Modeling Optimal Carbon Assimilation across Terrestrial Plant Communities at PCCI

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Abstract

With atmospheric carbon dioxide hovering around 400 ppm today, a lot is being done by scientists and policy-makers to determine the overall effect this will have on our planet as well as mitigation options. Green plants are the number one "fixer" of CO_2 and hold great potential to mitigate the effects of global climate change, storing excess carbon in biomass as well as soils. However, different plants and plant community types vary in their photosynthetic efficiency and rates of growth. Over the 2009 and 2013 growing seasons, leaf-level photosynthesis rates were measured as a function of light intensity for varying species in five different plant communities on the Pierce Cedar Creek Institute (PCCI) property in Hastings, MI. Using the light use efficiency curves for each plant species, an ecological model was created using leaf area index, canopy gap-light analysis and total species composition to estimate the total amount of carbon dioxide assimilated, the gross primary productivity (GPP), of the terrestrial plant communities at PCCI.

Key words: Global climate change; Photosynthesis; Carbon assimilation; GPP; PCCI; LUE

Introduction

Terrestrial ecosystems play a significant role in the stability of atmospheric carbon dioxide. The balance between gross primary productivity and heterotrophic respiration determines whether or not an ecosystem is actively absorbing carbon dioxide from the atmosphere or releasing it (Arnone et al. 2008). Utilizing solar energy, plants convert atmospheric carbon dioxide and soil-derived water into organic molecules. About 50% of the carbon photosynthesized is returned to the atmosphere through plant respiration over its lifetime; however, the remaining 50% is assimilated and used to build the essential parts of the plant, some of which will be sequestered as soil organic matter. Sequestered organic carbon is eventually locked into a relatively stable soil complex called humus which typically accounts for 60-80% of the total organic matter present in soil. Soil can be viewed as a potential reservoir for the excess carbon dioxide in the atmosphere (Hillel & Rosenzweig 2009).

Since the beginning of the Industrial Revolution in the late 1800s there has been a marked increase in atmospheric carbon dioxide, rising from 270 ppm to around 400 ppm today. This increase, coupled with the increase of other greenhouse gases, may have driven a 0.6 C˚ rise in average global temperature over recent decades. This trend is expected to continue (Hillel & Rosenzweig 2009). Under the Land Use, Land-Use Change and Forestry sector of the Kyoto Protocol, strong emphasis was placed on terrestrial carbon sinks and their potential for carbon dioxide uptake (Land Use, Land-Use Change 2013). Quantification of carbon uptake potential in various terrestrial biomes must be measured before mitigation efforts can be valued (Lal et al. 2003, Lal 2004, Lal 2010, Luo et al. 2001,).

Prairies composed primarily of C_4 monocots have been identified as potentially important carbon dioxide sinks (Kucharik et al. 2001). Additionally, forests have also been traditionally important carbon dioxide sinks, and are regarded as having the largest potential to act as sinks (DeLucia et al. 1999, Luo et al. 2001, Bauer 2001). Management of these plant community types offers potential to accumulate a significant quantity of carbon in soils. It is important to note that under varying environmental conditions, however, individual plant response can differ from community response (Bauer 2001).

Two methods have been traditionally used to characterize plant and community response and overall net primary productivity (NPP). The first method involves measuring the girth of the tree trunk at 1.37 m (4.5 feet) over subsequent years in correlation with species-specific equations (Heiligmann et al.). The second utilizes elaborate computer models that detect shapes and measure the shade or intensity of green on satellite photographs (Stagakis et al. 2007).

During the summers of 2009 and 2013, a third method for measuring individual plant and community productivity and landscape-level GPP was developed and evaluated on diverse natural ecosystems at Pierce Cedar Creek Institute (PCCI): restored prairie dominated by C_4 grasses, C_3 monocot field, shrubby field and early and late successional mixed deciduous forest. This method is based on empirical measurement of light use efficiency (LUE) curves, which report the photosynthetic rate of a specific plant across a range of light intensities under specified and controlled conditions. By coupling this photosynthesis data with averaged species composition of various plant communities and canopy light interactions, the quantity of carbon dioxide fixed per unit of land area were scaled up to the ecosystem level using the LUE curve relationships of each species.

