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Radiation use efficiency and leaf CO_2 exchange for diverse C_4 grasses

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Abstract

Biomass accumulation of different grass species can be quantified by leaf area index (LAI) development, the Beer–Lambert light interception function, and a species-specific radiation-use efficiency (RUE). The object of this field study was to compare RUE values and leaf CO_2 exchange rates (CER) for four C_4 grasses. Biomass, LAI, and fraction of photosynthetically active radiation (PAR) intercepted were measured during three growing seasons. CER was measured on several dates and at several positions in the canopies. Switchgrass (*Panicum virgatum* L.) had the greatest RUE whereas sideoats grama [*Bouteloua curtipendula* (Michaux) Torrey] had the lowest. Big bluestem (*Andropogon gerardii* Vitman) and eastern gamagrass [*Tripsacum dactyloides* (L.) L.] values were intermediate. The two species with the greatest differences in RUE, switchgrass and sideoats grama, had similar relative amounts partitioned to roots. Likewise differences among species in the accumulation of soil carbon showed trends similar to total shoot biomass production. The light extinction coefficients (k) of switchgrass, big bluestem, and eastern gamagrass were smaller than for sideoats grama, implying that light was more effectively scattered down into the leaf canopy of the first three grasses. Whole canopy CER values were calculated with a stratified canopy approach, using LAI values, the Beer–Lambert formula with appropriate extinction coefficients, and CER light response curves. Differences among species in RUE were similar to these values for estimated whole-canopy CER divided by the fraction of light that was intercepted. High LAI along with low k contributed to higher RUE in switchgrass, in spite of lower values for single-leaf CER. © 1999 Elsevier Science Ltd. All rights reserved.

Keywords: Light interception; Leaf area index; Beer–Lambert formula; Radiation-use Efficiency

1. Introduction

Modelling grass biomass accumulation requires knowledge of rate-limiting processes to accurately simulate growth. Increased understanding of factors controlling grass biomass production will help define productivity of different environ-

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Nomenclature

CER	leaf CO_2 exchange rates
FIPAR	fraction of incident PAR intercepted by the leaf canopy
k	light extinction coefficient for the Beer–Lambert formula
LAI	leaf area index
PAR	photosynthetically active radiation
RUE	aboveground radiation use efficiency
Switch 1	switchgrass planted as seedlings
Switch 2	switchgrass planted by sowing seeds in the four replications of the main plots.

ments. Thus, limitations due to stress or due to canopy architecture and leaf area can be better understood.

Radiation-use efficiency (RUE) is an effective and efficient approach to quantifying plant biomass accumulation. A species' RUE may be defined as the aboveground dry weight increase per unit intercepted photosynthetically active radiation (PAR). Values for C_4 grasses such as bluestems, indiangrass [*Sorghastrum nutans* (L.) Nash], johnsongrass [*Sorghum halepense* (L.) Pers.], and elephantgrass (*Pennisetum purpureum* Schum.) can be similar to those of the C_4 crops maize (*Zea mays* L.) and sorghum [*Sorghum bicolor* (L.) Moench]. A grassland in Kansas dominated by big bluestem, little bluestem (*Schizachyrium scoparium* (Michaux) Nash) and indiangrass, had RUE values of 1.4–3.4 g MJ^{-1} *absorbed* PAR [1]. This is equivalent to 1.1–2.7 g MJ^{-1} of *intercepted* PAR, assuming 80% of intercepted PAR is absorbed [2]. Johnsongrass in Texas had an RUE of 2.3 g MJ^{-1} intercepted PAR [3]. In Florida, elephantgrass RUE [4] was 2.9 g MJ^{-1} intercepted PAR when forage yields [5] were 4700 g m^{-2}. Mean RUE of maize for several locations, using intercepted PAR, was 3.5 g MJ^{-1} and the mean for sorghum was 2.8 g MJ^{-1} [6].

The relationship between forage RUE and leaf CO_2 exchange rate (CER) is interesting from an application viewpoint and for the basic understanding of the physiology of biomass production. Close correlation between RUE and total canopy CER per unit intercepted PAR would provide better understanding of interspecies differences in RUE. Differences in canopy structure, as described with the extinction coefficient in the Beer–Lambert formula [7] and the leaf area index (LAI) could help explain species differences in RUE.

