxa emerged; interestingly, *R. hispidus* had the greatest number of emerged seedlings in his study, as well. Other wetland seed bank studies have shown woody plants to be absent or poorly represented, likely because most have short-lived seeds (Leck 1989).

In the plot of the discriminant analysis (Figure 1), seedlings of rushes and woody plants separated open canopy fen soils from closed canopy fen and floodplain soils. Figure 1 further indicates that floodplain soils were separated from fen soils by sedge and grass seedlings. These patterns of emerged seedlings may correspond to differences in hydrologic regime but bear little similarity to the standing vegetation. For ex-

Table 4. Mean (± S.E.) cover of five plant types in herbaceous layer of 1 × 1 m^2 plots in three study areas. Across rows, values followed by the same letter are not significantly different at $P > 0.0067$.

Plant Type	Closed Canopy	Open Canopy	Floodplain
Woody	5.7 ± 1.0a	5.7 ± 1.2a	3.0 ± 0.6a
Grasses	1.4 ± 0.6b	13.3 ± 1.7ab	25.6 ± 4.5a
Sedges	10.8 ± 2.0b	25.0 ± 3.9a	2.0 ± 0.6b
Rushes	1.6 ± 1.1a	5.9 ± 1.5a	8.8 ± 4.4a
Forbs	0.9 ± 0.2b	2.2 ± 0.3ab	8.1 ± 2.6a

ample, the open canopy fen was the wettest of the three areas, with the water table remaining within 10 cm of the surface during most of 1994–1995 (Rossell et al. in press). The seed bank in this area produced the greatest number of rush seedlings but was lowest in overall taxonomic richness. The standing vegetation, however, was characterized by a low cover of rushes and a greater proportion of sedges than the other areas. In the closed canopy fen, where transpiration losses are greater, the water table dropped more then 30 cm below the surface on several occasions during the growing season. The seed bank in this area produced the most woody seedlings and the greatest overall taxonomic richness. The closed canopy fen is dominated by mature trees and other woody species that would continually drop seeds into the seed bank. However, the presence of woody plants in its herbaceous layer did not differ from the other areas. The floodplain, which is drained by numerous ditches, was the driest of the three areas, with the water table frequently dropping more than 60 cm below the surface. The seed bank in this area produced the most sedge and forb seedlings and was intermediate in taxonomic richness. The standing vegetation had a greater cover of forbs and grasses than the closed canopy fen but only differed from the open canopy fen in having less sedge cover.

In other studies, the species composition of wetland seed banks has sometimes resembled the standing vegetation but often has not (Leck 1989, Poiani and Dixon 1995, Hanlon et al. 1998). At our site, the seed bank and the standing vegetation in all three study areas were both characterized by a large proportion of graminoids. However, although the open canopy fen had woody seedlings in its standing vegetation, no woody seedlings germinated from its seed bank. In contrast, rushes constituted less than 10% cover in any of the study areas, but the open canopy seed bank produced an abundance of rush seedlings. Similarly, sedges contributed only 2% cover in the floodplain vegetation, but the floodplain seed bank produced the most sedge seedlings.

One of the wetland restoration goals for this site is to restore the original plant communities in the floodplain. It is not known whether restoration activities in the floodplain will influence the hydrology and vegetation dynamics in the adjoining closed and open canopy regions of the fen. Historical aerial photographs show that the floodplain was forested prior to disturbance, and it is likely that the vegetation resembled that in the closed canopy fen. Current restoration plans include planting some trees and shrubs in the floodplain, allowing others to regenerate on their own, and monitoring the herbaceous assemblages that develop. Since few woody seedlings emerged from floodplain soils in our study, most woody species that establish in this area will probably be contributed by the seed rain from surrounding forested areas. The seed bank in the floodplain will most likely lead to the establishment of graminoids and forbs. Later in succession, the composition of the restored plant communities might be influenced more by vegetative reproduction of shade-tolerant species (Bierzychudek 1982, Hanlon et al. 1998).