The two goals of this study were to quantify total carbon dioxide assimilation for PCCI during the 2009 and 2013 growing seasons, and then to compare GPP of plant species and communities at PCCI. The underlying objectives needed to accomplish these goals are as follows: (1) to characterize and delineate plant communities, (2) to measure photosynthesis rates of plant species which make up a significant proportion of each plant community in order to determine GPP and (3) to analyze canopy light interactions of each plant community.

Methods and Materials

Research took place on the 267 ha (661 acre) property of Pierce Cedar Creek Institute (PCCI) in Hastings, MI between the months of April and August of 2009 and 2013. This location was ideal because it contained a wide variety of plant communities, including areas that were farmed within the past decade, having a significant potential for additional soil organic carbon (SOC) storage.

Plant communities were delineated across the PCCI property using maps, aerial photographs, soil maps and historical landscape-use information. They were then confirmed at the ground level by walking a grid across the property. This information was compiled into a GIS map of seven predominant plant communities: prairie, field, shrubby field, early successional forest, late successional forest, mixed swamp, and sedge/fen. The wetland communities were dropped in the 2013 study and emphasis was placed on the other five terrestrial communities.

Six to ten GPS points were assigned at random to each of the five plant communities. The GPS points served as replicates for the plant communities as well as locations at which to estimate percent species composition. Species composition and percent coverage were estimated at each point in four cardinal directions and this data was used to determine key species. Soil samples from the uppermost 20 cm were collected at the end of May and analyzed for soil organic carbon (SOC) content. Individual core samples were collected from four random spots within ten meters of each GPS point using a hand soil probe. Composite soil samples were sent to A&L Laboratories, Inc. (Fort Wayne, Indiana) for analysis.

Using a Licor 6400xt portable gas exchange meter, Light Use Efficiency (LUE) curves were generated for each of the selected species (Figure 1). This was done using the light curve program on the instrument, with light levels set at 2000, 1600, 1200, 800, 500, 250, 100, 50 and 0 µmol m^{-2} s^{-1} with CO_2 level held constant at 400 ppm. Photosynthetic rate was logged at each light level, producing points that make up a curve, illustrating for each species the optimum light level at which photosynthesis is most efficient and the quantity of carbon dioxide fixed across a wide range of potential light intensities.

