

Identifying Trade-offs Between Biomass Production and Biological Diversity in Wisconsin's Forests and Grasslands to Meet Tomorrows Bioenergy and Biofuel Needs

Final Report November 2011

PREPARED BY:

CHRISTOPHER WEBSTER, ASSOCIATE PROFESSOR; DAVID FLASPOHLER, PROFESSOR; AMBER ROTH, PHD CANDIDATE; AND MAX HENSCHELL, MASTER OF SCIENCE SCHOOL OF FOREST RESOURCES AND ENVIRONMENTAL SCIENCE, MICHIGAN TECHNOLOGICAL UNIVERSITY, HOUGHTON, MI 49931

This report was funded through the Environmental and Economic Research and Development Program of Wisconsin's Focus on Energy.

ENVIRONMENTAL AND ECONOMIC RESEARCH AND DEVELOPMENT PROGRAM

Date of Report: September 23, 2011 (Revised: November 28, 2011)

Title of Project: Identifying trade-offs between biomass production and biological diversity in Wisconsin's forests and grasslands to meet tomorrow's bioenergy and biofuel demands

Investigators (include titles): Christopher Webster, Associate Professor; David Flaspohler, Professor; and Amber Roth, PhD Candidate

Institution: School of Forest Resources and Environmental Science, Michigan Technological University, Houghton, MI 49931

Research Category (from RFP): Environmental and Economic Research and Development Program-- Environmental and economic impacts of biomass and biofuel energy production and use to offset electricity generation and natural gas use in Wisconsin.

Project Period: July 1, 2008 to May 31, 2011

EXECUTIVE SUMMARY:

This research project examined trade-offs within two bioenergy production systems, grasslands in southern Wisconsin and aspen forests in northern Wisconsin. Our primary goal was to quantify the potential benefits and costs of producing bioenergy feedstocks and maintaining wildlife populations on the same piece of land within these systems. The factors that influence the costs and benefits of the emerging bioeconomy are complex and will require a synthetic and data rich approach. Key trade-offs examined included biomass productivity in grasslands and aspen forests and biodiversity within the production system.

Grassland fields spanned a range of plant community diversity from virtual monocultures to diverse restored prairies. In planted grasslands, bird species abundance was influenced by the evenness of the distribution of plant functional groups and the landscape context of the field. In general, landscapes with fewer forest patches and more regular patterning of non-woody perennial cover were associated with higher abundances of grassland birds. While individual species models were idiosyncratic and variable between years, they suggest that increasing the representation of planted grasslands on the landscape would enhance local grassland bird abundance. Our vegetation results suggest that productivity in planted grasslands may be substantially correlated with the floristic quality of the plant community. In other words, the productivity of a field was higher when the vegetation was comprised of native plant species with low tolerance for human disturbance. Consequently, plantings with an even distribution of functional groups (i.e., groups of species with similar morphological traits) comprised of locally adapted native plant species could provide high-levels of biomass production as well as valuable habitat for grassland birds.

Aspen forests ranged from clear-cut with no legacy tree retention to clear-cut with scattered hardwood trees retained and clear-cut with scattered conifer trees retained. Each of these three aspen forest management types was represented by a range of aspen age classes. Aspen forests with legacy trees supported a more diverse breeding bird community and legacy trees were a very important habitat component for several species of high conservation concern including the Golden-winged Warbler (*Vermivora chrysoptera*). Retention of legacy trees enhanced wildlife value with minimal short-term impacts on aspen stand-level productivity. Reductions in aspen growth due to shading by dispersed and clumped residual overstory trees were minor and initially offset by growth of residual trees. Retention of hardwood legacy trees did not reduce aspen biomass but conifer retention at the levels in this study reduced aspen biomass production for the first decade and a half after harvest; however, there was a strong indication in our data that aspen in conifer retention stands would "catch up" to the other treatments at approximately 35 years post harvest. Another advantage of legacy tree retention was that stands had greater standing stocks of biomass than no retention stands for the first three decades following harvest.

Funding from Focus on Energy, together with project support provided by the National Science Foundation, has allowed us to train two masters students (Chad Fortin, Max Henschell), and one Ph.D student (Amber Roth, expected defense February 2012). The students gained valuable new field and analytical skills that will serve them well in their careers. We expect to publish several articles in peerreviewed journals in the next year or two which will further establish the research credentials of the students involved. We have also given numerous talks at professional meetings and talks to local teacher and high school groups (see Publications and Presentations Resulting from this Research at the end of this report). Amber Roth plans to continue to develop outreach programs around current conservation and ecological issues so this has been an important experience for her professional interests.

INTRODUCTION

Wisconsin's public and private lands are in a unique position to capitalize on a variety of new feedstock sources to meet bioenergy and biofuel demands in the coming decades. Throughout the U.S., public land management has moved away from a strict emphasis on economic productivity to policies that seek to balance multiple resource values while maintaining ecosystem health. One way of doing this has been to increase species richness of plant communities with the expectation that higher trophic levels will become more diverse as a result. The retention of structural and plant species diversity in forest and grassland systems may provide valuable wildlife habitat on the same acres being managed for commodity production. There is considerable theoretical evidence that these two objectives can coexist on the same land. However, empirical tests of this idea are lacking and almost no research has examined potential trade-offs between competing land management objectives. In order for public lands to accommodate demand for multiple products, including an expanding bioenergy economy, we need information on the potential trade-offs of a variety of different systems for growing bioenergy feedstocks while maintaining biological diversity.

Few studies have explicitly examined the impacts of bioenergy production on wildlife and most feedstock production systems (e.g., corn) provide few sustainable economic or environmental benefits and represent modest to zero reductions in greenhouse gas emissions. With little data available on the trade-offs between feedstock production and other values such as wildlife habitat, land use change related to expanding bioenergy markets is likely to resemble past land use change related to agriculture and forestry. To increase commodity production, whether for food or ethanol feedstock, natural habitats have traditionally been altered in ways that best suit the focal commodity species. The effects of this process on biodiversity are well documented. On a field or stand scale, as species-rich and structurally diverse native plant communities are replaced by monocultures with little structural diversity, most species of wildlife decline in abundance. Historic and more recent widespread population declines in North American grassland birds are examples of this predictable response by many wildlife species to plant community simplification.

We examined grassland and forest ecosystems in Wisconsin to determine if win-win management scenarios can be identified that can produce high yields of biomass and support diverse ecological communities.

Objective 1: To evaluate diversity of bird and herbaceous plant communities in grasslands and aspen forests across three management treatments.

Objective 2: To quantify biomass production in grasslands and aspen stands across three management treatments.

METHODS

Study Design

In both systems, we selected study sites along existing continuums of plant community diversity. We selected a continuum of native grass plantings in southern Wisconsin (much of which was covered by prairies and savannas prior to Euro-American settlement). We selected 11 fields that range in plant diversity from near monoculture plantings of native switchgrass to restored prairies (composed of mixtures of native grasses and wildflowers; Figure 1). Evidence is mounting that native grass plantings may provide a renewable and reliable source of biomass, with far fewer inputs (e.g., fertilizer) and soil disturbance than conventional row crops.

Figure 1. Three grasslands in southern Wisconsin representing a gradient of plant species richness. A: switchgrass monoculture; B: 6-grass CRP planting; C: highly diverse prairie remnant dominated by warm season grasses and forbs. Photos by C. Webster, Oct. 2005.

In the grasslands, we quantified biomass production directly by clipping and weighing vegetation on sample plots at the end of each growing season. Plant community diversity was monitored on these plots as well to facilitate a direct comparison between diversity and productivity.

We quantified bird species diversity by recording individual bird observations along line transects. Habitat quality was assessed by mapping territories of focal species of conservation concern and estimating territory size. As habitat quality increases, territory size decreases since birds do not have to defend as much area to acquire an adequate food supply while breeding. This method is a better indicator of habitat quality than species diversity alone.

In northern Wisconsin, we have focused on forest stands dominated by and managed for aspen (*n*=27). This species is fast growing, easily regenerated by clearcutting, and is a potentially important source of biomass in the northern temperate forest zone. Forest managers have been adjusting the techniques used to regenerate this species in response to societal demands for improved aesthetics and wildlife habitat. Generally, this alternative management involves the retention of longer lived tree species (oaks and pines) at the time of harvest, but stands without retention of these species can still be found (Figure 2). Nevertheless, surprisingly little is known about the effects of this legacy-tree retention on productivity or plant and bird diversity. Consequently, this continuum from zero retention to high overstory tree retention sites available on the landscape provides an excellent opportunity to examine the trade-offs associated with managing for both high production and diversity.

