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ORIGINAL PAPER

Primary Productivity in 20-year Old Created Wetlands in Southwestern Virginia

Robert B. Atkinson · James E. Perry · Gregory B. Noe · W. Lee Daniels · John Cairns Jr.

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Abstract Thousands of depressional wetlands accidentally formed as a result of pre-1977 contour coal mining in the Appalachian Mountains. Eleven 20-yr old sites were found in a watershed that did not receive acid mine drainage. The purpose of this study was to quantify and model above- and below-ground plant biomass in these created wetlands and to evaluate functional development. Sampling was stratified by weighted average of two plant communities, which corresponded to shallower and deeper water levels, facultative wetland and obligate wetland communities, respectively. In 1994, peak above-ground biomass averaged 473.7 g m^{-2} in the facultative wetland community and 409.5 g m^{-2} in the obligate wetland community. *Scirpus cyperinus* exhibited the highest peak above-ground biomass (51.8% of total biomass) and *Typha latifolia* ranked second. Canonical correspondence analysis detected positive effects of longer soil exposure to the atmosphere and greater sediment depth on above-ground biomass at the site (wetland ecosystem) level. Within communities, forward stepwise regression identified positive association of above-ground biomass with water soluble reactive P, water soluble NH_3, decomposition rate over 507 d, live *S. cyperinus* tissue P content, and sediment depth. When these results are combined with prior studies conducted at the same 20-yr old sites, it appears that both structural and functional development has been arrested at a somewhat immature state resulting primarily from soil and hydrologic factors.

Keywords Functional performance · Nutrient limitation · Peak standing crop · Tissue nutrient content

Introduction

Contour surface mining for coal disturbed over 385,000 hectares in the Appalachian Mountains (National Wetland Inventory maps, e.g., Flat Gap Quadrangle) prior to enactment of the Surface Mining Control and Reclamation Act of 1977 (SMCRA, P.L. 95-87). Topographic features left by pre-SMCRA mining included vertical and relatively flat areas, known locally as high-walls and benches, respectively. The benches consisted of severely compacted spoil with bulk density of 1.7 g cm^{-3} (Daniels and Amos 1982) and water and sediment collected in many small depressions on the benches. As a result, hydroperiods lengthened and hydrophytic vegetation colonized the depressions (Atkinson et al. 2005). Although hundreds of small depressions formed per hectare of benches, few studies are available that describe the functions of these

R. B. Atkinson · J. Cairns Jr.
Department of Biology,
Virginia Polytechnic Institute and State University,
Blacksburg, VA 24061, USA

J. E. Perry
Virginia Institute of Marine Science,
Gloucester Point, VA 23062, USA

G. B. Noe
U.S. Geological Survey, 430 National Center,
Reston, VA 20192, USA

W. L. Daniels
Department of Crop Soil and Environmental Science,
Virginia Polytechnic Institute and State University,
Blacksburg, VA 24061, USA

Present Address:
R. B. Atkinson (✉)
Center for Wetland Conservation,
Christopher Newport University,
Newport News, VA 23606-2998, USA
e-mail: atkinson@cnu.edu

inadvertently formed wetlands. Thus, little is known of their ecological role in the mined mountain landscape.

Primary production is a critical function that supports a myriad of ecosystem services that are provided by wetlands (Sather and Smith 1984; Odum 1989). Several studies have reported above-ground vegetative production in naturally occurring nontidal freshwater wetlands (e.g., Westlake 1963; Auclair et al. 1976; Klopatek and Stearns 1978; Doumlele 1981; Dickerman et al. 1986) and a few studies have investigated above-ground production in created wetlands, all of which are less than 10 years old (Barnes 1983; Garver et al. 1988; Cole 1992; Whigham et al. 2002; Anderson and Cowell 2004), but no studies were found in which created wetland primary productivity was modeled.

Primary productivity of natural wetlands can vary according to soil nutrient and hydrologic factors (Brinson et al. 1981), soil, water and tissue nutrient concentrations (Boyd and Hess 1970; Emery and Perry 1995; Olde Venterink et al. 2003), and species composition along topo-edaphic conditions (Kirkman et al. 2000). Many of these factors also influence productivity across a range of altitudes (ChangTing et al. 2008).

In this study, peak standing crop above-ground biomass (PAG) for two years and below-ground biomass (PBG) in a single year is reported for eleven circa 20-yr old created wetlands that formed on bare compacted spoils and that received no management following creation. Environmental factors related to biomass production were also investigated. These wetlands provide an opportunity to evaluate the long-term efficacy of created wetlands to develop ecological functions beginning under harsh conditions and without active management. The purpose of this study was 1) to describe the above- and below-ground biomass of the 11 sites and contrast biomass parameters at two scales including community (facultative wetland and obligate wetland) and site (wetland ecosystem), and 2) to use environmental parameters to model above- and below-ground biomass at both scales in roughly 20-yr old created wetlands.