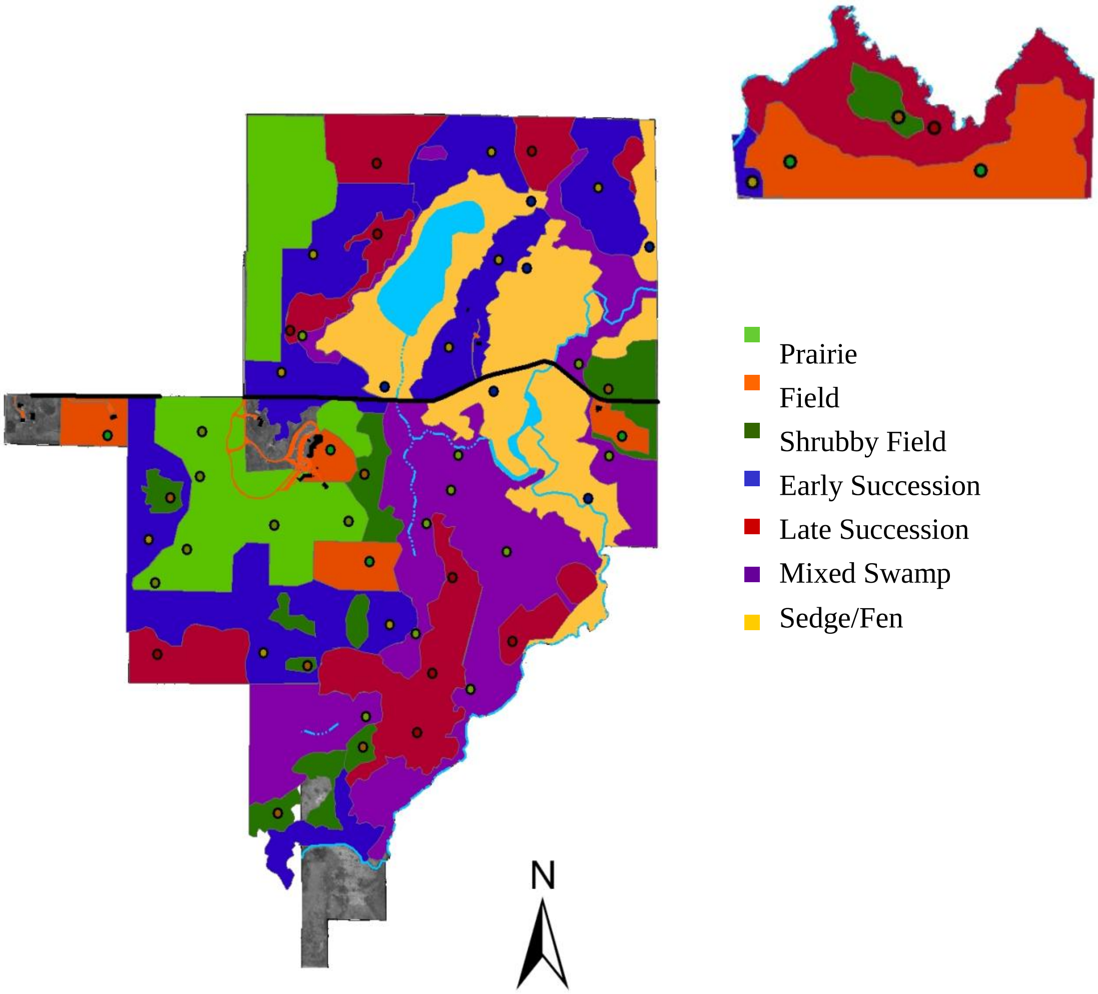

Figure 1 – This GIS layer was constructed by Andrew Wiersma and displays the seven plant communities delineated on PCCI's property during the 2009 study as well as the randomly selected GPS points, which represent the six to ten replicates of each plant community.

