

High Biomass Removal Limits Carbon Sequestration Potential of Mature Temperate Pastures

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Decades of plowing have depleted organic C stocks in many agricultural soils. Conversion of plowed fields to pasture has the potential to reverse this process, recapturing organic matter that was lost under more intensive cropping systems. Temperate pastures in the northeast USA are highly productive and could act as significant C sinks. However, such pastures have relatively high biomass removal as hay or through consumption by grazing animals. In addition, the ability to sequester C decreases over time as previously depleted stocks are replenished and the soil returns to equilibrium conditions. The objective of this research was to use eddy covariance systems to quantify CO_2 fluxes over two fields in central Pennsylvania that had been managed as pastures for at least 35 yr. Net ecosystem exchange measurements averaged over 8 site-years suggested that the pastures were acting as small net C sinks of $19 \text{ g C m}^{-2} \text{ yr}^{-1}$ (positive values indicate uptake). However, when biomass removal and manure deposition were included to calculate net biome productivity, the pastures were a net source of $-81 \text{ g C m}^{-2} \text{ yr}^{-1}$ (negative values indicate loss to the atmosphere). Manure generated from the hay that was consumed off site averaged $18 \text{ g C m}^{-2} \text{ yr}^{-1}$. Returning that manure to the pastures would have only partially replenished the lost C, and the pastures would have remained net C sources. Heavy use of the biomass produced on these mature pastures prevented them from acting as C sinks.

DECADES of plowing have depleted organic C stocks in many agricultural soils. It has been estimated that most agricultural soils in the Midwestern USA, for example, have lost 30 to 50% of their original C pool (Lal, 2002). Conversion of plowed fields to pasture has the potential to reverse this process, recapturing organic matter that was lost under more intensive cropping systems (Schnabel et al., 2001; Soussana et al., 2004). This conversion could result in an average C storage over 50 yr of $50 \text{ to } 100 \text{ g C m}^{-2} \text{ yr}^{-1}$ (IPCC, 2000). However, theory suggests that the ability of soils to sequester C decreases over time as previously depleted stocks are replenished and the soil returns to equilibrium conditions (Smith, 2004). The time it takes for soils to return to equilibrium is highly variable but may be as long as 100 yr in temperate locations. The relationship between pasture age and C sequestration is not always straightforward. When comparing C fluxes at nine European sites, Soussana et al. (2007) found that permanent semi-natural grasslands were large sinks, whereas newly sown grass-clover mixtures were as likely as not to experience a net loss of C. Kucharik (2007), on the other hand, found that the annual C sequestration rate declined as prairie age increased from 4 to 5 yr at the time of sampling to 11 to 16 yr.

Temperate pastures in the northeast USA are highly productive and could act as significant C sinks. Follett et al. (2001) estimated that the 18 million ha of pastureland in the USA could sequester an additional $10 \text{ to } 130 \text{ g C m}^{-2} \text{ yr}^{-1}$ through improved management practices. However, temperate pastures experience frequent defoliation and have relatively high assimilate partitioning to shoots, the majority of which is removed as hay or consumed by grazing animals. The pasture C balance, therefore, is a function not only of net ecosystem C exchange (NEE), which integrates plant photosynthetic uptake and ecosystem respiration, but also of net biome productivity (NBP), which includes losses through processes such as fire or export of harvested biomass and inputs from manure deposition or other C sources (Ammann et al., 2007). In highly disturbed systems, NBP can be near zero or negative even when NEE is positive (Suyker et al., 2003; Owensby et al., 2006).

The purpose of the current study was to determine NEE and NBP for two mature, grazed pastures in the humid, temperate region of the northeastern USA. These pastures had been in perennial vegetation for approximately 35 yr at the beginning of the experiment and were routinely grazed or cut for hay three to four times per year. Thus, their age and management history made it questionable as to whether these

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Abbreviations: NEE, net ecosystem exchange; NBP, net biome productivity.

pastures were acting as C sinks or if they had reached an equilibrium condition with balanced annual C inputs and outputs.

Materials and Methods

The study was conducted on two pastures at the Pennsylvania State University Haller Research Farm located about 10 km north-east of State College, Pennsylvania (40.9°N; 77.8°W). Soil type was a Hublersburg silt loam (Typic Hapludault) with 3 to 8% slopes. The first eddy covariance system was installed in May 2002 on a grass-dominated permanent pasture that had been traditionally cut once in the spring for hay and then rotationally grazed three to four times per year by beef cattle. The second system, installed in January 2003, was on an adjacent, alfalfa-dominated pasture typically managed for hay production during spring and summer and then grazed in the fall. Both locations had been sown to perennial forage species since the university purchased the farm in 1968. The grass-based pasture was last reseeded in 1982 and was dominated by a mixture of cool-season grasses, including orchardgrass (*Dactylis glomerata* L.), tall fescue (*Festuca arundinacea* Schreb.), and Kentucky bluegrass (*Poa pratensis* L.). Other common species included smooth brome grass (*Bromus inermis* Leyss.), dandelion (*Taraxacum officinale* L.), and alfalfa (*medicago sativa* L.). The alfalfa-based pasture was planted as an alfalfa monoculture in 1995. Intermixed with the alfalfa when CO₂ flux monitoring began in 2003 were patches of orchardgrass, smooth brome grass, dandelion, Kentucky bluegrass, and tall fescue. The proportion of alfalfa decreased from about 50 to 75% of plant cover in 2003 to 5% in 2006, possibly because of wet conditions in 2003 and 2004. By 2006, the predominant species in the alfalfa pasture were reed canarygrass (*Phalaris arundinacea* L.) and orchardgrass.