Site Description

Sites were located in small depressions on the benches of pre-SMCRA mines in Wise County in southwestern Virginia. Wetlands formed following the cessation of mining activity, which ranged from 1970 to 1974, and were 50–775 m^2 in size (Table 1). Selection criteria included the presence of hydrophytic vegetation and depressional wetland hydrology, and the absence of significant acid mine drainage inputs. Each wetland exhibited two plant community types, including 1) a shallower community primarily dominated by *Scirpus cyperinus* (L.) Kunth. and other facultative wetland species including *J. effusus* L. and *Salix nigra* Marsh., and 2) a deeper community primarily dominated by *Typha latifolia* L. and other obligate species including *Potomogeton pulcher* Tuck., *Juncus acuminatus* L., *Sparganium americanum* Nutt., and *Ludwigia palustris* (L.) Ell. (Atkinson et al. 2005). Adjacent mined upland benches were characterized by herbaceous species, including *Festuca rubra* L., *Lespedeza cuneata* (Dum. Cours.) G. Don, *Trifolium repens* L., and *Solidago gigantea* Aiton. Terrestrial vegetation dynam-

Table 1 Site reference number, age (year formed), area, and hydrology (water depth, SEI and hydrology modifier) for 11 wetlands in this study

Site	Year formed	Area (m^2)	Water depth (cm)	Facultative wetland community		Obligate wetland community		Hydrology
				SEI in 1993	SEI in 1994	SEI in 1993	SEI in 1994	
1	1975	64	40.1	47.6	42.9	0.0	0.0	H
2	1974	167	89.4	35.7	35.7	0.0	0.0	H
3	1974	50	17.7	71.4	38.8	64.3	14.3	C
4	1973	89	17.8	75.0	71.4	57.1	38.8	C
5	1973	775	61.7	75.4	64.3	55.4	4.8	C
6	1973	62	20.1	58.3	28.6	41.7	4.8	G
7	1974	217	44.1	61.9	61.9	0.0	0.0	H
8	1970	69	8.4	75.0	69.4	50.0	38.8	C
9	≅1970–4	148	60.0	66.7	47.6	29.2	0.0	G
10	≅1970–4	206	32.0	64.3	52.4	46.4	9.5	G
11	≅1970–4	143	72.5	50.0	50.0	0.0	0.0	H
Mean		181	42.2	61.9	51.2	31.3	10.1	
SE		62.0	7.85	3.92	4.28	7.95	4.50	

Water depth is presented as maximum measured depth in cm. SEI, soil exposure index, is the probability of drawdown frequency and duration. Modifiers are based on Cowardin et al. (1979) for palustrine system and emergent class include nontidal water regime modifiers: C = seasonally flooded, G = intermittently exposed, and H = permanently flooded ics in the region were discussed elsewhere by Holl and Cairns (1994).

Methods

In August of 1992 and 1994 plant community composition was assessed using aerial cover estimates in 1-m^2 plots (detailed methods and results were presented by Atkinson et al. (2005)) adjacent to each plot where biomass was harvested. Communities were designated based on weighted average (WA, also known as Prevalence Index) that was calculated within the 1-m^2 plots using species wetland indicator status (Reed 1988) and relative cover (Wentworth et al. 1988; Atkinson et al. 1993). Designated communities included WA 1.0–1.5 (*obligate wetland*, n=31) or WA 1.5–2.5 (*facultative wetland*, n=32), for a total of 63 plots (usually three plots in each community of each wetland).

Peak Biomass Estimates

Above-ground standing crop (peak above-ground biomass, PAG) was harvested in one 0.25-m^2 quadrat (n=63) adjacent to each plot. Collections were made during a two-week period from late August to early September in 1993 and 1994. Plants were sorted by species, placed in labeled paper bags and transported back to the lab. Concurrently, litter (a surface layer of undecomposed plant remains) was collected in both years within these plots. After live standing crop biomass and litter were removed in 1994, peak below-ground biomass (PBG) was estimated by excavating soil from the quadrat to the depth of compacted substrate, separating roots and soil in the lab, and rinsing roots. All biomass and litter samples were dried at 100°C to a constant mass.

Environmental Parameters

From the material harvested in each plot in 1994, litter and above-ground biomass tissue-nutrient content were measured for the most dominant species in each community, *S. cyperinus* and *T. latifolia*. Harvesting at the peak of the growing season ensured that plant biomass was near the peak of tissue nutrient content (Garver et al. 1988). Samples were ground using a Wiley Mill to pass through a 20-mesh screen. Total-N was measured by Kjeldahl analysis (AOAC 1990). After perchloric acid digestion, total P content was determined via molybdate blue colorimetry. Ash-free dry weight was determined by ashing subsamples.

Decomposition rates for *S. cyperinus* and *T. latifolia* were estimated using recently senesced plant material harvested from a 12th small depression and dried at 40°C to a constant mass. On March 6, 1994, 2.0-g bundles of each species were placed in separate plastic mesh bags and deployed adjacent to the same plots in which biomass was sampled (n=63). Bundles were retrieved after 2, 161, 258, 364, and 507 d, thoroughly rinsed, dried at 100°C for 2 d, and percent mass remaining was calculated for each species. Details of the decomposition work are published elsewhere (Atkinson and Cairns 2001).