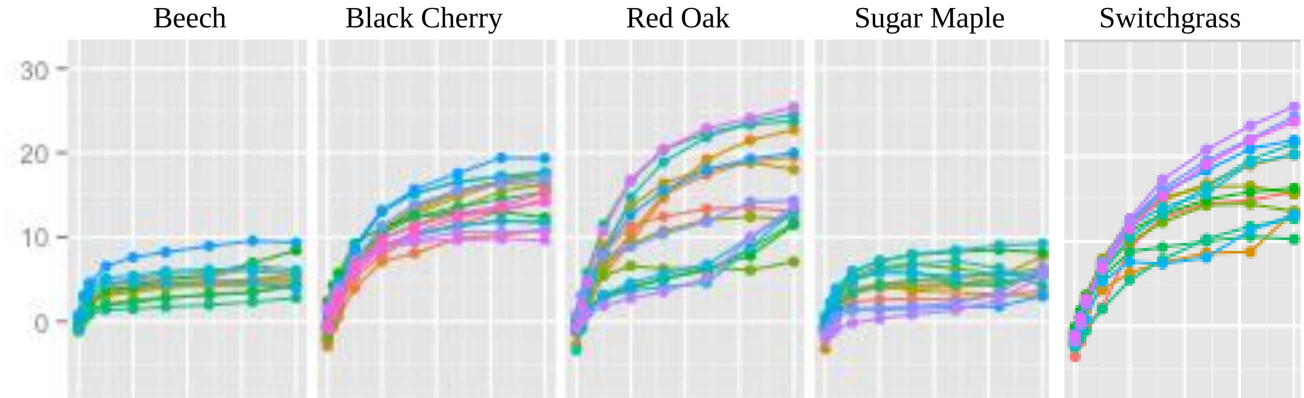

Figure 2 –LUE curves obtained for five species with the Licor 6400xt portable gas exchange meter using the light curve program, which logged photosynthesis rates at light levels of 2000, 1600, 1200, 800, 500, 250, 100, 50 and 0 µmolm^{-2}s^{-1} with CO_2 level held constant at 400 ppm.

A preliminary study determined that plants of the same species have statistically-similar LUE curves across plant communities so that species in more than one community, such as tall fescue, would only have to be measured once (Wiersma and Boersma, 2009). LUE was determined from measurements taken on three leaves of three different plants of each species at three different times throughout the growing season. Data was collected on sun-adapted leaves that could be reached with a six-foot tripod and which were large enough to fill the 2x3 cm IRGA (infrared gas analyzer) chamber. Once all LUE curves were obtained for each species, photosynthetic rates were averaged so that there was one curve for each species for three different times throughout the growing season. From these curves fourth order equations were generated for each species (with R^2 values of 0.98 or higher) to be used in final calculations (Table 1).

Table 1 –Fourth order equations generated from the LUE curves obtained for each species during the growing season.

Species	**x4**	**x3**	**x2**	**x**		**R^2**
Beech	-4.00E-12	2.00E-08	-3.00E-05	1.87E-02	3.20E-01	9.70E-01
Black cherry	-5.00E-12	3.00E-08	-5.00E-05	3.90E-02	-4.97E-01	1.00E+00
Red oak	-5.00E-12	2.00E-08	-4.00E-05	3.67E-02	-6.55E-01	1.00E+00
Sugar maple	-5.00E-12	2.00E-08	-4.00E-05	2.39E-02	-5.07E-01	9.80E-01
Goldenrod	-5.00E-12	2.00E-08	-4.00E-05	3.57E-02	-2.19E-01	1.00E+00
Autumn olive	-4.00E-12	2.00E-08	-3.00E-05	1.88E-02	-1.19E+00	1.00E+00
Tall fescue	-4.00E-12	2.00E-08	-4.00E-05	2.68E-02	-9.08E-01	9.90E-01
Switch grass	-4.00E-12	2.00E-08	-4.00E-05	3.92E-02	-1.41E+00	1.00E+00
Corn	-7.00E-13	9.00E-09	-3.00E-05	3.20E-02	-2.33E+00	1.00E+00
Black walnut	-6.00E-12	3.00E-08	-5.00E-05	4.08E-02	-5.12E-01	1.00E+00
American elm	-4.00E-12	2.00E-08	-3.00E-05	1.88E-02	-7.83E-01	9.80E-01

Digital photography was used to determine leaf area index (LAI) at each data point. Three photos were taken at random points within ten meters of each GPS point using a Nikon SLR camera equipped with a hemispherical lens. The camera was set on an automatic timer and placed on the forest floor pointing upward towards the canopy. The photos were then analyzed using Gap Light Analyzer (GLA) free-ware. The GLA application integrates a contrast image from the camera image to generate a single number estimating the number of leaf layers present at that spot in the canopy. The LAI values were then averaged for each plant community to be used in calculations.

A quantum light sensor was used to determine how much photosynthetic active radiation penetrated through the plant canopy at all data points. This was done by placing a LI-191 Line Quantum Sensor on the forest floor at four random spots within 10 meters of each GPS point. A total of four readings were taken at each spot and combined for an average to improve accuracy, as sunflecks can add variability to overall light intensity. All measurements were taken on clear, sunny days.

