Biomass harvest of invasive Typha promotes plant diversity in a Great Lakes coastal wetland

Citation	Lishawa, S. C., Lawrence, B. A., Albert, D. A., & Tuchman, N. C. (2015). Biomass harvest of invasive Typha promotes plant diversity in a Great Lakes coastal wetland. [Article in Press]. Restoration Ecology. doi: 10.1111/rec.12167
DOI	10.1111/rec.12167
Publisher	John Wiley & Sons, Inc.
Version	Accepted Manuscript
Terms of Use	http://cdss.library.oregonstate.edu/sa-termsofuse

Biomass harvest of invasive *Typha* promotes plant diversity in a Great Lakes coastal wetland

Keywords: biodiversity, biomass energy, conservation, hybrid cattail, Lake Huron, seed bank

Manuscript submission category: Research Paper

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Author contributions

SL, DA, NT conceived the idea; SL, DA, NT, BL designed the experiments and sampling protocols; DA provided taxonomic expertise; SL, BL performed the experiments and managed data; SL analyzed the data and wrote the manuscript; BL, DA, NT edited the manuscript.

Abstract

Ecological and financial constraints limit restoration efforts, preventing the achievement of desired ecological outcomes. Harvesting invasive plant biomass for bioenergy has the potential to reduce feedback mechanisms that sustain invasion, while alleviating financial limitations. *Typha* × *glauca* is a highly productive invasive wetland plant that reduces plant diversity, alters ecological functioning, its impacts increase with time, and is a suitable feedstock for bioenergy. We sought to determine ecological effects of *Typha* utilization for bioenergy in a Great Lakes coastal wetland by testing plant community responses to harvest-restoration treatments in stands of two age classes and assessing community resilience through a seed bank study. Belowground harvesting increased light penetration, diversity, and richness, and decreased *Typha* dominance and biomass in both years post-treatment. Aboveground harvesting increased light and reduced *Typha* biomass in post-year 1 and in post-year 2, increased diversity and richness and decreased *Typha* dominance. Seed bank analysis revealed that young stands (<20 years) had greater diversity, richness, seedling density, and floristic quality than old stands (>30 years). In the field, stand-age did not affect diversity or *Typha* dominance, but old stands had greater *Typha* biomass and slightly higher richness following harvest. Harvesting *Typha* achieved at least two desirable ecological outcomes: reducing *Typha* dominance and increasing native plant diversity. Younger stands had greater potential for native recovery, indicated by more diverse seed banks. In similar

degraded wetlands, a single harvest of *Typha* biomass would likely result in significant biodiversity and habitat improvements, with the potential to double plant species richness.

Key Words

biodiversity, biomass energy, conservation, hybrid cattail, Lake Huron, seed bank

Implications for Practice

- Both aboveground and belowground harvest of *Typha* stands increased plant diversity and richness for two years following treatment, indicating that these passive restoration methods (without planting) are viable in northern Great Lakes coastal wetlands with relatively intact seed banks.
- Younger *Typha* stands had a more intact and diverse seed bank than older stands.
- Harvesting *Typha* biomass for bioenergy production may be an appropriate alternative to herbiciding and burning methods in Great Lakes wetlands.

Introduction

The extent and intensity of ecological restoration is limited by ecological and financial constraints (Miller & Hobbs 2007). A degraded ecosystem reaching an alternate stable state becomes resistant to restoration efforts or requires significantly more intense management to overcome ecological thresholds (Suding et al. 2004; Zedler 2009). Dominant invasive wetland plants can drive an ecosystem into an alternate state by causing significant changes to soil nutrients and carbon (Tuchman et al. 2009) and depleting native seed banks (Frieswyk & Zedler 2006; Hall & Zedler 2010). These environmental changes may correspond with the length of time that invaders have been established (Strayer et al. 2006; Mitchell et al. 2011). We predict that plant community responses to restoration efforts will depend in part upon invasive species residence time and that time since establishment can be a useful proxy for an ecosystem's restorability.

Harvesting invasive plant biomass could reduce feedback mechanisms that sustain the invaded state (Zedler 2009). For example, periodic removal of dense litter and aboveground biomass from invaded wetlands could simultaneously remove nutrient-rich plant tissue, increase light penetration to the soil surface, and increase plant diversity. In addition to the ecological potential of harvesting, utilization of invasive plant and other biomass residues for energy production could directly offset restoration costs (Quinn et al. 2013), thereby reducing the financial constraints on restoration activities. For instance, Nackley et al. (2013) illustrated that within a 1.1 million ha *fuelshed* around a biomass power facility in Washington, the use of invasive shrubs for energy would entirely offset restoration, harvesting, and biomass transportation costs.

In other regions, highly productive invasive plants have similar potential to serve as biomass fuel stocks (Jakubowski et al. 2010; Quinn et al. 2013).

Cattails (*Typha* spp.) have long been considered as possible bioenergy crops due to their high productivity, the potential for harvest to remove nutrients from polluted lakes and wetlands, and recently for the generation of carbon credits (Dubbe et al. 1988; Cicek et al. 2006; Grosshans et al. 2012). In eastern North America, *Typha* × *glauca*, an invasive hybrid between native *T. latifolia*, and invasive *T. angustifolia* (Smith 1987), may be an appropriate species for bioenergy production linked with ecological restoration because of high productivity, undesirable ecological impacts (Tuchman et al. 2009), and the potential for harvesting to restore ecosystem structure and function. Harvesting of *T.* × *glauca*'s congener, *T. domingensis*, maintains biodiversity in central Mexican wetlands (Hall et al. 2008) and repeated *T.* × *glauca* harvesting resulted in increased native graminoid cover in an urban Wisconsin wetland (Hall & Zedler 2010). These findings suggest that harvesting has the potential to be a viable restoration method for *T.* × *glauca* invaded wetlands.