Soil analyses were conducted at all 63 plots in 1994. Sediment depth to compacted substrate was calculated as the mean of three estimates taken with a soil probe diagonally across each 1.0-m^2 square plot. Soil samples were collected in 0.25-m^2 nested subplots and roots were removed from soil. Samples were dried at 100°C to a constant mass and ground using a Wiley Mill to pass through an 80-mesh screen. Total-N was determined using the Kjeldahl procedure (Bremner and Mulvaney 1982). Plant-available P was measured using the Bray P-2 method as described by Olsen and Sommers (1982). Total-C was measured by dry combustion using a LECO Carbon Analyzer (LECO Corporation, St. Joseph, MI).

Three replicate surface-water chemistry samples were taken near the deepest point of each site in June or July of 1993 and 1994 and were filtered through Whatman #42 filter paper. Nitrite+nitrate-N and ammonium-N were measured spectrophotometrically (APHA 1989), total-P via ICPES, ortho-P by molybdate blue colorimetry, and dissolved Fe, Mn, and Ca were measured using flame atomic absorbance spectrophotometry (APHA 1989). The replicates within each wetland were averaged to yield site means.

Depth of standing water was measured at a permanent stake in the deepest point of each wetland every two weeks during the 1992, 1993, and 1994 growing seasons, which is from May 5 to October 9 in Wise County (USDA, NASS 2009). To estimate mean depth of standing water for each plot, plot elevation was measured (mean of three elevation estimates recorded diagonally across each 1.0-m^2 plot using a transit and stadium rod) relative to the elevation and mean water depth at the permanent stake (Fig. 1). To characterize the probability of drawdown frequency and duration, a Soil Exposure Index (SEI) was calculated for each plot based on relative elevation of the plot and permanent stake, and the mean and standard deviation of water level that was measured biweekly at the permanent stake for each of the 1992, 1993, and 1994 growing seasons (Table 1):

$$\mathrm{SEI} = 100 - \mathrm{x},$$

where x = percent of positive results, i.e. inundated, for seven separate water level calculations including mean relative plot depth and mean relative plot depth ±1, 2, or 3 standard deviations of water level. Thus, SEI ranges from 0 (never exposed) to 100 (always exposed) and as an example, a plot tending to exhibit shallow inundation with occasional drawdown, would have four positive results

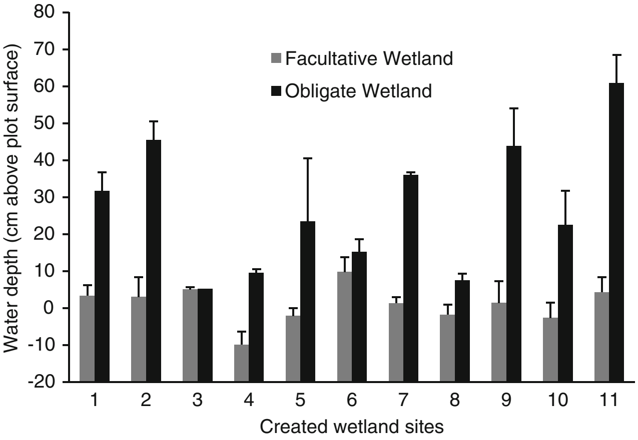

Fig. 1 Mean depth to standing water from April through September, 1994 for facultative wetland and obligate wetland communities at 11 created wetlands. Error bars represent 1 standard deviation of the mean water level among plots, except in the obligate wetland community at site 4 where only a single plot was sampled

(standing water) consisting of the mean water depth and each of the three positive standard deviations of that mean: $\mathrm{SEI} = 100 - (4 \div 7 = 57\% \text{ of calculations}) = 43$.

Soil saturation was not measured directly and appeared to have persisted during times of soil exposure (Atkinson, personal observations). Precipitation rates for 1993 and 1994 were described by the Palmer Drought Severity Index (NCDC 1999).

Data Analysis

Above-ground biomass, below-ground biomass, and litter mass were contrasted at the community scale for the facultative wetland and obligate wetland community types for each year and at the site scale for each year in the 11 wetland sites using Paired *t*-tests (Sigma Stat for Windows, version 3.11, Systat Software, Inc., 2004). The contribution of environmental parameters (Table 2) to community patterns of above-ground biomass in the 63 plots in 1994 (some environmental parameters were not available for 1993) was evaluated using canonical correspondence analysis (CCA) followed by Monte Carlo Permutation test (Canoco for Windows, version 4.02, ter Braak and Smilauer, Center for Biometry, Wageningen, The Netherlands, 1999). Mean above- and below-ground biomass in the 32 facultative wetland plots and the 31 obligate wetland plots were modeled using forward stepwise regression of all environmental parameters (Sigma Stat for Windows, version 3.11, Systat Software, Inc., 2004). Correlations among PAG and PBG measures were tested using Pearson product-moment correlation. Data were tested for normality using the Kolmogorov-Smirnov Test, and non-normally distributed data were log-transformed. A *p*-value of ≤0.05 was used to indicate statistical significance.

