

Response of seasonal pond plant communities to upland forest harvest in northern Minnesota forests, USA

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ABSTRACT

Small seasonally flooded forest ponds have received increased attention due to a growing recognition of their abundance in many landscapes, their importance as habitat for a variety of organisms, and the contributions they make to species and ecosystem diversity. There also is concern over potential negative effects of forest management in adjacent uplands on seasonal pond ecology. Several studies have examined invertebrate and songbird responses to upland harvest around seasonal ponds. Less attention has been given to examining how seasonal pond plant communities respond to adjacent forest harvesting. We studied the response of seasonal pond plant communities to adjacent upland timber harvests, assessing whether buffers around ponds (15.25 m uncut and partially cut) mitigated changes in species abundance and community composition, relative to changes in ponds that were clearcut to the pond margin. We addressed our objective using an operational-scale experiment in northern Minnesota, which included pre-harvest sampling, replicated treatments, and uncut controls. After treatment, changes in tree basal area and canopy openness in the pond basins reflected reductions in upland basal areas. Specifically, control ponds had significantly higher basal area and lower openness than ponds cut to their margins, while ponds with uncut buffers and partially cut buffers were intermediate. Changes in plant communities were evident in the ground layer and shrub/large regeneration layer. After treatment and over time, the control stands did not change significantly in ground layer structure or shrub/large regeneration layer composition. The three upland harvest treatments displayed increasingly greater deviation from their starting conditions and from the control along a gradient of increasing treatment intensity, from the buffer treatment to the partially cut buffer to the clearcut. The response in the ground layer was largely associated with increased sedge and grass cover, while the response in the shrub/large regeneration layer was associated with increases of *Salix* sp., *Alnus incana*, and *Populus tremuloides*. Our results indicate that adjacent upland timber harvest can lead to altered plant communities within seasonal ponds, at least temporarily. Moreover, uncut forest buffers (~15.25 m) surrounding seasonal ponds can mitigate plant community changes to some degree. If seasonal ponds are an important resource on the management landscape and a high percentage of upland forest is in a recently cut condition at any given time, than use of harvest buffers around seasonal ponds may be an appropriate approach for mitigating short term alteration of pond plant communities.

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1. Introduction

Small seasonally flooded forest ponds (hereafter seasonal ponds) have received increased attention from ecologists and natural resource managers in recent years (Tiner, 2003; Zedler, 2003; Colburn, 2004; Calhoun and DeMaynadier, 2007). This interest is due in part to a growing recognition of the abundance of seasonal ponds in many forest landscapes (Gibbs, 1993; Brooks et al., 1998; Calhoun et al., 2003; Palik et al., 2003; Tiner, 2003), their impor-

tance as habitat for amphibians, invertebrates, and other species (Brooks, 2000; DeGraff and Yamasaki, 2001; Batzer et al., 2004; Colburn, 2004; Francl, 2008), and the unique contributions seasonal ponds make to species and ecosystem diversity in a landscape (Hunter, 2007; Flinn et al., 2008). There also is concern about the potential effects of forest management in adjacent uplands on seasonal pond biota and ecology (Batzer et al., 2000; Palik et al., 2001).

The small size of seasonal ponds, often much less than 0.5 ha (e.g., Calhoun et al., 2003; Calhoun and DeMaynadier, 2007; Palik et al., 2007) results in high perimeter-to-area ratios, which may increase the potential for edge effects and interaction with the adjacent upland forest (Palik et al., 2006). For example, seasonal ponds gain substantial particulate organic matter from plant litter originating in adjacent uplands (Oertli, 1993; Palik et al., 2006),

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thus leaf fall from the uplands may be the major energy source for some pond organisms. An adjacent overhead canopy also mediates light availability at the pond surface (Batzer et al., 2000; Palik et al., 2001; Hanson et al., 2009). It follows that disturbances and successional changes in the adjacent forest may alter radiation and organic matter input, as well as water chemistry and hydrology (Semlitsch and Bodie, 1998; Skelly et al., 1999; Palik et al., 2001; Batzer et al., 2000; Hanson et al., 2009), potentially resulting in changes in biotic communities in seasonal ponds. This relationship has been demonstrated for invertebrate communities in several studies (Batzer et al., 2000; Hanson et al., 2009, 2010).

Less attention has been given to characterizing plant communities in seasonal ponds (Colburn, 2004; Flinn et al., 2008; Bried and Edinger, 2009), or examining how these communities may change in response to adjacent forest harvesting. One reason for this is that the value of ponds as invertebrate and amphibian breeding habitat may not be dependent on the specific composition of plant communities in a pond (Calhoun et al., 2003; Batzer et al., 2004), or because there may be few obligate seasonal pond plant species (Cutko, 1997; Colburn, 2004). However, changes in the abundance of plant functional groups within ponds in relation to adjacent forest age after clearcutting have been demonstrated (Batzer et al., 2000), and this in turn may influence the variety and abundance of other organisms in the pond. Moreover, alteration of seasonal pond plant communities in relation to upland disturbance may be indicators of environmental changes that ultimately will affect other biota such as invertebrates.

Retention of forested buffers around seasonal ponds may mitigate direct environmental changes associated with adjacent clearcut timber harvest, as has been shown with headwater streams (Wallace and Gurtz, 1985; Stone and Wallace, 1998; Kiffney et al., 2004). As a result, forested buffers around seasonal ponds have been suggested as a tool for minimizing effects of disturbance associated with adjacent timber harvesting (Dodd and Cade, 1998; Semlitsch, 1998; Minnesota Forest Resources Council, 1999). However, we are aware of no experimental studies evaluating the efficacy of forested buffers for mitigating changes in seasonal pond animals, plants, or hydrology.

With this need in mind, we studied the response of seasonal pond plant communities to adjacent upland timber harvests in northern Minnesota, assessing whether forested buffers (uncut and partially cut) mitigated short-term changes in plant communities. Specifically, we sought to (1) quantify the magnitude of change in pond plant communities in response to timber harvesting in the adjacent upland forest, (2) determine the degree to which uncut forest buffers could mitigate changes, and (3) assess whether partially cut buffers provided any mitigation. We evaluated these objectives using a planned silvicultural experiment that included pre-harvest sampling, replicated treatments, and uncut controls.