Efforts at finding a relationship between plant biomass productivity and single-leaf CER frequently fail. This was the case for comparisons among cultivars within C_3 species [8–10], for comparisons among different C_3 species [11–14], and for comparisons between C_3 and C_4 species [14,15]. Even Zelitch, who argued that such studies did not adequately integrate CER over the leaf canopy and over the season [16] admitted that the difference in productivity between two tobacco (*Nicotiana tabacum* L.) cultivars was primarily due to different leaf areas and thus different photosynthetic area and sink size [17]. When comparing big bluestem, switchgrass, and indiangrass, Polley et al. [2] concluded that differences in total canopy CER among species were more related to morphological differences than to single-leaf CER. Similarly, when Wullschleger et al. [18] studied several switchgrass populations at three locations, they found no relationship between single-leaf CER and forage yield. However lowland (tetraploid) switchgrass populations had 10–15% greater photosynthetic rates than upland (octoploid) switchgrass populations.

One trait contributing to differences among species for plant growth rate or RUE is the leaf orientation. More erect leaf types might cause

> spreading of the incoming light over more leaf area, decreasing the average light intensity intercepted by an individual leaf, [resulting in] more efficient conversion [of light] and greater yield [19].

Using the light extinction coefficient value (*k*) in the Beer–Lambert formula to quantify efficiency of light interception per unit leaf area index, more erect leaf types have smaller *k*. Growth rate was negatively correlated with *k* for different C_3 grass species [11,13] and for different perennial ryegrass selections [20], supporting the erect leaf advantage concept. Techniques of combining the Beer–Lambert formula to determine leaf illumination down in the canopy, with functions for CER response to PAR have provided realistic estimates of whole canopy productivity [21,22].

Leaf nitrogen (N) concentration has been described as a factor in plant biomass productivity, especially in N-deficient conditions [23]. Leaf CER was shown to be related to leaf-N concentration for guineagrass (*Panicum maximum*) [24], for big bluestem and indiangrass [2], and for new and old rice cultivars [25].

Differences in partitioning to roots and shoots could cause erroneous conclusions when comparing productivity among species if only the aboveground biomass is measured. Ideally, productivity should be analyzed in terms of shoots, roots, and soil carbon to compare leaf CER measurements with plant productivity.

The objective of this field study was to quantify the RUE of four C_4 grasses: sideoats grama, big bluestem, eastern gamagrass, and switchgrass. The LAI and light extinction coefficients were determined for these species to quantify how the grasses intercepted PAR. Single-leaf CER was measured and root:shoot ratios and specific leaf nitrogen were measured to assess how these contributed to differences in RUE among species. Total canopy CER was calculated by stratifying the leaf canopies into layers. Thus canopy CER was related to RUE without undertaking the complexities of diffuse:direct beam radiation [26] or the distribution of leaf nitrogen [27]. These results should help simulation modellers focus their efforts on predicting biomass production at sites dominated by C_4 grasses.

2. Methods

Studies were carried out on four C_4 grass species at the Grassland, Soil and Water Research Laboratory near Temple, Texas on Houston Black clay (fine, montmorillonitic, thermic Udic Pellustert). The grasses were located in three plot areas. In the main area, Alamo switchgrass (Switch 2), Haskell sideoats grama, and Kaw big bluestem were established by broadcasting on 18 January 1993. Plots were 5×75 m, arranged in a randomized complete block of four replicates. A plot (6.5×27 m) of eastern gamagrass (Experimental Line 1209 from Woodward, OK) planted before 1990 at a plant density of 0.97 plants m^{-2} and a plot (7×21 m) of Alamo switchgrass planted as seedlings at 1.66 plants m^{-2} (Switch 1) in 1992 were also used. The eastern gamagrass and the Switch 1 plots were each divided into three subplots of similar area.

On 24 February 1995, 100 kg N ha^{-1} as 33-0-0 and 45 kg P ha^{-1} as P_2O_5 were applied to all plots with an additional 100 kg N ha^{-1} as 33-0-0 on switchgrass. The additional N was applied to switchgrass because of the greater potential biomass for this species. This extra N did not increase the percent N in the biomass of switchgrass relative to the other species, as discussed below. In 1996, 224 kg N ha^{-1} was applied to all plots as urea (46-0-0) on 23 February. In 1997, plots were not fertilized and relied on residual N from the previous year. Grasses were burned on 22 February 1995, on 13 February 1996, and on 24 February 1997.