Quantum light measurements were also taken through three leaf layers for each species. This was done by first taking a reference with a LI-190 Quantum Sensor to see how much light was reaching it with no obstructions. Then measurements were taken after placing one, two and three leaves on top of the sensor subsequently, recording between each layer. The three leaves were taken from three different trees of each species, for a total of three replicates. Four readings were taken for each set of leaves and averaged. This helped to determine how much sunlight was reaching each leaf layer (as indicated by LAI) of each species. In 2009 the analysis of light penetration through leaf layers demonstrated that once the sunlight has filtered through the top canopy there was on average only 7% and 1% incidence of sunlight in the second and third leaf layer. Based on these results in 2009, only two leaf layers were included in the 2013 calculations of assimilated carbon by each plant community.

Finally, hourly solar radiation was obtained from the onsite weather station for the period between April 14 and August 25. This data was obtained from an online database through the Michigan State University Weather Station Network (MAWN) online. Because the data was collected hourly throughout this entire period it accounts for both night and day and for all weather conditions. Once the hourly solar radiation was catalogued into an Excel spreadsheet and the units converted from KJm^{-2} to $\mu molm^{-2}s^{-1}$ the data could be applied to each plant at each GPS point according to its LUE curve equation. The purpose of the spreadsheet calculations was to scale up from the units of photosynthesis, µg of carbon dioxide assimilated $m^{-2}s^{-1}$, to an estimate of the total carbon dioxide assimilated in metric tons by PCCI terrestrial green space area over the entire growing season. However, these calculations required that the relative contribution of each plant had to be determined for each GPS point. First, the LUE equation of the given plant was applied to 100% solar radiation in the first leaf layer. Second, the LUE equation was applied to the second leaf layer based on light penetration and LAI values for each plant community. Finally, the resulting figure had to be adjusted to the percent canopy coverage represented by that plant. Then the relative contributions of each plant could be summed to determine the µg of carbon dioxide assimilated m^{-2} at each GPS point. Once this value was determined for each GPS point and the six to ten replicates of each plant community averaged, the mean values could be multiplied by land area coverage on the PCCI property according to the plant community GIS layer constructed in 2009. To determine the metric tons of carbon dioxide assimilated by PCCI terrestrial green space area throughout the growing season, the units were converted and the relative contributions of each plant community were summed. Calculations were performed in Microsoft Excel and data was analyzed by analysis of variance (ANOVA) using *Statistix 9.1* software.

Results and Discussion

Our calculations showed that a total of 71 metric tons of carbon dioxide was assimilated by the terrestrial plant communities at PCCI between April 14 and August 25, 2013. The 2009 calculations estimated a total of 80 metric tons. The difference between the 2009 and 2013 estimations could be explained by climate differences, growing conditions during August 2009 were favorable in comparison with 2013, changes in canopy composition on the PCCI property (Table 2), and random error. Climate information obtained from the weather station at PCCI showed slightly higher mean temperatures in 2013 compared to 2009 with similar levels of precipitation (Enviro-weather 2011).

Table 2 – A comparison of climate conditions between the 2009 and 2013 growing seasons. The information was gathered from the MSU Weather Station Network.

Year	**2009**				**2013**			
	May	June	July	August	May	June	July	August
Ave Min Temp (C)	7.2	12.8	11.5	13.6	8.6	13.2	15.2	12.9
Ave Max Temp (C)	20.7	24.6	24.6	25.4	23.2	25.6	27.7	25.9
Mean Temp (C)	13.9	18.7	18.1	19.5	15.9	19.4	21.4	19.4
Total Precipitation (mm)	91	122	30	164	100	135	48	106

Though 2009 and 2013 demonstrated differences in productivity, in both years the prairie was observed as the plant community with the highest rate of carbon assimilation per unit area and the field community was observed as the lowest. Additionally, in both years early successional forest was observed to be a more productive community than late successional forest. As demonstrated in Figure 3, over the 2013 growing season the prairie community accounts for 22% of terrestrial land area, yet accounts for 30% of total carbon assimilated compared to the field community, which accounts for 12% of the land area and only 5% of the carbon assimilated. Similarly, early successional forest accounts for 36% of carbon assimilated while occupying only 30% of terrestrial land area and late successional forest accounts for only 21% of the carbon assimilated while occupying 27% of the land area.

