Photosynthetic Capacity of 26 Dominant Plant Species of the Mixed-grass Prairie

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Quantifying photosynthesis parameters for rangeland plant species not only allows for an assessment of the value of photosynthesis in plant competitive success but also is useful for modeling photosynthesis of plant communities under changing climate regimes.

Summary
Literature data show mixed results on the photosynthetic capacity of grasses vs. forbs growing on the prairies. This hampers our ability to quantify carbon flow and balance in prairie ecosystems. Our measurements suggest that the dichotomy of grasses vs. forbs cannot capture the true variation in photosynthetic capacity among these species. Of the 26 species studied, six forbs (mostly from the Asteraceae family) had a higher intrinsic photosynthetic capacity than the other species.

Introduction
Photosynthesis is the basis of plant growth. In the past 30 years, the biochemical model of photosynthesis proposed by Farquhar–von Caemmerer–Berry (FvCB) (Farquhar et al. 1980) has been used extensively to quantify carbon flow and balance in natural ecosystems (Harley et al. 1992). However, the application of the FvCB model requires a reliable estimation of parameters describing photosynthetic capacity (we use this term more generally than the typical usage of maximum photosynthetic rate) and biochemical limitations, which can be obtained through the construction of photosynthesis - intercellular CO_2 (A-Ci) response curves (Wullschleger 1993), in which net photosynthetic rate is measured under different intercellular carbon dioxide (CO_2) concentrations. An A-Ci curve simulates the net outcome of the interaction between the stomates (which control the supply of atmospheric CO_2 to plants) and the chloroplast (which dictates the demand of CO_2 of the enzyme-driven carbon reduction system).

Recently, Gu et al. (2010) incorporated new statistical concepts into a computer-intensive procedure for a rigorous estimation of the parameters of the FvCB model, overcoming important shortcomings of the methods used in the past decades. Despite past efforts to document photosynthetic capacity of prairie plants (McAllister et al. 1998, Lee et al. 2001, Reich et al. 2003, Tjoelker et al. 2005), relevant data covering some of the dominant plant species in the mixed-grass prairie are still limited.

The objective of our study is to measure and compare photosynthetic parameters of 26 plant species grown in a common greenhouse. This includes species that are so short in stature that their leaf photosynthesis is difficult to measure in the field.

Procedures
Seeds of 15 species, 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 April 20, 2012, seeds were sown in plastic pots (3 by 3 by 3 inches) in replicates of four, using a local prairie soil. Root cuttings of two shrubs and transplants of 11 more species were planted in pots in May and June 2012. The plant species measured include seven grasses, one sedge, 18 forbs and two shrubs (Table 1). Pots were placed in a greenhouse and watered as needed.

The A-Ci curve measurements were made using a Li-Cor 6400 Portable Photosynthesis System from July 7 through Aug. 13, 2012, with four replicates of each species. The A-Ci curves were fitted to the FvCB model according to Gu et al. (2010) and implemented through http://leafweb.ornl.gov/Pages/LeafWeb.aspx. The estimated eight parameters (see Table 2 for definitions and Table 3) were scaled to the standard values at 77º F, and principal component analysis (PCA) was used to identify the general trend of the multidimensional data sets. Differences in photosynthetic parameters among plant species were tested using analysis of variance (ANOVA). (Currently the LeafWeb Project is developed for C_3 species. In this report, results from the two C_4 grass species are omitted.)

Results and Discussion

The first axis of the PCA (Figure 1) is correlated with photosynthetic capacity and the second (vertical axis) with the mesophyll conductance (see Table 2 for definition of terms and Table 4 for correlation coefficients).

Six forbs (five species in 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 are Kentucky bluegrass, smooth brome and common dandelion. As Kentucky bluegrass grew poorly under greenhouse conditions, perhaps due to higher temperatures than in field conditions, and some with insect infestations, we selected the unaffected leaves to make the measurement. The low photosynthetic capacity in this species also is seen under field conditions (Tables 5-7).

Because the common dandelion also was affected with insects inside the greenhouse, we used plants growing outside to make the measurement.