***Typha* × *glauca* in Great Lakes coastal wetlands**

Great Lakes coastal wetlands provide critical habitat for diverse plants communities (Albert & Minc 2004), fish (Uzarski et al. 2005), migratory waterfowl and shorebirds (Prince et al. 1992; Ewert & Hamas 1995), and provide ecosystem services important to human well-being (Sierszen et al. 2012). Northern Lake Huron wetlands remain some of the highest quality, least disturbed coastal wetlands in the U.S. Great Lakes (Uzarski et al. 2013). Plant species in these ecosystems tend to sort into three distinct moisture dependent zones (wet meadow, emergent marsh, and submergent marsh). Characteristically, the wet-meadow is dominated by sedges (*Carex stricta*, *C. aquatilis*, *C. lacustris*) and blue-joint grass (*Calamagrostis canadensis*); the emergent marsh by bulrushes (*Schoenoplectus acutus, S. pungens*), spike rushes (*Eleocharis* spp.), rushes (*Juncus* spp.) and cattails (*Typha latifolia*); and the submergent marsh by pondweeds (*Potamogeton* spp.), water-lilies (*Nymphaea odorata* and *Nuphar* spp.) and bladderworts (*Utricularia* spp.) (Albert et al. 2005). Presently, these wetlands are undergoing widespread macrophyte invasions (Lishawa et al. 2010; Tulbure & Johnston 2010). Prolonged low water levels in the Great Lakes since 2000 (NOAA 2013), have reduced wave energy and exposed mud flats along the gently sloping shorelines (Albert et al. 2013), stimulating the establishment and proliferation of invasive plants (Tulbure et al. 2007). Predicted future water level declines associated with climate change (Angel & Kunkel 2010) will likely exacerbate invasion.

Typha × *glauca* (hereafter *Typha*) is invading highly disturbed and otherwise intact, diverse, and high-quality Great Lakes coastal wetlands (Lishawa et al. 2010). Once established, *Typha* is a superior competitor, spreading rapidly via rhizome expansion (Boers & Zedler 2008), and tolerating variable water levels (Harris & Marshall 1963). Because it is many times more productive than the native plants it replaces, deep organic sediments accrue in *Typha* stands accompanied by changes in microbial communities, soil nutrients, and biogeochemical cycling (Angeloni et al. 2006; Tuchman et al. 2009; Lishawa et al. 2013; Lishawa et al. 2014). Dead standing culms persist and accumulate as slowly decomposing aboveground litter (Vaccaro et al. 2009), preventing the penetration of light, buffering soil surface temperatures, and resulting in reduced plant diversity (Larkin et al. 2012). The effects of *Typha* on floristic and edaphic factors vary temporally. Mitchell et al. (2011) found that litter increased within 10-years, plant diversity decreased after 15 years, and soil organic matter (SOM) increased between 10-35 years following Great Lakes coastal wetland invasion. Similarly, Lishawa et al. (2014) found *Typha* stand-age negatively correlated with plant diversity and positively correlated with SOM. Furthermore, seed banks in older and highly disturbed *Typha* stands may be more depleted of native species than younger stands (Frieswyk & Zedler 2006; Hall & Zedler 2010). Thus, we expect passive restoration (i.e. no additional planting) will promote more diverse plant community recovery in recently invaded wetlands.

We are unaware of any investigations of *Typha* restoration or seed bank studies in northern Great Lake coastal wetlands that tend to have high floristic quality and low disturbance. In a *Typha* invaded northern Great Lake coastal wetland we asked: 1) *How do harvest-restoration methods and time since-invasion affect plant community response?* and, 2) *Do seed banks of more recently invaded stands have a higher capacity for passive restoration than those invaded for longer periods?* We experimentally implemented two restoration treatments (aboveground and belowground biomass harvest) in *Typha* stands of two ages (old >30 years; young < 20 years), and evaluated plant community response over three-years (one-year pre-treatment and two-years post-treatment). Additionally, we conducted an experimental seed bank study investigating seedling emergence from field-collected sediments exposed to three water levels.

We hypothesized that: (H1) both restoration treatments would increase native plant diversity compared to controls, and belowground harvest would yield the greatest increase in diversity by removing rhizomes which can re-sprout following aboveground harvesting, (H2) young stands would have greater capacity for native plant community recovery than old stands, as indicated by a more diverse plant response, and likewise, (H3) soil seed banks in younger stands would have higher diversity and density of emergent seedlings than those from older stands.

Methods

Study Site

We conducted experimental restoration and seed bank studies in Cheboygan Marsh, a Great Lakes lacustrine open-embayment wetland (Albert et al. 2005) on northern Lake Huron near the city of Cheboygan, Michigan (lat 45°39'N, long 84°28'W). As compared to the relatively oligotrophic wetlands characteristic of the region, Cheboygan Marsh has elevated sediment nutrient levels, likely resulting in part from the adjacent City of Cheboygan wastewater treatment facility and in part from internal nutrient loading (Tuchman et al. 2009; Lishawa et al. 2010). *Typha* first established in Cheboygan marsh in the late 1940's and by 2010 over 62% of the 23 hectare wetland was dominated by *Typha* (Lishawa et al. 2013). Within the invaded portion of the marsh, *Typha* is highly dominant, making up greater than 99% of aboveground biomass (Angeloni et al. 2006; Tuchman et al. 2009).

Field Experiment

During 2011-2013, we implemented a *Typha* management experiment testing the effects of stand-age (2 levels) and restoration treatment (3 levels). Using *Typha* stand-age maps created by aerial photo interpretation between 1963-2010 (Lishawa et al. 2013), we identified polygons of similar areas from two age classes (hereafter *stands)*, old (>30 years; 6.37 ha) and young (<20 years; 6.41 ha). We used a 2-stand × 3-treatment factorial design with four replicates, for a total of 24 plots; within each stand we randomly assigned twelve, 16-m^2 plots (4 × 4-m) to one of three restoration treatments (aboveground harvest, belowground harvest, or control). We established plots in July 2011 and implemented treatments in August 2011. Water levels were below the sediment surface in all plots at the time of harvest. Aboveground harvest treatments consisted of cutting all stems at the sediment surface using an aquatic weed-wacker (Weeders Digest LLC, New Hope MN, USA) and removing biomass and all standing litter from the plot. Belowground harvest consisted of aboveground harvesting followed by hand removal of all rhizomes from the sediment. Hand removal was accomplished by cutting organic sediments into ~0.25-m^2 blocks, removing rhizomes, and returning all non-rhizome material to the plot. To isolate our treatment areas and prevent translocation of nutrients and carbohydrates from outside plots, in 2011 and 2012 we severed belowground connections along all plot perimeters by cutting through roots and rhizomes using heavy-duty ice scrapers. Within each 16-m^2 plot, we established four 1-m^2 subplots located 0.5 m from the perimeter at plot corners.