Results

Precipitation patterns were normal in 1994, but drought conditions were reported in 1993 during August (severe drought) and to a lesser extent during July, September, October and November (mild drought) (NCDC 1999). In the facultative wetland communities, mean SEI among sites in 1993 (61.9, SE 3.92) was higher than in 1994 (51.2, SE 4.28) (paired *t*-test, $p=0.044$, $n=11$). Within the obligate wetland community, mean SEI in 1993 (31.3, SE 7.95) was higher that in 1994 (10.09, SE 4.50) ($p=0.017$) (Table 1).

Comparative Evaluation of Primary Production

Peak Above-ground Biomass Mean PAG among sites in 1993 (535.7 g m^{-2}, SE 70.6 g m^{-2}) was higher than in 1994 (435.3 g m^{-2}, SE 51.7 g m^{-2}) (paired *t*-test, $p=0.014$, $n=11$). Within the facultative wetland community, mean PAG in 1993 (594.6 g m^{-2}, SE 72.8 g m^{-2}) did not differ from that in 1994 (473.7 g m^{-2}, SE 40.8 g m^{-2}) ($p=0.055$). In the obligate wetland community, mean PAG in 1993 (522.0 g m^{-2}, SE 122.1 g m^{-2}) was also similar to that in 1994 (409.5 g m^{-2}, SE 75.5 g m^{-2}) ($p=0.126$). Facultative wetland PAG was not significantly higher than that for the obligate wetland community either year (Table 2).

When 1994 data from both communities were combined, *S. cyperinus* exhibited the highest PAG biomass (51.8% of total) and second highest relative cover (23.0%); and PAG for *T. latifolia* ranked second (23.6% of total) and relative cover ranked highest (32.0%). Within the facultative wetland community, *S. cyperinus* occurred in 28 of 32 plots and represented 78.3% of total PAG biomass, and in the obligate wetland community, *T. latifolia* occurred in 26 of 31 plots and represented 58.9% (Table 3).

Litter, Below-ground Biomass, Soil Carbon, and Shoot to Root Ratio Mean litter mass in the facultative wetland community (746.8 g m^{-2}, SE 99.3 g m^{-2}) was higher than in the obligate wetland community (494.4 g m^{-2}, SE 86.4 g m^{-2}) (paired *t*-test, $p=0.049$, $n=11$) in 1994, but litter mass did not differ in 1993 ($p=0.758$) (Table 2). Drought conditions did not seem to effect litter mass in either community; litter mass in 1993 did not differ from 1994 for either the facultative wetland ($p=0.150$) or the obligate wetland community ($p=0.136$).

Mean PBG among sites in 1993 (603.1 g m^{-2}, SE 64.5 g/m^2) was not different than in 1994 (633.1 g m^{-2}, SE 81.1 g m^{-2}) ($p=0.481$). Mean PBG in 1994 was higher in the facultative wetland community (586.8 g m^{-2}, SE 87.4 g m^{-2}) than in the obligate wetland community (370.2 g m^{-2}, SE 96.3 g m^{-2}) ($p=0.057$, Table 2). In 1994, PBG was positively correlated with PAG ($r=0.41$, $p=0.030$, $n=11$).

Table 2 Environmental parameter and primary production data for 11 sites

Parameter	Facultative wetland community			Obligate wetland community			Paired *t*-test
	MEAN	SE	*n*	MEAN	SE	*n*	*p*
1992 SEI	43.6	5.8	11	2.4	1.7	11	*0.003*
1993 SEI	61.9	3.9	11	31.3	7.9	11	*<0.001*
1994 SEI	51.2	4.3	11	10.1	4.5	11	*<0.001*
Sediment depth (cm)	19.0	6.2	11	29.3	5.9	11	*0.013*
Soil N (TKN, %)	0.23	0.03	11	0.24	0.03	11	0.938
Soil P (Bray2 extractable, mg g^{-1})	1.58	0.28	11	1.02	0.20	11	0.091
Soil C (%)	3.9	0.2	11	4.1	0.6	11	0.783
Soil C:N (mass)	19.8	2.1	11	18.6	1.4	11	0.689
Tissue N (TKN, %)	0.89	0.04	10	1.00	0.08	10	0.251
Tissue P (μg g^{-1})	1795.8	74.7	10	1998.6	168.3	10	0.365
Tissue N:P (mass)	5.0	0.2	10	5.0	0.2	10	0.868
Tissue C (%)	44.3	0.3	10	43.8	0.1	10	0.119
Tissue C:N (mass)	51.3	2.3	10	50.5	6.4	10	0.940
Litter N (TKN, %)	0.96	0.04	11	1.00	0.06	11	0.928
Litter P (μg g^{-1})	927.2	59.4	11	1123.5	86.3	11	*0.043*
Litter N:P (mass)	10.7	0.5	11	9.7	0.8	11	0.228
Litter C (%)	40.6	1.3	11	39.8	1.2	11	0.581
Litter C:N (mass)	46.2	2.3	11	41.6	2.3	11	0.167
D2	92.7	0.4	11	92.8	0.5	11	0.839
D161	83.0	3.4	11	75.8	3.8	11	*0.041*
D258	82.2	1.2	11	74.9	1.9	11	*0.005*
D364	81.1	1.1	11	72.6	1.7	11	*<0.001*
D507	77.5	2.4	11	65.7	2.6	11	*0.002*
1993 PAG (g m^{-2})	594.6	72.8	11	522.0	122.1	11	0.545
1994 PAG (g m^{-2})	473.7	40.8	11	409.5	75.5	11	0.295
1994 PBG (g m^{-2})	586.8	87.4	11	370.2	96.3	11	0.057
1994 PAG:PBG	1.0	0.20	11	1.5	0.28	11	0.140
1993 Litter mass (g m^{-2})	606.2	79.3	11	584.8	62.9	11	0.758
1994 Litter mass (g m^{-2})	746.8	99.3	11	494.4	86.4	11	*0.049*