For reasons unknown to us, (higher temperatures, perhaps) smooth brome did not grow well in the greenhouse, either. However, field measured data suggest that the photosynthetic capacity of smooth brome is comparable to plants of the intermediate group grown in greenhouse. Also, the value of the second PCA axis for smooth brome is quite high (Fig. 1).

Interestingly, three other species (stiff goldenrod, western yarrow and prairie rose) with high photosynthetic rates as measured under field conditions (Tables 5-7) also had relatively high values in the second PCA axis. The maximum carboxylation rate (reflecting mainly the Vcmax in the first PCA axis) and the mesophyll conductance (the second PCA axis) appear to compensate to give similar maximum photosynthesis.

Past studies indicate that the photosynthetic capacity of prairie forbs were similar to grasses (Reich et al. 2003), higher (Lee et al. 2001) or lower (McAllister et al. 1998, Tjoelker et al. 2005) than grasses. Our results suggest a more varied photosynthetic capacity in prairie forbs than grasses, implying that a more accurate characterization of photosynthetic capacity of prairie plants would be required for modeling community photosynthesis. Some species, especially forbs with low photosynthetic capacity, may rely on other life history strategies, such as a large number of seeds, extensive network of vegetative propagules, rapid early season growth, etc., rather than leaf photosynthesis for their competitive success in the plant community.

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

Scientific Name	Abbreviation	Photosynthetic Pathway	Longevity/ Functional Group	Native Status	Common Name
Achillea millefolium L.	Achmil	C_3	perennial forb	native	common yarrow
Ambrosia psilostachya DC.	Ambpsi	C_3	perennial forb	native	western ragweed
Antennaria neglecta Greene	Antneg	C_3	perennial forb	native	field pussy-toes
Artemisia absinthium L.	Artabs	C_3	perennial forb/ subshrub	introduced	wormwood, absinthium
Artemisia frigida Willd.	Artfri	C_3	perennial subshrub	native	fringed sagewort
Artemisia ludoviciana Nutt.	Artlud	C_3	perennial forb	native	white sage, cudweed sagewort
Bouteloua gracilis (Willd. ex Kunth) Lag. ex Griffiths	Bougra	C_4	perennial grass	native	blue grama
Bromus inermis Leyss.	Broine	C_3	perennial grass	introduced	smooth brome
Carex inops L.H. Bailey ssp. *heliophila* (Mack.) Crins [*Carex heliophila* Mack.]	Carhel	C_3	perennial sedge	native	sun sedge
Cirsium arvense (L.) Scop.	Cirarv	C_3	perennial forb	introduced	Canada thistle
Cirsium flodmanii (Rydb.) Arthur	Cirflo	C_3	perennial forb	native	Flodman's thistle

Elymus repens (L.) Gould [*Agropyron repens* L.]	Agrrep	C_3	perennial grass	introduced	quackgrass
Geum triflorum Pursh	Geutri	C_3	perennial forb	native	prairie smoke
Grindelia squarrosa (Pursh) Dunal	Grisqu	C_3	biennial/ perennial forb	native	curly-cup gumweed
Helianthus pauciflorus Nutt. ssp. *pauciflorus [Helianthus rigidus* (Cass.) Desf.]	Helrig	C_3	perennial forb	native	stiff sunflower
Melilotus officinalis (L.) Lam.	Meloff	C_3	annual/biennial forb	introduced	yellow sweetclover
Nassella viridula (Trin.) Barkworth [*Stipa viridula* Trin.]	Stivir	C_3	perennial grass	native	green needlegrass
Oligoneuron rigidum (L.) Small var. *rigidum* [*Solidago rigida* L.]	Solrig	C_3	perennial forb	native	stiff goldenrod
Oxalis stricta L.	Oxastr	C_3	perennial forb	native	yellow wood sorrel
Pascopyrum smithii (Rydb.) Á. Löve [*Agropyron smithii* Rydb.]	Agrsmi	C_3	perennial grass	native	western wheatgrass
Poa pratensis L.	Poapra	C_3	perennial grass	native/ introduced	Kentucky bluegrass
Rosa arkansana Porter	Rosark	C_3	shrub	native	prairie rose
Schizachyrium scoparium (Michx.) Nash var. *scoparium* [*A. scoparius* Michx.]	Andsco	C_4	perennial grass	native	little bluestem
Solidago canadensis L.	Solcan	C_3	perennial forb	native	Canada goldenrod
Solidago missouriensis Nutt.	Solmis	C_3	perennial forb	native	Missouri goldenrod
Symphoricarpos occidentalis Hook.	Symocc	C_3	shrub	native	western snowberry, buckbrush
Symphyotrichum ericoides (L.) G.L. Nesom var. *ericoides* [*Aster ericoides* L.]	Asteri	C_3	perennial forb	native	white aster, heath aster
Taraxacum officinale F.H. Wigg	Taroff	C_3	perennial forb	native/ introduced	common dandelion