Figure 2. Three aspen forest silvicultural treatments in north-central Wisconsin. A: aspen clearcut with no legacy tree retention, B: aspen clearcut with conifer legacy tree retention, and C: aspen clearcut with northern hardwood legacy tree retention. Photos by A. Roth, 2006.

To assess biomass production in the forested ecosystem, we examined growth rates of both aspen and retained trees through the use of tree ring analysis. The methodology related annual diameter growth to biomass production through the use of widely available allometric equations, which relate tree diameter to biomass. The second task was to quantify plant community diversity based on a network of previously established vegetation monitoring plots. This data was collected in tandem with tree productivity so we can link these variables spatially. Bird diversity and bird abundance was assessed via line transect surveys and territory mapping of focal species of conservation concern.

Avian and Herbaceous Plant Diversity

In both forests and grasslands, bird diversity, or species richness, was estimated using unlimited distance transect surveys using a double-observer method (Nichols et al. 2000, Buckland et al. 2001). Transect surveys were conducted twice during the breeding season (late May to late June) in 2008 and 2009 and also in 2010 for the aspen portion of the study. From these data, species richness and diversity were calculated for each treatment.

Plant diversity and productivity in each forest stand was measured within ten randomly placed nested sample plots per stand. Overstory tree diversity was measured on a $1000 \text{--} m^2$ circular plot. Within this plot, vegetation structural diversity was sampled on two randomly placed $1-m^2$ subplots. To specifically address the influence of legacy-tree regeneration on plant species diversity, we measured the cover of each plant species within three $1-m^2$ subplots at 30, 150, and 270 degrees placed at a distance of 5m from the center of the 1000-m² circular plot. Additional species present outside of the subplots but within the 1000-m² circular plot were also noted. To assess plant diversity and productivity in the grasslands, we established 30 1-m² plots in each 12 fields, for a total of 360 sample plots. Plant species were tallied on these plots at three times over the course of the growing season to capture changes in plant dominance in the community with the passing of the season.

Avian Territory Mapping and Habitat Quality

We mapped territories of focal species of conservation concern (e.g., Golden-winged Warbler, Sedge Wren) based on singing male locations (International Bird Census Committee 1970). Each male's territory was visited a minimum of four times thus four maps were produced per territory. Singing male locations were flagged and later logged into a global positioning system unit (GPS).

Grassland Productivity

Half of the field plots $(n=180)$ were clipped annually at the end of the growing season to estimate biomass production. Clipped samples were bagged, oven dried and weighed.

Aspen Forest Productivity

To estimate tree productivity, as indicated by whole-tree above ground biomass and annual growth rates, we randomly established ten 1000-m² circular plots in each stand separated by at least 30 m. A sample of all woody species with diameter at breast height (DBH) greater than 10 cm was measured and cored. For each stand, increment cores were sampled from a maximum of 15 trees for each legacy species (three from each of five crown classes—dominant, co-dominant, intermediate, overtopped, and suppressed) and a stratified sample of aspen trees. A 100-m² nested plot was centered at the same point as the 1000-m² plot and all woody plants taller than 1 m and with $DBH < 10$ cm measured. Within the 1000-m² plot, two 1-m² subplots were randomly located at least 10 m apart; all woody plants were tallied and a sample of five from each species measured.

Woody plant cores and clippings were analyzed in the lab to determine annual growth increments and biomass accumulation. Whole-tree above ground biomass was estimated using published species-specific allometric equations (Smith and Brand 1983). Preference was given to equations developed for trees in the Great Lakes Region.

Analytical Methods

To determine bird territory area, GPS locations for bird territories were transferred into a geographic information system and territory areas estimated using the Animal Movements Tool in ArcMap (ESRI 2010) to create minimum convex polygons.

In the grassland portion of the study, we computed several indices describing the composition of the vegetation community in each field. These include a Floristic Quality Index (FQI) (Swink and Wilhelm 1979), a mean Coefficient of Conservatism (*C*) as a modification of the FQI (Taft et al. 1997), Shannon's Diversity Index (H`), and species richness (S) annually for each plot. FQI was originally developed for use in the Chicago, IL region for determining the conservation value of natural areas (Swink and Wilhelm 1979). This index has been adapted to the flora of many states including Michigan (Herman et al. 1997), North Dakota (Mushet et al. 2002), Florida (Cohen et al. 2004), Kansas (Jog et al. 2006), and Wisconsin (Bernthal 2003). FQI is also routinely used as a method to determine the relative success of ecological restoration projects (Taft et al. 2006). An FQI is assigned after the completion of a floristic quality assessment, in which the vegetation of the site of interest is quantified. Native plant species are assigned an integer value from 0-10 while exotic species are typically not scored. These scores for native species are referred to as the coefficient of conservation. This score is based on a species' tolerance to primarily anthropogenic disturbance and its fidelity to a particular habitat (Swink and Wilhelm 1979). A score of 0 indicates a ruderal species that thrives in heavily disturbed areas and has little fidelity to a particular natural community. A score of 10 indicates a species with a narrow habitat tolerance that is likely to only be found on sites with little or no human disturbance. Scores are determined by polling botanists familiar with the requirements of plant species within a region (Bernthal 2003). We modified the index by also scoring all exotic species as a zero (Bernthal 2003). FQI is determined by calculating a mean coefficient of conservation (*C*) and dividing that by the square root of the number of species found (Swink and Wilhelm 1979). In essence, this is species richness weighted by the conservatism of the species found within a site.

Shannon's Diversity (H`) was calculated using the highest percent cover for each species throughout the growing season. This approach allows analysis of a more complete vegetation community, rather than computing H` from a single sampling visit, when all species were not identifiable. This also allowed us to have a more complete picture of the entire vegetation community for comparison with FQI. Principle components analysis (PCA), centered on zero and scaled to have unit variance, was used on the soil nutrient data because preliminary data exploration indicated that these variables were highly correlated.

Nonmetric multidimensional scaling ordination (NMS) was performed on the plant grassland plant community to examine the relationship between environmental variables and the plant community within each field. NMS is often used to describe patterns within ecological community data and display these patterns graphically. NMS is well suited for ecological data because such data are often non-normal and NMS does not assume linear relationships and uses a rank system for analysis (McCune and Grace 2002). The analysis was performed using the Slow and Thorough Autopilot mode with Sorensen distance measure. The Autopilot mode uses a random starting coordinate with 6 dimensions, a stability criterion of 0.00001, with 40 runs using the real data, 50 runs using random data, and a maximum of 400 iterations for each data set. We used data from the clipped plots in both 2008 and 2009 in the ordination. Cover data were square-root transformed prior to analysis. We report only those environmental variables that showed a strong correlation $(r^2 > 0.25)$ to the plant community data in our analysis.

We developed multiple regression models for productivity as a response to a narrow set of biologically relevant predictors. Three models were developed, one for each year, 2008 and 2009, and of the two years combined. We used linear mixed effects multiple regression to account for potential issues of a nested sample design since there was more than one plot per field and fields were sampled in two consecutive years (Laird and Ware 1982). Models were reduced by removing the least significant predictor, as determined by having the highest *p*-value. The models were reduced until only predictors with a *p*-value of less than 0.05 remained. We then individually added previously dropped predictors to the final model and retained any whose *p*-value was less than 0.05. After this forward check, we removed predictors that were highly correlated $(r>0.75)$. This technique allows for the identification of multiple competing models in which case Akaike Information Criterion (AIC) was used to identify the most parsimonious model, with models within 4 points of the lowest score considered competitive models (Burnham and Anderson 2002). We computed mixed effects regression R^2 values following Nagelkerke (1991). Regression analyses were performed in R 2.10.1 (R Core Development Team 2009).

Land cover 1600 m from the edge of each field was digitized from 1-m resolution 2008 National Agriculture Imagery Program photographs. Digitizing was performed in ArcMap 9.3 (ESRI 2008). Land cover was digitized as forested, open land, developed (urban, suburban, rural farmsteads and roads) or open water. The digitized shapefile was then split into buffers of 100 m, 200 m, 400 m, 800 m and 1600 m, each larger buffer inclusive of the smaller buffers. Buffers were then converted to raster files for analysis in FRAGSTATS (McGarigal et al. 2002). We performed a principle components analysis (PCA) on the land cover data for each buffer because preliminary data exploration indicated that these variables were highly correlated. The scores from these principle components were used in subsequent regression. We included all components that contributed to at least 80% cumulative proportion of the variance. Land use change between years was minimal, so PCA scores were used for both years of data analysis.