In mid-July of each year (2011, 2012, 2013) we sampled the vegetation in each subplot by assigning aerial cover values (<1-100%) for total vegetative cover, detritus, and for each plant species. Additionally, we recorded the presence of all plant species within 16-m^2 plots. Total species richness in the plot and the mean cover value of the four subplots were used for analysis. In 2011, we estimated root and rhizome biomass by collecting sediment subsamples from the belowground treatment plots (25 cm^2 surface area × maximum rooting zone depth), washing sediment, separating roots from rhizomes, and oven drying samples. In 2011, aboveground *Typha* biomass was estimated for aboveground and belowground plots by subsampling aboveground biomass from 25-cm^2 quadrats, oven drying, and weighing the dry biomass. We calculated post-treatment aboveground biomass by collecting 50 culms of varied heights throughout Cheboygan Marsh and creating a stem height-to-dry biomass allometric equation (g = $0.5265e^{1.751*\text{height(m)}}$; $r^2 = 0.81$). We measured the heights of *Typha* stems in each subplot in 2012 and 2013, and calculated biomass values using this equation. In late July 2012, we measured light penetration using a LI-189 Quantum sensor (LI-COR inc. Lincoln, NE, USA). At each subplot center, we recorded Photosynthetically Active Radiation (PAR, µmols s^{-1} m^{-2}) at 2.0-m, 1.0-m, 0.5-m, and 0.0-m (sediment surface). Mean 2.0-m PAR was considered 100% light for each plot. We estimated light penetration through the canopy for each plot by averaging the four subplot PAR values at each height and relativized them by the mean 2.0-m PAR value.

Seed Bank Experiment

We used the seedling emergence method (van der Valk & Davis 1978) to estimate seed bank composition within the old and young *Typha* stands. In July 2011, we collected three, 5-cm deep sediment plugs with a bulb planter from each 16-m^2 field plot and composited subsamples. Sediment samples were cold stratified by storing them at 4ºC from July 2011-June 2012 when the experiment began. We removed detritus, rhizomes, and roots, composited within-stand samples, and thoroughly homogenized the sediments by hand. We spread a 1-cm thick subsample of homogenized sediment over the surface of 10-cm of autoclave sterilized sand in 9.5-cm diameter pots (70.9-cm^3 sediment per/pot). We randomly assigned pots to three different water level treatments (relative to soil surface): high (+ 5-cm), moist (0-cm), or low (-5-cm). Four replicates of each stand × water-level treatment were tested (24 total replicates). In June 2012, experimental pots were randomly placed in an environmental growth chamber under a fluctuating light and temperature regime approximating June conditions in the northern Great Lakes region: 16 hours light at 22.5°C, eight hours dark at 12.5°C. Throughout the six-month study period, water levels were maintained twice a week and every two weeks pot locations were re-randomized and seedlings were identified and counted. Positively identified seedlings were removed from the pots and unidentified seedlings were allowed to grow until identification was possible.

Statistical Analysis

Subplots within each plot were averaged and extrapolated to the plot level. We evaluated the effects of stand and year on plant community and environmental variables (Shannon diversity [H'], species richness, *Typha* dominance [% of total veg. cover], aboveground biomass [g/m^2], belowground biomass [g/m^2], and % light reduction) and change in plant community variables between pre- and post-treatment using repeated measures analysis of variance (ANOVA). We assessed differences between treatments within years using Tukey's honestly significant differences test (HSD). Using indicator species analysis (ISA; Dufrene & Legendre 1997) we evaluated correspondence of individual species with stand (old, young) and treatment (above, below, control) across the three years of the study (2011, 2012, 2013). Indicator values of plant species were tested via Monte-Carlo simulation using 1000 permutations. We tested the effects of year, stand, and treatment on multivariate plant communities using permutational multivariate analysis of variance (PERMANOVA; Anderson 2001). We used nonmetric multidimensional scaling (NMDS) ordination to characterize plant community differences by stand (old, young) and treatment (aboveground harvest, total harvest, control), and to evaluate associated variables as vectors (McCune & Grace 2002). Dissimilarity between plots was based on Bray-Curtis distances, plots were constructed using two dimensions, and measured variables were tested for significance as vectors by permutation procedure (10,000 replicate permutations): species richness (Richness), H', percent unvegetated (Unveg), percent vegetated (Veg), detritus cover

(Detritus), *Carex* spp. cover (*Carex*), *Juncus* cover (*Juncus*), *Typha* cover (*Typha*), and water depth (Water).

In the seed bank experiment, we tested the effects of *Typha* stand-age (old, young), experimental water treatments (low, moist, high), and age × water level on seed bank H', species richness, Floristic Quality (FQI; Herman et al. 2001), stem density (#/pot), *Typha* density (#/pot), and *Carex* spp. density (#/pot) using ANOVA with Tukey's HSD test.

All statistical analyses were conducted using R 2.12.1 (R Development Core Team 2009) with the labdsv package used for ISA (Roberts 2012) and the vegan package used for NMDS (Oksanen et al. 2006).

Results

Pre-treatment Plant Communities

In 2011 pre-treatment, 28 plant species occurred across the 24 plots: 7 graminoids, 14 forbs, 1 aquatic, 5 woody species, and *Typha* (Supplementary Table 1). There were no statistical differences by stand-age or by random treatment assignment among H', species richness, *Typha* dominance (% of total vegetation cover), or aboveground biomass (Table 1; Fig. 1). However, we found significantly greater root and rhizome biomass in old *Typha* stands than in young stands: root-old, (mean ± SE; g/m^2) 4,516 ± 637, root-young, 2,609 ± 724 (p<0.05); and rhizome-old, 2,678 ± 70, rhizome-young, 1,682 ± 391 (p<0.05). ISA revealed that a single species, *Symphyotrichum puniceum*, was indicative of old stands (IV 63.1%; p=0.04; Supplementary Table 2). Additionally, we found slight but significantly greater Cyperaceae species richness in young stands than in old stands (Table 2). NMDS illustrated some clustering of pre-treatment young plot and old plot communities in multivariate space and correlations with several variables: Water (r^2= 0.41, p<0.01); Richness (r^2= 0.72; p<0.01); *Carex* (r^2= 0.26; p=0.03); H' (r^2= 0.64; p<0.01); and *Typha* (r^2= 0.29; p=0.03); (Fig. 2a). However, PERMANOVA revealed no statistical difference between pre-treatment plant communities by age, assigned treatment, or age × treatment (Table 3).

Plant Community Response to Restoration

Species richness nearly doubled from pre-treatment sampling to 53 species in post-year 2. Over the three-year study, a total of 63 species were identified across all 24 plots (Supplementary Table 1). In the two years following treatment, species richness and aboveground *Typha* biomass varied by *Typha* stand-age; old stands had both greater richness (old: 12.71 ± 1.21; young: 10.17 ±1.41 species/ m^2; p=0.028) and greater *Typha* biomass (old: 407.5 ± 101.6; young: 309.1 ± 80.2 g/m^2; p=0.033) than young stands (Table 1). Neither H' nor *Typha* dominance showed a stand-age effect (p=0.80, p=0.21 respectively; Table 1).