2. Methods

2.1. Study area description

The study area is located in Aitkin and Cass Counties (46°50'–57'N, 93°40'–94°05'W), in northern Minnesota, USA, within the Northern Minnesota Drift and Lake Plains Section. Soil parent materials were deposited during Wisconsinan-age glaciations from multiple advances and retreats of up to 4 separate ice lobes. Due to these multiple glaciations, the area is composed of a variety of different landforms such as drumlins, lake plains, moraines, and outwash plains.

Mean annual precipitation of the study area is 71 cm and average snowfall is 137 cm (Nyberg, 1999; Richardson, 1997). Precipitation is distributed fairly evenly throughout the growing season,

but generally highest in June and July. Mean annual air temperature is 4.8°C and the length of the growing season based on a daily minimum temperature >0.0°C is approximately 110 days (Nyberg, 1999; Richardson, 1997). For this study, we worked specifically in forests located on gently rolling ground moraine (Hobbs and Goebel, 1982), with soil parent material consisting of thick (60–180 m) glacial till (Almendinger et al., 2000).

2.2. Pond selection and experimental design

Our study was conducted in four large upland forest areas. Study areas were chosen subjectively from a larger available pool so as to meet the following criteria: each study area was at least 64 ha in size; seasonal ponds were abundant in the landscape, upland forests were dominated by *Populus tremuloides* (trembling aspen), with lesser amounts of *Acer saccharum* (sugar maple); stands were 60–70-year-old second-growth forest with minimal evidence of recent disturbances (stands originated after initial logging in the first half of the 20th century); and *Fraxinus nigra* (black ash) and *P. tremuloides* were the dominant trees species within seasonal ponds. The four study areas were separated by 4–30 km.

In each study area, a 64 ha block was delineated and each block was divided into four 16-ha treatment stands. In each stand, one seasonal pond was selected randomly for sampling, although there may have been other ponds within the same stand. Ponds were general similar in biophysical characteristics including size and hydrology. Pond sizes ranged from 0.2 to 0.5 ha and all had seasonal hydroperiods; wet in the spring after snowmelt, becoming drier during the summer months, and sometimes rewetting in the fall. Hydrologic characteristic of the study ponds varied both within and among blocks, but were similar on average among blocks (Table 1).

The following four treatments were assigned randomly to the four stands and their seasonal ponds within each block: control (uncut forest); full buffer; partial buffer; and clear-cut (Fig. 1). The full buffer treatment consisted of an upland clearcut with a 15.25-m uncut zone around the pond margin, beginning at the seasonal high water mark and extending into the adjacent upland forest. In the partial buffer treatment, basal area was reduced by approximately 50% within the 15.25-m buffer zone. In the clear-cut treatment, the forest was harvested up to the pond margin. All harvesting was done during December 2000 to January 2001 on frozen ground with an approximately 60 cm snowpack.

2.3. Vegetation sampling

In the spring of 2000, before harvest treatments, we established one or two (depending on pond size) circular, fixed radius plots in each pond to sample overstory and sapling strata vegetation. The plots were centered on a transect that spanned the long axis of the pond. The center of the initial plot was located 12 m from the average high water mark of the pond, beginning from a randomly chosen end of the transect. The remaining plot (if there were two) was spaced equidistantly between the first plot and the opposite pond margin. Plot diameter and area were 11.28 m and 100 m², respectively. Data recorded included species and diameter of all woody stems with a diameter at breast height (dbh at 1.4 m height) ≥2.5 cm. Canopy openness was assessed using a spherical densiometer. Readings were recorded at each plot center at waist height below most woody vegetation. Four readings were taken at each plot center in cardinal directions (N, S, E, and W), averaged for the plot, and converted to percent openness.

Shrub species and regeneration of tree species that were less than 2.5 cm dbh, but greater than 0.5 m tall (hereafter called shrub/large regeneration), were sampled in two 2-m wide belt transects centered on the long and short-axes of each pond basin and running from high-water mark to high-water mark. The combined

Table 1
Pre-harvest (2000) hydrologic characteristics of 16 study ponds organized by eventual treatment within each of four blocks.

Treatment	Block 1			Block 2			Block 3			Block 4		
	Mean depth (m)	Max depth (m)	Ponding (days)	Mean depth (m)	Max depth (m)	Ponding (days) ^a	Mean depth (m)	Max depth (m)	Ponding (days)	Mean depth (m)	Max depth (m)	Ponding (days)
Control	1.1	1.4	205	1.4	2.4	126	0.3	1.0	96	0.4	1.4	58
Buffer	0.4	1.1	77	1.1	1.8	120	0.4	0.9	141	1.0	1.3	189
Partial buffer	1.2	1.6	203	0.9	1.4	189	0.3	0.8	80	1.1	1.7	133
Clearcut	0.3	0.9	84	0.7	1.4	101	1.1	1.4	204	0.8	3.8	52
Mean ± SD	0.7 (0.5)	1.2 (0.3)	143 (72)	1.0 (0.3)	1.7 (0.5)	134 (38)	0.5 (0.4)	1.0 (0.3)	131 (56)	0.8 (0.3)	2.1 (1.2)	108 (65)

^a Cumulative days with water after ice out in 2000.

area sampled in these two transects varied among ponds depending on pond length and width. In these transects, the number and species of all appropriately sized woody stems were recorded.

Woody seedlings (<0.5 m tall) and broad classes of ground cover were sampled in eight 0.5 m² quadrats placed along the two transects described above. Six quadrats were placed equidistantly along the long-axis transect starting just below the high water mark, from a randomly determined end of the transect. Two additional quadrats were placed on the short axis transect, each equidistant between the center of the pond and the high water marks at the ends of the transect. In each quadrat, woody seedling numbers were recorded by species. Additionally, percent cover of major ground cover classes (sedges, grasses, forbs (i.e., non-graminoid herbs), bryophytes, and coarse woody debris) was estimated visually in the following classes: 0, <1%, 1–5%, 5–15%, 15–30%, 30–60%, 60–100%. Coarse woody debris was defined as any piece of wood with a diameter of at least 10 cm within the quadrat. For this sampling, we were primarily interested in assessing changes in structural conditions of ground cover (e.g., sedges versus forbs or bryophytes versus coarse wood, etc.) and not changes in taxonomic composition per se.