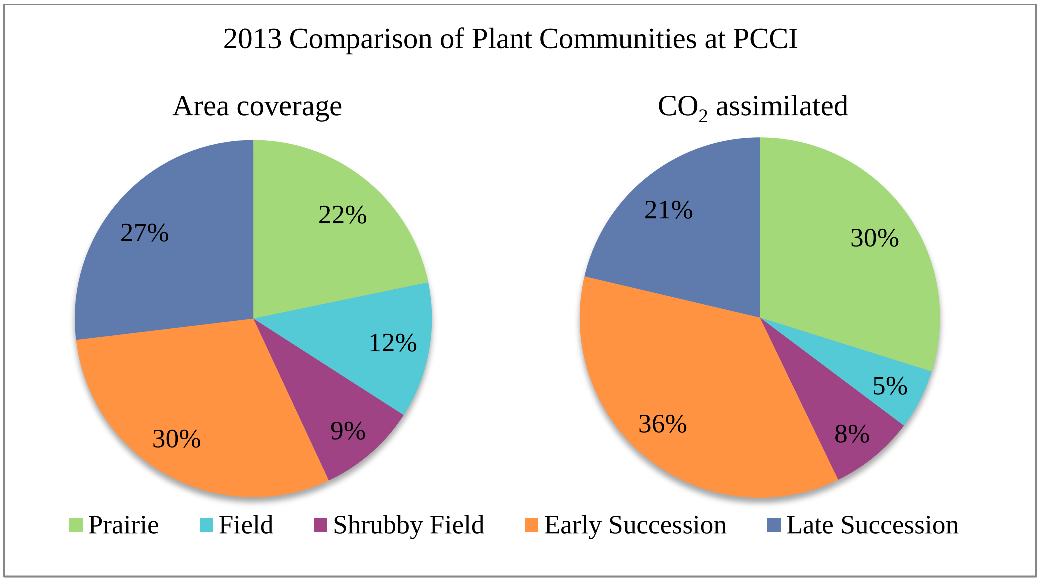

Figure 3 – A comparison of the land area coverage with the relative CO_2 assimilated during the 2013 growing season for each of the terrestrial plant communities at PCCI.

The difference in productivity per unit area among the plant communities, and between 2009 and 2013, can be explained at least in part by changes that occurred in canopy structure and composition. In 2009 the thirteen most abundant species in terrestrial plant communities included: oak (*Quercus* spp.), maple (*Acer saccharum*), black cherry (*Prunus serotina*), white ash (*Fraxinus americana*), beech (*Fagus grandifolia*), C_3 grasses and C_4 grasses (*Graminae*), goldenrod (*Solidago canadensis*), autumn olive (*Elaeagnus umbellata*) and elm (*Ulmus americana*). In 2013, white ash was not included as a key species as its presence in the canopy had been significantly diminished, due to the impact of emerald ash borer. Autumn olive presence in the canopy was also reduced due to Institute mitigation efforts. Additionally, black walnut and corn were added as key species demonstrating that there were indeed some changes in canopy composition among the years. The average canopy composition of each plant community in 2013 is displayed in Table 3.

Table 3 – The predominant species and percent canopy cover in each plant community for 2013.