Pastures were harvested three to four times per year between mid-May and mid-November. Management decisions were controlled by the Penn State University Dairy and Animal Science Department and varied from year to year based on pasture growth, weather constraints, equipment availability, and demands for the cattle by other research projects. The grass-based pasture was cut once for hay in May 2003, with all subsequent biomass removal by grazing. The alfalfa-based pasture was cut for hay once or twice in the spring and early summer and was grazed one to three times in the late summer and autumn. Pastures were subdivided into approximately 0.5-ha paddocks, and each paddock was typically grazed for 3 to 4 d by 10 to 25 cows or cow/calf pairs depending on the amount of available forage and cows. The grass-based pasture received N fertilizer as urea twice each year at rates of 56 kg N ha⁻¹ in April and 34 or 45 kg N ha⁻¹ in August, except in 2006 when the spring and late-summer rates were 67 and 22 kg N ha⁻¹, respectively. The alfalfa-based pasture was not fertilized until after the alfalfa had essentially disappeared and the pasture had become dominated by cool-season grasses. It then received 56 kg N ha⁻¹ in April 2005, 34 kg N ha⁻¹ in April 2006, and 22 kg N ha⁻¹ in September 2006. No attempt was made to quantify the amount of N fixed by the alfalfa.

Pasture-scale CO₂ fluxes were quantified using a Campbell Scientific (Logan, UT) eddy covariance CO₂ flux system featuring a LI-7500 open path CO₂/H₂O analyzer and CSAT3 3-D sonic an-

emometer (Campbell Scientific Inc., Logan, UT). This system uses micrometeorological techniques to monitor biosphere-atmosphere exchanges of CO₂ by correlating fluctuations in vertical wind velocity with CO₂ density (Dugas et al., 1991). Data were collected continuously at 10 Hz and averaged over 20-min intervals. The open-path CO₂/H₂O analyzer and CSAT3 3-D sonic anemometer were placed 1.75 m above the soil surface in the center of 7-ha (grass) and 9-ha (alfalfa) pastures, providing >200 m fetch in the direction of the prevailing winds. Neighboring fields also contained cool-season grass pastures, so that confounding features such as roads, other vegetation types, and farm buildings were all >200 m from the eddy covariance systems. Coordinate rotation, frequency response corrections (Moore, 1986), corrections for density effects due to heat and water vapor transfer (Webb et al., 1980), and corrections for internal and external heating of the LI-7500 (Burba et al., 2006) were applied to the raw CO₂ flux data. This report focuses on CO₂ fluxes from 1 Jan. 2003 through 31 Dec. 2006. The ecological sign convention is used throughout this report, where negative fluxes indicate CO₂ loss to the atmosphere and positive fluxes indicate CO₂ uptake into plants and soil.

Frequent gaps in eddy covariance data resulted whenever rain-water or dew coated the LI-7500 and CSAT3 sensors. Flux data also became unreliable when winds were calm and friction velocity decreased below about 0.12 m s⁻¹. Low friction velocity generally occurred at night and during early morning hours. Approximately 50% of the data typically need to be discarded because of the frequent rainfall (about 1000 mm yr⁻¹) and low wind velocity characteristic of this study site. Gap-filling procedures were used to replace spurious and missing values. In a few cases, when three or fewer consecutive 20-min values were missing, gaps were filled by interpolating between valid data points. Most nighttime missing data were estimated by regressing nighttime NEE against soil temperature (Xu and Baldocchi, 2004). Nighttime NEE vs. soil temperature equations were used to estimate all missing nighttime NEE values and daytime NEE during wintertime whenever pastures were covered with snow or when air temperature was <0°C. When there was no snow cover and air temperatures were >0°C, daytime missing values were estimated from light response curves derived from daytime NEE regressed against photosynthetically active radiation.

The exponential relationship $NEE = ae^{bT}$, where a is ecosystem respiration rate at 0°C and b represents the sensitivity of ecosystem respiration to temperature (T), was used to describe the response of nighttime NEE to temperature. The parameter “ a ” provides a baseline estimate of NEE and is related to inherent plant and soil properties that affect respiration, such as size of the active soil C pool, litter and manure inputs, and above- and belowground plant biomass. The parameter “ b ” was used to calculate Q_{10} values based on the equation $Q_{10} = e^{10b}$.