The fraction of PAR intercepted (FIPAR) was measured on seven dates in 1995, six dates in 1996, and six dates in 1997. There were at least five measurements of PAR above the canopy, at least ten below at different positions, and at least five more above, in rapid succession. The below measurements were always below the leaf canopy. There were three sets of these readings within each of the main replications and five sets of these readings in Switch 1 and eastern gamagrass. PAR was measured with a 0.8 m long Sunfleck Ceptometer PAR light bar sensor (Decagon Devices Inc., Pullman, WA) while moving the sensor across the plot and avoiding harvested areas. Light measurements were taken between 10 a.m. and 2 p.m. local time. Measurements taken several times during a day indicated that FIPAR measurement in this time interval were within 2% of the weighted daily mean FIPAR. The weights were the incident PAR during each measurement. Thus our data are in agreement with Monteith's [28] statement that:

> Direct measurements of radiation in crops support...that the (diurnal) variation in *k* is usually small enough to neglect, at least over the central 8 hours of the day when most assimilation takes place.

This "*k*" is the extinction coefficient in the Beer–Lambert formula.

The summed intercepted PAR was determined by linearly interpolating FIPAR to get daily estimates of this fraction. Daily incident PAR was calculated as 45% of the incident total solar radiation [29,30] measured with a standard weather station 200 m or less from the plots. Daily values for intercepted PAR were summed for each plot. RUE was determined by fitting a linear regression using the GLM procedure of SAS [31] for aboveground dry biomass as a function of intercepted PAR. The slope was the RUE. Within each grass species, differences among years in RUE were analyzed by using indicator variables for slope and intercept [32], looking for significant differences in the slope among years.

Aboveground biomass was harvested on several dates each year, from three randomly selected 0.25×0.25 m areas per plot. On the same dates, one randomly selected plant was harvested from each of the three subplots of eastern gamagrass and of Switch 1. A "plant" of eastern gamagrass was the equivalent of 1.03 m^2 of ground area and a "plant" of Switch 1 was the equivalent of 0.59 m^2 of ground area. There were seven biomass harvest dates in 1995, six dates in 1996, and five dates in 1997. All samples were dried in a forced-air oven at 70°C until weight stabilized, for as long as 8–10 days for harvests late in the season.

Green leaf and stem area was estimated by measuring the area of three to five tillers, weighing fresh, and determining total fresh weight of green material in the entire sample. The area of the green leaves and stems of the sampled tillers was measured with a LiCor LI-3100 leaf area meter (LiCor Inc., Lincoln, Nebraska). Total green area was calculated by multiplying this measured leaf and stem area by the ratio of total fresh weight of green material divided by fresh weight of the green material from subsampled tillers. Plant N concentrations were determined by the total Kjehdal Digest procedure by the Soil, Water, and Forage Testing Laboratory at Texas A&M University. Plant N concentration was expressed as g N cm^{-2} of leaf plus stem area.

We measured CER on leaves in the upper, middle, and lower third of the leaf canopies, maintaining original leaf angles and inclinations during measurements. For leaves too small to fill the chamber, leaf dimensions in the chamber were measured with calipers. The chamber was left on a leaf for more than four measurements in order to obtain a stable set of readings. Each leaf uptake measurement required 30 s. The incident photosynthetic photon flux density was measured for each leaf with a sensor mounted in the handle. There were seven CER measurement dates in 1995, three dates in 1996, and three dates in 1997. Measurements were taken throughout the day on each date. Thus PAR differences among measurements were due to positions in the leaf canopy and due to variations in incident PAR during the day. We used a CI-301PS Photosynthesis System (CID, Inc., Vancouver, WA) with a 4.5×10^{-5} m^3 cylindrical leaf chamber. Outside air was drawn through the chamber at 8×10^{-6} m^3 s^{-1}. To stabilize the CO_2 concentration, air was drawn from 4.2 m above the soil surface.

Light response curves for CER were calculated using the NLIN iterative procedure of SAS [31].

