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Leaf Photosynthesis and Plant Competitive Success in a Mixed-grass Prairie: With Reference to Exotic Grasses Invasion

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Abstract

The widespread invasion of exotic cool-season grasses in mixed-grass rangeland is diminishing the hope of bringing back the natural native plant communities. However, ecophysiological mechanisms explaining the relative competitiveness of these invasive grasses over the native species generally are lacking. We used experimental data collected in south-central North Dakota, USA to address this issue. Photosynthetic potential was obtained from the net assimilation (A) vs. internal CO_2 (Ci) response curves from plants grown in a greenhouse. Plant success was defined as the average frequency measured over 25 years (1988 to 2012) on overflow range sites across five levels of grazing intensity. Also, estimated leaf area index of individual species under field conditions was used to indicate plant success. The correlation between photosynthetic potential based on A/Ci curves and plant frequency was negative. The correlation between leaf photosynthesis and plant success (defined as leaf area within a unit land area) was also negative, although statistically weak. These results suggest that the two cool-season grasses, *Poa pratensis* and *Bromus inermis*, do not rely on superior leaf-level photosynthesis for competitive success. Instead, some other traits, such as early and late-season growth, may be more important for them to gain dominance in the mixed-grass prairie. We propose that the negative photosynthesis-frequency relation as observed in this study results from a strong competition for limited soil nutrients in the mixed-grass prairie. It has implications for the stability and productivity of the grassland under various human disruptions influencing the soil nutrient status.

Keywords: *Bromus inermis*; Invasive species; Leaf area index; Photosynthetic potential; *Poa pratensis*; Principal component analysis; Rangeland management

Introduction

Worldwide, invasive plants pose profound impacts on plant communities and ecosystem function [1]. In the mixed-grass prairie of North America, the widespread invasion of exotic cool-season grasses, such as *Poa pratensis* L. and *Bromus inermis* Leyss., is diminishing the hope of bringing back the natural native plant communities [2-3]. A best management strategy for these rangelands, based on several plant community studies [4-6], is perhaps to utilize these cool-season exotics while reducing their cover and increasing diversity. However, knowledge of the ecophysiological mechanisms that explain the relative competitiveness of these cool-season invasive grasses over the native species generally is lacking [7].

Photosynthesis is the basis of plant growth and production. Although plant productivity is strongly associated with integrated seasonal photosynthetic activity [8], it is difficult to quantify seasonal photosynthesis simultaneously for many plant species. Leaf-level instantaneous photosynthesis is frequently measured [9-11], despite the difficulty of obtaining consistent results contrasting the native and invasive species [12,13]. Leaf-level photosynthesis was positively related to plant success in the C_4 grass-dominated tallgrass prairie [14]. Whether this similar broad comparison exists in the highly invaded mixed-grass rangelands has important management implications because cool-season exotic grasses have already dominated these rangelands both in terms of herbage production [15] and cover [4]. This paper compares leaf-level photosynthesis of 26 plant species co-occurring in the mixed-grass prairie near Streeter, N.D. USA. The highlight is on the correlations between photosynthetic potential and plant success, with special reference to exotic invasive grasses *Poa pratensis* and *Bromus inermis*.

Materials and Methods

Field site and plant frequency data collection

The field site is located at the Central Grasslands Research Extension Center – NDSU near Streeter, N.D. USA. The climate is of the continental type with January mean temperature of -17°C and August mean temperature of 20°C. Mean annual precipitation is 458 mm, 70 percent of which occurs from May to September. The vegetation is dominated by grasses, followed by forbs (20 percent aboveground production) and shrubs (two percent) [16]. The rangeland had not been plowed for at least 50 to 60 years. Starting in 1988, a long-term cattle grazing intensity study was initiated on a land area of 156 ha, which was subdivided into 12 equal-size pastures stocked at four levels of season-long grazing (light, moderate, heavy and extremely heavy grazing) with yearling beef cattle. The light treatment left 65 percent of forage produced in an "average year" remaining at the end of the grazing season, moderate treatment left 50 percent, heavy treatment left 35 percent, and extreme treatment left 20 percent [15]. Frequency of occurrence of all plant species was monitored each year since 1988 in fifty 25 cm×25 cm frames along a 50 m transect on each site. Species frequency was defined as the number of frames in which the

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species occurred divided by the total number of frames used [17]. Data collected from the overflow range site and all grazing intensities combined [15] were used in this study because plants growing on this range site presumably experienced less resource stress and thus the measured frequency would reflect the species' intrinsic characteristics.