Ancillary data were collected at 20-min intervals at each site and included air temperature and relative humidity (HMP45C temperature and RH probe; Vaisala, Woburn, MA), net solar radiation (Q7.1 net radiometer; REBS, Seattle, WA), photosynthetically active radiation (190SZ quantum sensor; Li-Cor, Lincoln, NE), soil temperature at a depth of 3 cm (model 107 soil temperature probe; Campbell Scientific), soil moisture at 5 and 30 cm depths

(model CS616 water content reflectometer; Campbell Scientific), and rainfall (TE525 tipping bucket rain gauge; Texas Electronics, Dallas, TX). Data were collected continuously, except for brief interruptions, since eddy covariance systems were installed at the grass site in May 2002 and at the alfalfa site in January 2003, with the exception that soil moisture data are missing from 2003. Aboveground biomass was determined monthly by clipping five 0.1-m² transects per pasture to the soil surface. Plant materials were separated by functional groups (grasses and legumes) into live and dead leaves and stems. Weekly estimates of standing biomass were also made using a rising plate meter that had been calibrated against clipped data (Sanderson et al., 2001). Plate meter readings from the weeks immediately before and after harvests were used to estimate biomass removal. Snow cover prevented collection of biomass samples in February 2004 and December 2005. Root biomass was determined by collecting 20 soil cores per pasture to a depth of 60 cm in September 2003 and 2006 and in March, May, July, September, and November 2004 and 2005. Cores were divided into 0- to 7.5-, 7.5- to 15-, 15- to 30-, and 30- to 60-cm depths, and roots were washed free of soil, dried, and weighed.

In constructing C budgets for each pasture, plant biomass was assumed to contain 40% C. All biomass removed as hay was permanently lost from the pasture because manure generated from on-farm feeding of the hay was not returned to the monitored pastures. In theory, CO₂ exchange by grazing animals could be directly monitored by the eddy covariance system, eliminating the need for adjustments for removal of grazed biomass or for manure deposition. In practice, however, the short duration, high stocking rate, and close proximity of cattle to the eddy covariance towers resulted in extremely erratic and variable flux data. Because of a lack of confidence in the eddy covariance data during grazing, data were discarded when the presence of cattle could be detected in the eddy covariance data and NEE was determined with gap-filling procedures. Harvest data from haying or grazing were used to calculate biomass removal. When pastures were grazed, 37% of the consumed biomass was considered to have been returned to the pasture as manure. Manure deposition rate was based on digestibility results from a nearby study using similar forage species and grazing management (Soder et al., 2006).

Results

The first 2 yr of the study (2003 and 2004) had greater-than-average precipitation and below-average to average temperature (Table 1). Water stress was not a significant factor in either year. Drought conditions existed during the summers of 2005 and 2006. In 2005, volumetric soil moisture content at 30 cm decreased to below 0.10 cm³ cm⁻³ by the end of June and remained low until mid-October (Fig. 1). Occasional precipitation during the summer of 2005 would temporarily wet the upper 5 cm of the soil profile but was never sufficient to appreciably increase water content at the 30-cm depth. In 2006, soil moisture stress also occurred during much of the summer, although rainfall in June and in September provided some relief from the drought. Mean temperatures in 2005 and 2006 were greater than the 30-yr average. However, mean daily maximum temperature was greater than the

Table 1. Annual precipitation and daily mean temperature (T_{mean}), daily minimum temperature (T_{min}), and daily maximum temperature (T_{max}) for 2003–2006 at the Penn State University, Haller Beef Research Farm in central Pennsylvania.

Year	Precipitation mm	T_{mean} °C	Mean T_{max} °C	Mean T_{min} °C
2003	1108	9.0	13.8	4.2
2004	1189	9.6	14.2	4.8
2005	738	9.9	14.8	4.8
2006	864	10.7	15.6	5.5
30-yr average	1014	9.7	15.0	4.5

30-yr average only in 2006, whereas daily minimum temperature was greater than average in 2004, 2005, and 2006.

Daily NEE was generally negative during the wintertime, which ran from about mid-November to the end of March (Fig. 2). Rapid uptake began in early April and continued until the first harvest, which ranged from early May to early July. After the first harvest, the pastures could be C sources or sinks on any given day during the remainder of the summer and early autumn, depending on a combination of environmental conditions and management practices. Drought stress, cloud cover, and recency of the last harvest contributed to pastures being C sources during the growing season. The first harvest each year occurred earlier in the grass than in the alfalfa pasture (mean, 23 d; range, 3–34 d). Averaged over the 4 yr, cumulative NEE at the time of the first harvest for

