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Harvested perennial grasslands provide ecological benchmarks for agricultural sustainability

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ABSTRACT

Perennial vegetation can provide multiple ecosystem services essential for sustainable production more effectively than production systems based on annual crops. However, the ability of annually harvested, unfertilized perennial systems to sustain long-term yields while also maintaining ecosystem services has not been widely studied. Here we compare the impacts of harvested perennial grass and annual crop fields on ecosystem functioning in KS, USA. Despite the lack of mineral fertilizer applications, the aboveground harvests of perennial fields yielded similar levels of N compared to those of conventional high-input wheat (*Triticum aestivum*) fields and at only 8% of the in-field energy costs. Their 75-yr cumulative N yield per ha was approximately 23% greater than that from the region's wheat fields. In terms of aboveground food webs, perennial fields harboured greater numbers and/or diversity of insect pollinators, herbivores and detritivores. Belowground, perennial grass fields maintained 43 Mg ha^{-1} more soil carbon and 4 Mg ha^{-1} more soil nitrogen than annual crop fields in the surface 1 m. Soil food webs in perennial fields, as indicated by nematode communities, exhibited greater food web complexity and stability than did those in annual crop fields. In surrounding watersheds, increased annual cropland was correlated with higher riverine nitrate-nitrogen levels. Given their benefits, harvested perennial grasslands provide valuable ecological benchmarks for agricultural sustainability.

1. Introduction

Of human activities, agriculture is perhaps the most disruptive to the functioning of ecosystems around the world. While supplying most of our food calories, a large portion of our fibre needs and an increasing amount of our energy demands, farmed landscapes generally exhibit degraded soil, air, water and wildlife habitat conditions compared to those maintained by natural ecosystems (Cassman and Wood, 2005). As Foley et al. (2005) have illustrated, tradeoffs between ecosystem services and agricultural productivity are typical but may not be absolute. An ideal agricultural system would produce abundant yields over long time periods and support ecosystem services at similarly high levels as natural ecosystems, but would not require energy intensive inputs that pose environmental risks.

Perennial crops can provide multiple ecosystem services essential for sustainable production more effectively than production systems based on annual crops (Boody et al., 2005; Tilman et al., 2006; Glover et al., 2007; Jordan et al., 2007). Previous studies of perennial grasslands from which aboveground biomass has been removed for long periods of time indicate their potential to serve as a model for highly sustainable agricultural systems. For example, levels of total soil nitrogen (TSN) in unfertilized perennial grass plots in the Continuous Hay Experiment at Rothamsted did not decline after twice-annual harvests over a 120-yr period (Jenkinson et al., 2004); nor did biomass yields decline (Jenkinson et al., 1994). Studies of unfertilized harvested grasslands in the Russian Chernozem revealed that TSN and soil organic carbon (SOC) stocks had not been reduced after more than 50 yrs of annual harvesting when compared to unharvested grasslands (Mikhailova et al., 2000; Mikhailova and Post, 2006).

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For North America's prairie region, less well-documented reports of harvested grasslands indicate that yields can be maintained for decades with no fertilizer inputs (Shortridge, 1973). Questions remain, though, as to the long-term yields and soil quality of harvested grasslands (Russelle et al., 2007) and little is known about the long-term impacts on other factors such as nutrient yields, energy requirements, aboveground and belowground food webs and water quality. Additional information is also needed on how current cropping systems compare in terms of providing similar ecosystem services.

To fill in some of these information gaps, we used three studies focused on harvested perennial grasslands in North Central Kansas, USA and the surrounding watersheds (Fig. 1a–d) to evaluate a suite of ecosystem components. Based in part on the assessment framework of the Millennium Ecosystem Assessment (MEA, 2003), we considered ecosystem provisioning, regulating and supporting services as well as human inputs required for production (Table 1). Two of the studies, the *long-term study* and the *conversion study*, examine field scale impacts of perennial and annual production systems. Culman et al. (2010) and DuPont et al. (2010) provide additional details on the results of the soil studies for those two studies respectively. The *watershed study* examines impacts of converting perennial grasslands to annual croplands at the watershed scale.