Belowground harvest significantly altered a suite of plant community measures in post-year 1 and differences persisted in post-year 2 (Table 1; Table 2; Fig. 1). In both years H' was greater than either aboveground harvest and control treatments (both p<0.05). Species richness more than doubled from pre-treatment (7.00 ± 0.63) to post-year 1 (13.00 ± 1.22) and post-year 2 (14.13 ± 0.90 species/m^2), and was significantly greater than in control plots both years following treatment (both p<0.05). *Typha* dominance and aboveground *Typha* biomass were lower than aboveground and control treatments both years (both p<0.05). Cyperaceae and

Juncaceae species richness were greater (both $p<0.05$) in belowground plots than in control or aboveground plots in both years following harvest (Table 2). ISA analysis revealed that in post-year 1, six species were significant indicators of belowground harvest treatment, *Juncus nodosus* (IV 93.4%; $p<0.001$), *Schoenoplectus tabernaemontani* (IV 93.2%; $p<0.001$), *Ranunculus sceleratus* (IV 92.7%; $p<0.001$), *J. alpinoarticulatus* (IV 84.2%; $p<0.01$), *Sparganium eurycarpum* (IV 79.1%; $p<0.01$) and *Alisma triviale* (IV 70.7%; $p=0.02$). In post-year 2, five species were indicative, *J. nodosus* (IV 85.2%; $p<0.01$), *S. tabernaemontani* (IV 84.9%; $p<0.01$), *J. alpinoarticulatus* (IV 83.8%; $p<0.01$), *Alisma triviale* (IV 70.7%; $p=0.02$), and *S. acutus* (IV 70.7%; $p=0.02$; Supplementary Table 2).

Compared to controls, aboveground harvest reduced aboveground *Typha* biomass in post-year 1 ($p<0.05$) but did not differ in post-year 2 (Fig. 1d). However, other aboveground harvest treatment effects did not emerge until post-year 2. In post-year 1, aboveground harvest had no significant effect on H', species richness, or *Typha* dominance, but in post-year 2, each of these factors differed between aboveground harvest and controls (all $p<0.05$; Fig. 1). Aboveground harvest increased species richness from 7.25 (± 4.53) pre-treatment to 11.5 (± 5.95) post-year 1, and 14.00 (± 5.83) post-year 2 (Fig 1b) and richness was significantly greater in treatment than in control plots in post-year 2 ($p<0.05$; Fig. 1b; Table 2). Native and Cyperaceae species richness were also greater than the control in post-year 2 ($p<0.05$; Table 2). The native grass *Calamagrostis canadensis*, was a significant indicator of aboveground treatment in both post-year 1 (IV: 74.6%; $p=0.02$) and post-year 2 (IV: 82.8%; $p=0.01$; Supplementary Table 2).

In both years following treatment, multivariate community assemblage differed by Year, Treatment, Year × Treatment, and Stand-age × Treatment (PERMANOVA; Table 3). Treatment plots clustered in mulitvariate space, and were correlated with several variables (Fig. 2b): Unveg (r^2= 0.46, p<0.01); Veg (r^2= 0.26, p<0.01); Detritus (r^2= 0.50; p<0.01); Richness (r^2= 0.29; p<0.01); *Carex* (r^2= 0.27; p<0.01); H (r^2= 0.75; p<0.01); *Juncus* (r^2= 0.26; p<0.01); and *Typha* (r^2= 0.78; p<0.01) .

Light Penetration Response to Restoration

In post-year 1, the percentage of PAR penetration differed significantly by treatment at all three heights above the marsh sediment surface (1.0m; 0.5m; 0.0m). Light was almost entirely prevented from reaching the sediment surface in the control plots (1.37 ± 0.15% light penetration); whereas belowground harvest dramatically increased light penetration (58.60 ± 3.01%) and aboveground harvest plots had an intermediate effect (29.13 ± 2.20%; Fig. 3).

Seed bank analyses

The high water (+5-cm) treatment prevented any seedlings from emerging in all but 2 replicates (1 old, 1 young), and was therefore eliminated from statistical analyses. Stand-age impacted several important measures of seed bank composition, with young stands exhibiting significantly greater H', seedling density, richness, *Carex* spp. density, and FQI than old stands (all p<0.05; Fig. 4; Table 4). Water level treatment impacted *Typha* seedling emergence; moist (0-cm) had significantly greater *Typha* seedling density (2.75 ± 0.98 seedlings/ pot) than the low (-5-cm) treatment (0.13 ± 0.13 seedlings/ pot; p=0.03; Fig. 4e; Table 4). Age × water level significantly impacted FQI; old-moist treatment had significantly lower FQI than any other age × water level treatment (p=0.01; Fig. 4f; Table 4).

Discussion

Harvesting invasive plants achieved at least two desired ecological outcomes in our study 1) reducing *Typha* coverage, and 2) increasing native plant diversity. As predicted (H1), both aboveground and belowground (i.e. total biomass) harvest treatments increased native plant diversity, reduced *Typha* dominance and biomass, and increased light penetration in the two-years following treatment. Belowground harvest had more immediate and greater impact on all of these measures likely resulting from the elimination of rhizomatous *Typha* and some release of buried seeds as a result of sediment disturbance. However, despite the robust native plant response, harvesting belowground biomass is not likely feasible at large-scales without specialized machinery due to the time intensity of the method (we spent >32 person-hours per 16-m^2 plot). Our results indicate that in similar upper Great Lakes coastal wetlands, a single harvest of aboveground *Typha* biomass alone will result in significant biodiversity and habitat value improvements, with the potential to more than double native plant species richness.

Typha aboveground biomass is viable for fuel pellet production (Cicek et al. 2006; Grosshans et al. 2012) and preliminary research indicates it is also a suitable feedstock for biogas digestion (Lishawa et al. unpublished data). Secondly, we found that pre-treatment aboveground biomass in Cheboygan Marsh was greater than reported annual productivity of the bioenergy crop species *Panicum virgatum* (switchgrass) (*Typha*: 9.54 ± 0.87 dry mass t/ha this study; *P. virgatum*: 8 dmt/ha, McKendry 2002). Productivity varied following treatment, however. Harvesting biomass significantly reduced aboveground biomass one-year following harvest, but in the second-year following harvest, biomass did not differ from the control. Control biomass was also lower post-treatment, however, probably resulting from plot perimeter rhizome cutting (Fig. 1d). Our results indicate that repeated annual harvesting would likely maintain reduced *Typha* dominance but would yield diminishing quantities of biomass. Though feedstock viability and productivity values indicate the potential for linking restoration with bioenergy production, thorough economic analyses are necessary to assess regional feasibility. Examples of such analyses include evaluation of salt cedar and Russian olive in Washington State (Nackley et al. 2013) and switchgrass, hybrid poplar and willow in the northern Great Lakes region (Kells & Swinton 2014). Furthermore, the ecosystem service benefits of harvesting invasive plants, such as potential biodiversity enhancement, greenhouse gas mitigation, and nutrient removal, should be included in future feasibility studies.