Photosynthesis/intercellular CO_2 curves measured in greenhouse

Seeds of 12 species, both native and introduced, were collected during the summer and fall of 2011 on native prairies of the Central Grasslands Research Extension Center near Streeter, N.D. On 20 Apr 2012, seeds were sown in plastic pots (7.6 cm×7.6 cm×7.6 cm) in replicates of four, using a local prairie soil of the Towner-Barnes complex (black loamy fine sand) that was sifted before use. Root cuttings of two shrubs and transplants of 12 more species were planted in pots in May and June, 2012. Pots were placed in a greenhouse and watered as needed. The plant species measured were all C_3 species and included five grasses, one sedge, 18 forbs, and two shrubs (Table 1). The photosynthesis/intercellular CO_2 (A/Ci) curve measurements were made using a LI-COR 6400 Portable Photosynthesis System (LI-COR Bioscience, Lincoln, N.E. USA) from 7 Jul through 13 Aug 2012, with four replicates of each species. The chamber condition was set as: photosynthetic photon flux density (PPFD) 900 μmol $m^{-2}s^{-1}$; leaf temperature 28°C; relative humidity 26 to 29 mmol H_2O mol^{-1}; and flow rate 300 mol s^{-1}. The reference CO_2 was varied in 15 or 16 steps from 0 to 1500 ppm. The A/Ci curves were fitted to the FvCB model according to [18] and implemented through leafweb.ornl.gov. The A/Ci parameters were scaled to the standard values at 25°C and reported together with a global scale of datasets of A/Ci curves [19]. This paper provides additional analysis of this data set from North Dakota, focusing on the linkage between photosynthesis and plant competitive success.

The pots were overwintered by placing them in a shallow trench located on a sloping field on 8 Nov 2012. The tops of the pots were level with the soil surface, with soil around each tray of pots. They then were covered with an eight-inch thick layer of straw fastened down by a wire mesh. The pots were lifted on 5 May 2013, returned to the greenhouse and watered when needed. The photosynthesis survey of the major species was conducted from 11 Jun to 19 Jun 2013 under conditions similar to that for the A/Ci curve measurement survey in 2012. Leaf samples were collected on 25 June 2013 for total nitrogen content analysis. Also, specific leaf area was measured in order to convert leaf nitrogen content from the dry matter to leaf area basis.

Leaf photosynthetic rates measured under field conditions

Leaf photosynthetic rates for a wide range of plant species were measured on 13 days in 2008 (from 18 Jun to 18 Sep), 12 days in 2009 (1 Jun to 24 Sep) and eight days in 2010 (19 May to 21 Sep). The measurements were made within two 10 m×10 m exclosures located in one moderately grazed pasture and one extremely heavy grazing pasture. The vegetation within the exclosure was clipped to mimic the removal of herbage by cattle grazing. Photosynthesis measurements

Scientific name	Abbreviation	Longevity/Functional group	Native status	Common name
Achillea millefolium L.	Achmil	perennial forb	native	common yarrow
Ambrosia psilostachya DC.	Ambpsi	perennial forb	native	western ragweed
Antennaria neglecta Greene	Antneg	perennial forb	native	field pussy-toes
Artemisia absinthium L.	Artabs	perennial forb/ subshrub	introduced	wormwood, absinthium
Artemisia frigida Willd.	Artfri	perennial subshrub	native	fringed sagewort, prairie sagewort
Artemisia ludoviciana Nutt.	Artlud	perennial forb	native	white sage, cudweed sagewort
Bromus inermis Leyss.	Broine	perennial grass	introduced	smooth brome
Carex inops L.H. Bailey ssp. *heliophila* (Mack.) Crins [*Carex heliophila* Mack.]	Carhel	perennial sedge	native	sun sedge
Cirsium arvense (L.) Scop.	Cirarv	perennial forb	introduced	Canada thistle
Cirsium flodmanii (Rydb.) Arthur	Cirflo	perennial forb	native	Flodman's thistle
Elymus repens (L.) Gould [*Agropyron repens* L.]	Agrrep	perennial grass	introduced	quackgrass
Geum triflorum Pursh	Geutri	perennial forb	native	prairie smoke, torch flower
Grindelia squarrosa (Pursh) Dunal	Grisqu	biennial/ perennial forb	native	curly-cup gumweed
Helianthus pauciflorus Nutt. ssp. *pauciflorus* [*Helianthus rigidus* (Cass.) Desf.]	Helrig	perennial forb	native	stiff sunflower
Melilotus officinalis (L.) Lam.	Meloff	annual/biennial forb	introduced	yellow sweetclover
Nassella viridula (Trin.) Barkworth [*Stipa viridula* Trin.]	Stivir	perennial grass	native	green needlegrass
Oligoneuron rigidum (L.) var. *rigidum* [*Solidago rigida* L.]	Solrig	perennial forb	native	stiff goldenrod
Oxalis stricta L.	Oxastr	annual/ perennial forb	native	yellow wood sorrel, common yellow oxalis
Pascopyrum smithii (Rydb.) Á. Löve [*Agropyron smithii* Rydb.]	Agrsmi	perennial grass	native	western wheatgrass
Poa pratensis L.	Poapra	perennial grass	native/ introduced	Kentucky bluegrass
Rosa arkansana Porter	Rosark	shrub	native	prairie rose
Solidago canadensis L.	Solcan	perennial forb	native	Canada goldenrod
Solidago missouriensis Nutt.	Solmis	perennial forb	native	Missouri goldenrod
Symphoricarpos occidentalis Hook.	Symocc	shrub	native	western snowberry, buckbrush
Symphyotrichum ericoides (L.) G.L. Nesom var. *ericoides* [*Aster ericoides* L.]	Asteri	perennial forb	native	white aster, heath aster
Taraxacum officinale F.H. Wigg	Taroff	perennial forb	native/ introduced	common dandelion