Italicized fonts represent statistically significant differences ($p<0.05$). SEI = soil exposure index, D# = decomposition reported as mass remaining after # days, Tissue N:P mass based on tissues from *S. cyperinus* for the facultative wetland community and *T. latifolia* for the obligate wetland community

Mean soil C in 1994 in the facultative wetland community (3.9%, SE 0.2%) did not differ from that of the obligate wetland community (4.1%, SE 0.6%, $p=0.783$) (Table 2). In the facultative wetland community, soil carbon was negatively correlated with P content of soil ($r=-0.44$, $p=0.01$, $n=11$), of water (TP, mean: 0.081 mg L^{-1}, SE 0.018, $r=-0.45$, $p=0.01$), and tissues of *S. cyperinus* ($r=-0.39$, $p=0.026$); but soil C was not correlated with PAG, PBG, or litter content. In the obligate wetland community, soil carbon was positively related to P content in *T. latifolia* ($r=0.43$, $p=0.015$) and negatively related to 1994 SEI (wetter plots had more soil C, $r=-0.36$, $p=0.044$); however, PAG, PBG, and litter content were not significantly correlated with soil carbon.

Shoot/root ratio, the ratio of above- to below-ground biomass (PAG:PBG), was 1.40 (SE 1.50) in 1994 for all plots and PAG:PBG in the facultative wetland community (1.0, SE 0.20) was not different from the obligate wetland community (1.5, SE 0.28, $p=0.140$) (Table 2).

Predictive Model of Primary Production

Facultative Wetland Community For PAG in the facultative wetland community in 1994, Forward Stepwise Regression (FSR) selected both the decomposition rate over 507 d (faster decomposition was associated with greater PAG, $p<0.001$) and the live *S. cyperinus* tissue P content ($r=$

Table 3 Above-ground biomass of each species for each community and for both communities combined in 1994

Rank	Species	IS	Facultative wetland community PAG		Obligate wetland community PAG		Both communities PAG	
			Cumulative (gm^{-2})	Total (%)	Cumulative (gm^{-2})	Total (%)	Total species (gm^{-2})	Total (%)
1	*Scirpus cyperinus*	FACW	13591.2	78.3	380.0	3.9	13971.2	51.8
2	*Typha latifolia*	OBL	709.6	4.1	5670.0	58.9	6379.6	23.6
3	*Juncus acuminatus*	OBL	374.0	2.2	1896.0	19.7	2270.0	8.4
4	*Juncus effusus*	FACW	1320.0	7.6	0.0	0.0	1320.0	4.9
5	*Sparganium americanum*	OBL	5.2	0.0	718.0	7.5	723.2	2.7
6	*Sphagnum* sp.	OBL	246.4	1.4	344.0	3.6	590.4	2.2
7	*Eleocharis obtusa*	OBL	160.4	0.9	136.4	1.4	296.8	1.1
8	*Lobelia cardinalis*	FACW	148.8	0.9	72.0	0.7	220.8	0.8
9	*Solidago gigantea*	FACW	179.6	1.0	40.0	0.4	219.6	0.8
10	*Potomogeton pulcher*	OBL	4.4	0.0	192.0	2.0	196.4	0.7
11	*Festuca rubra*	FACU	177.6	1.0	0.0	0.0	177.6	0.7
12	*Agrostis tenuis*	NA	112.4	0.6	0.0	0.0	112.4	0.4
13	*Eupatorium perfoliatum*	FACW	96.4	0.6	0.0	0.0	96.4	0.4
14	*Potomogeton foliosus*	OBL	22.8	0.1	71.2	0.7	94.0	0.3
15	*Cyperus esculentus*	FACW	33.2	0.2	56.0	0.6	89.2	0.3
16	*Galium* sp.	NA	18.4	0.1	26.4	0.3	44.8	0.2
17	*Eupatorium fistulosum*	FACW	44.4	0.3	0.0	0.0	44.4	0.2
18	*Epilobium coloratum*	OBL	28.8	0.2	0.4	0.0	29.2	0.1
19	*Aster* sp.	NA	22.8	0.1	0.0	0.0	22.8	0.1
20	*Schoenoplectus americanus*	OBL	0.0	0.0	20.0	0.2	20.0	0.1
21	*Rumex crispus*	FACU	14.4	0.1	0.0	0.0	14.4	0.1
22	*Salix nigra*	FACW	14.0	0.1	0.0	0.0	14.0	0.1
23	*Liparis loeselii*	FACW	11.2	0.1	0.0	0.0	11.2	0.0