Prior to restoration treatments, old (>30 years) and young (<20 years) *Typha* stands exhibited nearly indistinguishable aboveground plant community characteristics. These data support Mitchell et al.’s (2011) findings that *Typha* density, litter mass, H’, and species richness all varied with stand-age in a Great Lakes coastal wetland, but did not differ significantly beyond 15 years post-invasion. We found that old *Typha* stands had greater belowground biomass than young stands and following treatment, aboveground *Typha* biomass re-growth was greater in old stands, likely owing to larger carbohydrate reserves. Despite this aboveground response, and counter to our expectations (H2), native plant communities did not respond more vigorously to experimental harvest in younger stands. The complete removal of the *Typha* litter layer presumably eliminated differences between age classes as litter accumulation is the principal mechanism through which native plants are excluded from *Typha* invaded wetlands (Farrer & Goldberg 2009; Vaccaro et al. 2009; Larkin et al. 2012). We expect that over the long-term, faster recovery of aboveground *Typha* biomass in old stands would be accompanied by more rapid litter accumulation and concomitant depletion of native species diversity, though continued monitoring would be required to confirm this hypothesis. Additionally, it may be possible that the two age classes we identified had both surpassed an ecological threshold, beyond which the impact of stand-age is muted. Testing our harvest treatments on more recent invasions (<10 years) may have resulted in more diverse community responses.

As predicted (H3), several measures of seed bank community composition were more robust in young stands than in the old stands including H', richness, seedling density, and *Carex* spp. density. Based on these data, higher diversity and abundance of native species in the experimental young plots in the field would be expected, but we did not see this response. This discrepancy may have resulted in part from the vegetative expansion of clonal species, though we did not differentiate between seedling and clonal resprouts. Despite the differences between our field harvest treatments and seed bank data, the young *Typha* stands evaluated in this study clearly had a more intact seed banks than old stands, and therefore greater plant community resilience (Frieswyk & Zedler 2006). Additionally, we observed widespread flowering and seed production by native plants in our aboveground and belowground study plots, indicating that harvesting may have the potential to replenish the seed bank.

Our results indicate that harvesting *Typha* biomass is a viable alternative restoration practice to burning and herbiciding. In contrast with Hall & Zedler (2010), who used similar methods in a highly disturbed urban wetland and concluded that restoration required annual harvesting for many years with associated planting, we documented increasing ecological returns through two-years following a single aboveground harvest. Our results indicate that there is strong potential for passive (i.e. no planting) restoration of native plant communities in sites with undisturbed hydrology and relatively diverse seed banks, such as within Great Lakes coastal wetlands along the shorelines of northern Lake Huron and the St. Marys River. Wetlands in this region are some of the highest quality in the Great Lakes (Uzarski et al. 2013) and are presently experiencing widespread invasion by *Typha* associated with low Great Lakes water levels (Lishawa et al. 2010). Though repeated harvesting would likely be required to maintain diversity over the long-term, management efforts could occur on three or more year rotations. We recommend larger scale implementation of above-ground harvest at or near the sediment surface in these wetland complexes to limit biomass accumulation which reinforces the invaded state. Additionally, there is a need to experimentally examine the effects of aboveground harvest on fish and bird habitat, ecosystem functions such as greenhouse gas flux, and the floral and ecological responses to annual and biennial harvesting in these ecosystems, as repeated harvesting may more accurately reflect bioenergy-focused management. While farm equipment has been used to manage *Typha* without affecting soil bulk density (Osland et al. 2011), care should be taken to avoid sediment disturbance and compaction, such as using harvesting equipment designed for wetland applications.

Management practices involving the utilization of invasive plant biomass for bioenergy may help to offset costs associated with ecological restoration (Miller & Hobbs 2007; Jakubowski et al. 2010; Nackley et al. 2013; Quinn et al. 2013). While conceptually encouraging, it remains unclear under what circumstances harvesting invasive plants will achieve traditional ecological restoration goals like increased biodiversity and ecosystem function. Our findings illustrate that in the case of *Typha* × *glauca*, there is great potential for linking restoration and bioenergy production.

Acknowledgements

Funding came from EPA GLRI grant GL-00E00545. We thank D. Monks, K. Greene, E. Tuchman, M. Davern, E. Marcos, J. Albert, and B. Castillo for their Herculean efforts in the field and lab.

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Tables

Table 1. Results from repeated measures ANOVA model testing for effects of sampling year (2011, 2012, 2013), treatment (aboveground, belowground, control), and stand-age (old, young) on the *Typha* relative dominance, *Typha* cover (%), total vegetation cover (%), species richness, plant diversity (H'), and aboveground biomass.

Response Variable	Source	*df*	*MS*	F	*P*
Typha dominance	Treatment	2	1.23	35.06	<**0.001**
	Stand age	1	0.05	1.51	0.23
	Trmt × Age	2	0.02	0.53	0.60
	Error[a]	18	0.04		
	Year	1	0.87	38.69	<**0.001**
	Year × Trmt	2	0.35	15.36	<**0.001**
	Year × Age	1		0.03	0.87
	Error[b]	42	0.02		
Total vegetation	Treatment	2	1604.44	20.01	<**0.001**
cover	Stand age	1	30.46	0.38	0.55
	Trmt × Age	2	42.53	0.53	0.60
	Error[a]	18	80.20		
	Year	1	4914.00	51.43	<**0.001**
	Year × Trmt	2	856.40	8.96	<**0.001**
	Year × Age	1	1.10	0.92	0.92
Richness	Treatment	2	127.93	4.44	**0.03**
	Stand age	1	33.35	1.16	0.30
	Trmt × Age	2	25.18	0.87	0.43
	Error[a]	18	28.80		
	Year	1	363.00	48.07	<**0.001**
	Year × Trmt	2	24.94	3.30	<**0.05**
	Year × Age	1	16.33	2.16	0.15