We used regression to examine trends in two avian population metrics, relative abundance and territory size, as functions of within-field vegetation indices and landscape metrics, via principle components. We used forward selection to determine which predictors were best to add to the model. We modeled sqrt (relative abundance) for each species for each year of the study individually using linear regression. We

also modeled territory size for the three focal species, Sedge Wren, Common Yellowthroat, and Song Sparrow for each year of the study individually using linear regression. To investigate how variation at different spatial scales influenced bird response variables, we developed both types of models in three ways: as a function of within-field vegetation indices, as a function of landscape metrics, and as a function of both vegetation and landscape measures. Variables whose α-level was <0.10 were retained in the model. We selected models using AIC. All models within 4 points of the minimum AIC score were considered valid models (Burnham and Anderson 2002).

For the aspen portion of the study, mean Golden-winged Warbler territory area was calculated by averaging four annual territory area estimates per site. Golden-winged Warbler territory area was compared among legacy tree treatments using one-way analysis of variance (ANOVA) in SigmaStat (Systat 2006). Understory plant species richness for aspen forests was analyzed using a two-way analysis of variance using SigmaStat. We used the indicator species analysis tool in PCORD (McCune and Grace 1999) to evaluate which species best represent aspen stand legacy tree treatments and age-classes. Understory plant richness in aspen forests was analyzed using a two-way ANOVA in SigmaStat.

RESULTS

Grasslands

Avian Relative Abundance and Diversity

We recorded 20 species of passerines throughout the two-year study: 18 species in 2008 and 19 species in 2009 (Tables $1 \& 2$). The most frequently occurring species in both years were the Common Yellowthroat, Red-winged Blackbird and Song Sparrow (Tables $3 \& 4$). The most abundant species in both years were the Common Yellowthroat and Song Sparrow.

We modeled the relative abundance for our three focal species, Sedge Wren, Common Yellowthroat and Song Sparrow as well as the combined relative abundance of all passerine species that require grassland cover during the breeding season (Sample and Mossman 1997) in each year, 2008 and 2009 (Tables 5 & 6, respectively).

The most competitive Common Yellowthroat models in 2008 consisted of two landscape principle components, the first component from the 1600 m buffer and the second from the 200 m buffer (Table 5). The 1600 m principle component was dominated by landscape contagion (CONTAG) and landscape Shannon's evenness of cover types (SHEI). More Common Yellowthroats were associated with 1600 m landscapes that were less spatially heterogeneous, as measured by CONTAG, while fewer were associated with landscapes in which the landscape covertypes were more evenly represented, as measured by SHEI. The highest loadings in the second component of the 200 m buffer were forested interspersion and juxtaposition (IJI) and forested nearest neighbor index (ENN_AM), which were both negatively associated with Common Yellowthroat abundance. The second 2008 model consisted of the importance value of two native functional groups, C4 grasses and composites. Both were associated with fewer Common Yellowthroats. The 2009 model for Common Yellowthroat included two plant community metrics, FQI and functional group evenness. FQI was associated with fewer Common Yellowthroats, while higher functional group evenness (E) was associated with more Common Yellowthroats.

Song Sparrow abundance was driven exclusively by within-field vegetation indices in both years of the study (Tables 5 & 6). The 2008 model was driven by litter depth; deeper litter was associated with more Song Sparrows (Table 5). The 2009 model consisted of FQI and functional group evenness. Higher FQI values were associated with fewer Song Sparrows, while more evenly represented functional groups was related to more Song Sparrows in 2009 (Table 6).

The models for Sedge Wren in 2008 typically included within-field vegetation characteristics, particularly plant species evenness and functional group evenness. A more evenly represented plant community was consistently associated with fewer Sedge Wrens, while more evenly represented functional groups were associated with more Sedge Wrens in second 2008 model (Table 5). The most competitive model in 2008 included the third principle component from the 1600 m buffer and litter depth. The landscape metrics with the highest loadings from this component are the open land Euclidean nearest neighbor index (ENN_AM) and the percent of forested land cover (PLAND). These metrics show a positive and negative relationship, respectively, with Sedge Wren abundance. Deeper litter was associated with more Sedge Wrens in this model. The 2009 model for Sedge Wren relative abundance consisted of the importance value of native legumes and the importance value of native composites.

We found no measured variables as significant predictors of grassland species relative abundance in 2008. The 2009 model consisted of the importance value of native legumes, which showed a negative association with abundance, and the third principle component of the 800 m landscape (Table 5). The landscape metrics with the highest loadings from this component are the open land Euclidean nearest neighbor index (ENN_AM) and open land interspersion and juxtaposition (IJI). More grassland passerines were found in landscapes that had patches of isolated open land, as measured by open land ENN AM, while fewer grassland passerines were associated with landscape patches that were adjacent to different covertypes, as measured by IJI.

Avian Territory Area

We modeled the territory area for our three focal species, Sedge Wren, Common Yellowthroat and Song Sparrow in each year, 2008 and 2009 (Tables 5 $\&$ 6). The Common Yellowthroat was the most abundant breeding species in both years, with a mean of 7 and 7.75 territories per field in 2008 and 2009, respectively (2008 range $= 3-14$; 2009 range $= 4-14$). Common Yellowthroat territory area ranged from 132 m^2 to 2702 m^2 in 2008 (mean = 610 m²) and from 102 m² to 2261 m² in 2009 (mean = 656 m²). We mapped an average of 5.5 Sedge Wren territories per field in 2008 (range = 1-10) and an average of four per field in 2009 (range = 2-9). The average Sedge Wren territory area in 2008 was 662 m² (range = 51- (3730 m^2) and the 2009 average was 735 m² (range = 253-1983 m²). We mapped an average of 5.8 Song Sparrow territories per field in 2008 (range $=1-12$) and an average of 4.4 territories in 2009 (range $= 1-8$). The average Song Sparrow territory area was 1439 m^2 in 2008 (range = 312-3359 m²) and 1515 m^2 in 2009 (range = $362 - 2616$ m²).

The 2008 model for the Common Yellowthroat included the density of woody stems 1-2 m tall (Table 5). The density of woody stems was associated with larger territories in 2008. The 2008 model also included the importance of C3 grasses, which was positively associated with larger territories. The 2009 model contained the density of woody stems >2 m tall. High woody stem density of this height class was associated with smaller territories. The 2009 model also included the third principle component from the 200 m landscape buffer (Table 6). The highest loadings within this component were from forested shape and open land SHAPE_AM. Larger territories were associated with 200 m landscapes in which the forested areas were less square, while Common Yellowthroat territories were smaller in 200 m landscapes in which the open land patches were squarer, as measured by SHAPE_AM.

The 2008 model for Song Sparrow territory size was comprised exclusively of the first two principle components of the 400 m landscape. The highest loadings for the first component were the percentage of open land (PLAND) in the 400 m landscape, which was associated with larger territories, and the evenness of landscape cover types (SHEI) within 400 m of the field edge, which was associated with smaller territories. The highest loadings from second component of the 400 m landscape were two measures of forest cover, forested interspersion and juxtaposition (IJI) and forested Euclidean nearest neighbor index (ENN_AM). Song Sparrow territory size increased as the forested cover within 200 m was next to multiple cover types, as measured by IJI, and as the distance between forested patches increased, as measured by ENN_AM. The 2009 model for Song Sparrow territory size was comprised of the importance value of native C4 grasses, which was positively associated (i.e. larger) with territory size, and the first component of the 800 m landscape. The highest loadings in this component are landscape cover type diversity (SHDI), landscape cover type evenness (SHEI) and the percent of open land (PLAND) in the landscape. Song Sparrow territory size decreased with increasing diversity and evenness and increased with increased open land cover in the landscape.