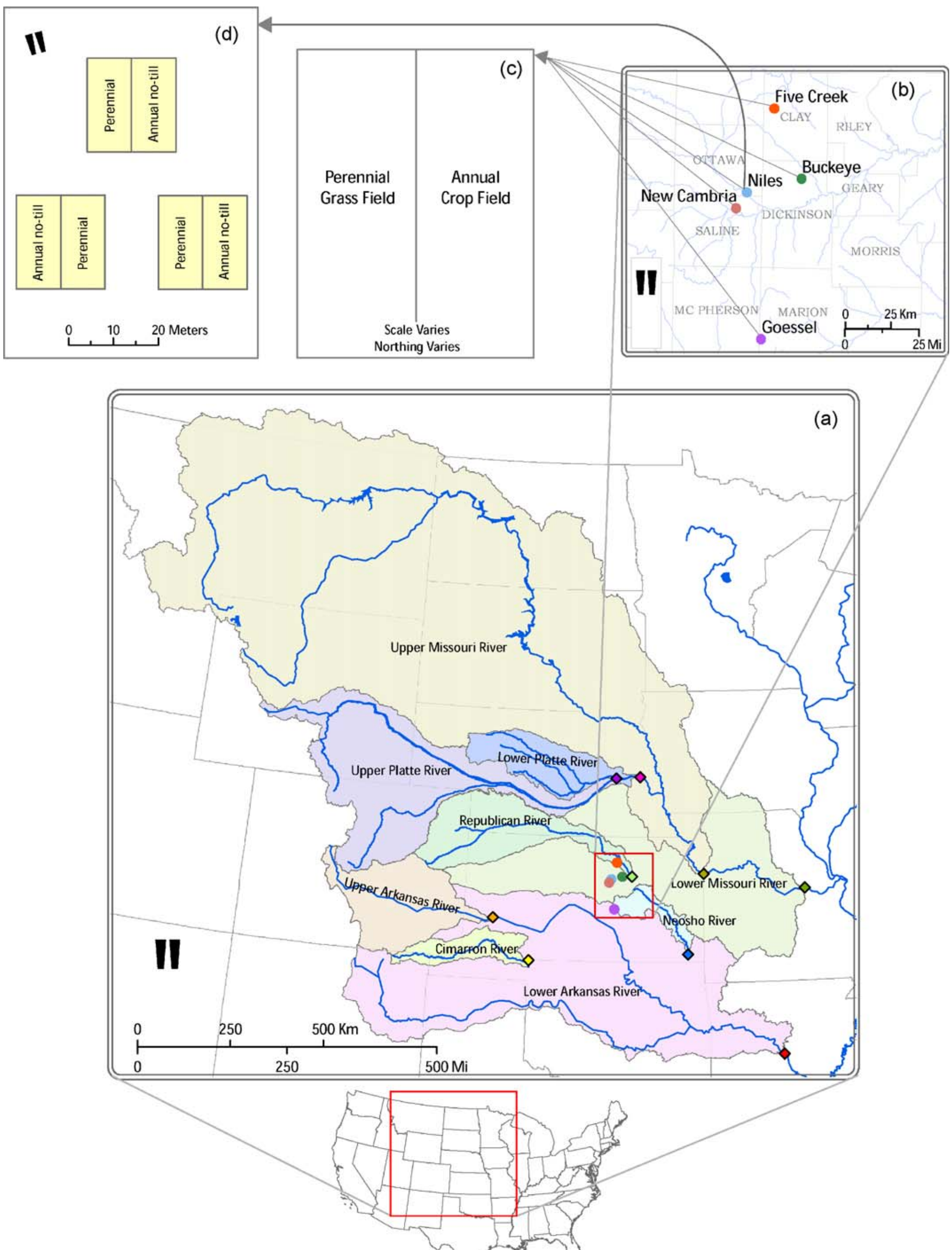

Fig. 1. Area of study in central USA. Watershed monitoring stations (indicated by colored diamonds in a), field site locations of the long-term study (indicated by solid circles in a and b), and research layout of the long-term study (c) and of the conversion study (d).

Table 1
Ecosystem components studied and type and source of data collected.

Ecosystem components	Attributes measured	Data source
Human inputs		
Energy	In-field energy requirements	Conversion study; scientific literature
Provisioning		
Yield	Harvested biomass and nitrogen	Long-term study; conversion study; historical data
Regulating		
Plant community	Plant community composition	Long-term study
Aboveground food web	Insect community composition	Long-term study
Belowground food web	Soil nematode community composition	Long-term study; conversion study
Supporting		
Soil and water properties	Root carbon, soil organic carbon, total soil nitrogen, soil water content, nitrate-nitrogen below root zone, and surface water nitrate concentration	Long-term study; conversion study; watershed study

2. Materials and methods

2.1. Study descriptions

2.1.1. Long-term study

The *long-term study* included five perennial grassland sites in KS, USA from which the aboveground biomass had been annually removed for use as hay (livestock fodder) for approximately 75 yrs or more (Fig. 1a–c). The unfertilized grasslands, which have been annually harvested for 75 yrs or more, provided us the opportunity to study a suite of ecosystem components (Table 1) associated with an agricultural system receiving few anthropogenic inputs. They are relatively unique in that they have not been converted from the native vegetation despite being located on fertile, level landscape positions that otherwise were almost entirely converted to annual crop productions in the late 19th and early 20th centuries.

Management histories were determined in interviews with landowners or managers. The perennial fields have typically been cut to a height of 8–10 cm once per year in mid-summer; hay production practices have changed little over the past century and are largely consistent amongst landowners (Shortridge, 1973; Towne and Ohlenbusch, 1992). Although all the sites are classified by the USDA's Natural Resources Conservation Service as Prime Farmland with few constraints for agricultural production, the sites have been maintained in perennial grass hay production because their irregular shape and/or relatively small size (2–20 ha) makes annual crop management impractical (the Five Creek, Buckeye and Niles sites) or because of long-standing landowner tradition (the New Cambria and Goessel sites). The New Cambria perennial field received infrequent application of herbicides in recent years to control annual cool-season grasses although plant community composition there was consistent with the composition of other sites. None of the landowners/managers reported any fertilizer application to their perennial fields and only the New Cambria site was reported to have been grazed (sporadically in the late nineteenth century).

On average, 79% of ground cover at the sites consisted of perennial grasses (69%), legumes (7%), and non-legume forbs (3%) native to the tallgrass prairie region of North America (Table 2). Non-native annual grasses accounted for an additional 4% of ground cover. A visual examination of soil diagnostic features below the rooting zone of perennial fields (3–3.5 m) indicated that water tables do not rise into the root zone and led us to conclude that the perennial fields were not being fertilized by N-enriched groundwater.

We selected farm fields immediately adjacent to the perennial fields with similar soil types that were primarily or exclusively used for winter wheat (*Triticum aestivum*) production over a similar period of time to make comparisons at the field scale. Wheat production serves as a useful reference system because wheat is, and was during the 20th century, the most widely grown crop in the region. It is also the most extensively grown crop globally (FAOSTAT, 2008) and much of global wheat production occurs in temperate grassland regions such as KS, the leading wheat-producing US state (US Department of Agriculture-National Agricultural Statistics Service [USDA-NASS], 2009). The 3.0 Mg ha^{-1} yr^{-1} average wheat yield of the five counties included in our study (USDA-NASS, 2009) is similar to the global average of 2.8 Mg ha^{-1} yr^{-1} (FAOSTAT, 2008).

During the period of study, wheat straw was not removed from the crop fields after harvest. In recent years at some sites, farm managers have used short rotations of wheat, sorghum (*Sorghum bicolor*), and/or soybeans (*Glycine max*) and/or have used no-tillage practices for varying periods. Field management followed typical practices for the region (KSUAES, 1996, 1997).

Table 2
Location of field sites and species number and percent cover of plant groups in perennial grass fields.