Table 1
Mean monthly weather averages, precipitation totals and vapour pressure deficit (VPD) values measured 200 m or less from the plots

Month	Maximum temperature °C	Minimum temperature °C	Solar radiation MJ m^{-2} d^{-1}	Precipitation mm	Average maximum daily VPD kPa
1994					
August	34.6	21.0	–	69	
September	31.5	16.6	–	47	
October	25.4	13.8	–	208	
November	20.5	9.5	–	54	
December	15.4	4.9	–	155	
1995					
January	15.6	3.4	10.3	20	
February	17.7	4.8	10.6	25	
March	20.1	9.6	13.5	91	0.94
April	25.2	12.9	19.9	91	1.39
May	27.9	16.9	19.6	136	1.39
June	31.4	20.7	24.9	75	2.11
July	35.1	22.7	24.2	68	3.29
August	35.3	23.3	22.0	36	2.79[a]
September	31.9	19.8	17.9	34	
October	28.1	14.4	17.2	17	
November	20.3	8.3	12.2	40	
December	16.9	6.1	9.4	19	
1996					
January	16.4	1.1	11.2	4	
February	20.2	6.5	12.3	0	
March	19.9	6.0	16.9	62	1.69
April	27.6	12.3	22.3	49	2.88
May	32.1	20.9	20.9	127	2.78
June	33.3	21.6	24.6	64	2.99
July	36.8	23.7	24.4	24	4.24
August	33.8	22.7	19.4	129	3.17
September	29.9	19.2	18.1	167	
October	25.9	14.9	13.2	14	
November	20.5	9.5	9.7	100	
December	17.4	5.2	9.7	56	
1997					
January	13.8	3.0	9.7	32	
February	15.1	6.7	9.5	129	
March	21.4	10.6	13.5	54	1.44
April	21.9	11.7	18.1	201	1.45
May	27.0	17.5	19.9	129	2.14
June	30.6	21.3	22.5	105	2.73
July[b]	34.1	22.3	27.1	15	2.75

[a] First 9 days of August.

[b] For the first 23 days of July.

Within a year, measurements were ranked by the PAR value. Means of PAR and CER were calculated for several ranges of PAR within each year. These data values were used to fit a rectangular hyperbola of the form:

$$\mathrm{CER} = a\,\mathrm{PAR}/(\mathrm{PAR} + b). \tag{1}$$

CER is the leaf CO_2 exchange rate (micromol m^{-2} s^{-1}), PAR is the photosynthetically active radiation (micromol m^{-2} s^{-1}), and a and b are fitted values. The value for a is the asymptote for the curve and the value for b is the PAR value when predicted CER is half maximum. Relative values for CER were calculated from the predicted value for sideoats grama at 2500 μMol m^{-2} s^{-1}. This allowed easier comparison among species each year for CER.

We sampled belowground biomass by taking six 0.041 m diameter cores per plot for the entire depth of the soil, three on grass plants and three between grass plants, on 13 July 1995 and 30 July 1996. The depth to the impermeable layer varied with position in the plots, ranging from 1.15 to 2.75 m. The mean depth was 1.70 m. In 1995, these cores were from replication 2 of sideoats grama, big bluestem, and Switch 2, and from the plots of Switch 1 and eastern gamagrass. In 1996, cores were from each species in replications 2 and 3 and from Switch 1 and eastern gamagrass. We washed each 0.25 m increment of each core, collected plant material on a window screen with squares 0.23 × 0.23 mm, dried the roots at 65°C for 48 h, and determined subsequent dry mass.

Soil organic carbon was determined with cores of the same diameter, taken to 1 m depth on 30 August 1995 and to 1.5 m depth on 20 July 1996. There were six cores 0.5 m apart on a transect. We also sampled cores on an adjacent cultivated field (in both years) and from a nearby native prairie (1996 only) for comparison. All six samples from a depth were combined and ground. Depth increments were 0.10 m in 1995 and 0.25 m in 1996. The roots were removed by screening. A subsample was then analyzed for organic matter, using the columetric variation of the modified Walkley–Black method [33] by the Soil, Water, and Forage Testing Laboratory at Texas A&M University.

Whole canopy CER was calculated for each species each year with the CER:PAR response curves, the LAI, and the Beer–Lambert formula, assuming incident PAR was 2500 μMol m^{-2} s^{-1}. For each year, the maximum LAI of the canopy was stratified into ten layers of equal leaf area, and the mean PAR on each layer calculated using the Beer–Lambert formula and the appropriate extinction coefficient for the species. Using the CER response to PAR for a species in a year, expected CER was calculated. Each of these CER values was multiplied by LAI/10 to get the CER for a leaf layer. The sum of these ten products was the whole canopy productivity. This was repeated with LAI equal to two-thirds the maximum for the year and equal to one-third of maximum. Means of these three estimates were then compared among species for each year.