The first Sedge Wren model for territory size in 2008 included both plant species and functional group evenness (E) (Table 5). Larger territory size was associated with more evenly represented functional groups, while smaller territories were associated with a more even plant community. The second model for 2008 was comprised of field area and the third principle component of the 200 m landscape. Larger fields were associated with larger territories (Table 5). The highest loadings for the third component of the 200 m landscape were from forested shape index (SHAPE_AM) and open land SHAPE_AM. Smaller territories were associated with 200 m landscapes in which the forested areas were less square. Territories were larger in 200 m landscapes in which the open land patches were squarer, as measured by SHAPE_AM. The first model for Sedge Wren territory size in 2009 was comprised of functional group evenness and native C3 grass importance value. Territory size was smaller with more evenly represented functional groups as well as with more native C3 grasses in a field. The second model for 2009 was comprised of the third component of the 200 m landscape and the second component of the 100 m landscape. The highest loadings for the third component of the 200 m landscape were from forested shape index (SHAPE_AM) and open land SHAPE_AM. Smaller territories were associated with 200 m landscapes in which the forested areas were less square, territories were larger in 200 m landscapes in which the open land patches were squarer, as measured by SHAPE_AM. The highest loadings in the second component of 100 m landscape were from the open land shape index (SHAPE_AM) and the open land interspersion and juxtaposition (IJI). Sedge Wren territory size decreased as the shape of the open patches within 200 m of the field edge became more square, as measured by SHAPE_AM, and territory size increased as the open areas within the 200 m landscape were more adjacent to different cover types.

that require grassianu nabitat uuring the breeding season (sample and mossinan 1997). Bird Species	ВM	DA	GS	HН	HL	HM	NK	OK	S ₁	S ₂	TG	Frequency
American Goldfinch												
(Spinus tristis)			$\pmb{\mathsf{X}}$	X	$\pmb{\mathsf{X}}$				X			$\overline{4}$
American Robin												
(Turdus migratorius)			$\pmb{\mathsf{X}}$			$\pmb{\mathsf{X}}$					$\pmb{\mathsf{X}}$	$\overline{3}$
Brown-headed Cowbird												
(Molothrus ater)*						$\pmb{\mathsf{X}}$		$\pmb{\mathsf{X}}$				$\overline{2}$
Bobolink												
(Dolichonyx oryzivorus)*	$\pmb{\mathsf{X}}$					$\pmb{\mathsf{X}}$		$\pmb{\mathsf{X}}$				3
Clay-colored Sparrow												
(Spizella pallid)*		Χ						$\pmb{\mathsf{X}}$	Χ	$\pmb{\mathsf{X}}$		$\overline{4}$
Common Yellowthroat												
(Geothlypis trichas)	$\pmb{\mathsf{X}}$	X	Χ	Χ	$\pmb{\mathsf{X}}$	$\pmb{\mathsf{X}}$	$\pmb{\mathsf{X}}$	$\pmb{\mathsf{X}}$	Χ	X	$\pmb{\mathsf{X}}$	11
Dickcissel												
(Spiza Americana)*	$\pmb{\mathsf{X}}$	$\pmb{\mathsf{X}}$				$\pmb{\mathsf{X}}$						3
Eastern Kingbird												
(Tyrannus tyrannus)			$\pmb{\mathsf{X}}$									$\mathbf{1}$
Eastern Meadowlark												
(Sturnella magna)*	$\pmb{\mathsf{X}}$			X	$\pmb{\mathsf{X}}$	$\pmb{\mathsf{X}}$						$\overline{4}$
Field Sparrow												
(Spizella pusilla)*		X						$\pmb{\mathsf{X}}$				$\overline{2}$
Grasshopper Sparrow												
(Ammodramus savannarum)* Henslow's Sparrow	$\pmb{\mathsf{X}}$							Χ				$\overline{2}$
(Ammodramus henslowii)*	$\pmb{\mathsf{X}}$							$\pmb{\mathsf{X}}$				$\overline{2}$
Red-winged Blackbird												
(Agelaius phoeniceus)	$\pmb{\mathsf{X}}$	$\pmb{\mathsf{X}}$	$\pmb{\mathsf{X}}$	X	$\pmb{\mathsf{X}}$	$\pmb{\mathsf{X}}$	$\pmb{\mathsf{X}}$	$\pmb{\mathsf{X}}$	X	$\pmb{\mathsf{X}}$	$\pmb{\mathsf{X}}$	11
Savannah Sparrow												
(Passerculus sandwichensis)*	$\pmb{\mathsf{X}}$											$\mathbf{1}$
Sedge Wren												
(Cistothorus platensis)*		$\pmb{\mathsf{X}}$				$\pmb{\mathsf{X}}$	$\pmb{\mathsf{X}}$	X	Χ	Χ	X	$\overline{7}$
Song Sparrow												
(Melospiza melodia)		Χ	$\pmb{\mathsf{X}}$	Χ	$\mathsf X$	$\pmb{\mathsf{X}}$	$\pmb{\mathsf{X}}$	$\pmb{\mathsf{X}}$	Χ	$\pmb{\mathsf{X}}$	$\pmb{\mathsf{X}}$	10
Swamp Sparrow												
(Melospiza Georgiana)									Χ			$\mathbf 1$
Willow Flycatcher												
(Empidonax traillii)						Χ		Χ				$\overline{2}$
Avian species richness	$\,8\,$	$\overline{\mathbf{z}}$	$\boldsymbol{6}$	5	5	10	$\overline{\mathbf{4}}$	11	$\overline{7}$	5	5	

Table 1. Passerine species occurrence during 2008 line transect sampling in study fields located in south-central Wisconsin. "X" indicates the species was present within the field. "*" indicates species that require grassland habitat during the breeding season (Sample and Mossman 1997).

that require grassianu habitat uuring the breeting season (bample anu Mossinan 1997).											
Bird Species	BM	DA	GS	HH	HL	HM	NK	OK	S ₂	TG	Count
American Goldfinch											
(Spinus tristis)	Χ	$\pmb{\mathsf{X}}$		$\pmb{\mathsf{X}}$		Χ		$\pmb{\mathsf{X}}$			5
American Robin											
(Turdus migratorius)				$\mathsf{X}% _{0}$		$\pmb{\mathsf{X}}$					$\overline{2}$
Brown-headed Cowbird											
(Molothrus ater)*	Χ	$\pmb{\mathsf{X}}$	X								3
Bobolink											
(Dolichonyx oryzivorus)*				Χ	$\pmb{\mathsf{X}}$			$\pmb{\mathsf{X}}$			3
Clay-colored Sparrow											
(Spizella pallid)*			X			Χ					$\overline{2}$
Common Yellowthroat											
(Geothlypis trichas)	Χ	$\pmb{\mathsf{X}}$	Χ	Χ	$\pmb{\mathsf{X}}$	Χ	$\pmb{\mathsf{X}}$		$\pmb{\mathsf{X}}$	$\pmb{\mathsf{X}}$	9
Eastern Meadowlark											
(Sturnella magna)*	Χ			Χ	$\pmb{\mathsf{X}}$	X		$\pmb{\mathsf{X}}$			5
Field Sparrow											
(Spizella pusilla)*			X			Χ					$\overline{2}$
Gray Catbird											
(Dumetella carolinensis)						$\pmb{\mathsf{X}}$					$\mathbf{1}$
Grasshopper Sparrow											
(Ammodramus savannarum)*	Χ							$\pmb{\mathsf{X}}$			$\overline{2}$
Henslow's Sparrow											
(Ammodramus henslowii)*	Χ							$\pmb{\mathsf{X}}$			$\overline{2}$
Red-winged Blackbird											
(Agelaius phoeniceus)	Χ	$\pmb{\chi}$	X	X	$\pmb{\chi}$	X	X		X	$\mathsf{\chi}$	9
Savannah Sparrow											
(Passerculus sandwichensis)*			X			X					$\overline{2}$
Sedge Wren											
(Cistothorus platensis)*	Χ	$\pmb{\mathsf{X}}$	Χ	$\pmb{\mathsf{X}}$	$\pmb{\mathsf{X}}$		X		$\pmb{\mathsf{X}}$		$\overline{7}$
Song Sparrow											
(Melospiza melodia)	Χ	$\pmb{\mathsf{X}}$	Χ	Χ	$\pmb{\mathsf{X}}$	$\pmb{\mathsf{X}}$	X		$\pmb{\mathsf{X}}$	$\pmb{\mathsf{X}}$	9
Swamp Sparrow											
(Melospiza Georgiana)			X				$\pmb{\mathsf{X}}$				$\overline{2}$
Willow Flycatcher											
(Empidonax traillii)			X	Χ		Χ			$\pmb{\mathsf{X}}$		4
Yellow Warbler											
(Dendroica petechia)			Χ			x					$\overline{2}$
Field Richness	9	$6\,$	11	$\boldsymbol{9}$	6	12	5	5	5	$\mathsf 3$	

Table 2. Passerine species occurrence during 2009 line transect sampling in study fields located in south-central Wisconsin. "X" indicates the species was present within the field. "*" indicates species that require grassland habitat during the breeding season (Sample and Mossman 1997).

	during their breeding cycle" (Sample and Mossman 1997).								
Field	Common Yellowthroat	Sedge Wren	Song Sparrow	Grassland Species					
BM	1.67	0.00	0.00	1.67					
DA	5.33	2.67	5.33	3.00					
GS	2.33	0.00	6.00	0.33					
HH	5.33	0.00	5.33	0.33					
HL	5.67	0.00	2.67	0.67					
HM	6.33	0.33	5.00	3.67					
NK	4.33	6.33	4.00	6.33					
OK	5.00	0.00	0.67	17.67					
S ₁	7.67	1.00	4.33	1.33					
S ₂	5.00	1.00	1.33	1.67					
TG	2.00	1.67	7.67	1.67					

Table 3. Relative abundance (mean individuals/transect) of select species of passerines occupying fields in the study area located in south-central Wisconsin during the 2008 study period. The 'Grassland Species" category includes all passerines listed as "species that require grasslands

Table 4. Relative abundance (mean individuals/transect) of select species of passerines occupying fields in the study area located in south-central Wisconsin during the 2009 study period. The "Grassland Species" category includes all passerines listed as "species that require grasslands during their breeding cycle" (Sample and Mossman 1997).