Table 1: List of C_3 species used in the photosynthesis-CO_2 response curve measurement.

were made on clear or mostly clear days from 9 AM to 12 PM at a leaf temperature of 16.4 to 32.9ºC, PPFD of 500 to 1330 μmol m^{-2} s^{-1}, and relative humidity of 28.3 to 65.5 percent. Measurements made on days when the volumetric soil water content at 23 cm depth of soil was lower than 0.2 (permanent wilting point in this prairie soil) are not included as we are interested in photosynthesis under less stressful conditions. During each of the three years, 16 to 20 plant species were measured in the exclosures (with each species measured four to 20 times). Grand averages of photosynthetic rates for each species under different grazing pressures were used in further analysis linking photosynthesis with leaf area index.

Leaf area index for individual plant species

A leaf area survey was conducted monthly four times during the growing season, May to September, for three years (2009 through 2011). A 1-m^2 frame was placed on two designated plots in the vicinity of the photosynthesis measurements. Four subplots within each frame were delineated and the percent contribution of total leaf area to the whole frame was noted for each. Separately, each subplot was visually surveyed to estimate leaf area by species. For each subplot, the value of each species' contribution was adjusted to total 100 percent. The percent value of each species was then multiplied by the contribution of the subplot to the total frame. This information was combined with the total leaf area index within the 1-m^2 frame measured using a LP-80 Ceptometer (Decagon Devices, Pullman, Wash. USA) to obtain the total leaf area of the frame by species.

Data analysis

The estimated eight parameters (Table 1) were subjected to principal component analysis (PCA) to identify the general trend of the multi-dimensional data sets. Differences in photosynthetic parameters among plant species were tested using one-way analysis of variance (ANOVA). As 'photosynthetic capacity' is often used to refer to maximum photosynthetic rates under no resource limitations, we denote the PCA-summarized variable as 'photosynthetic potential.' This is correlated with the long-term averaged frequency data for the 26 species. Also, grand averages of photosynthetic rates of dominant species were correlated with the corresponding leaf area indices estimated from field surveys from the same location. Data of leaf area index were square root transformed in order to meet the assumptions of the correlation analysis.

Results and Discussion

The first axis of PCA (Figure 1 - horizontal) is correlated with photosynthetic carboxylation (V_{cmax}) and electron transport (J_{max}) and the second (vertical axis) with the mesophyll conductance (G_{meso}) (Table 2). Six forbs (five from the Asteraceae family and one legume) had a greater intrinsic photosynthetic capacity than the remaining species, which occupied the middle or lower range of variation. Located at the lowest end of the horizontal axis were *Poa pratensis*, *Bromus inermis* and *Taraxacum officinale* F.H. Wigg. It appears that the maximum carboxylation rate (reflecting mainly the V_{cmax} in the first PCA axis) and the mesophyll conductance (the second PCA axis) may compensate to give similar maximum photosynthesis. In this respect, *Achillea millefolium* L. and *Rosa arkansana* Porter exhibited different patterns

Parameter[1]	PC1 (48.4%)	PC2 (21%)	PC3 (16%)
V_{cmax}	0.76*[2]	-0.05	0.48*
J_{max}	0.88*	-0.36	-0.07
R_{dlight}	-0.22	-0.89*	0.09
G_{meso}	0.51*	0.53*	0.56*
Γ^*	-0.51*	-0.26	0.72*
Γ	-0.87*	-0.14	0.22
A_{net}	0.84*	-0.43*	-0.01

[1]=Abbreviations: V_{cmax}, maximum rate of carboxylation limited by the amount, activity and kinetics of rubisco; J_{max}, maximum rate of carboxylation limited by electron transport; R_{dlight}, rate of respiration in the presence of light; G_{meso}, mesophyll CO_2 conductance; Γ^*, chloroplast CO_2 photo-compensation point without considering R_{dlight}; Γ, CO_2 compensation point considering R_{dlight}; A_{net}, net photosynthesis estimated at the transition from RuBP-limited to the TPU-limited photosynthesis.

[2]*=correlations are statistically significant (p=0.05).