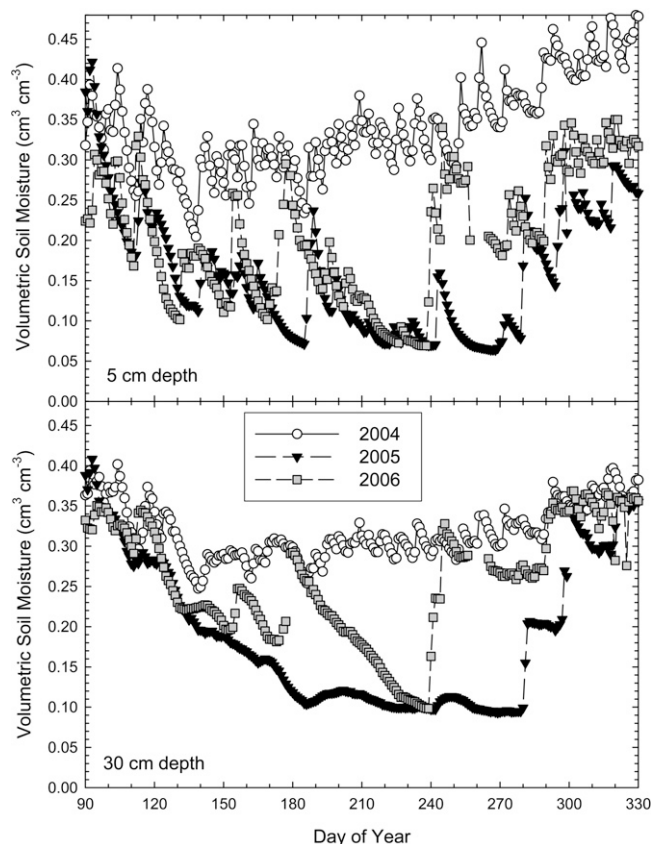


Fig. 1. Growing season volumetric soil water content at 5 and 30 cm depths for the grass-based pasture. Data from the alfalfa-based pasture were almost identical to the grass-based pasture. No data were available for 2003 because of instrument problems.

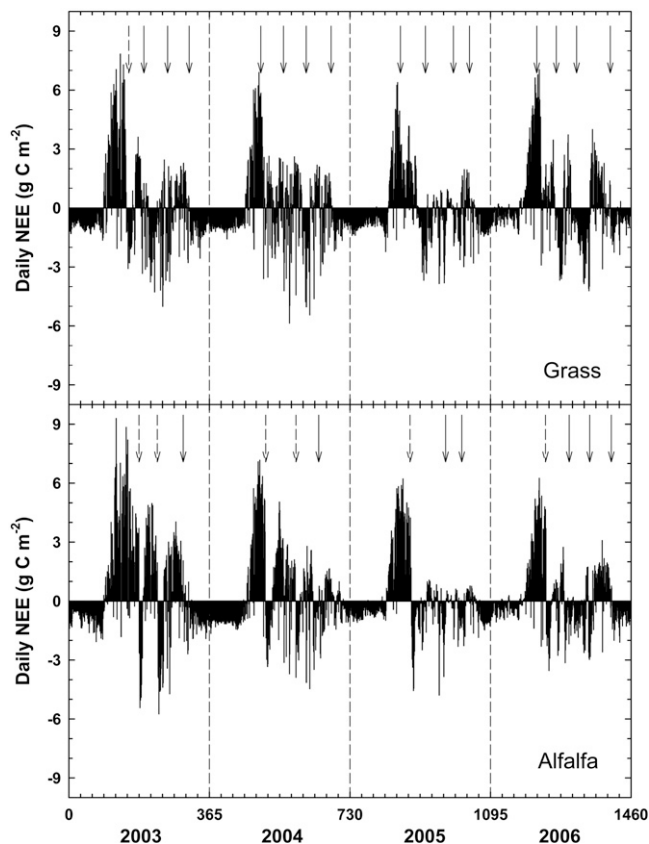


Fig. 2. Daily net ecosystem exchange (NEE) for grass- and alfalfa-based pastures from 2003 to 2006. The ecological sign convention is used, whereby positive values represent C uptake by the pastures and negative values represent C loss to the atmosphere. Solid arrows indicate grazing events, and dashed arrows identify dates when the pastures were cut for hay.

the grass pasture was $46 \pm 24 \text{ g C m}^{-2}$, compared with $115 \pm 23 \text{ g C m}^{-2}$ for the alfalfa pasture at its first harvest.

Average monthly daytime NEE was positive from April through November, with the greatest uptake occurring in April and May of each year (Fig. 3). Nighttime NEE was low

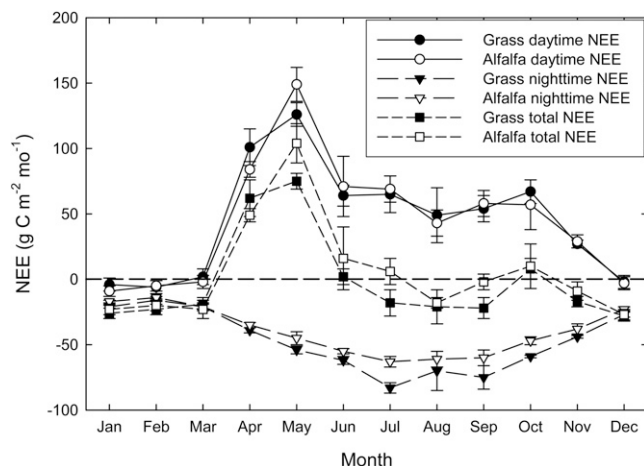


Fig. 3. Mean monthly daytime, nighttime, and total net ecosystem exchange (NEE) for grass- and alfalfa-based pastures averaged over 4 yr. Standard error bars show variability among years within each month.