	Autumn Olive	**Elm**	**Beech**	**Black Cherry**	**Black Walnut**	**Corn**	**Goldenrod**	**Maple**	**Oak**	**C4 Grasses**	**C3 Grasses**
Prairie							41%			57%	
Field					3%	33%	15%				48%
Shrubby Field	14%	4%		21%	14%		11%	9%	2%		21%
Early Successional Forest		5%		15%	24%			22%	24%		
Late Successional Forest		2%	20%		3%			32%	34%		

While many plant species were present in more than one community, each community showed distinct combinations and densities of plant species. Since photosynthetic rates vary among species, canopy composition is an important factor in the GPP of a community. Data obtained from the Licor 6400xt portable gas exchange meter allowed us to compare the photosynthetic rates of eleven predominant species of PCCI's terrestrial plant communities.

Though stomatal conductance was the same for all species across all light levels ($p<0.001$), when GPP rates were averaged across light levels there was a statistically significant difference between species ($p<0.001$). GPP rates also differed among different light levels when averaged across species ($p<0.001$). Our data also showed that the decline of photosynthetic rate between light levels varied significantly for each species, providing a uniquely-shaped LUE curve for each species ($p<0.001$). These findings support the idea that plants vary in their ability to perform photosynthesis and assimilate carbon because of species-specific differences in physiology as well as in responses to varying climate conditions, especially solar radiation levels. LUE curves best reflect the differences in photosynthesis across all light levels among species, however, comparing the maximum photosynthesis rate (P_{max}), or the rate of photosynthesis at the highest light level (2000 $\mu molm^{-2}s^{-1}$), is a useful means of assessing species differences. The maximum rates of the dominant species are recorded in Table 4.

Table 4 – The maximum photosynthesis rate of each species at the 2000 $\mu molm^{-2}s^{-1}$ light level.

Species	**P_{max} ($\mu CO_2m^{-2}s^{-1}$)**
Corn	20.54
Switch Grass (C4 grasses)	17.93
Oak	16.47
Goldenrod	15.81
Black Walnut	14.75
Black Cherry	14.71
Autumn Olive	10.37
Tall Fescue (C3 grasses)	9.08
Maple	5.64
American Elm	5.42
Beech	5.36

Canopy composition is not the only factor that influences the productivity of a plant community. The density of the canopy, reflected in the LAI, is also important in determining the rate of carbon assimilation per unit area (Table 5). When both the structure and foliar composition of a plant community is taken into account, the resulting carbon assimilation rate more accurately describes the GPP of that community than what may be implied by the photosynthesis rates of the species it includes. For instance, though corn dominated in several locations of the Field community and had the highest rate of photosynthesis, the mean LAI of the Old field replicates was the lowest of all plant communities. As a result, the naturally denser Prairie on PCCI's property proves more productive than the sparser Old field despite the fact that Corn has the highest rate of photosynthesis and accounts for 33% of the Old field community composition.

Table 5 – The mean Leaf Area Index (LAI) of each plant community and statistically significant categories among communities (communities with the same letter are not different).

Plant Community	LAI	Tukey HSD
Prairie	2.3	AB
Old Field	1.2	C
Shrubby Field	1.7	BC
Early Successional Forest	2.6	A
Late Successional Forest	3	A

The interplay between LAI and canopy composition observed on PCCI's property produced significant differences in GPP among the terrestrial plant communities. As shown in Figure 4, the Prairie and Young Forest communities possessed the highest GPP followed by the Shrubby Field and Old Forest communities. Old Field had the lowest GPP due primarily to low foliage density.