	Error[b]	42	28.80		
H’	Treatment	2	5.11	16.45	**<0.001**
	Stand age	1	0.04	0.13	0.73
	Trmt × Age	2	0.02	0.05	0.95
	Error[a]	18	0.31		
	Year	1	4.42	39.70	**<0.001**
	Year × Trmt	2	1.36	12.21	**<0.001**
	Year × Age	1	0.10	0.89	0.35
	Error[b]	42			
Aboveground biomass	Treatment	1	234342	5.10	**0.04**
	Stand age	1	36570	0.80	0.38
	Trmt × Age	1	216893	4.72	**0.04**
	Error[a]				
	Year	1	4355801	41.78	**<0.001**
	Year × Trmt	2	813246	3.90	**0.03**
	Year × Age	1	28554	0.27	0.60

[a] Between-subject error; [b] Within-subject error

Table 2. Year-specific plant species richness responses to restoration treatments (mean number of species per $16m^2$ plot [SE]). Plants grouped into geographic origin (Native, Non-native), form (Woody, Forbs), and dominant wetland plant families (Cyperaceae, Juncaceae, Poaceae). Within-year (PT: pre-treatment; PY1: post-year 1; PY2: post-year 2) statistical differences between treatments (O: old; Y: young; C: control; A: above; B: below) represented by non-overlapping subscript letters (Tukey HSD).

Year-Treatment*		Total Richness	Native	Non-native	Woody	Forbs	Cyperaceae	Juncaceae	Poaceae
PT	O	6.1 (0.2)	4.8 (0.3)	1.3 (0.1)	0.5 (0.0)	3.8 (0.2)	0.2 (0.1)^{A}	0.0 (0.0)	0.1 (0.1)
	Y	7.0 (0.5)	5.8 (0.5)	1.2 (0.0)	0.6 (0.0)	4.0 (0.2)	1.2 (0.2)^{B}	0.0 (0.0)	0.0 (0.0)
PY1	C	7.9 (1.0)^{a}	6.4 (0.9)	1.5 (0.3)	1.0 (0.3)^{a}	4.5 (0.6)	0.6 (0.2)^{a}	0.0 (0.0)^{a}	0.3 (0.3)
	A	11.5 (6.0)^{ab}	9.6 (2.0)	1.6 (0.3)	0.9 (0.3)^{ab}	5.1 (1.2)	1.6 (0.3)^{a}	0.8 (0.3)^{a}	0.9 (0.2)
	B	13.0 (1.2)^{b}	11.0 (1.1)	1.4 (0.2)	0.1 (0.1)^{b}	4.5 (0.6)	3.1 (0.5)^{b}	2.3 (0.3)^{b}	0.8 (0.3)
PY2	C	7.8 (1.0)^{A}	6.4 (0.9)^{A}	1.4 (0.2)	0.1 (0.1)	5.1 (0.7)	0.8 (0.3)^{A}	0.0 (0.0)^{A}	0.3 (0.3)
	A	14.0 (5.8)^{B}	11.6 (1.9)^{B}	1.5 (0.2)	0.4 (0.3)	6.1 (1.2)	2.8 (0.6)^{B}	0.8 (0.3)^{A}	1.3 (0.3)
	B	14.1 (0.9)^{B}	12.5 (0.9)^{B}	1.5 (0.2)	0.0 (0.0)	5.0 (0.9)	4.5 (0.5)^{C}	1.8 (0.3)^{B}	1.1 (0.4)

*No statistical differences between Old and Young stands in PY1 and PY2.

Table 3 Results of PERMANOVA (Adonis function) testing the effects of year (2011, 2012, 2013), stand-age (old, young) and treatment (above, below, control) on multivariate plant communities.

	All years (2011-2013)					Pre-treatment (2011)					Post-treatment (2012, 2013)				
	df	*SS*	*F*	R^2	*p*	*df*	*SS*	*F*	R^2	*p*	*df*	*SS*	*F*	R^2	*p*
Year	1	1.08	11.18	0.9	**0.01**	-	-	-	-	-	1	0.24	2.70	0.03	**0.04**
Age	1	0.16	1.64	0.01	0.16	1	0.08	1.92	0.08	0.13	1	0.19	2.06	0.02	0.11
Treatment	2	3.23	16.62	0.27	**0.01**	2	0.07	0.80	0.07	0.62	2	4.72	25.80	0.49	**0.01**
Year * Age	1	0.15	1.53	0.01	0.20	-	-	-	-	-	1	0.10	1.12	0.01	0.34
Year * Treatment	2	1.06	5.45	0.09	**0.01**	-	-	-	-	-	2	0.56	3.08	0.06	**0.01**
Age * Treatment	2	0.35	1.79	0.03	0.08	2	0.11	1.36	0.11	0.17	2	0.45	2.45	0.05	**0.05**
Year * Age * Treatment	2	0.27	1.39	0.02	0.15	-	-	-	-	-	2	0.13	0.70	0.01	0.72

Table 4 Effects of *Typha* stand-age (old: >30 years; young: <20 years) and experimental water treatments (low: -5cm; moist sediment: 0cm) on seed bank Shannon diversity (H'), species richness, floristic quality, stem density, *Typha* density, and *Carex* spp. density at Cheboygan Marsh.

	Age				Water level				Age × Water			
Characteristic	*df*	*SS*	*F*	*p*	*df*	*SS*	*F*	*p*	*df*	*SS*	*F*	*P*
Shannon diversity (H')	1	5.80	70.25	**<0.001**	1	0.17	2.02	0.18	1	0.05	0.55	0.46
Species richness	1	72.25	102.00	**<0.001**	1	1.00	1.42	0.26	1	0.00	0.00	1.00
Floristic quality (FQI)	1	35.70	9.77	**<0.001**	1	9.78	2.67	0.13	1	31.08	8.51	**0.01**
Stem density (# stems)	1	2756.25	49.89	**<0.001**	1	182.25	3.30	0.09	1	20.25	0.58	0.56
Typha density (# stems)	1	0.06	0.01	0.91	1	27.56	6.15	**0.02**	1	0.56	0.13	0.73
Carex spp. density (# stems)	1	45.56	6.81	**0.02**	1	7.56	1.13	0.31	1	3.06	0.46	0.51

Figure legends

Figure 1. Four measures of vegetation response to experimental *Typha* management, Shannon diversity (H') (a), species richness (b), *Typha* dominance (% of total cover) (c), and aboveground biomass (g/m^2) (d) to three treatments (aboveground harvest, belowground harvest, and control) over three years, pre-treatment (2011) and two-years following treatment (2012 and 2013) at Cheboygan Marsh. Within each year, treatments that do not share a common letter indicate significant differences (Tukey HSD).