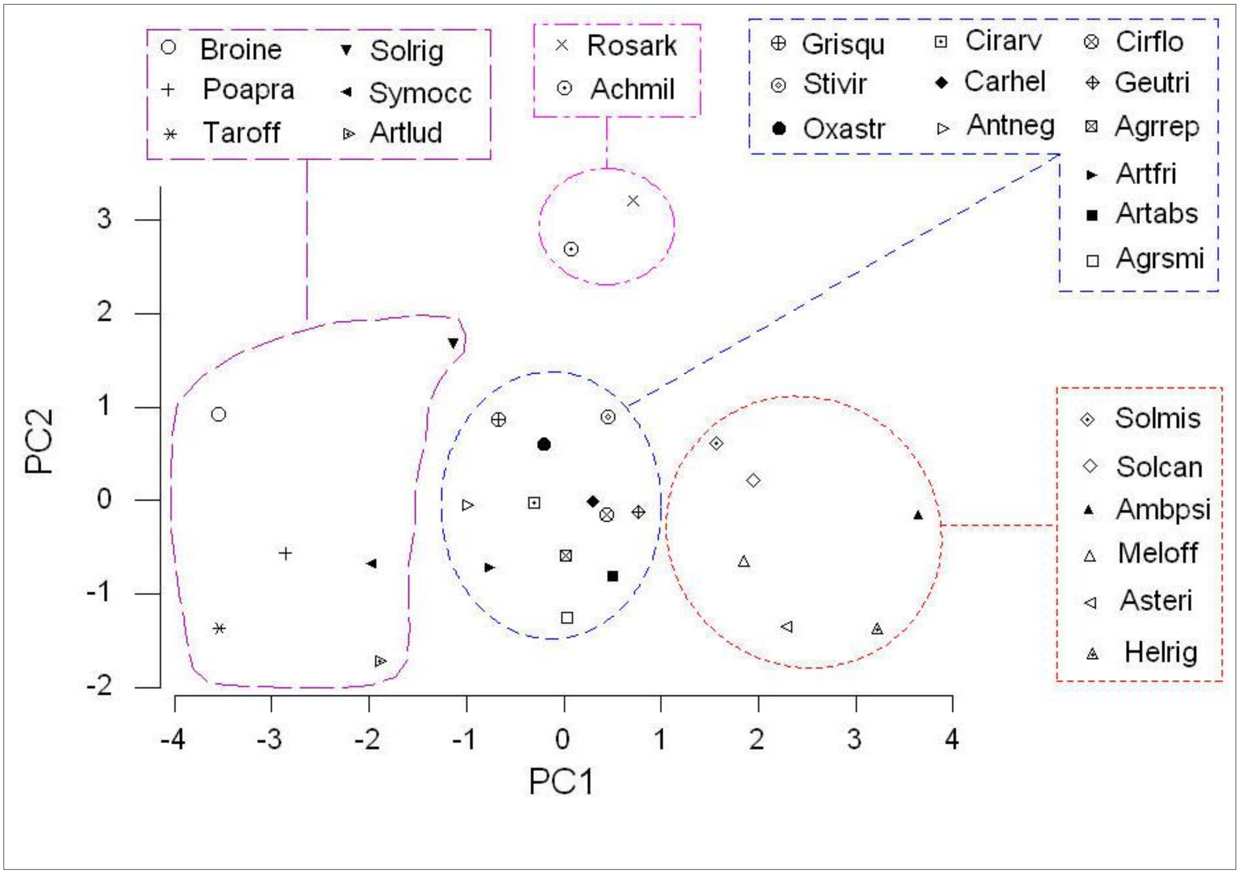

Figure 1. Principal component analysis (PCA) of seven parameters (Vcmax, Jmax, Rdlight, Gmeso, Γ*, Γ and Anet) of the FvCB model based on the automated analysis scheme available at http://leafweb.ornl.gov/Pages/LeafWeb.aspx. Abbreviations of plant species are defined in Table 1 and the model parameters 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.

Table 2. Description of major photosynthetic parameters.

Parameter	Description
Vcmax	A critical step of photosynthesis carbon fixation is the carboxylation of the riboluse-1,5-bisphosphate (RuBP, a five-carbon molecule serving as the “acceptor” for CO_2). This carboxylation step is catalyzed by the enzyme riboluse-1,5-bisphosphate carboxylase/oxygenase (Rubisco). Vcmax presents the maximum apparent activity of Rubisco. This process occurs in the stroma of the chloroplast.
Jmax	For all the C3 plants, the CO_2 is first fixed as three-carbon acid, 3-phosphoglycerate (3-PGA), which is reduced to form triose sugar-phosphate using the energy (ATP) and reducing power (NADPH) generated from the light-harvesting electron transport chains within the chloroplast thylakoids. While some triose phosphate molecules are to be transported out of the chloroplast for storage or other pathways of carbon metabolism, the majority of them are to be recycled back to renew the depleted RuBP for continuing CO_2 fixation. Jmax indicates the maximum rate of the electron transported-based RuBP regeneration capacity.
Tpu	The capacity of triose sugar-phosphate utilization, which occurs at high CO_2 and high-light conditions. The “Tpu” parameter for some species is lacking (see Table 3), mostly because measured net photosynthesis did not reach a stabilized plateau or started to reduce near the highest range of the CO_2 concentration. Under such a condition, the capacity of triose phosphate utilization can be considered as very high.
Rdlight	Estimated mitochondrial respiration under light condition. This is to be differentiated from photorespiration, which happens only under light and involves the chloroplast and mitochondrion, as well as the peroxisome.
Gmeso	This indicates the relative ease of diffusion of CO_2 from the substomatal cavity to the chloroplast.
Γ*	Chloroplast CO_2 photo-compensation point without considering Rdlight (at which the photorespiratory efflux of CO_2 equals the rate of photosynthetic CO_2 uptake).
Γ	CO_2 compensation point considering Rdlight.
Anet	Net photosynthesis estimated at the transition from RuBP-limited to the Tpu-limited photosynthesis.

Table 3. Photosynthetic parameters (at 77º F) for 26 dominant plant species of the mixed-grass prairie near the Central Grassland Research Extension Center, Streeter, N.D. The chamber condition was set as: photosynthetically active radiation 900 µmol $m^{-2}s^{-1}$; leaf temperature 82.4°F; humidity 26 to 29 mmol H_2O mol^{-1} and flow rate 300 mol s^{-1}. The reference CO_2 was varied in 15 to 16 steps from 0 to 1,500 parts per million. Within each column, numerals not labeled by common letters are statistically different (P=0.05).