Cumulative PAG per community based on the sum of PAG for a species in plots within the facultative wetland community (32 plots) and in the obligate wetland community (31 plots), excluding species with a total above-ground biomass of <10 g. Total PAG for both communities represents the sum for all 63 plots. Rank based on both communities combined, Indicator Status (IS) presented as indicator code in which OBL = obligate wetland, FACW = facultative wetland, FAC = facultative, FACU = facultative upland, and NA = not available (USDA, NRCS 2009)

0.85, $p<0.001$, $n=26$). For PBG in the facultative wetland community in 1994, FSR selected both the live *S. cyperinus* tissue N:P (positive association, $p=0.004$) and the concentration of SRP in water (mean: 0.019 mg L^{-1}, SE 0.002) ($r=0.61$, $p=0.033$).

Obligate Wetland Community For PAG in the obligate wetland community in 1994, FSR selected both the concentration of NH_3 in water (positive association, mean: 0.090 mg L^{-1}, SE 0.026, $p=0.002$, $n=26$) and sediment depth (positive association, $r=0.73$, $p=0.007$). For PBG in the obligate wetland community in 1994, FSR selected both litter N:P (positive association, $p=0.002$) and the depth to water table in the previous year (1993) (i.e., plots drier in 1993 exhibited greater PBG in 1994, $r=0.67$, $p=0.027$).

Wetland Ecosystem Scale According to the CCA based on 63 plots, sediment depth and SEI for 1993 and 1994 structured gradients of species-specific patterns of productivity (greater sediment depth and more drawdown was positively associated with productivity). However, soil nutrient concentrations of N and P did not contribute to the model (Tables 4 and 5).

Discussion

Comparative Evaluation of Primary Production

Annual above-ground biomass in this study (mean PAG in 1993: 558.3 g m^{-2} and in 1994: 441.6 g m^{-2}) was within the range reported for other created wetlands. PAG in our study was higher than reported for 10-yr old restored emergent, non-tidal freshwater wetland sites in Maryland (mean across 3 yrs and three communities was 214–249 g m^{-2}, Whigham et al. 2002). DeBerry and Perry

Table 4 Canonical Correspondence Analysis of above-ground biomass for both communities in 1994

Axes	1	2	3	4	Total inertia
Eigenvalues	0.855	0.687	0.630	0.565	5.487
Species-environment correlations:	1.000	0.999	0.989	0.973	
Cumulative percentage variance					
of species data:	15.6	28.1	39.6	49.9	
of species-environment relation:	15.6	28.4	40.1	50.7	
Sum of all canonical eigenvalues					5.392

(2004), working in a 3-yr old created palustrine wetland in the coastal plain of Virginia, measured PAG ranging from 146 to 896 g m^{-2}. Bailey et al. (2007), working in the same wetland three years later found PAG ranged from 580 to 790 g m^{-2}.

Peak above-ground biomass in the facultative wetland community in the current study, 594.6 g m^{-2} in 1993 and 473.7 g m^{-2} in 1994, was somewhat higher than that reported for temporarily flooded communities in twelve 10-yr old created wetlands in the coastal plain of Maryland (3-yr mean ranged from 297.6 to 358.6 g m^{-2}, Whigham et al. 2002).

In the obligate wetland community, PAG was lower for emergent/seasonally flooded communities in 10-yr old restored wetlands (3-year mean ranged from 167.8 to 232.3 g m^{-2}, Whigham et al. 2002) than in the current study (522.0 g m^{-2} in 1993 and 409.5 g m^{-2} in 1994). *Typha latifolia* exhibited the highest dominance in the obligate wetland community within most of the 11 sites in this study, but exhibited low productivity compared to natural wetlands. In this study, *T. latifolia* averaged 309.8 g m^{-2} for the plots that it occurred in during 1994 and 236.3 g m^{-2} in 1993; however, Hill (1987) provided results from several studies of *Typha* spp. that ranged in peak above-ground standing crop from 404 to 2,252 g m^{-2}.

Mean 1994 PBG was lower in both the facultative wetland community (586.8 g m^{-2}, SE 87.4 g m^{-2}) and the obligate wetland community (370.2 g m^{-2}, SE 96.3 g m^{-2}) than Schalles and Shure (1989) measured in a dystrophic Carolina Bay (910 g m^{-2}). In a literature survey of below-ground biomass, de la Cruz (1978) reported a range of 371–1,300 g m^{-2} for *T. latifolia*. Garver et al. (1988) planted 21 g root stock of *Typha* sp. and measured 271, 341, and 338 g m^{-2} below-ground rhizome production in years one, two, and three, respectively, which was slightly lower than below-ground biomass in the considerably older obligate wetland community of our study. Along with the PBG predictive model results, this suggests that shallow sediment depth inhibited below-ground productivity in the obligate wetland community.