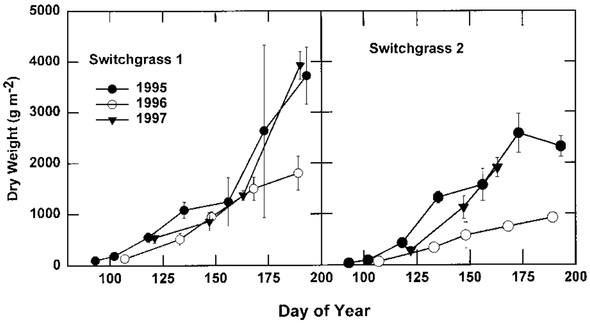

Fig. 1. Above-ground biomass of two areas of switchgrass (see text). Vertical bars are the SE values.

3. Results and discussion

In 1995, adequate rainfall precluded drought stress during the growing season, from early April to mid July (Table 1), and mean monthly maximum temperatures were greater than 31°C from June to August. Incoming solar radiation means were above 19 MJ m^{-2} d^{-1} from April to August. Rainfall from August 1995 to March 1996 was insufficient to refill the soil profile. This resulted in drought stress during the 1996 growing season, as evidenced by leaf rolling, especially for eastern gamagrass and Switch 2. This caused a shorter period of active growth in 1996. Rainfall was greatest in 1997 and plants did not suffer from drought stress.

3.1. Dry matter and leaf area index

Switchgrass had more biomass than the other

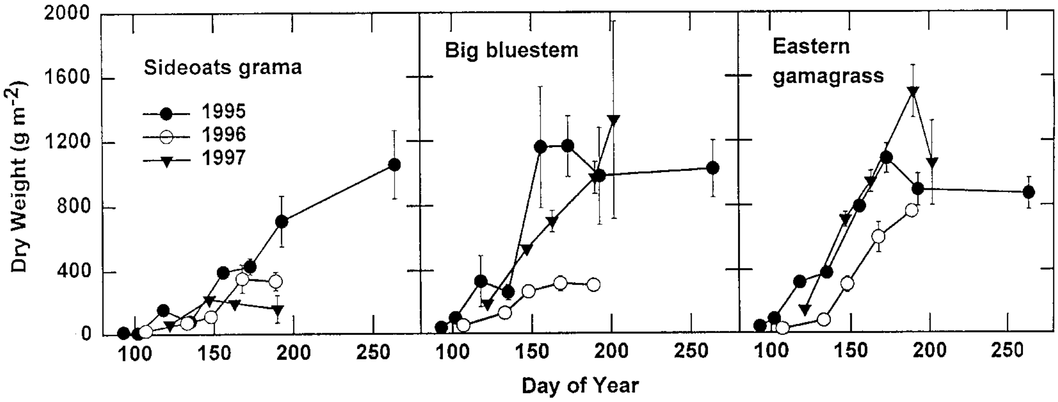

Fig. 2. Above-ground biomass of three species of grasses. Vertical bars are the SE values.

species throughout the growing seasons (Figs. 1 and 2). Sideoats grama had the least biomass and eastern gamagrass and big bluestem were intermediate. Final biomass of switchgrass in 1995 and 1997 was greater than biomass of Alamo switchgrass measured previously at several Texas locations [34]. These other locations in Texas received 67 or 134 kg N ha^{-1}, less than the 200 kg N ha^{-1} in the present study. The maximum biomass values in 1995 for Switch 2 and Switch 1 yields in the present study were 2579 and 3720 g m^{-2}. In 1997 these maximum values were 1903 and 3929 g m^{-2}. Similar values for Alamo switchgrass were reported in Auburn, AL with 2439 g m^{-2} for an August 1990 harvest and 3696 g m^{-2} for the total 1990 production [35].

Leaf area index (LAI) values were usually greatest in 1995 and 1997 (Figs. 3 and 4). In these 2 years, maximum LAI values were 17.7 and 15.7 for Switch 1, 12.9 and 11.1 for Switch 2, and 1.7 and 1.6 for sideoats grama, respectively. In these 2 years, eastern gamagrass had maxima of 4.3 and 4.8 and big bluestem had 7.7 and 7.6, respectively. The big bluestem maxima were similar to values of 5.8 to 8.0 for "Pawnee" big bluestem in 2 years in Nebraska [36]. The switchgrass maxima were greater than those in the Nebraska study for "Trailblazer" switchgrass, with maxima of 4.9 and 7.7 in 2 years.