Site	Location	Plant species number	Percent ground cover			
			Perennial grasses	Annual grasses	Legumes	Non-legume forbs
Buckeye	N39°2.34′ W97°7.8′	35	66	5	6	7
Goessel	N38°15.3′ W97°22.4′	30	64	4	4	0
Five Creek	N39°22.7′ W97°18.8′	25	63	0	14	2
New Cambria	N38°53.5′ W97°32.6′	28	77	0	3	2
Niles	N38°58.2′ W97°28.6′	26	73	11	9	2
Average		29	69	4	7	3

Table 3
In-field energy inputs for perennial grass hay and no-till winter wheat production.

Inputs	Units	MJ unit^{-1}	Perennial grass		No-till annual wheat	
			Amount	MJ ha^{-1}	Amount	MJ ha^{-1}
Equipment MTR[a]				186[b]		360[c]
Diesel	L	36.6	11.1	408	27.1	992
Nitrogen	kg	57.5	0	0	77	4424
Phosphorus	kg	7	0	0	25.0	176
Seeds	kg	5.6	0	0	134.4	749
Herbicides	kg	267	0	0	0.9	240
Insecticides	kg	285	0	0	0.1	14
Fungicides	kg	289	0	0	0.1	29
				594		6984

[a] Manufacturing, transportation and repair.
[b] MTR energy values are from Table 7, West & Marland (2002) for harvest operations.
[c] Embodied energy values for equipment manufacturing, transportation and repair are from Table 7, West and Marland (2002) and include equipment for planting, harvest, fertilizer, and herbicide application operations.

2.1.2. Conversion study

The long-term study sites are limited by the fact that differences in soil properties may be artefacts of the region's early agricultural practices for which better alternatives have been more recently developed (e.g., no-tillage practices). In August 2003, therefore, we established three, 20 m $\times$ 20 m research blocks in the perennial grass field at the Niles site, in order to conduct more detailed studies of soil and ecosystem properties following the conversion of perennial grass plots to annual cropping using no-tillage practices (Fig. 1d; hereafter referred to as *the conversion study*). We imposed a randomized complete block design over the annually harvested grassland, with two treatments and three blocks. The two treatments included: (i) continuation of the annual harvest regime that had been in place for 75 yrs or more and (ii) conversion of the grassland into annual cropland using best management practices through herbicide application and without tillage. DuPont et al. (2010) provide specific seeding and application rates and harvested yields.

2.1.3. Watershed study

In order to study larger scale impacts of perennial grass and annual crop production, we used digitized historical water quality data (1906–1912) collected from US Geological Survey (USGS) river monitoring stations (Fig. 1a) reported by Clarke (1924) to assess impacts of land use changes on water quality in eight watersheds encompassing our five study sites. Prior to European settlement 75–150 yrs ago, these watersheds primarily supported perennial grassland vegetation. The USGS National Water Information System (USGS, 2007) provided modern data for the years 1974–1997. We compiled and digitized Census of Agriculture county-level data regarding land use practices, crop and livestock production, and human population, converted them to units per watershed area, and compared them to watershed NO_3-N concentrations using geographic information system software (ArcGIS).

We based our selection of monitoring stations and years on the completeness of NO_3-N concentration data sets, which were most complete for the years 1906–1912, 1974–1978 and 1993–1997. Land use data were compiled from digitized data files obtained from the US Bureau of the Census (USBC), Census of Agriculture reports for 1905 (Haines, 2004), 1978 (USBC, 1990), and 1997 (USBC, 2001). S-Plus 2000 (MathSoft, Inc., 1999) was used to develop a multiple regression model of watershed NO_3-N concentration. An initial exploration of the data revealed that data from a single monitoring station were consistently influential, as measured by Cook's *D* test, and severely impacted the model coefficients. The data for this watershed were removed based on its influence and the unusual conditions in the watershed: at the first sampling date, its human and cattle population densities were both several times greater than any other watershed. A model was fitted using the "lm" function of S-Plus that included the natural logarithm of NO_3-N concentrations as the response and the following predictors: fraction of the watershed cropland planted to annual crops, cattle inventory per watershed area, human population per watershed area, year, and watershed. Next, the "step.lm" function was used for model selection via backward elimination.

Recognizing that several of our study watersheds are nested within other study watersheds, we developed a test to determine if a difference exists between nested and independent watersheds regarding the relationship between NO_3-N concentrations and annual cropland. Using 49 additional watersheds from the same dataset presented in this study, we identified the watersheds as independent if they were not encompassed by another study watershed. Nested watersheds are embedded within other study watersheds. A regression analysis of the 1993–1997 data showed that nitrate concentrations are significantly related to the fraction of a watershed in annual cropland for both the independent and nested categories ($p < 0.0001$, $r^2 = 0.61$, $n = 34$ and $p = 0.0013$, $r^2 = 0.56$, $n = 15$, respectively). Analysis of covariance (ANCOVA) showed that the slope and intercept of the regression lines were not significantly different ($p = 0.807$ and $p = 0.125$, respectively). We concluded that the nested watersheds in our analysis are not statistically different from the independent watersheds. Because the nested watersheds are not different from independent watersheds, we chose to use all possible watersheds for the analysis with adequate data from 1906 that lie within the study area.

2.2. Yield assessments

2.2.1. Contemporary yield comparisons

We based contemporary yield estimates on measurements of perennial grass and annual wheat fields gathered over a period of 5 yrs (2002–2004 and 2006–2007). Sites were omitted from this estimate if the crop fields were not used for wheat production that year, or if the grass fields were harvested by the producers before yield estimates could be made. As a result, contemporary yield estimates were based on a total of 10 side-by-side comparisons of wheat and grass hay yields.

Simulating typical hay production practices, we determined perennial grass field yields by clipping aboveground biomass at a height of 8–10 cm in mid-summer in 10 1-m^2 quadrats at each sample site. Clipped biomass was dried to constant weight at 60 °C and weighed to determine dry yield. Biomass N contents, as determined by Kansas State University's soil testing laboratory

(KSU-STL), ranged from 1.10 to 1.40 g N kg^{-1} grass hay (dry weight); we used the average value of 12.3 g N kg^{-1} for calculations of N yields.