Table 2: Correlation coefficients between the first three axes of the principal component analysis (PCA) and the seven photosynthetic parameters used in the PCA analysis. The analysis was based on the averaged data from photosynthesis-intercellular CO_2 concentration curves for 26 C_3 rangeland plant species. Measurements were made at 28ºC, but the parameters were scaled to 25ºC. The percentages of variance of the original seven parameters explained by the PCA axes are included in the parentheses.

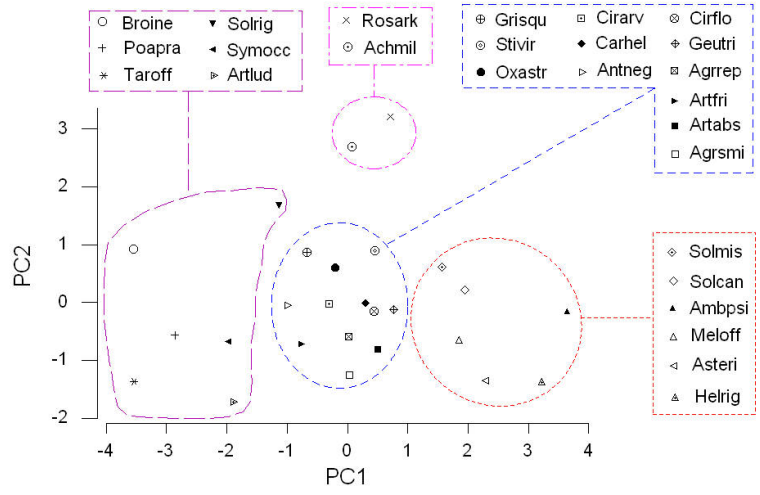


Figure 1: Principal component analysis (PCA) of seven parameters (V_{cmax}, J_{max}, R_{dlight}, G_{meso}, Γ^*, Γ, and A_{net}) of the FvCB model based on the automated analysis scheme available at leafweb.ornl.gov. Abbreviations of plant species are defined in Table 1 and the abbreviations of parameters are defined in Table 2. The horizontal and vertical axes stand for the first and second axes of PCA, respectively, which account for 70 percent of the variance of the seven original parameters.

from other species (Figure 2). As shown in Figure 3, frequency was negatively correlated with photosynthetic potential of prairie plants, though the correlation was stronger when the information from the first two PCA axes were combined (Figure 3b, r=-0.435, p=0.026). Also, there was a positive correlation between photosynthetic rates and leaf nitrogen in these species (Figure 4). Furthermore, using our leaf photosynthesis data collected from 2008 through 2010 and leaf area index data for 25 species collected from 2009 through 2011, we

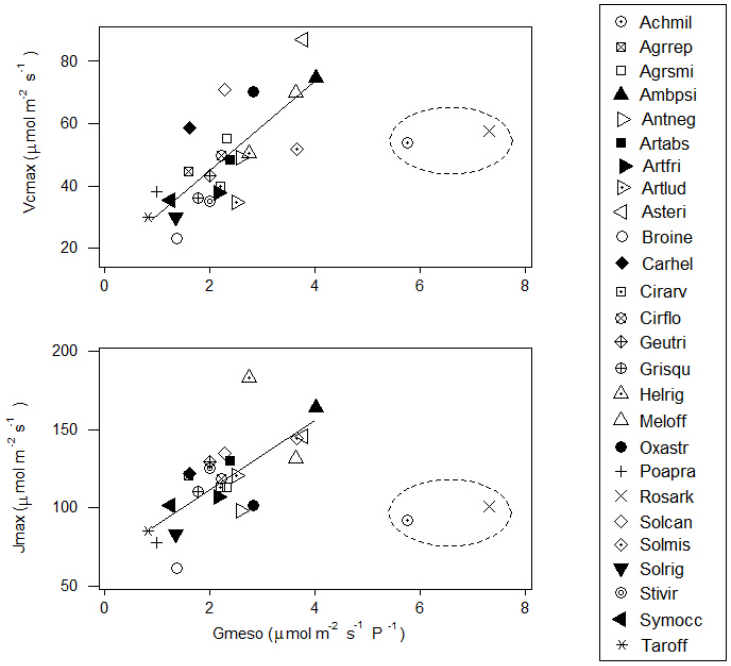


Figure 2: Relationships between maximum carboxylation limited photosynthesis (V_{cmax}) and mesophyll conductance (G_{meso}) (top panel) and electron transport limited photosynthesis (J_{max}) and mesophyll conductance (G_{meso}) (lower panel).