Field	Common Yellowthroat	Sedge Wren	Song Sparrow	Grassland Species
BM	1.50	2.00	0.50	9.75
DA	5.50	4.00	4.25	5.00
GS	2.40	2.20	4.00	3.40
HH	5.17	0.17	5.83	1.67
HL	3.83	1.33	3.17	2.17
HM	3.75	0.00	3.50	3.00
NΚ	4.60	1.80	2.60	2.40
OK	0.00	0.00	0.00	4.80
S ₂	4.50	1.00	4.50	2.50
TG	1.67	0.00	1.00	0.00

							Likelihood Ratio
Species	Model	ΔAIC	Predictor	Estimate	P-value	value	P
Common	Model 1	0	Intercept	1.662	< 0.001	3.662	0.002
Yellowthroat			1600m PC1	-0.113	0.0014		
			400m PC3	0.138	0.014		
	Model 2	1.91	Intercept	4.444	< 0.001	2.709	0.005
			Native C4 IVI	-4.472	0.002		
			Native Composite IVI	-2.235	0.007		
Song Sparrow	Model 1	0	Intercept	-0.248	0.397	-0.094	< 0.001
			Litter	0.053	< 0.001		
			Woody stems 1-2m	0.287	0.032		
Sedge Wren	Model 1	$\pmb{0}$	Intercept	-2.455	0.025	-5.815	0.018
			Field size	-0.437	0.012		
			1600m PC3	0.340	0.010		
	Model 2	1.88	Intercept	-0.587	0.754	-6.021	0.035
			Plant species E	-5.990	0.020		
			Functional group E	7.723	0.031		
	Model 3	3.74	Intercept	2.403	0.115	0.069	-6.949
			Litter	0.0312	0.066		
			Plant species E	-4.124	0.074		
Grassland	Model 1	$\mathbf{0}$	Intercept	1.156	< 0.001	-9.250	0.027
Species			800 m PC4	-0.414	0.027		

Table 5. Linear regression models for the relative abundance of selected species of passerines occupying fields in the study area located in south-central Wisconsin during the 2008 study period. The 'Grassland Species" category includes all passerines listed as "species that require grasslands during their breeding cycle" (Sample and Mossman 1997).

Table 6. Linear regression models for the relative abundance of selected species of passerines occupying fields in the study area located in south-central Wisconsin during the 2009 study period. The 'Grassland Species" category includes all passerines listed as "species that require grasslands during their breeding cycle" (Sample and Mossman 1997).

Vegetation Diversity

We recorded 155 herbaceous species and 22 woody species in 2008 and 157 herbaceous species and 25 woody species in 2009. The species that occurred in the most plots in both 2008 and 2009 was *Taraxacum officinale* F.H. Wigg followed by *Solidago canadensis* L. in both years. The most common woody shrubs were *Rubus* spp., while trees were dominated by *Prunus serotina* Ehrh. The most common native C4 grass was *Andropogon gerardii* Vitman. Plot H` ranged from 0 to 2.84 in 2008 and from 0 to 2.71 in 2009. Zero-value H` plots consisted solely of the exotic *P. arundinacea* L. Plant species richness ranged from 1 to 25 species m^2 in 2008 and from 1 to 29 species m^2 in 2009. Plot-level dry weight biomass estimates ranged from 1455 kg/ha to 10,438 kg/ha in 2008 and from 626 kg/ha to 10,707 kg/ha in 2009.

The plant community was best described by a 3-dimensional NMS ordination. The final stress of this ordination was 18.51 and it had a final stability of 0.00001. The cumulative variance explained by the ordination was 70.8%. Axis 2 explained the most variation, 26.2%, followed by axis 3 at 22.4% and axis 1 at 22.2%. Ordination results suggest that while within field vegetation community differences were small, between field differences were relatively large (Figures $3 \& 4$). Axis 1 was significantly associated with several environmental variables, particularly the soil attributes pH $(R^2=0.46, P<0.001)$, magnesium $(R^2=0.26, P<0.001)$, and potassium-magnesium ratio $(R^2=0.34, P<0.001)$ (Table 7). Axis 1 was also associated with plant community metrics including FQI (Floristic Quality Index; R^2 =0.35, P<0.001) and *C* (average Coefficient of Conservation; $R^2 = 0.32$, P<0.001) (Table 7). Axis 3 was highly correlated with $C (R²=0.31)$ and FQI ($R²=0.26$). Although Axis 2 explained the most variation, it was not significantly correlated with any measured environmental variables.

Table 7. Environmental variables and associated correlations with the 3 dimensional NMS ordination axis scores across all sampled plots in southern Wisconsin, USA. Only those environmental variables with a correlation greater than 0.25 with at least one ordination axis are listed.

			Axis 1				Axis 2			Axis 3		
Variable	$Mean \pm 1SE$	Min	Max	$\mathbf r$		p -value	$\mathbf r$		p -value	\mathbf{r}		p -value
\mathcal{C}	1.8 ± 0.1	$\overline{0}$	5.875	0.563	0.316	< 0.001	0.367	0.134	< 0.001	0.558	0.311	< 0.001
FQI	6.5 ± 0.3	$\boldsymbol{0}$	24.140	0.593	0.352	< 0.001	0.309	0.095	< 0.001	0.506	0.256	< 0.001
pH	6.3 ± 0.0	5.8	τ	0.679	0.461	< 0.001	0.211	0.044	< 0.001	--		
Mg	916.3 ± 18.5	638	1494	0.513	0.263	< 0.001	0.203	0.041	< 0.001	--		--
K: Mg	0.1 ± 0.0	0.05	0.24	-0.584	0.341	< 0.001	0.014	0.0001	< 0.001	--		

Figure 3. Nonmetric multidimensional scaling ordination showing axes 1 and 2 of prairie plantings in southern Wisconsin. Fields within our study are coded by field plant species richness (A.). Symbols represent average field axes scores, with error bars representing one standard error. Joint plot vectors for selected environmental variables are represented in B (clockwise from 12 o'clock: pH, magnesium, FQI, *C***, potassium- magnesium ratio). Note differences in scale between A. and B. Environmental variables were selected based upon strong** correlations with at least one axis $(r^2 > 0.25)$.

 plantings in southern Wisconsin. Fields within our study are coded by field plant species Figure 4. Nonmetric multidimensional scaling ordination showing axes 2 and 3 of prairie richness (A.) Symbols represent average field axes scores, with error bars representing one standard error. Joint plot vectors for selected environmental variables are represented in B (clockwise from 12 o'clock: FQI and *C***). Note differences in scale between A. and B. Environmental variables were selected based upon strong correlations with at least one axis** $(r^2>0.25)$.

Aboveground Dormant Season Biomass (ADSB)

We developed separate models for ADSB based on the time frame of interest. In 2008, ADSB was best predicted at the plot level by H` (*P*<0.016) and FQI (*P*<0.001), and litter depth (*P*<0.001). We removed litter as a predictor because of issues regarding circularity in inference. Our final model for 2008 was $ln(ADSB) = 8.665 - 0.477*ln(H^+) + 0.172*ln(FQI)$ (*P*=0.005, *R*²=0.076). S was not a significant predictor of plant biomass in 2008 (*P*=0.139) (Table 8).

In 2009, ADSB was best predicted by H` $(P<0.001)$ and FQI ($P=0.003$). Our final model for the 2009 data was $ln(ADSB) = 8.515 - 0.905*ln(H^{\prime}) + 0.204*ln(FQI) (P<0.001, R^2=0.193)$ (Table 8). For the multi-year model, ADSB was also associated with H` (*P*<0.001) and FQI (*P*<0.001). Our final multi-year model was $ln(ADSB) = 8.554 - 0.682*ln(H^+) + 0.206*ln(FQI)$ (*P*<0.001, $R^2 = 0.319$) (Table 8).