Despite some variation in legume abundance at each site, legumes comprised only a small portion of overall biomass at any site and biomass N contents were not correlated with legume abundance. Although the USDA provides a higher estimate of 15 g N kg^{-1} for average bluestem grass hay harvests (USDA, 2009), we chose to use the more conservative value derived directly from our sites for calculations of N yields. Wheat seed yields were based on similar methods as for perennial biomass yields or on farmer reports. The average N content of hard red winter wheat grain (20.3 g kg^{-1}; equivalent to 12.7% protein) was obtained from USDA data (USDA, 2009).

2.2.2. Historical yield comparisons

We estimated cumulative 75-yr wheat yields based on: (a) an average of yields reported in USDA's Census of Agriculture (USDA-CA) for 1934, 1940, 1945 and 1949; (b) interpolation of USDA-CA data for 1954, 1959, 1964 and 1968; and (c) annual yield data reported by USDA-NASS. A single average value was used for the period 1934–1949 because reported wheat yields in the five counties did not significantly change during that period. Wheat yields reported in the census years between 1954 and 1968 significantly increased as fertilizer use became more widespread. Thereafter, we used annual yield figures which became available following 1968. Using the average N content for winter wheat (20.3 g kg^{-1}), wheat grain yields were converted to N yields. Similarly, we used a N yield of 45.4 kg N ha^{-1} yr^{-1} for the perennial grass fields based on the average biomass yield of all five grass fields and the measured N content of 2007 plant samples (12.3 g kg^{-1}) to calculate estimated 75-yr N removal totals.

2.3. Energy requirements

We used reported energy requirements for equipment, chemical inputs, field operations and harvesting from West and Marland (2002) and Tilman et al. (2006). For wheat production we assumed no-tillage practices typical for the region based on O'Brien et al. (2007). Because the harvested hay may have multiple end uses, each of which could have specific energy requirements, only the in-field energy requirements for production and harvesting of both crops were considered.

2.4. Insect communities

Insects were sampled in June 2007 at the long-term study sites using a sweep net along 11, 22 m long transects (242 sweeps per 484 m^2) within perennial grass and annual wheat fields at each site except for Buckeye where the annual crop field was not in wheat production that year. Adult insects were sorted to morphospecies within family (Trippelhorn and Johnson, 2005).

2.5. Root and soil characteristics

In June 2007, five, 12.5-cm diameter soil cores to a depth of 2 m were collected from the perennial grass and the annual wheat field at the Niles site. The cores were sectioned into 20-cm sections and separated the roots from soil by repeated rinsing on fine mesh screen. Following extractions, roots were dried and weighed to determine root mass per area and sent samples to KSU-STL for analysis of C content. The Missouri Agricultural Experiment Station (MAES) provides details of analytical methods used at KSU-STL (MAES, 1998). Because root samples were collected only from the perennial grass and wheat fields at one site, data were not statistically analyzed.

Five 4-cm diameter soil samples were collected in June 2007 to a depth of 1 m in each of the perennial and annual fields in the long-term study. The five samples were bulked from each field by depth and the roots and other plant material were removed from the samples. Samples were analyzed for SOC and TSN at KSU-STL and for readily oxidizable carbon (ROC; Weil et al., 2003). We determined nematode community compositions in soil samples collected in June 2006, October 2006 and June 2007. For each sample date, five 4-cm diameter soil cores were collected to a depth of 1 m from the long-term study and four 4-cm diameter soil cores from the conversion study. The samples were bulked by depth, removed roots and other plant material and refrigerated the samples until nematode extractions were completed. Nematodes were extracted from 200 to 300 g soil using a combination of decanting–sieving and Baermann funnel methods (Barker, 1985) and identified to genus or family within a week following extraction or preserved in 4% formalin until identifications could be made. DuPont et al. (2010) provide additional details on extraction and identification.

We used standardized indices of food web structure and function based on characteristics of nematode assemblages to determine the effects of environmental stress, and dominant decomposition channels (Bongers, 1990; Wardle et al., 1995; Lenz and Eisenbeis, 2000; Ferris et al., 2001; Ferris and Matute, 2003). Soil food web indices were calculated based on Ferris et al. (2001). The Structure Index (SI) reflects the relative abundance of nematodes in higher trophic groups and cp levels indicate soil food web length and connectance. The Basal Index (BI) enumerates the predominance of nematode groups that are tolerant to disturbance.

To determine NO_3-N concentrations below root zones in the conversion study plots, three, 2-cm diameter soil cores were collected from the 3.0–3.2 m depths in each plot in October 2007. Nitrate-nitrogen was extracted with KCl (Robertson et al., 1999) and analyzed at KSU-STL. We also monitored soil moisture content in the conversion study plots using time domain reflectometry probe readings (Jarrell et al., 1999) at 20 cm intervals to a depth of 1 m approximately twice per month from November 2006 through October 2007.

2.6. Statistical analysis of long-term and conversion study data

Yield, soil, and soil water data were analyzed with analysis of variance using PROC MIXED for those data collected from long-term study sites and PROC GLM for those data collected from conversion study sites (SAS Institute, Cary, NC). Long-term study sites were treated as random effects and management history as a fixed effect. Nematode index data were analyzed over all dates, with date treated as repeated measure. We transformed the insect data ($\sqrt{y}+1$) and performed a Type IV analysis of variance using SPSS statistical software (SPSS v.15.0, Chicago, IL, USA).