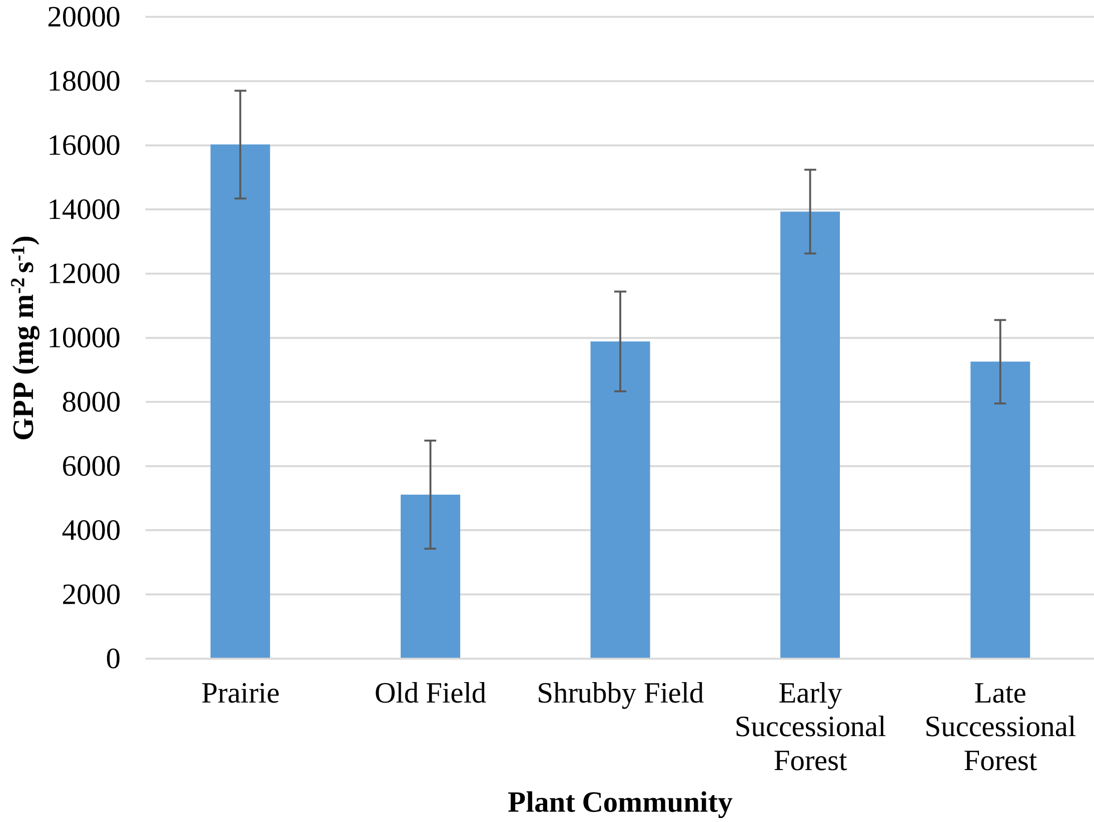

Figure 4 – Gross Primary Productivity, measured in mg of CO m^{-2} s^{-1}, of each plant community.

Because significant differences exist between terrestrial plant communities, certain land management practices could benefit the productivity of a property. Based on our results the greatest potential for improving the carbon assimilation rate of a piece of land in the PCCI area would be to restore old fields into prairies dominated by C_4 grasses and wildflowers. In addition, our results suggest that selective logging and thinning of late successional forests could increase the productivity of this community by allowing younger trees and early successional species to grow into the canopy. Such management strategies could increase a property's rate of carbon assimilation over a growing season; however, it is less clear how the temporary storage of carbon in plant tissue over the growing season impacts the more permanent storage of carbon in soils. The soil samples we collected did not show any statistically significant variability in SOC content among plant communities. They did show an overall low amount of SOC consistently across all plant communities (mean of 2.4%), which can be explained by the fact that PCCI land was previously used for agriculture, depleting the soils of their nutrient content. The low carbon content supports our idea that PCCI has great potential to store more carbon in their soils.

Conclusion

With growing concern over climate change, the potential for storing carbon through plants becomes increasingly important. An effective model for scaling up carbon assimilation measurements to plant communities and entire properties would better inform land management practices and also assist in the development of a carbon credit system that incentivizes preserving and restoring green space. Because our model includes canopy structure and composition as well as real-time measurements of photosynthesis it offers an effective method for assessing the potential for carbon storage at the landscape level using empirical data.

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