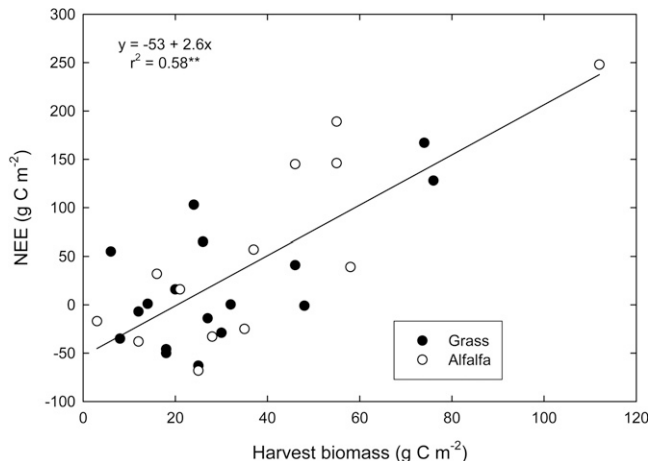


Fig. 4. Relationship between net ecosystem exchange (NEE) and harvested biomass for each growth period. Net ecosystem exchange for the first harvest of each year was calculated from 1 April rather than from the beginning of the year.

during the winter and increased from March through July before decreasing again in late summer and autumn. When summed on a monthly basis, April and May were the only months that consistently were important C sinks. Nighttime NEE was exponentially related to mean monthly air temperature (Fig. 5), with Q_{10} values ranging from 1.5 to 2.0 in the grass pasture and from 1.6 to 1.9 in the alfalfa pasture. When data from both pastures were combined, a significant linear relationship existed between annual precipitation and Q_{10} ($r = 0.88$; $P < 0.001$).

Summing fluxes for the entire year revealed that NEE was positive all 4 yr in the alfalfa-based pasture but was positive only in 2006 for the grass-based pasture (Table 2). Annual daytime NEE was identical for the two pastures, averaging 543 ± 49 and $544 \pm 53 \text{ g C m}^{-2} \text{ yr}^{-1}$ for the grass-based and alfalfa-based pastures, respectively (Table 3). However, nighttime NEE was 19% greater in the grass pasture, averaging $-571 \pm 30 \text{ g C m}^{-2} \text{ yr}^{-1}$ compared with $-480 \pm 27 \text{ g C m}^{-2} \text{ yr}^{-1}$ for the alfalfa pasture. When NBP was calculated, taking into account biomass removed by the harvests and manure added back by the grazing animals, both pastures and all 4 yr were net C sources (Table 2). Averaged across the 4 yr, the grass-based pasture lost $113 \pm 28 \text{ g C m}^{-2} \text{ yr}^{-1}$, and the alfalfa-based pasture lost $48 \pm 7 \text{ g C m}^{-2} \text{ yr}^{-1}$.

Approximately 70% of the harvest biomass from the alfalfa-based pasture was removed as hay, whereas only 15% was removed as hay from the grass-based pasture. If the manure produced from feeding the hay generated by the pastures had been returned, it would have added an additional 7 and 30 $\text{g C m}^{-2} \text{ yr}^{-1}$ to the grass- and alfalfa-based pastures, respectively. Lee et al. (2007) suggested that approximately 45% of C added as manure was respired to the atmosphere during the first year after application. If manure had been returned after feeding the hay, and taking the potential respiratory loss into account, NBP for the grass-based pasture would have been $-109 \text{ g C m}^{-2} \text{ yr}^{-1}$, whereas NBP for the alfalfa-based pasture would have been $-32 \text{ g C m}^{-2} \text{ yr}^{-1}$.

Discussion

The pasture systems in this study were relatively productive, with maximum daily NEE each year ranging from 6 to 9 g C m⁻². These rates were similar to those observed for native tallgrass prairie in Texas and Oklahoma (Dugas et al., 1999; Suyker and Verma, 2001) and greater than those for northern temperate mixed-grass prairie (Frank and Dugas, 2001; Flanagan et al., 2002) or southern mixed-grass prairie (Sims and Bradford, 2001). However, daily NEE was less than newly established bermudagrass in Texas (Dugas et al., 1999) or newly established temperate grasslands in Switzerland (Ammann et al., 2007).