3. Results and discussion

3.1. Yield assessments

Significantly greater ($p < 0.001$; $n = 10$) amounts of biomass were harvested from perennial plots in the form of hay (3.83 Mg ha^{-1} yr^{-1}) than from adjacent wheat plots in the form of grain (2.35 Mg ha^{-1} yr^{-1}). This result might be expected given that most of the aboveground material in mid-summer is removed from the perennial fields and only the grain from the wheat fields. While others have used net energy yields to evaluate the productivity of perennial grass systems for biofuels (Tilman et al., 2006; Schmer et al., 2008), the amount of harvested N provides a useful ecological metric for comparison of different

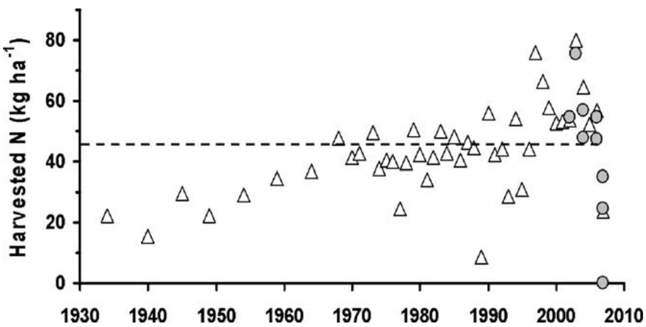

Fig. 2. Winter wheat N yield (kg N ha^{-1}) data for five North Central Kansas counties from 1933 to 2007 (based on planted acres). The triangles represent USDA data and the 10 closed circles represent yields of measured wheat plots adjacent to perennial grass plots used to calculate contemporary yields. The dashed line represents the average N yield (45.4 kg ha^{-1}) of the five perennial fields.

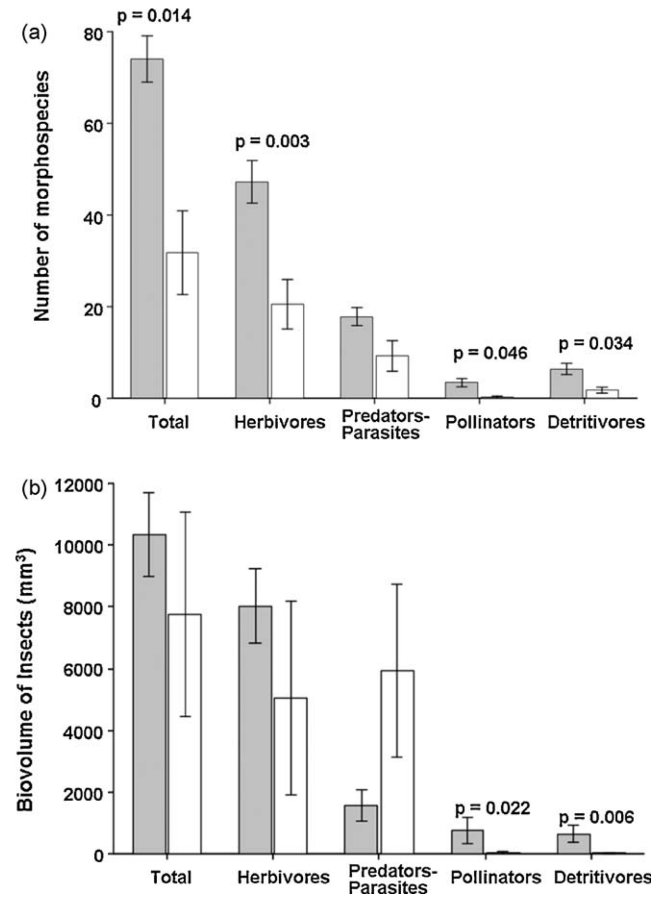

Fig. 3. Means (±1 S.E.) of insect (a) morphospecies richness and (b) biovolume in perennial grass (shaded bars) and annual wheat (open bars) fields (n = 5). Groups with significantly different means are denoted with respective p-values.

farming systems. Our measurements of N removed from perennial plots (47.9 kg ha^{-1} yr^{-1}), which have received no fertilizer applications, were statistically similar (p = 0.909; n = 10) to those removed from adjacent wheat plots (47.2 kg ha^{-1} yr^{-1}) receiving annual inputs of approximately 70 kg N ha^{-1} (Fig. 2). For comparison, estimated N removal rates based on 20-yr average wheat yields (2.5 Mg ha^{-1} yr^{-1}) obtained from USDA-CA for the five counties would be 50 kg N ha^{-1} yr^{-1} and the average annual N yield for the five perennial fields for 2004, 2006 and 2007 was 45.4 kg N ha^{-1} (Fig. 2).

Long-term yield data for perennial hay fields indicate that their yields can be maintained for decades (Shortridge, 1973; Jenkinson et al., 1994). Assuming our measured yields for the five perennial sites (45.4 kg N ha^{-1} yr^{-1}) have been maintained since harvesting commenced, over the past 75 yrs the perennial fields have yielded roughly 664 kg ha^{-1} more N than the average for wheat fields in the five-county region (Fig. 2).

3.1.1. Energy requirements

Increased expenditures of energy for agricultural production often result in greater financial and environmental costs. We used machinery, fuel and farm chemical inputs for regional no-tillage winter wheat and perennial hay production to assess in-field energy use (Table 3). Nitrogen fertilizer inputs to wheat fields accounted for over 60% of in-field energy use (Table 3) and typically accounts for more than 30% of total energy use in wheat production and transportation (Pimentel et al., 2008). Because of their high N requirements and greater number of field operations, wheat fields required 6984 megajoules (MJ) ha^{-1} or 11.75 times the energy requirements of the perennial grass fields (594 MJ ha^{-1}). In terms of harvested N, wheat fields required 148 MJ of energy inputs per kg harvested N. Perennial fields, in contrast, required only 12 MJ kg^{-1} harvested N.

3.1.2. Insect communities

Because insects span a wide range of trophic levels and provide a suite of aboveground ecosystem services including pollination, pest control, and contributions to nutrient mineralization through frass deposition and detritivore activity (Weisser and Siemann, 2004) we used insect community characteristics to assess system effects on aboveground food webs. We sampled insect pollinators, predators and parasites, herbivores, and detritivores as indicators of aboveground trophic interactions at the long-term study sites. Herbivores are often of concern in agricultural systems because they can damage or destroy plant tissues and thus reduce yield. Insect predators and parasites provide further information about the potential loss due to insect herbivores since predators and parasites may contribute to the regulation of populations of herbivorous insects. Pollinators can contribute to the yield and persistence of forb species through pollination and detritivores contribute to organic matter breakdown by feeding on litter, dung, or animal carcasses (Kaufman et al., 1998).