Species	**Vcmax** (µmol m^{-2} s^{-1})	**Jmax** (µmol m^{-2} s^{-1})	**Rdlight** (µmol m^{-2} s^{-1})	**Gmeso** (µmol m^{-2} $s^{-1}P^{-1}$)	**Tpu** (µmol m^{-2} s^{-1})	**Γ*** (Pa)	**Γ** (Pa)	**Anet** (µmol m^{-2} s^{-1})
Achillea millefolium	53.84±6.49[ab]	91.64±7.55[c]	1.60±0.74[a]	5.75±2.84[a]	6.31±0.41[abc]	3.76±0.74[a]	5.28±0.53[ab]	17.36±1.56 [cd]
Elymus repens	44.64±7.80[abc]	120.31±5.47[bc]	3.35±0.64[a]	1.61±0.16[ab]	8.42±0.18[abc]	3.67±0.95[a]	5.28±0.81[ab]	24.33±0.44[abcd]
Pascopyrum smithii	55.19±9.13[ab]	112.84±7.43[bc]	4.66±0.81[a]	2.32±0.52[ab]	7.67[abc]	3.40±0.50[a]	5.13±0.32[ab]	23.38±1.19[abcd]
Ambrosia psilostachya	74.71±9.83[a]	163.81±7.86[ab]	2.92±1.01[a]	4.03±1.05[a]	10.73[abc]	2.43±0.51[a]	4.11±0.31[bc]	31.00±0.80[a]
Antennaria neglecta	49.10±3.19[ab]	97.62±9.96[c]	3.06±1.48[a]	2.59±0.54[ab]		5.94±0.43[a]	5.19±0.08[ab]	20.48±2.98[bcd]
Artemisia absinthium	48.30±4.25[ab]	129.8±12.9[abc]	3.77±0.59[a]	2.38±0.09[ab]	8.07±0.63[abc]	3.37±0.43[a]	5.40±0.20[ab]	25.51±2.76[abc]
Artemisia frigida	37.69±5.40[abc]	106.59±7.65[c]	4.28±0.69[a]	2.16±0.27[ab]		3.36±0.84[a]	5.66±0.91[ab]	21.71±1.43[abcd]
Artemisia ludoviciana	34.87±2.45[abc]	120.01±9.07[bc]	4.52±0.64[a]	2.51±0.90[ab]		5.52±0.28[a]	7.42±0.22[a]	23.45±0.81[abcd]
Symphyotrichum ericoides	86.94±3.80[a]	145.42±6.32[ab]	4.32±1.82[a]	3.77±0.34[a]		4.43±0.69[a]	4.63±0.06[ab]	27.77±0.62[ab]
Bromus inermis	23.18±4.07[c]	61.09±5.7[cd]	3.32±1.76[a]	1.37±0.30[ab]	3.92±0.32[c]	3.13±1.26[a]	6.96±1.31[ab]	11.23±0.71[cde]
Carex inops var. *heliophila*	58.49±7.34[ab]	121.35±9.48[bc]	2.34±1.20[a]	1.62±0.09[ab]	8.67±2.56[abc]	4.48±0.35[a]	5.14±0.27[ab]	23.62±2.39[abcd]
Cirsium arvense	40.00±8.44[abc]	112.7±15.5[bc]	3.30±0.93[a]	2.21±0.44[ab]	8.28±0.07[abc]	3.35±0.83[a]	5.32±0.93[ab]	21.54±2.32[bcd]