Table 8. Plant productivity regression models. Productivity was modeled at 3 different time periods, 2008, 2009 and over the two years. H` refers to Shannon's Diversity Index, FQI refers to Floristic Quality Index (n=160 in 2008, n=141 in 2009 and n= 301 in the combined data).

Likelihood Ratio

Aspen Forests

Avian Relative Abundance and Richness

We detected 73 bird species on line transect surveys over three years across all aspen stand age-classes and legacy tree retention treatments (Table 9). The two most abundant species were Chestnut-sided Warbler with higher abundance in the younger aspen stands and Ovenbird with higher abundance in the older aspen stands (Table 9). Generally, avian species richness was at its highest during the first five years after the aspen harvest (Figure 5). This declines until around 20-years post-harvest and levels off and possibly begins to increase with time. Species richness tended to be consistently highest in the hardwood legacy tree retention treatment through time, lowest in the no legacy tree retention treatment, and intermediate between the other two retention treatments for conifer legacy tree retention stands.

Indicator species analysis results suggested that for most age-treatment combinations, there are one or more bird species that can be indicative of different compositional and structural conditions in aspen stands (Table 10). Sixteen species were considered good indicators of one age-treatment combination. Species typically associated with large pines, such as Pine Warbler, Black-throated Green Warbler, and Yellow-rumped Warbler, were not surprisingly associated with conifer legacy tree retention treatments. The hardwood legacy tree retention treatment had the greatest number of indicator species (9) perhaps due to generally having the largest number of species present overall but also it includes habitat specialists such as Golden-winged Warbler. Of the three age-classes, the young stands had the most indicator species (10) with a majority in the hardwood legacy tree retention stands (5) and the no legacy tree retention stands (4). This suggested that there are potentially more species that are specialists of young aspen forests and, in particular, aspen stands with hardwood legacy tree retention.

Table 9. Species richness and mean relative abundance of bird species on line transects (individuals/500 m) for 27 aspen forest stands in north-central Wisconsin, 2007-09. Line transects were surveyed twice per year. The maximum count within a year for each species was averaged across years. The highest value across age-classes and treatments is indicated in bold font for each species.

Table 10. Indicator species analysis results by treatment and stand age-class for 27 aspen stands with and without legacy tree retention, north-central Wisconsin, 2007-09. Only species with proportion (*p***) values equal to or less than 0.05 are included. Species in each treatment-age group are sorted by highest indicator value. Species not in bold font had nearly equally high indicator values in one or more of the other groups, thus only species in bold font are good indicators for one treatment-age group. See Table 9 for species scientific names.**

likely a good indicator of this treatment.

Figure 5. Avian species richness by legacy tree retention treatment in 27 aspen forest stands in north-central Wisconsin, 2007-2009.

Golden-winged Warbler Territory Area

Golden-winged Warbler territory areas appeared to differ between legacy tree treatments though we were unable to test this statistically as the variances were not equal despite efforts to transform the data (Table 11). This was likely due to the small annual sample sizes in the no legacy tree retention treatment and the highly variable area results within and among years

Legacy Tree	# Territories	Min Area	Max Area	Mean Area \pm se
Treatment & Year	Mapped	(ha)	(ha)	(ha)
No Retention				
2007	3	0.35	2.51	0.90 ± 0.26
2008	$\overline{2}$	0.47	0.64	0.56 ± 0.26
2009	$\overline{2}$	0.19	0.71	0.45 ± 0.26
2010	$\overline{4}$	1.49	3.04	2.26 ± 0.22
All Years	11			1.04 ± 0.13
Conifer Retention				
2007	15	0.11	1.73	0.57 ± 0.22
2008	13	0.14	1.44	0.56 ± 0.26
2009	13	0.14	1.24	0.49 ± 0.26
2010	10	0.26	1.21	0.67 ± 0.26
All Years	51			0.57 ± 0.12
Hardwood Retention				
2007	16	0.09	2.11	0.62 ± 0.22
2008	14	0.10	1.69	0.65 ± 0.22
2009	17	0.15	1.27	0.64 ± 0.22
2010	17	0.14	3.18	0.96 ± 0.22
All Years	64			0.72 ± 0.11

Table 11. Golden-winged Warbler territory area (ha) in aspen stands with no legacy tree retention $(n=3)$, with conifer legacy tree retention $(n=3)$, and with hardwood legacy tree retention $(n=3)$ in **2007-2010, north-central Wisconsin.**

Understory Plant Species Richness

We identified 203 understory plant species across the 27 aspen stands surveyed. Understory plant species richness did not differ significantly by legacy tree treatment $(F_{2, 18}, P=0.33)$, stand age class $(F_{2, 18}, F=0.33)$ *P*=0.18), or the interaction of these two independent variables ($F_{4, 18}$, $P=0.35$; Table 12).

Table 12. Mean understory plant species richness (± se) for 27 aspen stands in north-central Wisconsin, 2009-2010.

Aboveground Live Woody Biomass

Overstory tree basal area and density increased with stand age and sapling density generally decreased with stand age (Table 13). Though stands with legacy trees were categorized as hardwood retention or conifer retention, all stands had some biomass of both hardwoods and conifers (Table 14). Aboveground live woody biomass increased for all tree species and aspen species with stand age (Figures 6 and 7). The retention of legacy trees generated higher biomass than in stands without legacy trees for young stands (Figure 6). However the stands without legacy trees have a higher rate of annual growth such that there is no difference in biomass between treatments at around 30 years post-harvest.

Foresters are often concerned about suppression of aspen regeneration due to retention of large canopy trees. Retention of hardwoods did not appear to reduce aspen biomass as compared to the stands without legacy trees (Figure 7). The retention of conifers did appear to suppress aspen biomass though not immediately apparent in young stands. At around 15-years post-harvest, the annual rate of growth increases to match that of the other two treatments. However, it is unclear if these stands eventually are able to produce the same amount of biomass as the other two treatments prior to next aspen harvest rotation.

Table 13. Tree characteristics in 27 aspen stands in 2007-2008, north-central Wisconsin.

*CR=conifer retention, HR=hardwood retention, NR=no retention

		Above-ground Live Woody Biomass (kg/ha)											
				Overstory Trees				Saplings				Combined Total	
	Aspen												
Site	Age	All				All				All			
Code	(years)	Species	Conifers	Hardwoods	Aspen	Species	Conifers	Hardwoods	Aspen	Species	Conifers	Hardwoods	Aspen
		Conifer Legacy Tree Retention											
BRNW	9	47,862	37,992	9,870	18	5,941	0	5,941	5,028	53,803	37,992	15,811	5,046
CTYD	9	16,461	14,892	1,569	0	10,706	0	10,706	8,238	27,167	14,892	12,275	8,238
CFLN	11	19,832	19,714	119	0	5,922	24	5,898	4,690	25,754	19,737	6,017	4,690
BRSE	16	48,507	40,108	8,400	161	13,120	8	13,112	8,116	61,627	40,116	21,511	8,277
CTYN	16	40,981	39,229	1,752	37	9,226	284	8,942	7,064	50,208	39,513	10,694	7,101
BRSW	21	58,095	51,433	6,662	4,254	14,299	0	14,299	6,158	72,394	51,433	20,961	10,412
OLDC	24	59,520	55,057	4,462	4,045	10,092	21	10,071	5,985	69,612	55,078	14,533	10,031
CTYE	27	35,627	15,463	20,164	17,447	8,531	1,173	7,358	1,226	44,158	16,636	27,522	18,674
RVRD	27	49,724	11,897	37,827	17,423	9,018	136	8,882	2,192	58,742	12,033	46,709	19,615
		Hardwood Legacy Tree Retention											
BUCK	6	34,956	488	34,468	0	2,896	207	2,689	1,697	37,851	694	37,157	1,697
TLKR	7	7,031	2,179	4,852	0	8,367	153	8,213	5,925	15,397	2,332	13,065	5,925
CFDN	10	9,691	479	9,212	0	8,572	0	8,572	8,237	18,263	479	17,784	8,237
NLKW	11	8,709	83	8,625	0	14,675	1	14,674	10,834	23,384	84	23,299	10,834
BRNE	16	11,503	2,206	9,297	4,956	28,598	104	28,494	15,647	40,101	2,310	37,791	20,603
NLKE	20	22,004	0	22,004	5,687	39,370	69	39,301	8,412	61,373	69	61,305	14,099
MUSK	21	33,107	1,286	31,821	2,750	11,261	276	10,984	8,751	44,368	1,562	42,805	11,500
GLRD	29	52,055	505	51,549	27,942	10,342	0	10,342	897	62,396	505	61,891	28,838
BVLK	37	59,627	0	59,627	52,611	6,286	0	6,286	463	65,912	0	65,912	53,074
		No Legacy Tree Retention											
CTYY	6	0	$\mathbf 0$	0	0	4,473	0	4,473	4,206	4,473	$\boldsymbol{0}$	4,473	4,206
JRRD	6	2,590	2,161	429	0	3,772	35	3,736	2,079	6,362	2,197	4,165	2,079
KNFL	9	411	411	0	0	9,465	306	9,159	8,541	9,876	717	9,159	8,541
CFDS	12	281	281	0	0	9,055	150	8,906	7,773	9,336	431	8,906	7,773
CFLS	12	$\mathbf 0$	0	$\overline{0}$	$\mathbf 0$	14,207	98	14,109	12,422	14,207	98	14,109	12,422
TRCR	20	13,200	0	13,200	6,706	32,346	0	32,346	12,465	45,546	0	45,546	19,171
LLKR	21	18,029	0	18,029	14,555	26,490	0	26,490	17,118	44,519	0	44,519	31,673
WDLK	27	31,704	2,033	29,671	27,067	9,465	478	8,987	3,237	41,169	2,511	38,658	30,304
GRRD	28	52,716	3,288	49,428	26,655	15,469	0	15,469	1,445	68,186	3,288	64,898	28,100