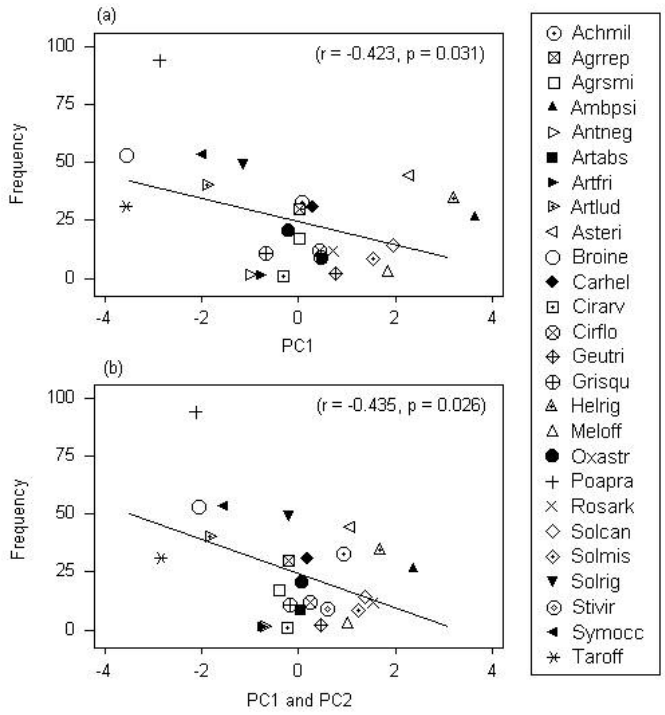


Figure 3: Correlation of plant frequency and photosynthetic potential defined as the first axis of the principal component analysis (PCA) of the seven photosynthetic parameters (a) and the combination of the first and second axes of the PCA analysis (b) for 26 C_3 plant species found in the mixed-grass prairie.

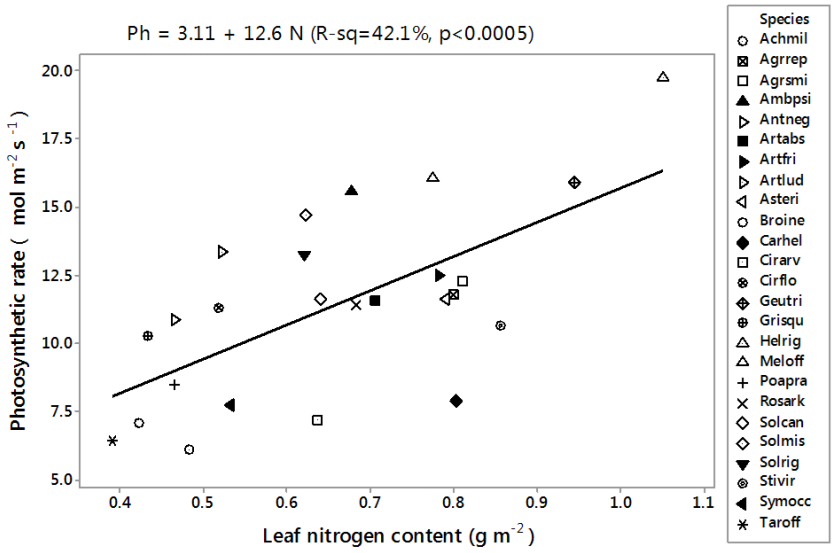


Figure 4: Relationship between photosynthetic rates and leaf nitrogen contents for prairie plants measured under common greenhouse conditions.

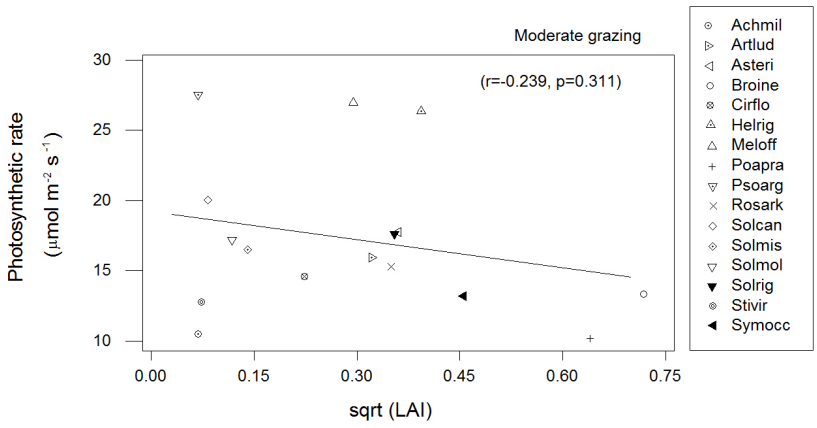


Figure 5: Correlation between photosynthetic rates and the square root of leaf area index of 16 plant species growing in a moderately grazed pasture. Photosynthetic rates were averaged based on measured values on 33 clear to mostly clear days during the growing seasons from 2008 to 2010, and leaf area indices were averaged values based on field surveys conducted in the same location from 2009 to 2011. Abbreviations of plant species are defined in Table 1, as well as: Psoarg=*Pediomelum argophyllum* (Pursh) J. Grimes [*Psoralea argophylla* Pursh] and Solmol=*Solidago mollis* Bartl.

observed also a negative correlation between leaf photosynthesis and plant success (here defined as leaf area within a unit land area) in both moderately and heavily grazed pastures, although the correlation was statistically weak (p=0.311 for moderate grazing and p=0.365 for heavy grazing), (Figures 5 and 6).