Cirsium flodmanii	49.80±4.58[ab]	118.4±11.7[bc]	3.37±0.53[a]	2.22±0.12[ab]	7.39±2.09[abc]	3.48±0.68[a]	4.61±0.1[ab]	22.35±2.36[abcd]
Geum triflorum	43.21±2.98[abc]	129.2±16.7[abc]	3.02±0.82[a]	1.99±0.46[ab]	9.08±1.25[abc]	2.96±0.82[a]	4.71±0.75[ab]	24.66±2.26[abc]
Grindelia squarrosa	36.23±4.88[abc]	110.32±5.99[bc]	2.01±0.99[a]	1.78±0.22[ab]	7.09±0.23[abc]	3.38±0.67[a]	5.67±0.07[ab]	20.35±2.21[bcd]
Helianthus pauciflorus	50.39±2.10[ab]	183±7.36[a]	3.55±0.77[a]	2.74±0.28[ab]	11.51±0.39[a]	2.98±1.07[a]	3.79±0.52[bc]	32.94±2.25[a]
Melilotus officinalis	70.00±14.2[a]	131.2±12.8[abc]	4.29±1.17[a]	3.63±0.99[ab]	10.7[abc]	2.91±0.71[a]	4.49±0.72[ab]	25.35±2.39[abc]
Oxalis stricta	70.12±1.25[a]	100.94±7.14[bc]	3.15±1.36[a]	2.83[ab]	6.23[abc]	4.33±0.58[a]	4.88±0.01[ab]	15.55±1.38[cd]
Poa pratensis	38.28±2.13[abc]	77.27±3.27[cd]	3.82±0.26[a]	0.98±0.12[b]	4.69±0.69[bc]	5.74±0.86[a]	6.07±0.63[ab]	15.82±0.48[d]
Rosa arkansana	57.50±14.3[ab]	100.34±2.91[c]	0.98±0.49[a]	7.32±4.39[a]	5.39±0.06[bc]	4.13±0.44[a]	5.52±0.83[ab]	19.98±0.64[bcd]
Solidago canadensis	70.80±24.9[a]	134.3±18.1[abc]	2.60±0.76[a]	2.28±0.57[ab]	8.65±0.94[abc]	2.96±0.52[a]	4.15±0.25[bc]	24.51±2.30[abcd]
Solidago missouriensis	51.92±5.76[ab]	144.3±15.3[ab]	1.91±0.64[a]	3.65±1.80[ab]	8.96±0.75[abc]	4.01±0.34[a]	4.75±0.37[ab]	26.43±2.12[abc]
Oligoneuron rigidum	29.95±1.63[abc]	82.64±8.31[cd]	2.01±0.61[a]	1.35±0.21[ab]	6.02±0.74[bc]	2.60±0.43[a]	4.65±0.55[ab]	15.46±0.98[d]
Nassella viridula	35.22±1.33[bc]	124.7±6.49[abc]	2.13±0.31[a]	2.00±0.17[ab]	7.59[abc]	2.48±0.47[a]	4.69±0.30[ab]	21.74±0.93[abcd]
Symphoricarpos occidentalis	35.29±5.96[bc]	100.96±7.94[c]	3.46±1.10[a]	1.25±0.18[ab]		4.87±0.80[a]	6.51±0.71[ab]	20.52±1.15[bcd]
Taraxacum officinale	30.07[abc]	84.49[abcd]	4.84[a]	0.83[ab]	5.47[abc]	5.04 [a]	7.27[abc]	15.42[abcd]