2.4. Statistical analyses

We employed a before-after-control-impact (BACI) experimental design, with one year of pretreatment sampling and multiple post-treatment samplings over a six-year period (Stewart-Oaten et al., 1986). All variables had one pretreatment measurement in 2000, but differed in post-treatment measurement frequency and interval, ranging from two to four post-treatment measurements between 2001 and 2006. All response variables were summarized at the pond-scale as means for each year of measurement. Means of overstory basal area and canopy openness were compared among treatments using a randomized block ANOVA, with block and treatment as fixed factors. We did not use a mixed-model, with block as a random factor, because we had only four study blocks to choose from and we could not choose these four randomly from a larger pool. If the overall test was significant ($p \leq 0.1$) then harvest treatments were compared amongst each other using Scheffe's test within a measurement year. Before analysis, we assessed variance and normality of the data and in some cases transformed the original data (square root or log) to better meet the assumptions of ANOVA. Analyses were run in SAS v. 9.2 (SAS Institute Inc.).

We used detrended correspondence analysis (DCA) to graphically display changes in pond vegetation composition and structure of the ground layer over time. We ran separate ordinations for ground cover, seedlings (<0.5 m tall), shrubs/large regeneration (stems ≥ 0.5 m tall and <2.5 cm dbh), saplings, and overstory. Input data for each analysis consisted of a matrix of 80 stands (4 treatments \times 4 reps \times 5 years) by species or ground cover groups, with data consisting of basal areas (overstory), densities (saplings, shrub/large regeneration, seedlings), or percent cover (ground layer). We choose DCA over nonmetric multidimensional scaling (NMDS) because, following the guidance of De'ath (1999), we were primarily interested in uncovering a hypothesized gradient in species distributions from control ponds to ponds within upland clearcuts, rather than representing species composition in ponds. Moreover, DCA reasonably displayed the vegetation differences among treatments and over time that we observed in the field. To better display temporal trends among treatments graphically, we averaged the four site (pond) scores for each treatment for each year of analysis to derive a mean score for a treatment at a given time. DCA's were run using PC-ORD v. 5 (MjM Software Design).

When DCA results suggested trends related to treatments, we examined these responses in more detail using principal response curves (PRCs) (ter Braak and Smilauer, 1998; Kedwards et al.,

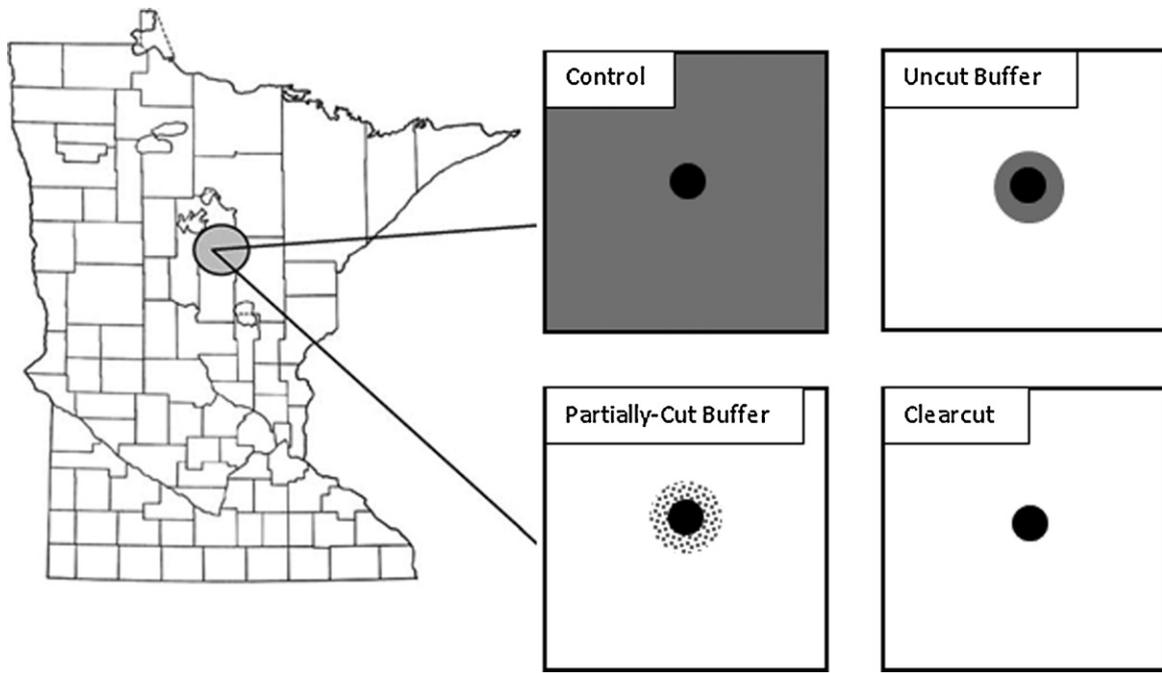


Fig. 1. Site study location and treatment design. Treatments include: control (uncut upland, uncut pond buffer); uncut buffer (upland clearcut, uncut pond buffer); partially cut buffer (upland clearcut, partially cut pond buffer); clearcut (upland clearcut, pond buffer clearcut).

1999a,b; Van den Brink and ter Braak, 1999). PRC is based upon partial redundancy analysis in which explanatory variables are used to account for variation in plant species data after first accounting for variation attributable to a third covariable data set (time in our case). In our study, explanatory variables were 12 dummy variables that consisted of all combinations of the three non-control treatments and four post-treatment times. This set of explanatory variables excludes variables that denote control treatments or pre-treatment times, ensuring that treatment effects were expressed as deviations from the control (ter Braak and Smilauer, 1998). Covariables consisted of dummy variables that indicated sampling year. In summary, PRC first accounted for variation in species composition due to time, allowing the remaining variation to be attributed to the treatments. The PRC was generated by plotting the first principle component of the treatment effects against time for each treatment group.

The significance of the PRC was assessed with a Monte Carlo permutation test, by permuting whole time series in the partial RDA from which the PRC was obtained. The null hypothesis was that treatment effect was zero for all times, treatments, and species. The interpretation of plant species responses in the PRC diagram is aided by a line graph of species weights, which are the species factor loadings on the first principal component. In our case, a positive weight indicates an increase in abundance following harvest, while a negative weight indicates a decline. Species with weights farther

from zero have increased or decreased in abundance by greater amounts than species with weights nearer zero. PRC analyses were run in Canoco v. 4.5 (Microcomputer Power).