Averaged over the growing season from May to September, the leaf area indices of *Poa pratensis* and *Bromus inermis* combined accounted for 46 percent and 24 percent of the total LAI in plots of moderately and heavily grazed pastures, respectively (Tables 3 and 4). In terms of leaf nitrogen on ground area basis, the two exotic species combined represented 30 percent and 15 percent of the total leaf nitrogen of the plant communities under the two grazing treatments.

Past studies indicate that photosynthetic capacities of prairie forbs when compared to grasses are similar [20], higher [21] or lower [14,22]. Our results suggest that photosynthetic capacity of prairie forbs is widely variable, which is not surprising considering the number of plant families and life forms represented. The negative correlation between photosynthesis and plant frequency as observed in our study contrasts the findings of McAllister et al. [14] done in a highly productive tallgrass prairie. We speculate that the negative photosynthesis-plant success relationship as found in our study might indicate an outcome of severe interspecific competition for soil resources in the mixed-grass prairie.

The data from this study has several implications for understanding plant community and ecosystem functions in the mixed-grass prairie. First, the negative correlation between leaf photosynthesis and plant success suggests that the instantaneous photosynthetic characteristics measured at leaf level can only represent shortly-lived trends of leaf carbon gain, which cannot portray the overall photosynthetic capacity of the plant species during the entire growing season. Our measurements were conducted in the warm months, and did not capture photosynthetic activity in early spring and late fall when *Poa pratensis* and *Bromus inermis* maintain photosynthesis and growth while many other species in the prairie are dormant. Taking advantage

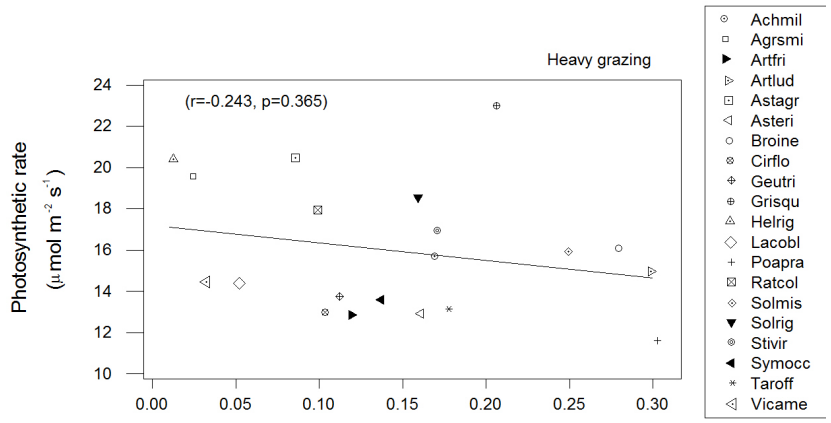


Figure 6: The same as in Figure 5 except that the measurements were made on 20 species in a heavily grazed pasture. Abbreviations of plant species are defined in Table 1, as well as: Astagr = *Astragalus agrestis* Douglas ex G. Don., Lacobl =*Lactuca tatarica* (L.) C.A. Mey. var. *pulchella* (Pursh) Breitung [*Lactuca oblongifolia* Nutt.], Ratcol=*Ratibida columnifera* (Nutt.) Woot. & Standl., and Vicame=*Vicia americana* Muhl. ex Willd. et al.

Species	‡LAI-2009	LAI-2010	LAI-2011	LAI-mean	N (g/m² ground area)§
Bromus inermis	0.3233	0.5416	0.6826	0.5158	0.2182
Poa pratensis	0.3081	0.4069	0.5165	0.4105	0.1908
Helianthus pauciflorus	0.1174	0.1496	0.1976	0.1548	0.1626
Symphoricarpos occidentalis	0.1746	0.196	0.2518	0.2075	0.1106
Aster ericoides	0.115	0.1257	0.1494	0.13	0.1029
Rosa arkansana	0.0882	0.1168	0.1618	0.1223	0.0834
Oligoneuron rigidum	0.0941	0.1178	0.1654	0.1258	0.0782
Melilotus officinalis	0.0316	0.0933	0.1355	0.0868	0.0672
Artemisia ludoviciana	0.0907	0.0941	0.1242	0.103	0.0537
Cirsium flodmanii	0.0301	0.042	0.0774	0.0499	0.0258
Solidago missouriensis	0.0237	0.0053	0.0299	0.0196	0.0122
*Solidago mollis**	0	0.0152	0.0259	0.0137	0.0090
*Tragopogon dubius**	0.0047	0.0187	0.0101	0.0111	0.0073
*Lotus purshianus**	0	0	0.0305	0.0102	0.0067
Stipa viridula	0.0021	0	0.0137	0.0053	0.0045
Solidago canadensis	0.0179	0	0.0023	0.0067	0.0043
Anemone cylindrica *	0.0005	0.0044	0.0127	0.0059	0.0039
*Psoralea argophylla**	0.0019	0	0.0119	0.0046	0.0030
*Asclepias ovalifolia**	0	0	0.0117	0.0039	0.0026
*Cirsium arvense**	0.0045	0.003	0.0044	0.004	0.0025
Achillea millefolium	0.0032	0.0038	0.0068	0.0046	0.0022
Carex spp.	0.0042	0.0023	0.001	0.0025	0.0020
*Phleum pretense**	0	0	0.0066	0.0022	0.0014
Taraxacum officinale	0.0025	0	0	0.0008	0.0003
Total	1.4383	1.9365	2.6297	2.0015	1.3156