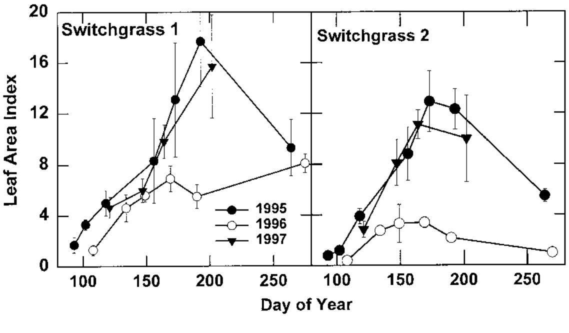

Fig. 3. Leaf area index of two areas of switchgrass (see text).

In the drier year, 1996, maximum LAI values were noticeably lower for switchgrass and big bluestem. Maxima were 8.1 for Switch 1, 3.4 for Switch 2, 2.4 for big bluestem, 1.5 for sideoats grama, and 4.2 for eastern gamagrass.

3.2. Light extinction coefficients

Pooling data across years, within each species, *k* was not significantly related to LAI for sideoats grama, switchgrass, or eastern gamagrass (Figs. 5 and 6). Thus one *k* value was sufficient for each of these grasses. The means for switchgrass and eastern gamagrass were similar, 0.33 and 0.31. The mean for sideoats grama was much greater, 1.05.

Big bluestem was the only grass which showed a trend of decreasing *k* with increasing LAI, similar to that reported for napier grass (*Pennisetum purpureum* Schumach) [37]. However, napiergrass *k* decreased from 1.1 to 0.4 as LAI increased from 2.8 to 15.3. Big bluestem *k* decreased only

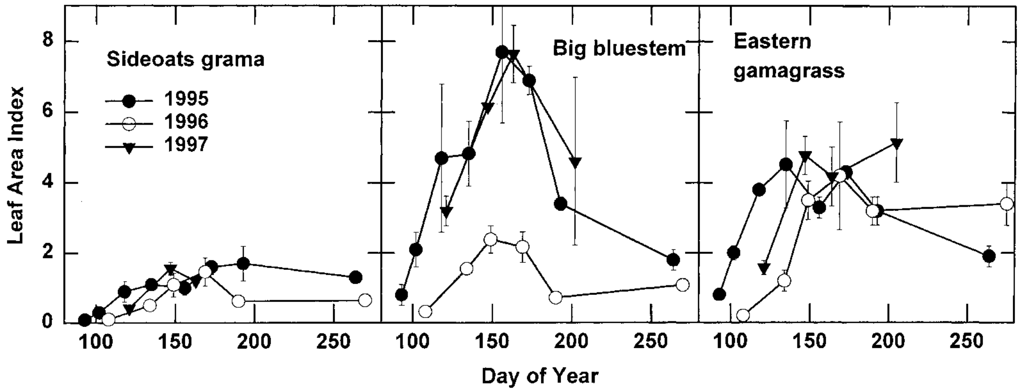

Fig. 4. Leaf area index of three species of grasses.

for LAI values less than 2.5. Above 2.5, mean *k* was 0.36, similar to switchgrass and eastern gamagrass. The values of *k* for three of the grasses in the present study were similar to the 0.3 value reported for grasses [29].

3.3. Radiation use efficiency

The data showed linear responses for dry matter as a function of cumulative intercepted PAR (Figs. 7–11, Table 2). There was no significant squared term, similar to results with crops [6]. RUE values (slope of the regression lines) were similar to the range reported in Kansas [1]. Sideoats had the lowest values, with a mean of 1.1 g MJ^{-1} and a CV of 35%. Switchgrass had the greatest mean, 4.0 g MJ^{-1} for the six data sets, with a CV of 32%. Eastern gamagrass mean was 2.1 g MJ^{-1} and the CV was 18%. Big bluestem RUE was 1.4 g MJ^{-1} and the CV was 34%.