Finally, we used indicator species analysis (Dufrene and Legendre, 1997) in PC-ORD v. 5 (MjM Software Design) to test for differences in selected plant species or ground cover groups among treatments. Indicator species analysis combines information on the abundance of species or groups and the frequency of occurrence of a species in that group. It produces indicator values for each species in each group which are then tested for statistical significance using a Monte Carlo permutation technique. Indicator values range from 0 (no indication or association with a group) to 100 (perfect indication). For this and previously described statistical tests, an alpha of 0.10 as considered significant.

3. Results

3.1. Changes in canopy structure

Prior to treatment, basal areas of the ponds, the surrounding riparian buffers, and the adjacent uplands did not differ significantly among treatments ($p=0.2$, upland; $p=0.7$, buffer; $p=0.6$, pond; Table 2). Basal areas within the ponds were measured again in 2006. At this time, there were still no significant differences in overstory basal area among the treatments ($p=0.9$; Table 2),

Table 2

Basal areas (m²/ha) of trees (dbh ≥ 10 cm at 1.4 m height) among treatments in ponds, riparian buffers around ponds, and in the adjacent upland. Values are means (±se) of four replicates. Means within a column followed by different letters were significantly different at $p < 0.1$.

Treatment	Pond			Riparian Buffer			Upland		
	Pre-harvest (2000)	Post-harvest (2002) ^A	Post-harvest (2006)	Pre-harvest (2000)	Post-harvest (2002)	Post-harvest (2006)	Pre-harvest (2000)	Post-harvest (2002)	Post-harvest (2006) ^B
Control	14.0 (4.7) a	na	11.8 (2.3) a	28.0 (4.2) a	25.6 (4.5) a	25.3 (4.4) a	29.7 (3.0) a	31.8 (5.1) a	na
Buffer	14.0 (6.1) a	na	10.9 (3.5) a	34.3 (10.3) a	26.8 (9.7) a	25.3 (10.1) a	19.1 (3.9) a	0.2 (0.2) b	na
Partial Buffer	22.0 (7.2) a	na	14.2 (3.7) a	22.4 (9.2) a	12.7 (4.6) a	12.3 (4.5) a	27.1 (7.9) a	0.4 (0.4) b	na
Clearcut	12.5 (6.4) a	na	10.3 (5.3) a	32.0 (8.0) a	0.6 (0.3) b	0.4 (0.2) b	35.2 (5.5) a	2.7 (1.3) b	na

^A Not measured in 2002.

^B Not measured in 2006.

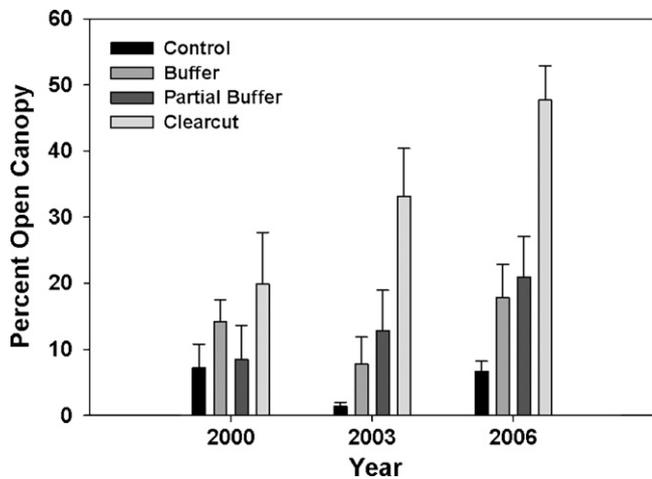


Fig. 2. Mean (\pm standard error) canopy openness over pond basins over time among different treatments. 2000 was the pretreatment year.

although pond basal areas were all somewhat reduced from the pre-harvest condition in all treatments. Basal areas within the uncut riparian buffers declined somewhat from the pre-harvest condition and treatment differences evident in both measurement years (2002, $p=0.004$; 2006, $p=0.003$). Basal areas were highest in the two uncut treatments (control and buffer), followed by the partially cut buffer, and then the clearcut buffer (Table 2). Only the latter was significantly less than the other treatments in either 2002 or 2006 (Scheffe's test, $p < 0.1$; Table 2). Post-harvest basal areas of the adjacent uplands were measured only in 2002. As expected, basal areas in upland harvest treatments were significantly lower than the uncut control (Scheffe's test, $p < 0.10$; Table 2).

Canopy openness over the pond basins paralleled the reductions in riparian and upland basal areas described above (Fig. 2). Openness was variable but significantly different among treatments in 2000 before harvest ($p=0.05$), however none of the contrasts among treatments were significant (Scheffe's test, $p > 0.1$). After harvest in both 2003 ($p=0.04$) and 2006 ($p=0.01$) treatment effects were significant. Specifically, the control had significantly lower openness than the clearcut treatment (Scheffe's test, $p < 0.1$), while the other treatment contrasts were not significantly different (Fig. 2).

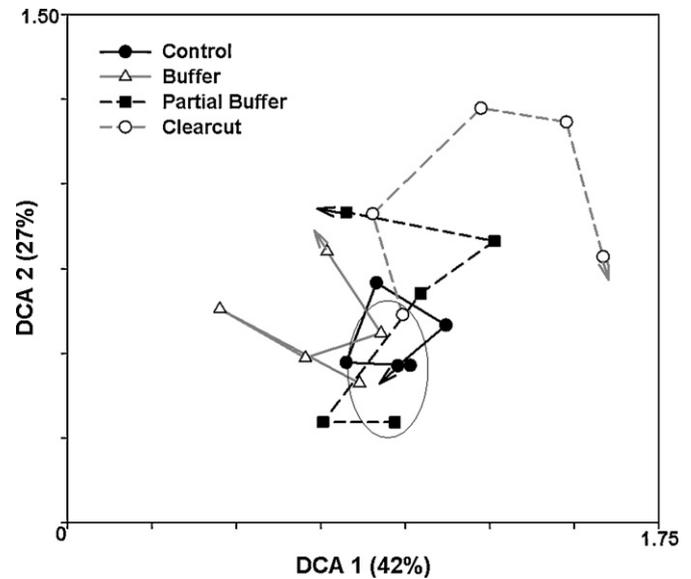


Fig. 3. Temporal detrended correspondence analysis of pond treatments based on ground layer cover groups. Each data point is the mean of four replicate site (pond) DCA scores for a year and treatment combination. Time periods include 2000 (pre-treatment), 2001 (1 year post-treatment), 2002, 2003, and 2006. Starting conditions in 2000 for all treatments fall within the oval on the graph.