Although daytime C uptake was often observed throughout the winter months (Skinner, 2007), daily NEE did not become positive until the first week of April each year. April and May were critical months for sequestering C (Fig. 3) because they were the only months that were substantial C sinks on a consistent basis. Although daytime NEE was relatively high from June through October, nighttime respiration was of equal or greater magnitude. Thus, the net balance was near zero for all months during the growing season other than April and May. Similar results were observed in a native grassland in western Canada where gross photosynthetic uptake occurred over 6 to 7 mo, yet NEE was positive for only a 2-mo period in May and June (Flanagan et al., 2002). A mountain grassland in the Italian Alps was also found to be a C sink for only 2 mo of the year, during May and June (Gianelle et al., 2004). Ammann et al. (2007) compared C fluxes over 3 yr in newly established intensively and extensively managed grasslands in Switzerland. Their study was conducted on a site with similar annual temperature and precipitation to the current study. The extensive grassland in all 3 yr and the intensive grassland in a drought year showed little or no net C uptake after about the end of May, whereas the intensive grassland continued to accumulate C through the end of October in years of normal or greater precipitation. Averaged over 3 yr, NEE for the intensive field was of 467 g C m⁻² yr⁻¹, compared with 254 g C m⁻² yr⁻¹ for the extensive pasture. In comparison, mean NEE in this study was -27 g C m⁻² yr⁻¹ for the grass pasture and 65 g C m⁻² yr⁻¹ for the alfalfa pasture (Table 2).

Table 2. Carbon budgets for mature humid-temperate pastures. The ecological sign convention is used, whereby positive values indicate C accumulation by the pastures and negative values indicate loss to the atmosphere.

Harvest dates†	Grass-based pasture				Alfalfa-based pasture				
	NEE‡	Biomass removed	Manure returned	NBP§	Harvest dates	NEE	Biomass removed	Manure returned	NBP
g C m ⁻²									
2003									
149	88	-74	0	14	183	164	-112	0	52
197	-1	-48	18	-31	232	39	-58	0	-19
253	-63	-25	9	-79	299	16	-21	8	3
315	1	-14	5	-8	365	-64	0	0	-64
365	-55	0	0	-55					
Total	-29	-162	32	-159	Total	155	-191	8	-28
2004									
139	46	-76	28	-2	142	53	-55	0	-2
189	0	-32	12	-20	223	57	-37	0	20
249	-14	-27	10	-31	277	-25	-35	13	-47
325	-35	-8	3	-40	366	-23	0	0	-23
366	-37	0	0	-37					
Total	-41	-142	53	-130	Total	62	-127	13	-52
2005									
125	-21	-6	2	-25	159	136	-55	0	81
198	41	-46	17	12	245	-68	-25	9	-84
273	-46	-18	7	-57	292	-17	-3	1	-19
312	-7	-12	5	-14	365	-41	0	0	-41
365	-47	0	0	-47					
Total	-81	-83	31	-133	Total	9	-83	10	-63
2006									
121	73	-24	9	58	143	113	-46	0	67
163	65	-26	10	49	205	-33	-28	10	-51
215	-29	-30	11	-48	249	-38	-12	5	-45
269	-50	-18	7	-61	313	32	-16	6	22
317	16	-20	8	4	365	-41	0	0	-41
365	-32	0	0	-32					
Total	44	-118	44	-31	Total	33	-103	21	-49
Mean	-27	-126	40	-113		65	-126	13	-48
SE	26	17	5	28		32	24	3	7

† Harvest dates indicate the day of year that the pasture was cut for hay (0 manure returned) or the midpoint of the grazing period, which usually lasted 3–5 d. The last day of the year is included to show net ecosystem exchange from the last harvest through the end of the year. No harvest occurred on that day.

‡ Net ecosystem exchange.

§ Net biome productivity (NBP) = NEE – biomass removed + manure returned.

Annual NEE was positive for 5 of the 8 site-years, which was less frequent than the results of Gilmanov et al. (2007), who found that 15 of 19 European grassland sites were C sinks. The sites that were C sources in Europe were associated with organic rich soils, grazing, and heat stress. Soussana et al. (2007) monitored CO₂ fluxes on nine European grasslands over 2 yr and found that all site-years were net C sinks. In the current study, 1 of the 3 site-years with negative NEE was a drought year (the grass-based pasture in 2005), but the others occurred during years of greater than average precipitation, and there was no significant relationship between precipitation and NEE. Soussana et al. (2007) also found that climate drivers such as precipitation failed to be good predictors of among site variability in annual NEE.

Soil management practices that increase fertility and productivity often lead to increases in soil organic C (Schnabel et al.,

Table 3. Annual daytime and nighttime net ecosystem exchange (NEE) for grass- and alfalfa-based pastures in central Pennsylvania.