Table 4. Pearson correlation coefficients among 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 82.4° F, but the parameters were scaled to 77° F for comparison with literature data. The percentages of variance of the original seven parameters explained by the PCA axes are included in the parentheses.

Parameter	**PC1 (48.4%)**	**PC2 (21%)**	**PC3 (16%)**
Vcmax[2]	0.76*[1]	-0.05	0.48*
Jmax	0.88*	-0.36	-0.07
Rdlight	-0.22	-0.89*	0.09
Gmeso	0.51*	0.53*	0.56*
Γ*	-0.51*	-0.26	0.72*
Γ	-0.87*	-0.14	0.22
Anet	0.84*	-0.43*	-0.01

[1] * = correlations are statistically significant. [2] The abbreviations of terms are defined in Table 2.

Table 5. Net photosynthetic rates of 16 plant species measured in two rangeland exclosures on 13 clear days from May 28 to Sept. 18, 2008. On each day, the photosynthesis measurement was made from 9 a.m. to noon at a leaf temperature of 61.5 to 91.2° F, photosynthetically active radiation of 500 to 1,330 μmol m^{-2} s^{-1}, and relative humidity of 28.3 to 65.5 percent.

Species	**Species Abbreviation**	**Photosynthetic Rate (μmol CO_2 m^{-2} s^{-1})**	**Replication (N)**
Poa pratensis	Poapra	13.6±1.1[b1]	17
Cirsium flodmanii	Cirflo	13.7±1.4[b]	10
Solidago canadensis	Solcan	14.6±2.0[ab]	2
Symphoricarpos occidentalis	Symocc	15.0±1.6[b]	18
Achillea millefolium	Achmil	15.1±3.5[ab]	3
Artemisia frigida	Artfri	16.8±2.0[ab]	9
Bromus inermis	Broine	17.4±1.2[ab]	23
Nassella viridula	Stivir	18.0±1.9[ab]	12
Oligoneuron rigidum	Solrig	18.1±1.0[ab]	19
Artemisia ludoviciana	Artlud	19.2±2.0[ab]	13
Solidago missouriensis	Solmis	20.4±2.1[ab]	8
Helianthus pauciflorus	Helrig	21.3±1.9[ab]	6
Rosa arkansana	Rosark	21.6±1.4[ab]	6
Geum triflorum	Geutri	21.9±2.0[ab]	3
Symphyotrichum ericoides	Asteri	22.1±1.4[ab]	2
Grindelia squarrosa	Grisqu	24.4±3.6[a]	6

[1] Values followed by the same letter are not significantly different at *P*=0.05.