3.2. Changes in plant communities

Compositional changes in plant communities among treatments were evident in the shrub/large regeneration layer, as were structural changes in the ground layer. We detected no obvious changes in the composition of the canopy, seedling layer (<0.5 m tall), or sapling layer (2.5 < dbh < 10 cm) and do not report on them further here.

The temporal DCA ordination of the ground layer accounted for 69% of total variation on the first two axes (Fig. 3). On average, the treatment ponds were similar in ground layer cover prior to treatment (relatively close together within the oval in Fig. 3). After treatment and over time, the control ponds did not change much in ground layer cover groups. In contrast, the three harvest treatments displayed increasingly greater deviation from their starting conditions and from the controls, along a gradient of treatment

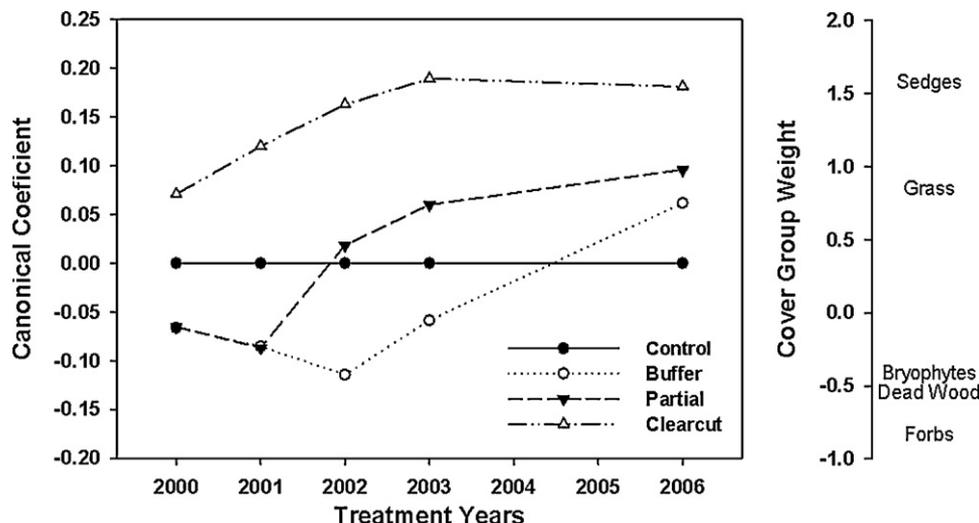


Fig. 4. First principle response curve (PRC) diagram, with ground layer cover group weights on the separately scaled graph on the right. The influence of harvest treatment is indicated by curves that depart from the reference condition (control). The vertical axis on the PRC graph represents 38% of the variation in the treatment regime. Year 2000 is the pretreatment year; 2001 is the first post-treatment year, etc.

Table 3

Seasonal pond ground cover (a–e) and shrub/large regeneration (f and g) indicator values by year and treatment. The shaded cells reflect significant indicator responses ($p \leq 0.10$).

		(a) Bryophyte	(b) Dead Wood	(c) Sedges	(d) Forbs	(e) Grasses	(f) Shrubs ^b	(g) <i>Populus tremuloides</i>
2000	Control	32 ^a	26	27	34	26	19	23
	Buffer	22	30	26	23	13	1	20
	Partial	15	12	10	24	10	8	21
	Clearcut	31	32	37	15	33	45	29
	<i>p</i>	0.610	0.343	0.224	0.450	0.773	0.307	0.852
2001	Control	32	20	24	27	14	15	33
	Buffer	16	32	24	36	3	0	7
	Partial	35	23	12	27	7	1	31
	Clearcut	17	25	40	10	53	48	21
	<i>p</i>	0.416	0.200	0.148	0.853	0.478	0.135	0.579
2002	Control	27	20	20 ^b	21	5	5	7
	Buffer	32	34	15	29	5	0	11
	Partial	20	35	19	38	42	32	13
	Clearcut	21	11	46	9	23	4	66
	<i>p</i>	0.811	0.187	0.007	0.251	0.578	0.534	0.100
2003	Control	45	10	13	26	9	1	46
	Buffer	25	24	17	32	6	1	23
	Partial	9	45	21	30	24	5	19
	Clearcut	21	9	49	12	39	18	12
	<i>p</i>	0.314	0.574	0.007	0.712	0.667	1.000	0.581
2006	Control	35	15	8	16	6	1	8
	Buffer	16	48	29	29	12	4	27
	Partial	10	28	30	30	7	50	32
	Clearcut	34	8	30	19	63	31	33
	<i>p</i>	0.544	0.544	0.859	0.929	0.066	0.173	0.848

^a Indicator values range from zero (no indication) to 100 (perfect indication). Perfect indication means that a given cover group indicates a particular treatment without error.

^b Includes *Salix* sp. and *Alnus incana*.

intensity, from the buffer treatment to the partial buffer to the clearcut (Fig. 3). In particular, the clearcut treatment displayed relatively large deviation from the other treatments over time. The full buffer and partial buffer treatments varied over time to larger degrees than the control treatment, but to a lesser degree than the clearcut treatment. Gradient lengths of treatment means on the *x* and *y* axes were 1.13 and 0.93 standard deviations, respectively (Fig. 3), suggesting almost one-half species turnover between extremes on each gradient (McCune and Grace, 2002).

The first axis of the ground layer PRC was significant ($p = 0.015$) and explained 38% of the variation in ground cover changes among treatments over time (Fig. 4). The PRC confirmed the patterns displayed in the temporal ordination. The treatments deviated somewhat in initial structure before harvest (Fig. 4), but this variation from the control changed over time to reflect the gradient of upland treatment intensity (i.e., buffer to partial buffer to clearcut). By the 6th year after treatment there was an obvious distinction in ground layer structure between the control and the clearcut treatment. The full buffer and partial buffer treatments were intermediate.