The shoot/root (PAG:PBG) for the facultative wetland community was 1.0 in this study, which was not significantly lower than that for the obligate wetland community (1.5). Kao et al. (2003) reported shoot/root for *S. cyperinus* of 1.7, the highest of five perennial macrophytes they studied (the lowest was 0.42). The shoot/root for the obligate wetland community in our study was higher than that reported by Klopatek and Stearns (1978) which concluded that annual *Typha* spp. below-ground net production equals that for above-ground. The grand mean for both communities in the current study (1.4) was somewhat higher than shoot/root for Carolina bays (0.15, Schalles and Shure 1989).

Predictive Model of Primary Production

PAG in the facultative wetland and obligate wetland communities, in contrast to the site scale, was positively associated with environmental parameters related to nutrient availability (tissue nutrient concentration, decomposition rate, and sediment depth) but was not related to SEI.

Facultative Wetland Community The positive associations of PAG with both decomposition rate over 507 d and with live *S. cyperinus* tissue P content, along with positive associations of N:P of live *S. cyperinus* and with SRP in water for PBG, suggest that P limits productivity in this community. In addition to soil and water nutrient concen-

Table 5 Monte Carlo Permutation results based on Canonical Correspondence Analysis of 63 plots in 1994

Variable	Marginal effects		Conditional effects	
	Lambda 1	Lambda A	*p*	*F*
Sediment Depth (cm)	0.43	0.43	0.005	6.63
1993 SEI	0.36	0.29	0.005	4.72
1994 SEI	0.32	0.22	0.005	3.69
Soil P (ppm)	0.22	0.03	0.835	0.61
Soil N (ppm)	0.07	0.03	0.860	0.52

trations, live tissue and litter nutrient content have been widely used to determine limiting nutrients (Koerselman and Mueleman 1996; Güsewell et al. 2003). *Scirpus cyperinus* live tissue P was 0.19% in our study, which is near the low end of the range of P-limited wetlands (0.10–0.64%; Bedford et al. 1999), but similar to above-ground *S. cyperinus* live tissue P (0.22%) reported by Kao et al. (2003). Litter tissue P in the facultative wetland community (0.09%) was also in the low end of the range for marshes (0.06–0.22%; Bedford et al. 1999).

Litter and plant tissues may have accumulated P over time and reduced its availability. The study of decomposition at these sites by Atkinson and Cairns (2001) reported considerable litter accumulation (746.8 g m^{-2}) and slow tissue decomposition rates, especially for *S. cyperinus* (80.9% mass remaining after one year, significantly slower than the rate reported for *T. latifolia*, 72.3%, Atkinson and Cairns 2001), which was slower than the *S. cyperinus* decomposition rate (78% mass remaining after 150 d) found by Kao et al. (2003). The litter accumulation may have reduced the P content of above-ground plant tissue as reported in northern fens by Weltzin et al. (2005). Furthermore, PBG in the *S. cyperinus*-dominated community was twice that of the *T. latifolia*-dominated community. Kao et al. (2003) reported that *S. cyperinus* exhibited the highest below-ground concentration of P (0.43%) for any of the five species in that study, suggesting some level of plant control over P availability.

However, N limitation was also indicated. Live tissue N (0.95%) was also within the low end of the range for North American marshes (0.83–4.20%, Bedford et al. 1999) and lower than *S. cyperinus* live tissue N (1.5%) reported by Kao et al. (2003). Litter N (0.98%) was an intermediately low value within the range for marshes (0.75–1.58%, Bedford et al. 1999). Koerselman and Mueleman (1996) reviewed 40 studies that addressed nutrient limitation in emergent vegetation systems and suggested that a tissue N:P (mass) ratio between 14 and 16 was optimal for community productivity, and that lower values, such as the N:P ratio of 5 in the current study, indicated N limitation. Thus, it appears that these communities are primarily N-limited, yet are also P-limited to a lesser but significant extent as indicated by the positive relationship between live tissue P and biomass. Olde Venterink et al. (2003) assessed productivity among 150 wetland sites in Western Europe and found N-limitation among most sites, but N and P co-limitation among nutrient poor sites.

Obligate Wetland Community Predictive environmental variables for productivity in this community included positive associations of NH_3 in water and sediment depth for PAG; and for PBG, predictive variables included litter tissue N:P (positive relationship) and the depth to water table in the previous year (1993, drawdown was positively associated with increased productivity). Because these sites formed accidentally after cessation of surface mining operations, sediment accumulation is likely to have been rapid in the years immediately after mining. Sedimentation rates should have declined once revegetation occurred, and Holl and Cairns (1994) reported 90% vegetative cover among 15–20-yr old reclaimed sites in reclaimed areas near our study sites. Live tissue N:P (5.0 SE 0.2) in *T. latifolia* was well below optimal values. These variables generally support an assertion of N-limitation for this community. Nitrogen limitation for *T. glauca* has been reported elsewhere for natural lacustrine marshes (Neill 1990).