Perennial fields supported overall greater insect species richness; in particular, they supported greater richness of insect herbivores, pollinators and detritivores (Fig. 3a). Greater biovolume of pollinators and detritivores was also measured in perennial fields (Fig. 3b). Pollinators were absent from three of the four annual fields but were found in all five of the perennial fields. Perennial fields likely provided a greater number and diversity of pollen sources which would account for the consistent presence of wild pollinators in the perennial fields. In contrast, annual wheat production, like much of annual crop production in general, leaves fields largely devoid of living plant cover for much of the year. Kansas wheat fields, for example, typically do not have living plant cover from July through September or October.

3.1.3. Root and soil characteristics

Differences in plant community composition and aboveground food webs interact with belowground conditions and food webs (Wardle et al., 2004). Although the specific nature of the interactions are not easily predictable, plant communities that provide more resources aboveground and belowground over longer periods of time would be expected to support more productive and complex food webs. Plant roots provide much of the C inputs to the soil ecosystem and differences in root characteristics have profound effects on soil C and N pools (Buyanovsky et al., 1987; Rice et al., 1998; Crews, 2005). Plant root

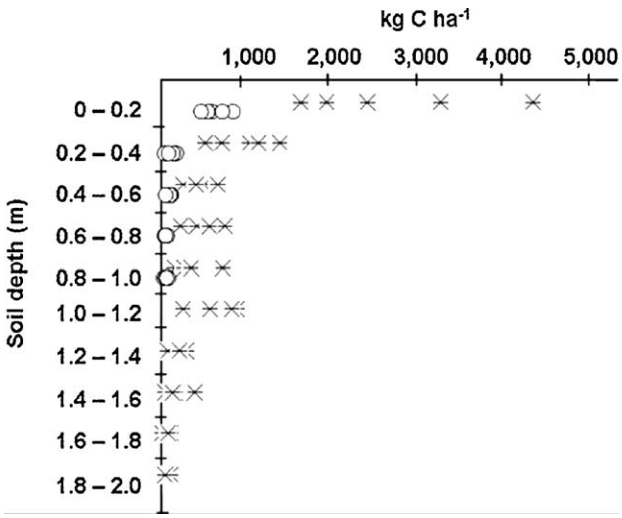

Fig. 4. Belowground carbon storage in root biomass of perennial fields (asterisks) and annual wheat fields (open circles) at the Niles field site. The data represent measurements taken from five soil cores collected from each field.

C, measured at the Niles field site, was 6.7 times greater and the rooting depth 1 m deeper in the perennial field than in the adjacent wheat field (Fig. 4). The proportion of total root C between grasslands and croplands at the Niles site was greater than that reported by Buyanovsky et al. (1987), who measured 2.3 greater root C in grasslands in the surface 50 cm. However, globally temperate grasslands average more than nine times greater root biomass than croplands, globally (Jackson et al., 1996).

These differences in root mass may explain the significantly greater ($p = 0.027$; $n = 5$) levels of SOC measured in the perennial fields (182.2 Mg ha^{-1}) compared to annual fields (138.8 Mg ha^{-1}) in the surface 1 m in the long-term study. Perennial fields in the long-term study also maintained significantly higher levels of TSN (15.4 Mg ha^{-1}; $p = 0.013$; $n = 5$) than did annual fields (11.7 Mg ha^{-1}) in the surface 1 m. Although we cannot conclude that soil C and N levels in the perennial fields have not declined since harvesting commenced, soil C or N levels in other studies of annually harvested grasslands did not decline over many decades (Jenkinson et al., 2004; Mikhailova and Post, 2006).

Soil food web structure strongly influences rates of C and N transformations (Chapin et al., 2002; Schroter et al., 2003). Culman et al. (2010) report that the perennial fields in our study supported bacterial and nematode communities in the 0–10, 10–20, and 20–40 cm depths that were significantly different in composition from those in the annual fields. Community compositions in perennial fields were also positively correlated with higher levels of SOC, TSN, readily oxidizable carbon (ROC) and water stable aggregates at those depths, suggesting strong linkages between the soil food webs maintained in perennial fields and enhanced soil quality. Additionally, perennial fields maintained nematode communities with 25–37% greater taxal richness ($p < 0.001$; $n = 5$) reflecting more diverse soil food webs.

Additional information on soil food web characteristics may be inferred by grouping nematode taxa according to their functions and rating populations using standardized indices such as the structure index and basal index (Ferris et al., 2001). A high structure index value indicates nematode communities rich in omnivores and predators—trophic groups associated with low disturbance environments. A high basal index indicates nematode communities associated with impoverished nutrient status and high stress environments.

In the long-term study, nematode communities in perennial fields had higher structure and lower basal index ratings than annual fields (Fig. 5a) indicating healthier soil environments with large, stable resource bases (Khan and Kim, 2007; Sánchez-Moreno and Ferris, 2007). Additionally, 3 yrs after conversion from perennial grass, annual no-tillage conversion study plots supported nematode communities with reduced soil food web structure ratings and increased basal index ratings in the surface 1 m (Fig. 5b). Although some soil properties such as SOC change slowly in response to management changes, nematode communities appear to be responding rapidly to changes in root structure and/or aboveground inputs due to conversion to annual cropping. DuPont et al. (2010) also report significantly reduced levels of ROC in the surface 40 cm of the converted no-till plots, indicating that soil carbon pools are also responding to management changes.