The response of the clearcut treatment was largely associated with increased sedge cover initially, followed by an increase in grass cover (Figs. 4 and 5). Sedges and grasses had high positive weightings on the first PRC axis (Fig. 4) and in general were more abundant in all treated ponds, but particularly in the clearcut treatment (Fig. 5). Results from the indicator species analysis confirmed this trend (Table 3). Sedges had significantly higher indicator scores in the clearcut treatment than other treatments in 2002 ($p = 0.001$) and 2003 ($p = 0.007$), while grasses had a significantly higher indicator score in the clearcut treatment than other treatments in 2006 ($p = 0.066$). The directional changes seen in some responses, e.g., forbs in the control treatment, presumably are due to the influence of a common driver (e.g., climate) that affects all treatments.

The temporal DCA ordination of the shrub/large regeneration layer accounted for 41% of total variation on the first two axes

(Fig. 6). On average, the treatment stands were similar in composition prior to treatment (relatively close together within the oval in Fig. 6). After treatment and over time, the treatment ponds changed to a greater degree than did the control ponds, with the clearcut and partial buffer treatments having the greatest degree of change, relative to their starting conditions and the control. By year six, the full buffer treatment was intermediate in composition between the control and other two treatments. Gradient lengths of treatment means on the *x* and *y* axes were 1.19 and 1.15 standard deviations, respectively (Fig. 3), suggesting about one-half species turnover between extremes on each gradient (McCune and Grace, 2002).

The first axis of the shrub/large regeneration layer PRC explained 32% of the variation in compositional changes among treatments over time (Fig. 7), however the Monte Carlo permutation test was not significant ($p = 0.25$). Still, the results confirmed the patterns displayed on the DCA plot. The treatments deviated somewhat in initial conditions before harvest (Fig. 7), but deviation from the control increased over time for all harvest treatments. By the 6th year after treatment there was an obvious distinction in composition between the clearcut and partial buffer treatments and the control. The full buffer treatment was intermediate, but closer to the other harvest treatments than the control.

The response of the shrub/large regeneration layer in the clearcut and partial buffer treatments was largely associated with increases of *Salix* sp. and *Alnus incana* by the last year of measurement and *P. tremuloides* in 2002 and 2003 (Figs. 7 and 8). *Salix* sp., *A. incana*, and *P. tremuloides* had relatively large negative weightings on the first PRC axis (Fig. 7), indicating that they were more abundant in all treated ponds, particularly the clearcut and partial buffer treatments (Fig. 7). However, these responses were highly variable within treatments (Fig. 8), largely because one of the four replicates in the relevant treatment by year combination did not show the same response as the others. Results from the indicator species analysis reflected this muted response (Table 3). The shrub

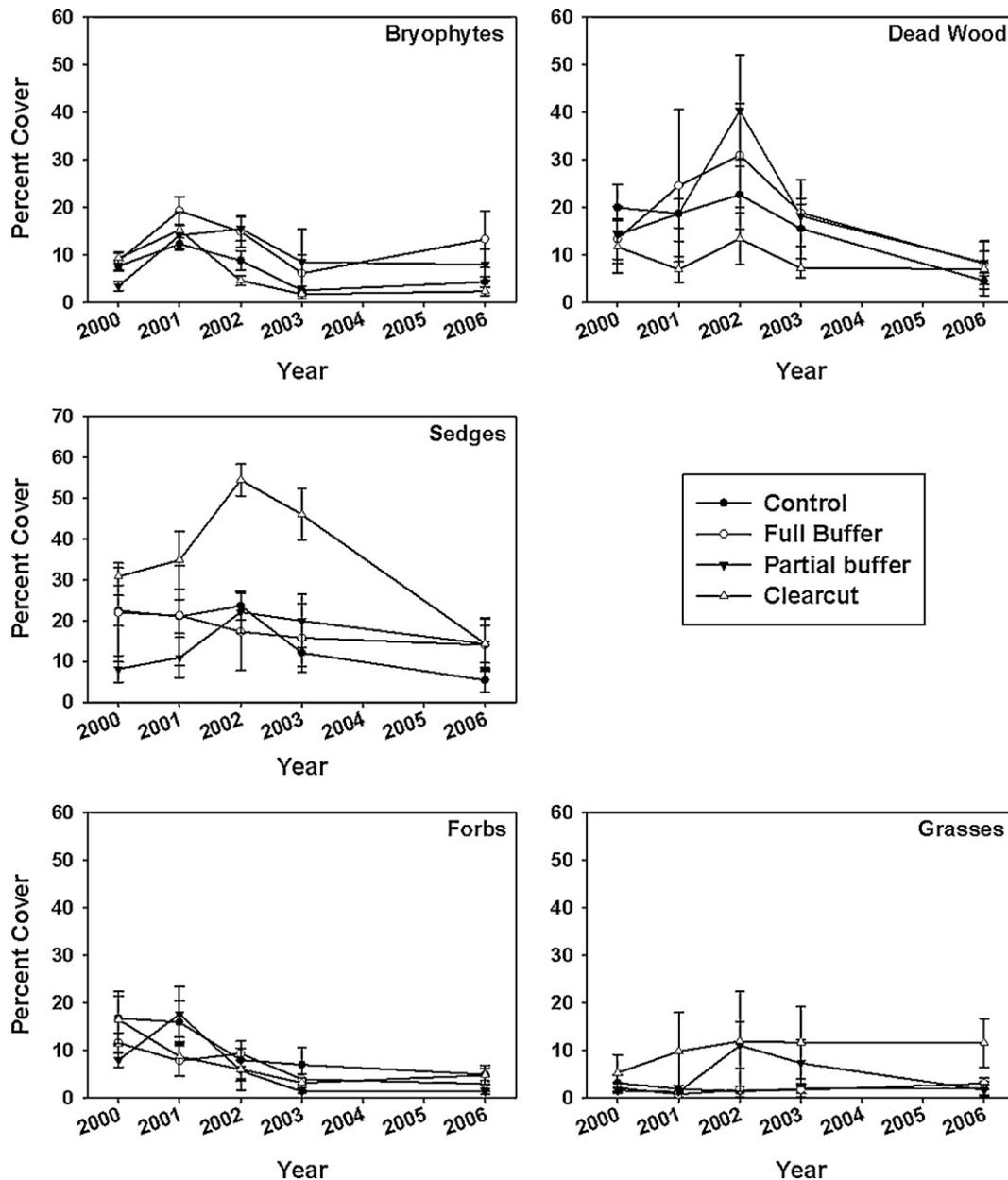


Fig. 5. Mean (\pm standard error) cover of major ground cover groups over time and among treatments.

response was not significant in any year and the response for *P. tremuloides* was significant in 2002 only.