However, live tissue P for *T. latifolia* was 0.19%, which is in the low end of the range for marshes (0.10–0.64%) and within the range of P-limited marshes (Bedford et al. 1999). Litter tissue P in the obligate wetland community (0.11%) was also in the low end of the range for marshes (0.06–0.22%; Bedford et al. 1999). Some studies of natural wetlands have reported that P in soil, water, and live plant tissues were all strongly positively correlated with standing crop of *T. latifolia* (Boyd and Hess 1970), while others suggest that P limitation only occurs with N additions (Neill 1990) or that N and P co-limitation occurs (Woo and Zedler 2002). Eight natural, *Typha*-dominated wetlands in Minnesota contained the same *Typha* P concentration as in the current study (0.2%), but PAG averaged 670 g m^{-2} (Emery and Perry 1995), compared to only 410 g m^{-2} in our study. As in the facultative wetland community, it appears that N, and to a lesser extent P, limit productivity of this community.

Wetland Ecosystem Scale At the wetland ecosystem (site) scale, hydrology (SEI) exerted a controlling influence on community composition, which has also been found for prairie potholes, whether they are naturally occurring (Stewart and Kantrud 1971) or restored (Seabloom and van der Valk 2003). The resulting species composition can also influence primary production (Hooper et al. 2005). *Scirpus cyperinus* occurred at a higher SEI than did *T. latifolia* (Atkinson et al. 2005) and represented nearly 52% of all PAG produced in 1994, while *T. latifolia* represented <24% of PAG.

Precipitation patterns at the site scale further support the importance of SEI and the effect of hydrology on nutrients. In a review of freshwater wetland functions including primary productivity and decomposition, Brinson et al. (1981) reported that inundation for long duration resulted in slow decomposition and low nutrient availability. Higher PAG in 1993 coincided with drought conditions that might have stimulated primary production by increasing decomposition rates in these sites. Connections between hydrology and tissue nutrient content have also been suggested from wetland mesocosm experiments (Anderson and Mitsch 2005).

Availability of N and P may have been influenced by land use, which changed over time at these sites. Nitrogen is predicted to be in low supply in mineral soils (Bedford et al. 1999) and to accumulate very slowly as soil organic matter accumulates in created wetlands (Bishel-Machung et al. 1996; Shaffer and Ernst 1999; but see Nair et al. 2001). In upland soils adjacent to sites in the current study, Li and Daniels (1994) reported that geologic N content (fixed NH_4^+ in micas etc.) was high immediately after mined land reclamation, but that plant-available forms accumulated slowly in mine soils as they weathered. Adjacent soil N concentrations were 0.2–0.3% in raw mine spoils and increased to >1.5% in 20-yr old upland mine soils (Li and Daniels 1994). Soil TKN in our study (0.23% for both communities) was higher than that reported for created wetland soils in Pennsylvania after 1–8 years (0.11%) (Bishel-Machung et al. 1996), but lower than reported for created wetlands in Ohio after 10 years (TN=0.32–0.36%; Anderson and Mitsch 2006). Langis et al. (1991) also reported N-limitation of plant productivity in created salt marshes with low soil organic content and low nutrient loading.

It would appear that either P inputs were low at these sites, or that P was initially more available. In the mined landscape of the study sites, mineral sources of P presumably would be abundant during early ecosystem development as P was deposited through sedimentation. Hogan et al. (2004) reported that retention of P by restored wetlands exceeded that of natural wetlands. As in our study, Anderson and Mitsch (2006) found greater sediment accumulation in open water than emergent zones, which may enhance P inputs (Mitsch and Gosselink 2007) and increase productivity (Belcher et al. 1995). However, as discussed earlier, P accumulation and slow decomposition in the facultative wetland community may have reduced P availability in both communities of the current study.

Conclusions

The ca. 20-yr old created wetlands sites in our study exhibited greater primary production for a drought year than during a year with normal precipitation, but exhibited primary production rates in the lower portion of the range reported for natural wetlands. The moderately low nutrient content of these sites may have influenced development of important functions such as decomposition and primary production.

While several studies have reported higher species richness associated with low to moderate nutrient conditions (Nygaard and Ejrnaes 2009), cover of *S. cyperinus* was negatively associated with species richness (Atkinson et al. 2005), perhaps as a result of the extensive accumulation of *S. cyperinus* litter that may act to limit germination and growth of other species. Further, the distribution of *S. cyperinus* in these sites is either stabilized or expanding and neither a species rich assemblage, nor woody physiognomy is becoming established (Atkinson et al. 2005). Thus plant community development and productivity in these sites are delayed as they remain in an immature state (sensu Odum 1969).

It appears that hydrology influences differences between plant communities in inadvertently formed wetlands in mined landscapes, but that nutrient availability determines productivity levels within communities and that productivity in these maturing ecosystems is co-limited by N and P. However, since species composition in these sites influences decomposition rates and since decomposition interacts with nutrient availability and SEI, functions at the two scales appear to be interdependent.

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