Table 14. Aboveground live woody biomass for trees in 27 aspen stands in 2007-2008, north-central Wisconsin.

Figure 6. Aboveground live woody biomass (saplings and overstory trees combined) increases with stand age at 27 aspen stands in north-central Wisconsin. Until around 30-years post-harvest, stands with legacy trees have greater biomass than stands with no legacy trees.

Aspen Species

Figure 7. Aboveground live woody biomass (saplings and overstory trees combined) increases with aspen stand age at 27 aspen stands in north-central Wisconsin. Retention of hardwood legacy trees do not reduce aspen biomass but conifer retention at the levels in this study reduce aspen regeneration.

DISCUSSION

Grasslands

Biomass Production

Our vegetation results suggest that productivity in planted grasslands may be substantially correlated with the floristic quality of the plant community. This pattern held at two different time scales, within year and between years. Measures of floristic quality (e.g., FQI and *C*) were consistently positively associated with aboveground plant biomass production. Areas with high floristic quality were composed of species that have a high fidelity to TGP ecosystems and associated disturbance regimes. This relationship between productivity and floristic quality may be driven by the presence of high biomass yield native C4 grasses species such as *P. virgatum*, *A. gerardii* and *Sorghastrum nutans* (L. Nash) as well as high biomass native forbs such as members of the genus *Silphium*, which have moderately high *C* values.

An increase in FQI, by definition, means more native prairie-specific plants are found in the plot and fewer exotics, particularly because of the penalty imposed on the calculation of FQI by scoring exotic species with a zero. Plots with higher quality plant communities, at a given level of plant species diversity, also had higher biomass yields, partially because of the inclusion of high-yield grasses which have moderately high *C* values. Co-evolution of native prairie species may have led to complimentary resource use for co-existence, whereas the introduction of exotic species likely results in interspecific competition with the invaders and one or more native species, potentially reducing native species prevalence (Yurkonis et al. 2005) and reducing productivity. High native plant diversity, however, may help grasslands resist invasion. For example, work at the Cedar Creek LTER (Knops et al. 1999, Tilman et al. 1997a, Kennedy et al. 2002) has consistently suggested that plantings with high native species richness may be more resistant to invasion as a result of reduced availability of soil nutrients via complimentary effects and low light levels at the soil surface. A high abundance of late successional prairie species in the initial planting mix and cultural treatments such as prescribed burning or mowing may also reduce the prevalence of native ruderals.

Avian Community

Our results suggest that avian species abundance in grasslands is influenced primarily by vegetation characteristics within a field. In both years, more even representation of functional groups within a field is consistently associated with higher abundance of both individual avian species as well as the abundance of species requiring grasslands. Plant community indices calculated at the species level (e.g., FQI, individual functional group IVI) are typically associated with lower abundance of individual avian species. FQI was only a significant predictor in two models, and in both higher FQI was marginally associated with fewer Common Yellowthroats and Song Sparrows. Given the strength and direction of the other predictors found in these models, FQI seems to have little utility in predicting the abundance of birds in this system. However, more research of individual obligate grassland bird species may be required to completely dismiss this index as a potential indicator of the abundance of such species.

The diversity of functional groups had a stronger influence on bird abundance than the importance of any single functional group. As an individual functional group becomes more important (i.e. dominant) within a field, others become less common, thus decreasing the evenness and diversity of functional groups. The influence of functional group diversity on individual avian species abundance could be a result of the services provided directly to birds by different plant functional groups. Higher availability of all functional groups likely provides increased cover because of increased structural diversity (Grime 1998) as well as increased food availability; composites such as sunflowers provide larger seeds**,** while legumes typically have higher arthropod loads due to foliage palatability by herbivorous arthropods (Reader and Southwood 1981).

Aspen Forests

Biomass Production

As one would expect, following harvest and as an aspen stand ages, on-site biomass increases. The retention of legacy trees reduces the overall fluctuation in on-site biomass by reducing the low point at the time of harvest and aspen removal. Following harvest, legacy trees continue to add biomass as the aspen stand regenerates. Our data suggest that aspen above ground biomass is added to the stand at very similar rates over time in both the no retention and the hardwood retention treatments. In sites where conifers were retained, accrual of new aspen biomass is slower in the first 10-15 years after harvest, but as the stand ages to 20-25 years, the slope describing aspen biomass accumulation increases to nearly match the slope for hardwood and no retention treatments. There is even a suggestion in the data that aspen in conifer retention sites might eventually grow more rapidly but additional older conifer retention stands would need to be examined to answer this question (because legacy tree retention was an unusual management choice 30 years ago, such sites are extremely rare if they exist at all).

Avian Community

Bird species were distributed across aspen age classes and across legacy tree retention treatments in ways that demonstrated the importance of these habitat features for avian breeding habitat selection. The youngest aspen stand had the highest bird species richness, likely reflecting a rapid growth of the aspen in the five years following cutting. High growth rates support large populations of arthropods, the primary food for most breeding migratory songbirds. Bird species richness was highest in stands containing legacy trees for middle- and older age classes, but not for the youngest aspen age classes. Those bird species most sensitive to age- and stand-related attributes were identified as "indicator species" for certain age-treatment combinations, with young aspen having the most indicator bird species. Indicators of aspen with hardwood retention appear to be among the most specialized bird species in terms of habitat preferences.

Golden-winged Warbler area was potentially larger in the no legacy tree retention treatment due to most of the males not acquiring mates. Female behavior often results in changes to territorial boundaries and in their absence, bachelor males were perhaps inclined to defend a larger area in hopes of attracting a mate even well into the breeding season. Also, males on no legacy tree retention sites often had few if any neighboring conspecific males which often limit territorial boundaries when present.

Understory Plant Community

For the 203 understory plant species identified within the 27 aspen stands, neither stand age, treatment type nor the combination showed a significant effect on understory plant species richness. Within a given location, understory plant community composition is known to be shaped by soil type, disturbance history (including forest management and herbivore browse intensity), and many other factors.

MANAGEMENT RECOMMENDATIONS

Grasslands

As the next generation of biofuel crops is being investigated and planted, our findings provide insight into the establishment and management of such operational fields and the potential benefits these fields might provide for wildlife. To promote sustainable high yields of biomass, it may be prudent to include a diverse suite of both native species and functional groups in planting mixes. Our study also suggests that high functional group diversity would promote habitat for grassland birds. High-yielding C4 grasses will likely comprise a substantial portion of the matrix in biomass production fields. Promoting high quality plant communities may act as a self-maintaining management strategy to reduce invasion of undesirable/ruderal plant species, decrease the rate of disease, and maintain higher trophic level diversity and associated ecosystem services such as pollination (Knops et al. 1999, Kennedy et al. 2002, Ebeling et

al. 2008). FQI may provide a valuable tool for monitoring the health and biomass production potential of TGP plantings intended for use as bioenergy feedstocks. These management suggestions will not only provide increased social benefit but also provide benefits to the wildlife that will be occupying these fields.

Aspen forests

Plant community structural and compositional diversity has long been understood to correlate positively with species richness among a variety of wildlife groups. Although it followed logically that retention of legacy trees in aspen clearcuts would enhance habitat diversity for understory plants compared to clearcuts lacking legacy trees, there was little empirical research to support this form of aspen management. To our knowledge, this study is the first to demonstrate that for a variety of bird species of conservation concern, legacy tree retention dramatically improves the quality of the aspen forest habitat.