4. Discussion

Our results support the contention that interactions with the adjacent upland forest may be an important influence on seasonal pond structure and function (Palik et al., 2006) and that timber harvesting in the upland can alter of this interaction (Semlitsch and Bodie, 1998; Batzer et al., 2000; Palik et al., 2001; Hanson et al., 2009). Specifically, our results indicate that shifts in plant communities within seasonal ponds can occur, even in a relatively short time period, as a result of clearcut forest harvest in the adjacent upland. Moreover, forested buffers around seasonal ponds appear to mitigate changes to some degree. Changes in composition were moderate overall, even in the clearcut treatment, as suggested by the length of gradients in the DCA ordinations (Figs. 3 and 6). Gradient lengths of 4 standard deviations reflect

complete species turnover between ends of a gradient (McCune and Grace, 2002); whereas our values, which were around 1 standard deviation between extremes, suggest about one-half change in species turnover.

The changes we observed in ground layer structure, specifically an increase in sedges and grasses, have been reported by others working in small seasonal wetlands in the southeastern USA (Batzer et al., 2000; Prenger and Crisman, 2001), suggesting a generalizable change in the structure of the ground layer in small wetlands disturbed in similar ways. The increase in abundance (although variable among ponds) of *P. tremuloides* in the shrub/large regeneration layer is consistent with the reproductive habit of the species. *P. tremuloides* often regenerates vegetatively as suckers from existing root systems. Suckering is stimulated by removal of the above ground stem (Frey et al., 2003) and can occur at substantial distances from the parent stump, at least up to 15 m (Barnes, 1966). Additionally, *P. tremuloides* is tolerant of moderately wet conditions, such as stream and wetland margins (Barnes and Wagner,

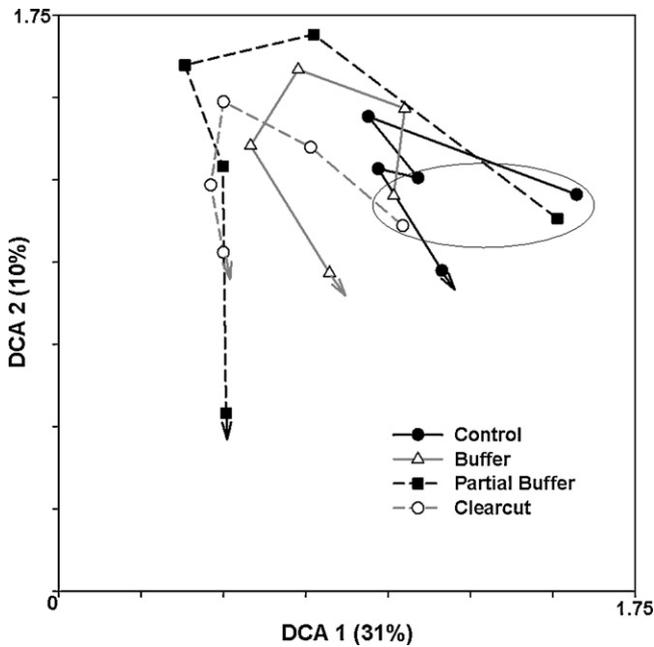


Fig. 6. Temporal detrended correspondence analysis of pond treatments based on shrub/large regeneration layer species. Each data point is the mean of four replicate site (pond) DCA scores for a year and treatment combination. Time periods include 2000 (pretreatment), 2001 (1 year post-treatment), 2002, 2003, and 2006. Starting conditions in 2000 for all treatments fall within the oval on the graph.

1981). As such, cut *P. tremuloides* within the 15.25 m buffer likely had root systems that extended into the outside margins of the pond basins and these roots may have initiated new suckers after treatment of the upland forest. However, the reduction in *Populus* density over time in the large regeneration layer, without a detectable increase in density in the sapling layer, suggests that conditions for longer term survival of *Populus* were not met even at the margin of ponds in the clearcut treatment. *A. incana* and *Salix* sp. also increased in abundance within the pond basins, particularly in the clearcut treatment. *A. incana* has been shown to increase in density with partial harvests that removed around 43% of initial basal area (Man et al., 2008).

Forested buffers around small seasonal ponds have been suggested as a tool for minimizing effects of pond disturbance from adjacent upland timber harvesting (Dodd and Cade, 1998; Semlitsch, 1998; Minnesota Forest Resources Council, 1999). Results from the both the ground layer and shrub/large regeneration layer analyses lend support to this suggestion. For both vegetation layers, the multivariate analyses suggest that the buffer treatments were intermediate between the ponds in uncut forest and the ponds in clearcut forest. For the ground layer, the two buffer treatments were similar in final structure (as measured in 2006) and both were arrayed largely intermediate between the other two treatments. In contrast, shrub/large regeneration composition in partially cut buffers was similar to the clearcut treatment, while composition in the full buffer treatment was intermediate between the control and other two treatments, although weighted towards the latter. These results suggest that uncut buffers around seasonal ponds can mitigate vegetation changes associated with adjacent upland clearcuts. Partially cut buffers are less effective at mitigation. In related studies from the same experiment, changes in wetland invertebrate and songbird communities were also mitigated to some extent by buffers around ponds, including both uncut and partially cut buffers (Hanowski et al., 2006; Hanson et al., 2010).

We did not detect changes in other vegetation layers among treatments or over time. Canopy and sapling layer abundance and composition would likely be unresponsive to change in the relatively short time period examined in this study, because of the extended time needed for individuals to recruit into these size classes. Conversely, establishment and mortality in the seedling layer can be highly dynamic even over short time periods (e.g., Streng et al., 1989), and probably responded to multiple environmental factors in addition to the study treatments, leading to high variability in seedling abundance of different species. Moreover, seedlings of some species that established or were released as a result of treatments may have rapidly grown out of the seedling size class in the first year or two after treatment, leading to the trends we detected in the shrub/large regeneration layer (e.g., *P. tremuloides*). As such, trends in response to treatments may have been hard to detect in the seedling size class.