Figure 2. Non-metric multidimensional scaling ordination of plot-level plant community data from Cheboygan Marsh. Points close together in ordination space indicate plots were similar in plant community composition; (a) pre-treatment (2011) data (n=24) illustrating *Typha* stand age (old: >30 years; young: < 20 years) and, (b) post-treatment data (2012 & 2013; n= 48) highlighting differences between treatments (aboveground harvest, belowground harvest, control). Dissimilarity was based on Bray-Curtis distances and plots were constructed using two dimensions. Fitted vector arrows are significant (p<0.05, by permutation procedure) and their length is proportional to their explanatory strength.

Figure 3. Penetration of photosynthetically active radiation (PAR) in 2012, one-year after conducting three restoration treatments (aboveground harvest, belowground harvest, and control) at three heights above the marsh sediment surface (1m; 0.5m; 0m) at Cheboygan Marsh. Within each height, non-overlapping letters (a,b,c) indicate significant differences between treatments (Tukey HSD).

Figure 4. Measures of seed bank composition from old (>30 years) and young (<20 years) *Typha* stands exposed to two water level treatments low (-5cm) and moist sediment (0cm); (a), Shannon diversity (H'), (b) stem density, (c) species richness, (d) *Carex* density, (e) *Typha* density, and (f) Floristic quality. All measures reflect per-pot responses; each pot contained 71 cm^3 of wetland sediment. Non-overlapping letters (a,b,c) indicate significant differences between treatments (Tukey HSD).

Figures

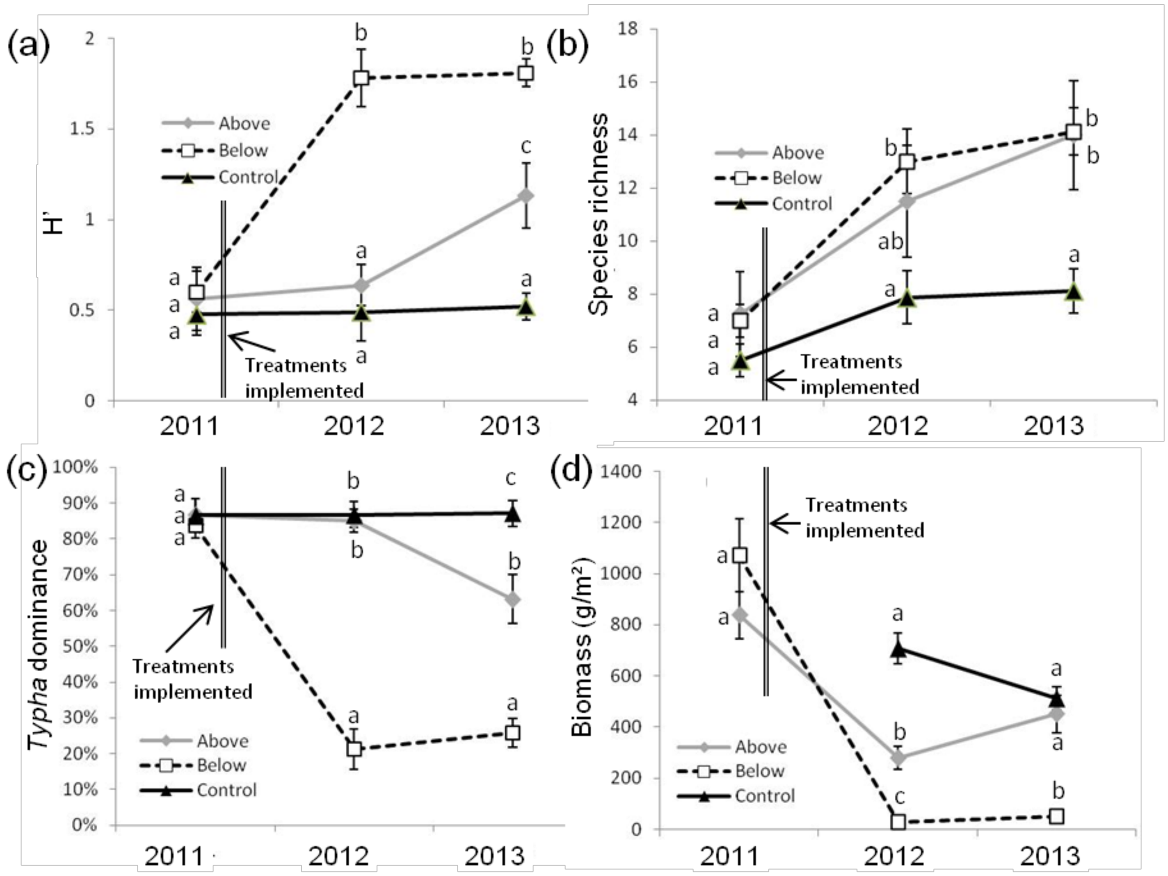

Figure 1.

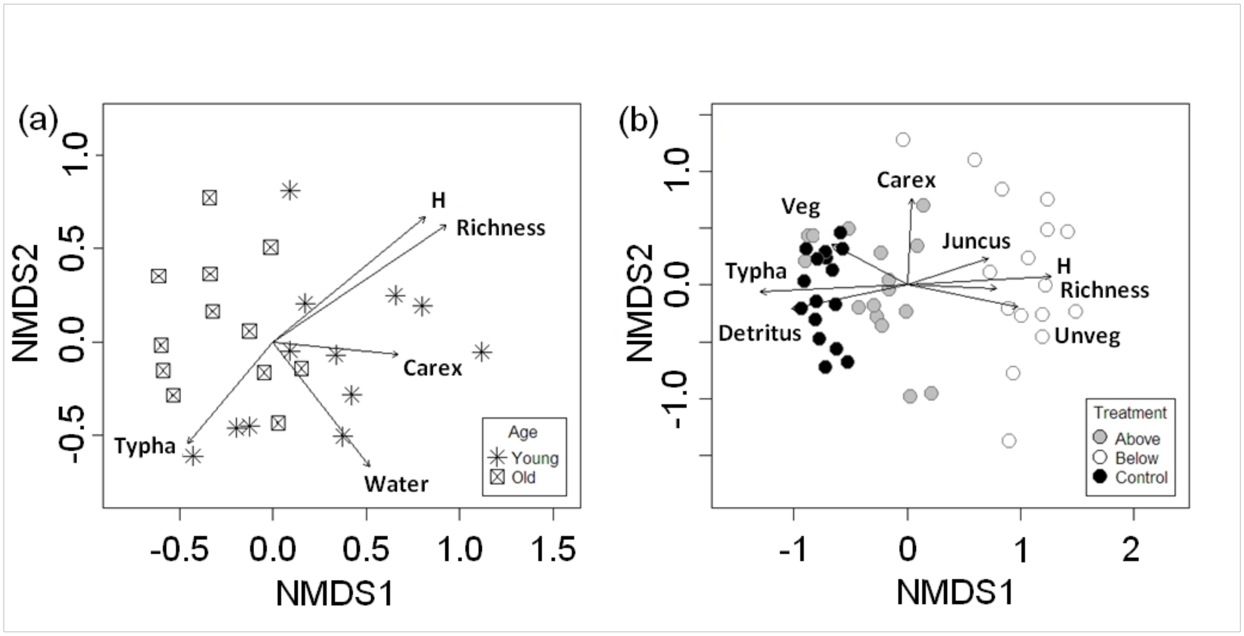
(a)
NMDS2
NMDS1
1.0
0.5
0.0
-0.5
-0.5
0.0
0.5
1.0
1.5
H
Richness
Carex
Typha
Water
Age
Young
Old
(b)
NMDS2
NMDS1
1.0
0.0
-1.0
-1
0
1
2
Carex
Veg
Juncus
Typha
H
Richness
Detritus
Unveg
Treatment
Above
Below
Control