‡LAI was measured five times from May to September in 2009 through 2011. Value for each species was estimated by the relative leaf area occurring within 1×1 m frames as well as the absolute total seasonal LAI measured using a ceptometer (see main text for detail).

§Leaf nitrogen per unit ground area for each species was estimated by multiplying LAI of each species by area-based leaf nitrogen concentration (based on Figure 4).

*Species for which leaf nitrogen was not measured and an average value of 0.66 g/m² (based on 25 species) was assumed.

Table 3: Leaf area indices (LAI) and leaf nitrogen per unit ground area for 24 plant species found in a moderately grazed pasture in the mixed-grass prairie near Streeter N.D., USA.

of ample spring soil water for rapid growth is especially important for the competitive success of these two exotic species. Second, maintaining a low photosynthetic rate for the most abundant species also reduces excessive depletion of soil resources, and thus favors a more diverse plant community. This can also be seen from the peak-season value of the ground area-based nitrogen for each species co-occurring in the moderate and heavy grazing pastures (Tables 3 and 4). We can see that on a unit ground area basis on this prairie, these two exotic species are strong competitors for nitrogen, especially in the moderately grazed pasture. This occurred despite their low nitrogen content and low photosynthetic rate per unit leaf area.

Soil in this mixed-grass prairie typically is low in nitrogen (N) and phosphorus (P) and fertilization of N and P can increase forage production [23]. At the same time, high N application tends to

Species	ǂLAI-2009	LAI-2010	LAI-2011	LAI-mean	N (g/m² ground area)§
Artemisia ludoviciana	0.0373	0.0788	0.1524	0.0895	0.0467
Poa pratensis	0.0321	0.0766	0.1665	0.0917	0.0426
Solidago missouriensis	0.0452	0.0665	0.0749	0.0622	0.0387
Bromus inermis	0.0301	0.0707	0.1337	0.0782	0.0331
Stipa viridula	0.0128	0.0245	0.0502	0.0292	0.0250
Aster ericoides	0.0115	0.0253	0.0407	0.0259	0.0205
Grindelia squarrosa	0.0353	0.047	0.0456	0.0426	0.0184
Oligoneuron rigidum	0.0111	0.0322	0.0328	0.0253	0.0157
Carex spp.	0.0199	0.019	0.0155	0.0181	0.0145
Achillea millefolium	0.008	0.0194	0.0584	0.0286	0.0138
Taraxacum officinale	0.0188	0.0367	0.0394	0.0317	0.0124
Geum triflorum	0.0038	0.0129	0.0209	0.0125	0.0118
*Bouteloua gracilis**	0.0081	0.0155	0.0286	0.0174	0.0114
Artemisia frigida	0.0134	0.0134	0.0158	0.0142	0.0111
Symphoricarpos occidentalis	0.0128	0.018	0.0255	0.0188	0.0100
Cerastium arvense	0.0054	0.0186	0.0176	0.0139	0.0089
Antennaria neglecta	0.0088	0.0143	0.0265	0.0165	0.0077
*Oxalis stricta**	0	0.0035	0.0309	0.0115	0.0076
*Dichanthelium wilcoxianum**	0.0043	0.004	0.0244	0.0109	0.0072
*Medicago lupulina**	0.0017	0.0104	0.0187	0.0103	0.0068
*Ratibida columnifera**	0.0018	0.0075	0.0202	0.0098	0.0064
*Stipa curtiseta**	0	0.0151	0.0112	0.0088	0.0058
Cirsium flodmanii	0	0.0069	0.0252	0.0107	0.0055
*Astragalus flexuosus**	0.0026	0	0.0198	0.0074	0.0049
*Astragalus agrestis**	0.0026	0.0121	0.0071	0.0073	0.0048
*Anemone cylindrica**	0.0028	0.0042	0.0143	0.0071	0.0047
*Viola pedatifida**	0.001	0.0043	0.0137	0.0063	0.0041
*Lactuca tatarica**	0.0006	0.0014	0.006	0.0027	0.0018
*Sphaeralcea coccinea**	0.0011	0.0031	0.0028	0.0023	0.0015
*Vicia americana**	0	0.0003	0.0027	0.001	0.0007
*Potentilla pensylvanica**	0.0003	0	0.0024	0.0009	0.0006
Pascopyrum smithii	0	0	0.0017	0.0006	0.0005
Ambrosia psilostachya	0.0008	0.0003	0	0.0004	0.0003
*Euphorbia serpyllifolia**	0	0.0013	0	0.0004	0.0003
Helianthus pauciflorus	0	0.0005	0	0.0002	0.0002
*Agrostis hyemalis**	0	0.0009	0	0.0003	0.0002
*Onosmodium, molle**	0	0.0008	0	0.0003	0.0002
*Polygonum convolvulus**	0	0.0001	0	0	0.0000
Total	0.3340	0.6661	1.1461	0.7155	0.4703