Increased light availability over the pond basins, as a result of adjacent clearcutting, may have been at least partially responsible for the changes in plant communities that we observed. While we did not measure light directly, canopy openness was signifi-

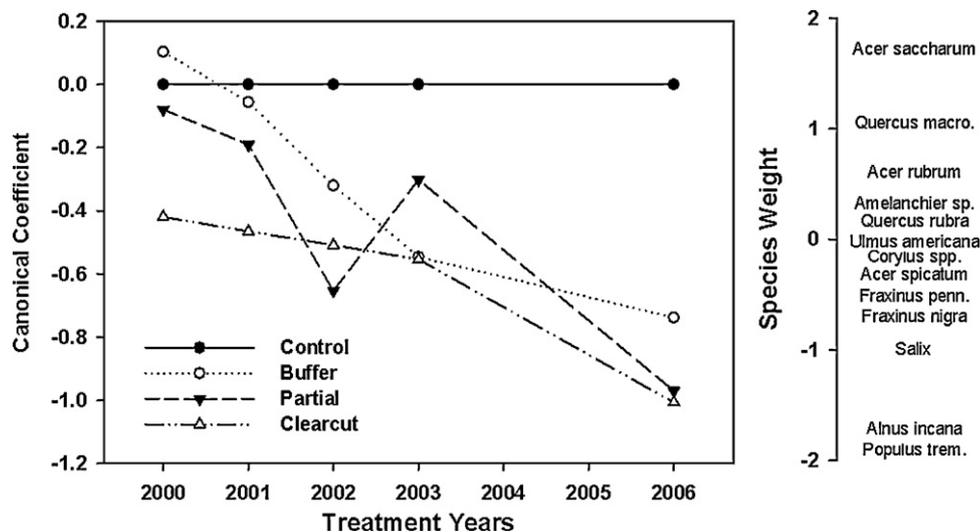


Fig. 7. First principle response curve (PRC) diagram, with shrub/large regeneration layer species weights on the separately scaled graph on the right. The influence of harvest treatment is indicated by curves that depart from the reference condition (control). The vertical axis of the PRC graph represents 32% of the variation in the treatment regime. Year 2000 is the pretreatment year; 2001 is the first post-treatment year, etc.

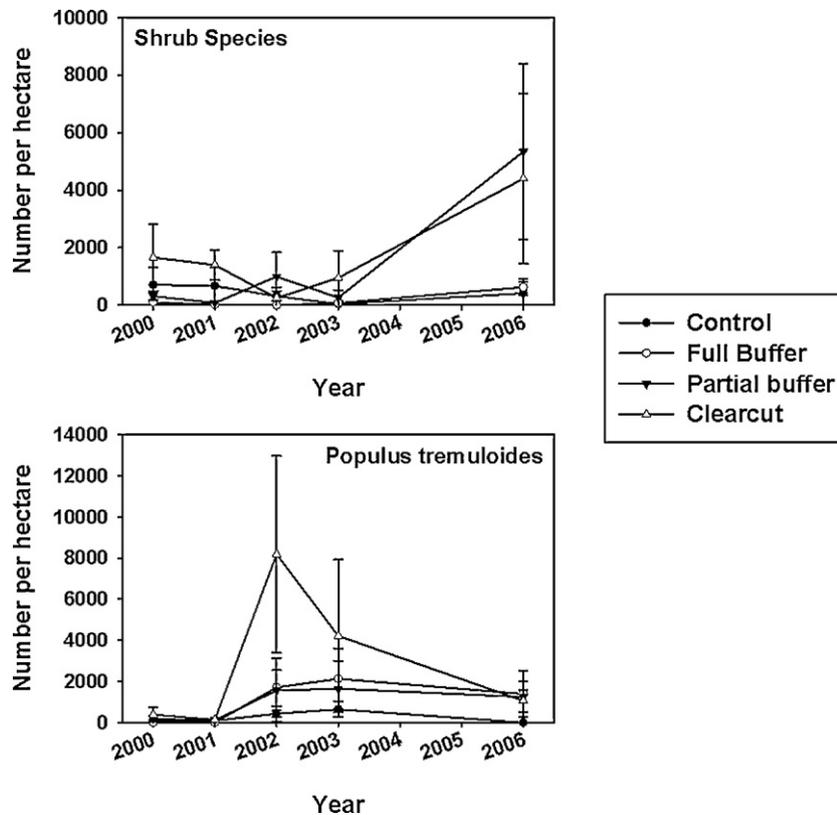


Fig. 8. Mean (\pm standard error) densities of shrubs (*Salix* sp. and *Alnus incana*) and *Populus tremuloides* in the shrub/large regeneration layer over time and among treatments.

cantly higher over the ponds embedded in clearcuts, compared to the controls and canopy openness over full-buffer ponds was closer to control ponds and openness over partially cut buffer ponds was more like ponds in the clearcuts. Changes in pond hydrology, including increased depth and duration of flooding when the adjacent forest is harvested, may also have influenced plant communities, as has been suggested in other studies (Palik et al., 2001; Hanson et al., 2009). In fact, preliminary analysis of hydrologic responses in our experiment suggests that all three buffer treatments resulted in increased water depth, relative to the control, for the first four years after treatment. Moreover, in the first year after harvest, the no buffer treatment had significantly greater water depth than the other three treatments. Water level differences were not significant by the fifth year after treatment (R. Kolka, unpublished data).

5. Management implications

To our knowledge, this experiment is unique; we are aware of no other study that experimentally manipulated adjacent upland forest conditions around small seasonal ponds and then tracked changes in pond plant communities over time. Previous reports from this experiment have documented changes in songbird and wetland invertebrate communities (Hanowski et al., 2006; Hanson et al., 2010).

Our results indicate that adjacent clearcut timber harvest results in measurably altered plant communities within the types of seasonal ponds we examined, at least temporarily. If a goal for resource managers is to minimize changes in plant communities of seasonal ponds that may occur after adjacent upland harvest, then our results also suggest that uncut forest buffers of 15.25 m width surrounding seasonal ponds can mitigate plant community changes to some degree. Mitigation occurred even though as much as 15% of mature trees within both unharvested and partially

harvested-buffers have blown down over the period of sampling (B. Palik, unpublished data). Presumably, wider buffers would mitigate changes to even a greater degree and would result in a lower percentage of total trees blown down after harvest. If seasonal ponds are an important or unique resource on the landscape and a high percentage of upland forest is in a recently cut condition at any given time, than use of harvest buffers around seasonal ponds may be an appropriate approach for mitigating short term alteration in seasonal pond plant communities.

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