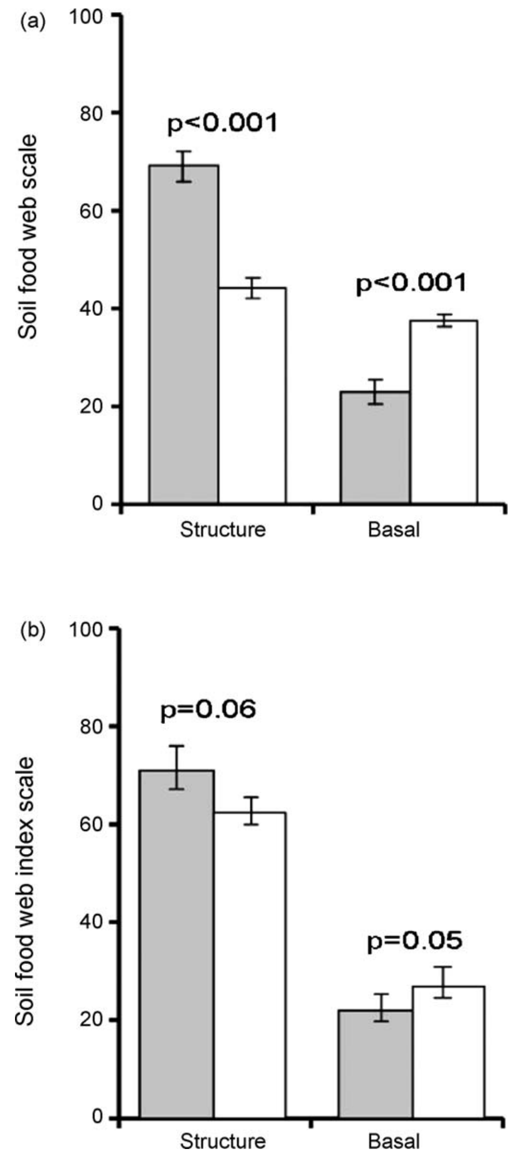

Fig. 5. Nematode community structure indices for perennial grass (solid bars) and annual crop (open bars) fields to a depth of 1 m in (a) long-term study sites ($n = 5$) and (b) conversion study plots ($n = 3$). Error bars indicate standard errors of means.

We used changes in soil moisture to a depth of 1 m to indicate water use over the growing season. Reductions in soil moisture in the 0.4–0.8 m soil depth were measured during the summer growing season in perennial conversion study plots (Fig. 6). These reductions likely reflect the greater water use in perennial grasslands compared to the annual no-tillage wheat crop. Additionally, greater water uptake over the growing

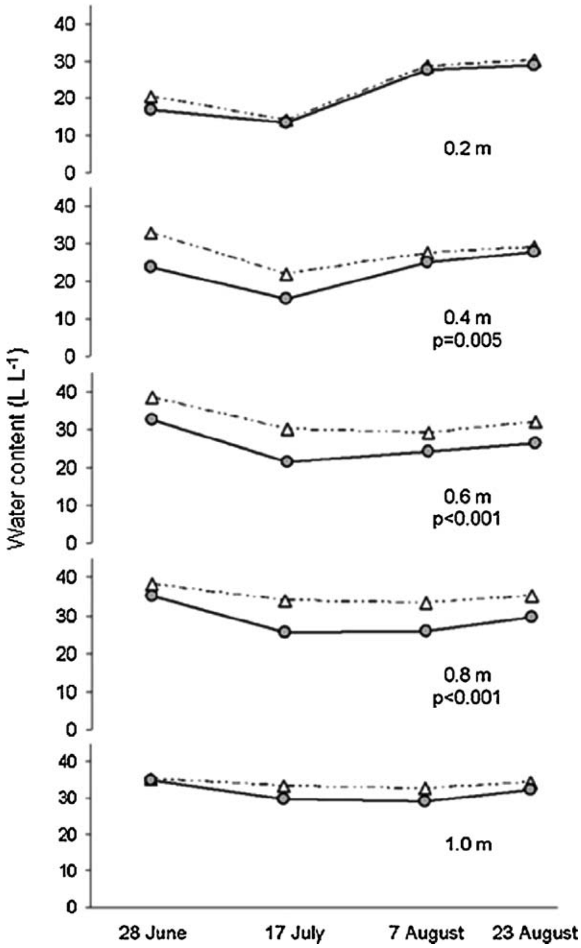

Fig. 6. Volumetric water content of perennial grass (shaded circles) and annual wheat (open triangles) plots. No differences were measured at any depth during the rest of the year.

season has been linked to reductions in nitrate-nitrogen losses to the surrounding environment (Randall et al., 1997; Huggins et al., 2001). At the end of the growing season the NO_3-N concentrations below root zones (3.0–3.2 m) were 24% lower ($p = 0.0459$; $n = 3$) in perennial plots than in annual no-tillage plots. Even with the use of modern no-tillage practices, annual crop cover decreased ROC stocks, negatively impacted soil food webs (DuPont et al., 2010) and resulted in greater losses of N below rooting zones.

3.2. Watershed study

The conversion of perennial grasslands to annual crop production in the Upper Midwest portion of the US has been linked to loss of nitrogen at the field (Huggins et al., 2001) and watershed (Turner and Rabalais, 2003) scales. We used 5-yr averaged historical water quality and land use data from eight watersheds encompassing our sites in 1906–1912, 1974–1978 and 1993–1997 (Fig. 1a) to assess the effect of annual croplands on regional riverine NO_3-N concentrations (Table 4). Taking into account the effects of sampling year and human and cattle population densities, the fraction of watershed cropland in annual crops significantly influences riverine NO_3-N concentrations ($r^2 = 0.72$; $p < 0.001$; $n = 24$). For example, for average human and cattle population densities across the watersheds in 1997, a plausible increase in the percent of watershed cropland in annual crops from 10 to 50% results in a predicted increase in NO_3-N concentrations from 0.35 to 1.85 ppm.

Crop and soil scientists reported the loss of soil N within the first decades following widespread conversion of the region's native grasslands to annual cropland and the resulting impacts on crop productivity (Swanson, 1915; Throckmorton and Duley, 1932; Hide and Metzger, 1939). Farmers enjoyed relatively high crop yields in the first few years after grasslands were ploughed out but yields quickly fell by 30% or more despite introductions of improved cultivars (Throckmorton and Duley, 1932). Yields began to significantly increase again in the late 1950s as use of nitrogen fertilizers became more widespread. Increased crop yields are desirable but greater applications of nitrogen typically result in a greater portion of the nitrogen applied being lost to the environment (Cassman et al., 2003). These losses result in higher input costs and energy requirements for production, impaired water quality, generation of greenhouse gas emissions, decreased biodiversity, and reduced soil quality (Galloway and Cowling, 2002; Cassman et al., 2003).