Table 6. Net photosynthetic rates of 19 plant species measured in two rangeland exclosures on seven days from May 26 to June 30, 2010. On each day, the photosynthesis measurement was made from 9:30 a.m. to noon at a leaf temperature of 65.3 to 91.2°F, photosynthetically active radiation of 564 to 2,054 μmol $m^{-2} s^{-1}$, and relative humidity of 25.8 to 70 percent.

Species	Species Abbreviation	Photosynthetic Rate (μmol CO_2 $m^{-2} s^{-1}$)	Replication (N)
Nassella viridula	Stivir	12.4±2.9[c1]	7
Artemisia frigida	Artfri	12.7±1.3[abc]	3
Taraxacum officinale	Taroff	13.1±0.1[abc]	2
Symphoricarpos occidentalis	Symocc	13.7±1.5[bc]	9
Geum triflorum	Geutri	13.9±2.3[abc]	4
Poa pratensis	Poapra	14.0±2.7[bc]	5
Solidago canadensis	Solcan	14.4[abc]	1
Aster ericoides	Asteri	15.7±1.9[abc]	8
Bromus inermis	Broine	15.8±3.0[abc]	5
Artemisia ludoviciana	Artlud	16.0±1.6[abc]	7
Solidago missouriensis	Solmis	16.2±1.6[abc]	7
Rosa arkansana	Rosark	16.3±1.9[abc]	3
Pascopyrum smithii	Agrsmi	16.8±2.0[abc]	5
Cirsium flodmanii	Cirflo	17.1±1.3[abc]	6
Oligoneuron rigidum	Solrig	18.7±1.3[abc]	8
Grindelia squarrosa	Grisqu	21.0±2.4[abc]	3
Achillea millefolium	Achmil	23.3±0.6[abc]	2
Helianthus pauciflorus	Helrig	23.8±3.5[ab]	6
Melilotus officinalis	Meloff	26.3±1.7[a]	7

[1] Values not labeled by common letters are statistically different (*P*=0.05).

Table 7. Net photosynthetic rates of 17 plant species measured in two rangeland exclosures on seven days from July 7 to Sept. 21, 2010. Location and conditions same as in Table 6.

Species	Species Abbreviation	Photosynthetic Rate (μmol CO_2 $m^{-2} s^{-1}$)	Replication (N)
Symphoricarpos occidentalis	Symocc	9.9±1.1[cd1]	5
Nassella viridula	Stivir	10.3±3.0[cd]	3
Poa pratensis	Poapra	13.2±3.0[bc]	5
Pascopyrum smithii	Agrsmi	13.9±0.8[abc]	3
Solidago missouriensis	Solmis	14.0±2.2[bc]	6
Bromus inermis	Broine	14.5±3.2[abc]	4
Cirsium flodmanii	Cirflo	14.5±0.9[abc]	4
Achillea millefolium	Achmil	14.8±4.9[abc]	3
Artemisia ludoviciana	Artlud	15.1±1.2[abc]	5
Artemisia frigida	Artfri	15.7[abc]	1
Rosa arkansana	Rosark	16.3±1.0[abc]	4
Oligoneuron rigidum	Solrig	17.0±2.0[abc]	6
Aster ericoides	Asteri	19.0±2.9[abc]	4
Grindelia squarrosa	Grisqu	24.6[abc]	1
Solidago canadensis	Solcan	25.0±1.8[ab]	3
Helianthus pauciflorus	Helrig	25.8±2.8[a]	6
Melilotus officinalis	Meloff	26.2±1.7[a]	4

[1] Within each column, values not labeled by common letters are statistically different (*P*=0.05).