Figure 2.

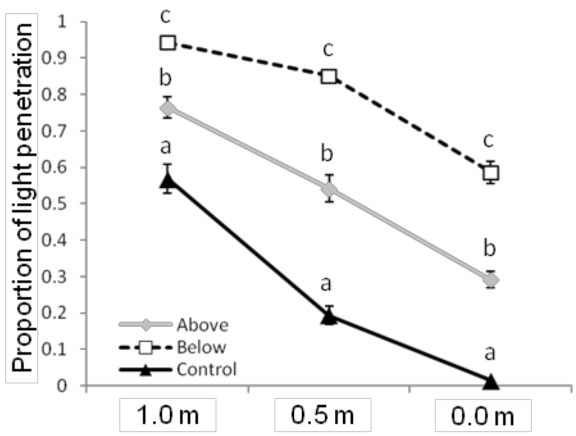
Proportion of light penetration
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
c
c
c
b
b
b
a
a
a
Above
Below
Control
1.0 m
0.5 m
0.0 m

Figure 3.

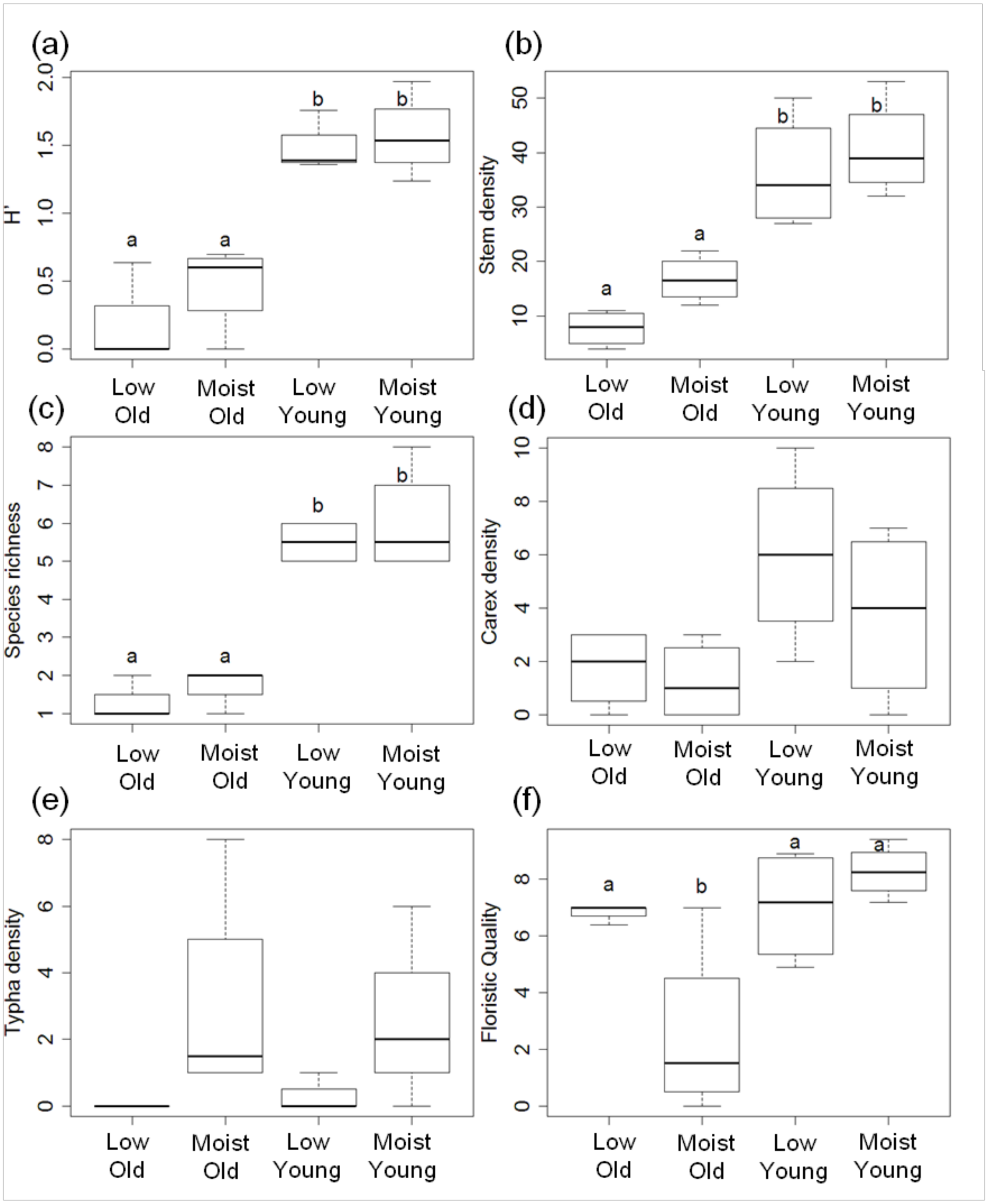
(a)
H'
(b)
Stem density
(c)
Species richness
(d)
Carex density
(e)
Typha density
(f)
Floristic Quality
Low Old
Moist Old
Low Young
Moist Young

Figure 4.