ǂLAI was measured five times from May to September in 2009 through 2011. Value for each species was estimated by the relative leaf area occurring within 1×1 m frames as well as the absolute total seasonal LAI measured using a ceptometer (see main text for detail).

§Leaf nitrogen per unit ground area for each species was estimated by multiplying LAI of each species by area-based leaf nitrogen concentration (based on Figure 4).

*Species for which leaf nitrogen was not measured and an average value of 0.66 g/m² (based on 25 species) was assumed.

Table 4: Leaf area indices (LAI) and leaf nitrogen per unit ground area for 38 plant species found in a heavily grazed pasture in the mixed-grass prairie near Streeter N.D., USA.

favor exotic grasses such as *Poa pratensis* and reduce plant diversity, depending on stocking history [24]. Studies in the tallgrass prairie [25,26] also demonstrate that nitrogen addition may encourage native warm-season grasses to be displaced by exotic cool-season grasses such as *Poa pratensis* and *Elymus repens* (L.) Gould. It has been estimated that atmospheric nitrogen deposition due to burning of fossil fuels, crop fertilization and intensive livestock operations may increase plant N supply by 10-25 percent in the tallgrass prairie [27]. The relative contribution of nitrogen deposition may be higher in the mixed-grass prairie, perhaps as high as 50 percent, considering an estimated annual N mineralization rate of 1.2 g m^{-2} [28] and an annual total atmospheric N deposition of 0.6 g m^{-2} based on data of NADP for the year 2000. *Bromus inermis* and *Poa pratensis*, which are considered invasive [3] and investing larger proportion of its production to belowground biomass compared with co-occurring natives [29], have been shown to increase in both biomass production and cover on the silty range sites of the mixed-grass prairie over past 26 years, especially under rest and light grazing situations [15]. Wedin and Tilman [27] used a positive feedback model to describe the interaction between tallgrass prairie natives and soil nitrogen cycling. Perhaps the same framework can be used to speculate why in the mixed-grass prairie *Poa pratensis* and *Bromus inermis* have extensively displaced native grasses and forbs may partly be due to the low photosynthesis/low nitrogen, and low litter quality nature of these exotic species. Nevertheless, as the positive

feedback system is inherently unstable, the future of the mixed-grass prairie will to a substantial extent be influenced by how the plant species, especially those representing a large fraction of LAI and per land area based nitrogen, such as *Poa pratensis* and *Bromus inermis*, allocate nitrogen among different organs and adjust their physiology strategies in response to various disturbances, including atmospheric N deposition at regional scale spanning tallgrass and mixed-grass prairies.

In addition to nitrogen deposition, other global change factors, such as increases in atmospheric CO_2 concentration and temperature, may have differential impacts to exotic vs. native species. A synthesis of available data suggests that invasive, noxious weeds have a larger than expected growth increase to both recent and projected atmospheric CO_2 increase as compared to native plant species [30]. Actually, it has been shown that, in *Poa pratensis,* increased atmospheric CO_2 concentration not only mitigated high temperature stress on net carbon gain, but also significantly increased root growth [31]. It will be interesting to test experimentally if this CO_2-related growth enhancement would increase the invasive potential of this and related species. Although our data showed a relative low photosynthetic potential in several invasive plants (Figure 1 and Table 2), the low mesophyll conductance measured in several invasive plants (Supplementary Table 1) suggests potentials for photosynthesis to increase under high atmospheric CO_2. To what extent this will be integrated into whole plant growth and competitive success is yet to be seen using manipulative experiments contrasting the invasive against the native plants, for which comprehensive data is merger yet critically important for understanding the integrity of rangeland ecosystems under future climate and land use changes [30]. As the invasion and naturalization of exotic plant species is influenced by not only biophysical but also social economic factors, including global trade [32], it will be a challenging task to constantly contain the vigor of the exotic species using a combination of tools, such as early grazing and prescribed fire targeted at the most vulnerable growth stages while maintaining the integrity of native species [4-6,33,34]. This highlights the importance of integrated, transdisciplinary studies for the rehabilitation of degraded rangelands [35].

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