	Grass-based pasture		Alfalfa-based pasture	
	Daytime NEE	Nighttime NEE	Daytime NEE	Nighttime NEE
	g C m ⁻² yr ⁻¹			
2003	598	-627	664	-508
2004	547	-588	563	-502
2005	406	-487	408	-399
2006	623	-582	542	-511
Mean	543	-571	544	-480
SE	49	30	53	27

2001). In a modeling exercise, Soussana et al. (2004) suggested that 5-yr-old pastures fertilized at 150 kg N ha⁻¹ could act as CO₂ sinks, whereas pastures receiving no fertilizer would likely be CO₂ sources. The Swiss pastures monitored by Ammann et al. (2007) were highly productive, with average harvested biomass export of 340 g C m⁻² yr⁻¹, compared with average export from the grass-based and alfalfa-based pastures in this study of 126 g C m⁻² yr⁻¹. It is possible that increased soil fertility and increased productivity could have increased NEE in the current study. However, the alfalfa pasture had greater NEE than the grass pasture, whereas harvested biomass was identical for the two pastures. Thus, differences in NEE between pastures in this study could not be explained by

differences in productivity. In general, pastures in the current study had annual and seasonal NEE dynamics that were similar to extensively managed European and North American grasslands rather than to more highly fertilized, intensive grasslands. This was despite the 50 to 100 kg N ha⁻¹ applied most years to pastures in the current study. Net ecosystem exchange represents a very small difference between two large fluxes, making process-level determination of the controls over NEE difficult (Sacks et al., 2006). Relatively small changes in photosynthesis or respiration could cause a site to shift from being a net sink to net source. Further research into these processes could prove useful in elucidating the reasons for differences between northeastern USA and European pastures.

The best predictor of differences between pastures in annual NEE in this study was the amount of time that the pastures were allowed to grow before the first harvest was taken in the spring. On average, the first harvest of the alfalfa-based pasture occurred 23 d later than for the grass-based pasture. Cumulative NEE when the first harvest occurred for the alfalfa pasture was 69 g C m⁻² greater than for the grass pasture when it was first harvested. This was enough to explain 75% of the 92 g C m⁻² yr⁻¹ difference in NEE between pastures (Table 2). A significant relationship was also observed within each growth period between the amount of harvested forage and NEE during that period (Fig. 4). It seems that harvest timing was more important than harvest method (cutting vs. grazing) or species identity in determining differences in NEE between these pastures. Allowing pastures to grow as long as possible before the first harvest in the spring or increasing the interval between subsequent harvests could increase NEE and have positive effects on C sequestration. However, increased NEE could occur at the expense of forage quality, which decreases as plants mature.

Based on data from 15 European forest ecosystems, Valentini et al. (2000) concluded that ecosystem respiration rather than gross primary production was the main determinant of differences in NEE among sites. In the current study, the grass pasture had 19% greater nighttime NEE than the alfalfa pasture, suggesting that total ecosystem respiration was greater in the grass pasture. Daytime NEE represents the net balance between photosynthetic uptake and respiratory loss. The fact that daytime NEE was identical between pastures (Table 3) probably resulted from the compensating effects of greater photosynthesis and respiration in the grass compared with the alfalfa pasture.

Factors affecting plant canopy C status and carbohydrate supply to roots can have a greater effect on soil respiration than physical properties of the ecosystem, such as temperature (Craine et al., 1999). Baseline respiration rate (parameter "a") was greater in the grass than the alfalfa pasture in all years except 2003 (Fig. 5). At the beginning of the monitoring period, the active soil organic C pool in the top 5 cm of the grass pasture was 1.26 mg C g soil⁻¹, compared with 0.88 mg C g soil⁻¹ in the alfalfa pasture (C.J. Dell, personal communication). Averaged across years, the grass pasture also had slightly greater aboveground litter (15 vs. 12 g C m⁻²) and greater average root biomass (173 vs. 152 g C m⁻²) than the alfalfa pasture. All these factors probably contributed to the greater baseline respiration in the grass pasture. The greater baseline respiration could explain why the grass pasture had lower NEE than the