The actual contribution that the seed bank makes to the plant communities that become established in the floodplain will depend on the hydrologic regime after restoration, the germination requirements of individual species (Leck 1989, van der Valk et al. 1992), and the depth that soil is disturbed, which could result in burial of some species (McGee and Feller 1993). It will also be influenced by the extent of additions to the seed bank from the local seed rain (Schneider and Sharitz 1986, Titus 1991) and on the microtopographical relief that is established (Golet 1969, Paratley and Fahey 1986). Virtually all of the microtopographical relief in the floodplain was obliterated when this area was graded during the attempted golf course construction, and the extent to which restoration can recreate microtopographic heterogeneity may exert a strong influence on the nature of the communities that develop.

ACKNOWLEDGMENTS

This study was funded by the Center for Transportation and the Environment. Additional funding was provided by the University of North Carolina at Asheville (UNCA) Biology Department. The UNCA Botanical Gardens kindly provided greenhouse space. We gratefully acknowledge the assistance of D. Ducharme, J. Lawrence, and C.R. Rossell, Jr. with field work, K. Johnson with greenhouse work, J. Perry with seedling identification, and J. Petranka and B. Elkin with statistical analyses. Helpful comments on earlier drafts of the manuscript were provided by C.R. Rossell, Jr. and three anonymous reviewers.

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Manuscript received 20 November 1997; revision received 23 December 1998; accepted 16 February 1999.

Appendix. Total number of seedlings of each taxon emerging in plots sampled in the three study areas.

Family	Taxon	Closed Canopy (N = 20)	Open Canopy (N = 20)	Floodplain (N = 12)
Sedges				
Cyperaceae	*Carex* spp.	325	420	399
Cyperaceae	*Cyperus retrorsus* Chapman	0	1	0
Cyperaceae	*Cyperus strigosus* L.	2	0	27
Cyperaceae	*Eleocharis obtusa* (Willd.) Schultes	2	5	1
Total sedges		329	426	427
Rushes				
Juncaceae	*Juncus* spp.	107	780	141
Grasses				
Poaceae	*Panicum dichotomum* L.	129	91	151
Poaceae	Unknown	28	145	76
Total grasses		157	236	227
Woody plants				
Aceraceae	*Acer rubrum* L.	1	0	0
Rosaceae	*Rosa palustris* Marshall	0	0	1
Rosaceae	*Rubus hispidus* L.	29	0	2
Vitaceae	*Vitis aestivalis* Michx.	4	0	0
Unknown	Unknown	4	0	2
Total woody plants		38	0	5
Forbs				
Asteraceae	*Erechtites hieracifolia* (L.) Raf.	4	1	2
Asteraceae	*Eupatorium perfoliatum* L.	19	1	2
Euphorbiaceae	*Acalypha rhomboidea* Raf.	0	0	7
Hypericaceae	*Hypericum mutilum* L.	83	72	74
Lamiaceae	*Lycopus virginicus* L.	2	0	0
Melastomataceae	*Rhexia mariana* L.	1	1	24
Onagraceae	*Ludwigia palustris* (L.) Ell.	8	11	0
Oxalidaceae	*Oxalis stricta* L.	0	0	2
Plantaginaceae	*Plantago* sp.	1	0	0
Polygonaceae	*Polygonum pensylvanicum* L.	0	1	0
Polygonaceae	*Polygonum punctatum* Ell.	1	1	5
Polygonaceae	*Polygonum sagittatum* L.	7	5	1
Rosaceae	*Potentilla* sp.	0	0	3
Rubiaceae	*Galium tinctorium* L.	7	16	0
Scrophulariaceae	*Lindernia dubia* (L.) Pennell	1	0	0
Scrophulariaceae	*Verbascum thapsus* L.	1	0	0
Violaceae	*Viola blanda* Willd.	19	6	23
Violaceae	*Viola primulifolia* L.	18	3	70
Unknown	Unknown dicots	32	11	10
Unknown	Unknown monocots	21	118	8
Total forbs		225	247	231
Grand totals (all taxa)		856	1689	1031