Clearly, one recommendation would be to retain legacy trees in intensively harvested aspen forest stands to enhance the value of the forest for a host of high value game and non-game birds. We also would hope that Focus on Energy and/or other groups would support research that quantifies the role of legacy trees for other groups of wildlife. Legacy tree retention also provided the means for reducing the loss of overall stand biomass and carbon during clearcutting and thus mitigates some of the negative effects of harvesting trees on the forest carbon balance.

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PUBLICATIONS AND PRESENTATIONS RESULTING FROM THIS RESEARCH

Publications

Fortin, C.R. 2009. Floristic quality as a potential driver of vegetative diversity-productivity relationships and arthropod habitat in restored grasslands. M.S. Thesis. Michigan Technological University.

Henschell, M.A. 2010. Biomass and birds: effects of potential planted grassland biofuel crops on plant productivity and the grassland avian community in the Upper Midwest. M.S. Thesis. Michigan Technological University.

Presentations

- Flaspohler, D. The relationship between biofuels, land use and biodiversity conservation. Presentation to Calumet High School Future Fuels Outreach. 16 March 2010.
- Flaspohler, D., A. Roth and C. Webster. Intensive management of native forests for bioenergy: Quantifying trade-offs between forest productivity and biodiversity. Invited talk for University of Hawaii-Manoa seminar series. March 2011.
- Flaspohler, D., C. Webster, and A. Roth. Development of cellulosic bioenergy in North America: Biodiversity issues. Invited talk at Beijing Forestry University, China. 16 July 2009.
- Flaspohler, D., C. Webster, and A. Roth. Intensive management of native forests for bioenergy: Quantifying trade-offs between forest productivity and biodiversity. Invited talk in symposium: Biodiversity and climate change: Direct and indirect linkages inadaptation and mitigation. XXIII World Congress International Union of Forest Research Organizations (IUFRO), Seoul, South Korea. August 2010.
- Henschell, M.A., D.J. Flaspohler, and C.R. Webster. Does floristic quality influence habitat quality for birds breeding in grasslands grown for biofuel feedstocks? Poster presented at 94th Annual Meeting of the Ecological Society of America, Albuquerque, NM. 4 August 2009
- Roth, A., D. Flaspohler, and C. Webster. Golden-winged Warbler ecology in aspen forests managed with legacy tree retention. Invited talk for special symposium at $127th$ Stated Meeting of the American Ornithologists' Union, Philadelphia, PA. 14 August 2009
- Roth, A., D. Flaspohler, and C. Webster. Cellulosic ethanol in the Northwoods: implications for our forests and wildlife. Presented to Coverts Workshop for private woodland owners, Woodruff, WI. 28 August 2009
- Roth, A., D. Flaspohler, and C. Webster. Balancing biodiversity and biomass for bioenergy in Wisconsin. Wisconsin Wildlife Society, Wausau, WI, Invited plenary talk. 4 March 2010.
- Roth, A., D. Flaspohler, and C. Webster. Golden-winged Warbler ecology in aspen forests managed with legacy tree retention. Invited presentation for the Golden-winged Warbler Conservation Workshop, Ithaca, NY. 3 August 2010
- Roth, A, Flaspohler, D. and C. Webster. Intensive management of native forests for bioenergy: Quantifying trade-offs between forest productivity and biodiversity. Invited talk in symposium: Ecological Forestry and Wildlife. 71st Midwest Fish and Wildlife Conference, Minneapolis, MN. 13 December 2010
- Webster, C, A. Roth, and D. Flaspohler. Legacy tree retention in intensively managed aspen forests. Invited talk to Society of American Foresters national convention, Orlando, FL. 1 October 2009

	Conifer Retention				Hardwood Retention		No Retention			
		Middle-			Middle-			Middle-		
Species Scientific Name	Young	Age	Mature Young		Age	Mature Young		Age	Mature	
Achillea millefolium	$\mathbf P$		\mathbf{P}	\mathbf{P}	\mathbf{P}	\mathbf{P}	\mathbf{P}	\mathbf{P}	\mathbf{P}	
Actaea pachypoda					\mathbf{P}				\mathbf{P}	
Actaea rubra	${\bf P}$	\mathbf{P}	$\, {\bf P}$	\mathbf{P}	\mathbf{P}			${\bf P}$	${\bf P}$	
Adiantum pedatum					\mathbf{P}					
Agrimonia gryposepala					\mathbf{P}					
Agropyron repens	${\bf P}$	\mathbf{P}		\mathbf{P}		\mathbf{P}		${\bf P}$	\mathbf{P}	
Agrostis gigantea	\mathbf{P}		\mathbf{P}	P	\mathbf{P}		\mathbf{P}			
Agrostis hyemalis	$\mathbf P$	$\, {\bf P}$	$\, {\bf P}$	\mathbf{P}	\mathbf{P}	${\bf P}$	$\mathbf P$	${\bf P}$	${\bf P}$	
Alnus crispa				\mathbf{P}						
Amphicarpaea bracteata					${\bf P}$			${\bf P}$		
Anaphalis margaritacea					\mathbf{P}					
Anemone americana				${\bf P}$	\mathbf{P}	${\bf P}$	$\mathbf P$	${\bf P}$	\mathbf{P}	
Anemone cylindrica								\mathbf{P}		
Antennaria neglecta						${\bf P}$	${\bf P}$			
Anemone quinquefolia	\mathbf{P}	\mathbf{P}	\mathbf{P}	\mathbf{P}	\overline{P}	\overline{P}	$\mathbf P$	${\bf P}$	\mathbf{P}	
Apocynum										
androsaemifolium	\mathbf{P}	$\, {\bf P}$	$\, {\bf P}$	\mathbf{P}	\mathbf{P}	\mathbf{P}	$\mathbf P$	\mathbf{P}	\mathbf{P}	
Aquilegia canadensis	${\bf P}$			\mathbf{P}	\mathbf{P}	\mathbf{P}		\overline{P}	\mathbf{P}	
Arabis drummondii								\mathbf{P}		
Arabis glabra							$\mathbf P$			
Aralia nudicaulis	${\bf P}$	\mathbf{P}	\mathbf{P}	\mathbf{P}	\mathbf{P}	\mathbf{P}	\mathbf{P}	${\bf P}$	\mathbf{P}	
Arctostaphylos uva-ursi							$\mathbf P$			
Argrostis hyemalis							\mathbf{P}			
Asclepias exaltata	${\bf P}$		\mathbf{P}	\mathbf{P}	\mathbf{P}			\mathbf{P}		
Aster ciliolatus	\mathbf{P}	${\bf P}$	\mathbf{P}	\mathbf{P}			$\mathbf P$			
Aster cordifolius				\mathbf{P}						
Athyrium filix-femina	\mathbf{P}	${\bf P}$	$\, {\bf P}$	${\bf P}$	\mathbf{P}	\mathbf{P}	$\mathbf P$	\mathbf{P}	\mathbf{P}	
Brachyelytrum erectum		${\bf P}$		${\bf P}$	${\bf P}$		${\bf P}$	${\bf P}$	${\bf P}$	
Bromus ciliolatus	\mathbf{P}		\mathbf{P}	\mathbf{P}	\mathbf{P}		\mathbf{P}	\mathbf{P}	\mathbf{P}	
Calamagrostis										
canadensis	${\bf P}$		\mathbf{P}	${\bf P}$	\mathbf{P}		\mathbf{P}	${\bf P}$		
Calystegia spithamaea	${\bf P}$		\mathbf{P}	\mathbf{P}	\mathbf{P}	\mathbf{P}	\mathbf{P}	${\bf P}$	\mathbf{P}	
Campanula rotundifolia							\mathbf{P}			
Carex arctata	${\bf P}$	$\, {\bf P}$	${\bf P}$	${\bf P}$	${\bf P}$	${\bf P}$	${\bf P}$	${\bf P}$	\mathbf{P}	
Carex brunnescens									${\bf P}$	
Carex communis				\mathbf{P}					\mathbf{P}	
Carex deweyana		$\, {\bf P}$	${\bf P}$	\mathbf{P}						
Carex intumescens				\mathbf{P}				\mathbf{P}		
Carex leptonervia			${\bf P}$							

Appendix A. Understory plants present (P) in 27 aspen forest stands in north-central Wisconsin, 2009-2010.

Acronym	Term
AIC	Akaike Information Criterion
DBH	diameter at breast height
FQI	Floristic Quality Index
GPS	global positioning system
NMS	nonmetric multidimensional scaling ordination
PCA	principle components analysis

Appendix B. Common acronyms from the text.