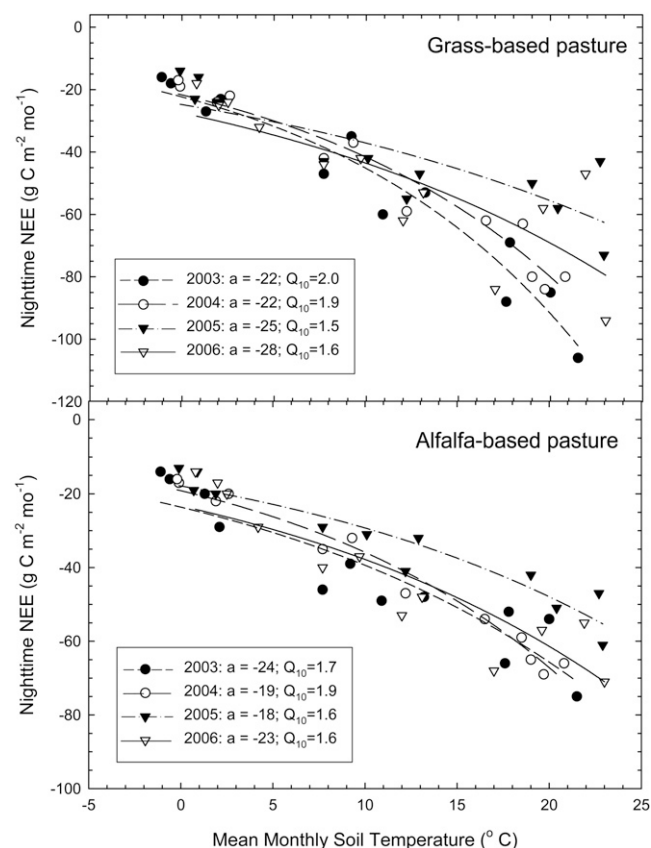


Fig. 5. Relationship between monthly nighttime net ecosystem exchange (NEE) and monthly soil temperature at a depth of 3 cm. Data were fit to an exponential equation of the form $NEE = ae^{bT}$, where a is ecosystem respiration rate at 0°C, and b represents the sensitivity of ecosystem respiration to temperature (T). Q_{10} values were calculated from b as follows: $Q_{10} = e^{10b}$ (Lee et al., 2007).

alfalfa pasture despite their similar productivity. Little difference in Q_{10} existed between the alfalfa and grass pastures (Fig. 5), indicating a similar responsiveness to temperature in the two pastures. A significant positive linear relationship existed between Q_{10} and total annual precipitation ($r = 0.92$; $P = 0.001$). Huxman et al. (2003) found that the Q_{10} for a high-elevation, subalpine forest was 1.9 in a relatively wet year and 1.5 in a relatively dry year. Suyker et al. (2004) also found that nighttime respiration and accompanying Q_{10} were significantly reduced during periods of moisture stress. In the current study, periods of moisture stress during 2005 and 2006 coincided with periods of high temperature. Thus, reduced respiration caused by drought would simultaneously reduce respiration at high temperatures and reduce Q_{10} .

Studies of several grasslands have found NBP to be near zero when all C sources and sinks were taken into account (Suyker and Verma, 2001; Gianelle et al., 2004; Owensby et al., 2006). However, a study of nine European grasslands showed an average NBP of $104 \pm 73 \text{ g C m}^{-2} \text{ yr}^{-1}$ (range, -266 to $462 \text{ g C m}^{-2} \text{ yr}^{-1}$) (Soussana et al., 2007). These sites represented mean annual temperatures between 6.3 and 10.5°C , mean annual precipitation ranging from 500 to $>1000 \text{ mm}$, and fertilizer applications ranging from 0 to $300 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. Thus, environmental conditions and management practices in the current study fell within the boundaries of the European study. However, NBP was negative for all 8 site-years in the current study, indicating that both pastures were net sources of C to the atmosphere (Table 2). It is possible that increasing productivity, perhaps through additional fertilizer applications, could have increased NEE. Allard et al. (2007) found that sink activity increased over time in an intensively managed, semi-natural grassland in France but declined after the first year when fertilizer was withheld from an extensively managed adjacent pasture. However, increased productivity in the current study would have also increased harvested biomass removal. It is not clear if NBP would have increased with increased productivity and, if so, if it would have increased enough to turn the pastures into net C sinks.

In the current study, the C content of harvested forage and returned manure was assumed to be 40% of total biomass. In a survey of 27 cool-season species, Poorter et al. (1997) found that leaf C content ranged from 38 to 47% (mean, 43%). Similarly, Griffin et al. (2005) found that C content of dairy manures ranged from 39 to 46% (mean, 43%). Substituting these values into the calculations of NBP in Table 2 gives mean biomass removal values of -121 to $-149 \text{ g C m}^{-2} \text{ yr}^{-1}$ for both pastures and mean manure returned values of 39 to 46 and 13 to $15 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the grass-based and alfalfa-based pastures, respectively. The resulting mean values for NBP would be -109 to $-149 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the grass-based pasture and -43 to $-69 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the alfalfa-based pasture.

Conclusions

Net ecosystem exchange measurements averaged over 8 site-years suggested that two mature temperate pastures were acting as net C sinks of only $19 \text{ g C m}^{-2} \text{ yr}^{-1}$. However, when biomass removal and manure deposition were included to calculate NBP, the pastures were a net source of $-81 \text{ g C m}^{-2} \text{ yr}^{-1}$. Two major

factors seemed to be responsible for differences between the grass- and alfalfa-based pastures. First, nighttime respiration was greater in the grass pasture, probably due to a larger active soil C pool and to greater C inputs from litter, roots, and manure. Second, delayed harvest of the alfalfa compared with the grass pasture contributed to greater annual NEE in the alfalfa pasture. Manure generated from the hay that was consumed off site averaged $18 \text{ g C m}^{-2} \text{ yr}^{-1}$. Returning that manure to the pastures would have only partially replenished the lost C, and the pastures would have remained net C sources. Heavy use of the biomass produced on these mature pastures prevented them from acting as C sinks.

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