4. Conclusions

We used a suite of ecosystem components to evaluate the ability of perennial grass and annual wheat production systems to sustainably provide harvests over many decades (Fig. 7). Despite the lack of mineral fertilizer applications, the aboveground harvests of perennial fields yielded similar levels of N compared to those of conventional high-input wheat fields and at only 8% of the in-field energy costs. Their 75-yr cumulative N yield per ha was approximately 23% greater than that from the region's wheat fields. In terms of aboveground food webs, perennial fields harboured greater richness and/or biovolumes of insect pollinators, herbivores and detritivores. Belowground, perennial grass fields maintained 4 Mg ha^{-1} more root C, 43 Mg ha^{-1} more SOC and 4 Mg ha^{-1} more TSN than annual crop fields in the surface 1 m. Belowground food webs in perennial fields were also more highly structured and less stressed than those in annual wheat fields, even those under modern no-tillage practices. At the watershed scale, increased annual crop cover was correlated with higher riverine nitrate-nitrogen (NO_3-N) levels.

The yields harvested from the perennial grasslands reported herein could likely be substantially increased with more inputs (Schmer et al., 2008) or through advances in plant breeding (DeHaan et al., 2005). Yield increases, however, should be weighed

Table 4
Statistical output of the multiple regression model used to determine the influence of annual crop cover and human and cattle population densities on nitrate-nitrogen concentrations in eight watersheds (Fig. 1a).

	Value	Standard error	t value	Pr(>|t|)
Intercept	−0.153	0.300	−0.664	0.515
Annual cropland	4.198	1.533	2.739	0.013
Cattle population	−37.573	6.510	−5.771	<0.001
Human population	17.389	7.468	2.328	0.031
Year	0.016	0.004	3.765	0.001

The resulting model had a p-value <0.001.

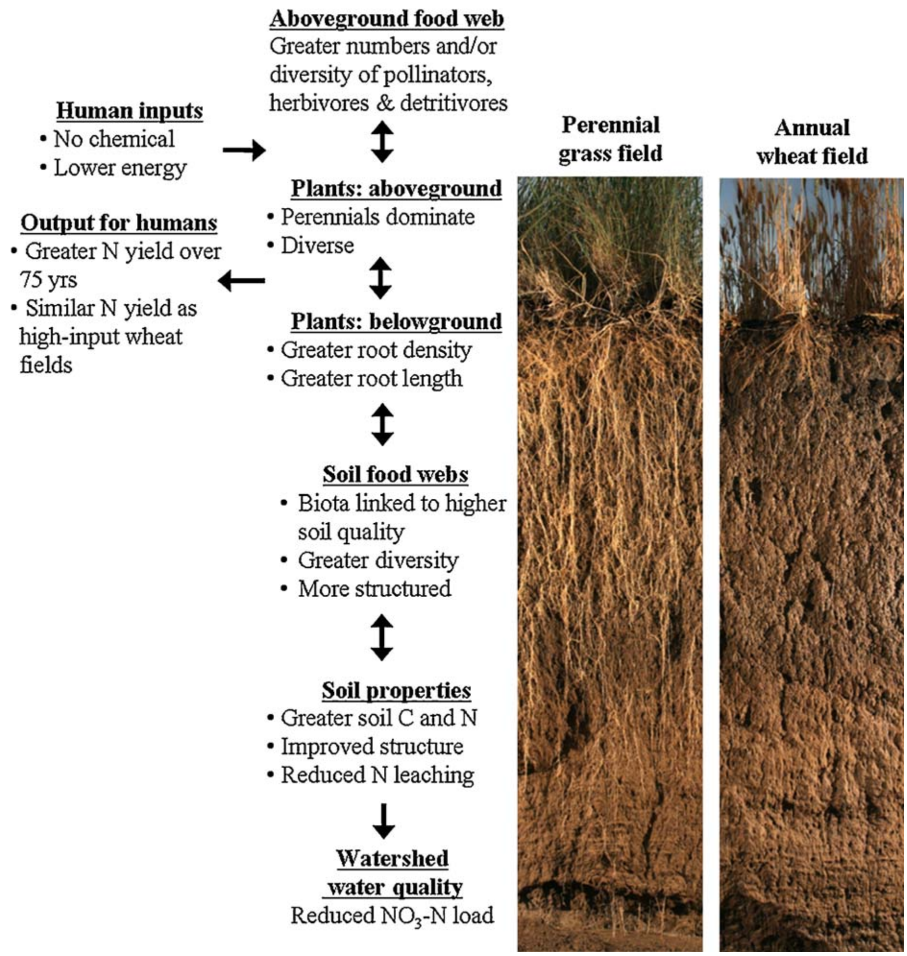

Fig. 7. Ecosystem attributes of harvested perennial grass fields (on left) compared to annual wheat fields.

against any negative impacts resulting from changes in management or plant community composition on ecosystem functions and soil and water quality.

Annual crops occupy over three quarters of harvested global crop area with our primary food crops—cereals, oil seeds, and pulses—covering 68% (Monfreda et al., 2008). Limited primarily to production of livestock fodder, perennial grass crops, even with increased yields, have little current potential to significantly expand onto those areas. Until recently, expanding the use of other perennial crops to provide the wide range of basic agricultural products primarily provided by annual crops was impractical or technically impossible. Achieving this transition is now more feasible because of advances in plant breeding, such as embryo rescue used in developing perennial grain crops (DeHaan et al., 2005; Cox et al., 2006; Glover et al., 2007), and innovations in post-harvest processing, such as bio-based production of chemicals, materials and fuels (Regauskas et al., 2006; Tilman et al., 2006; Nash, 2007; Schmer et al., 2008).

If efforts, such as those included in the Green Lands Blue Waters Initiative (2008), to develop new, economically competitive perennial crops and post-harvest processing technologies capable of utilizing more perennial crops prove successful, then large areas of land currently being degraded or at high risk of degradation under annual crop production could be farmed more sustainably. Given the time required to make significant changes in agricultural production, the extent to which perennial crops are featured on farms 20 yrs hence largely depends on current decisions made by agricultural scientists and policymakers.

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