In the 2 years with adequate soil moisture, RUE values for shoot biomass averaged 4.7 g MJ^{-1} of intercepted PAR for switchgrass, 2.2 for eastern gamagrass, 1.6 for big bluestem, and 1.2 for sideoats grama. In the year with drought-induced reduction in LAI and biomass, RUE values were 1.6 and 4.0 for switchgrass, 1.9 for eastern gamagrass, 1.0 for big bluestem, and 0.8

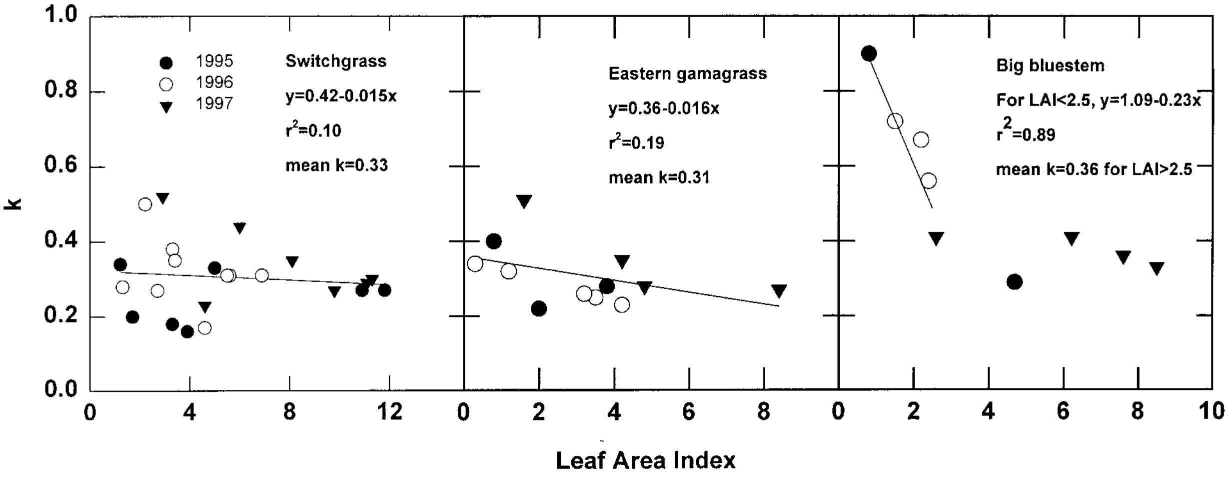

Fig. 5. Light extinction coefficients (*k*) for the Beer–Lambert formula for the three species over three years.

for sideoats grama. Using the Switch 1 1995 data set as the standard, regression analysis of the switchgrass data sets indicated that only the 1997 Switch 1 and the 1996 Switch 2 data had a significantly different slope ($\alpha = 0.05$). Slopes for sideoats grama in 1996 and 1997 were not significantly different from the slope in 1995. Thus the mean RUE of 1.1 g MJ^{-1} appeared to be adequate for sideoats across years.

For eastern gamagrass in 1997 and big bluestem in 1996 and 1997, RUE values were significantly different from the 1995 values. The dry conditions of 1996 significantly reduced big bluestem RUE. Eastern gamagrass RUE increased in response to the wet soil conditions in 1997.

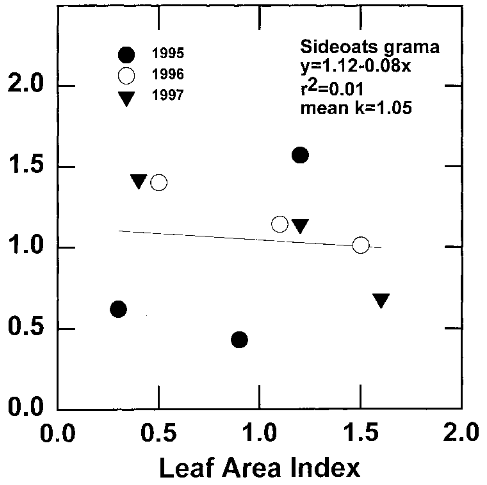

Fig. 6. Light extinction coefficients (k) for the Beer–Lambert formula for sideoats grama over three years.

Table 2
Radiation use efficiency (RUE) (mean ± SE) for above-ground biomass

	Switch 1	Switch 2	Sideoats grama	Big bluestem	Eastern gamagrass
			g MJ^{-1} intercepted PAR		
1995	4.0 ± 0.6	4.4 ± 0.5	1.0 ± 0.1	1.9 ± 0.3	1.9 ± 0.1
1996	4.0 ± 0.7	1.6 ± 0.3	0.8 ± 0.1	1.0 ± 0.1	1.9 ± 0.2
1997	5.3 ± 1.3	5.0 ± 0.8	1.5 ± 0.2	1.3 ± 0.6	2.6 ± 0.3
Means	4.4	3.7	1.1	1.4	2.1

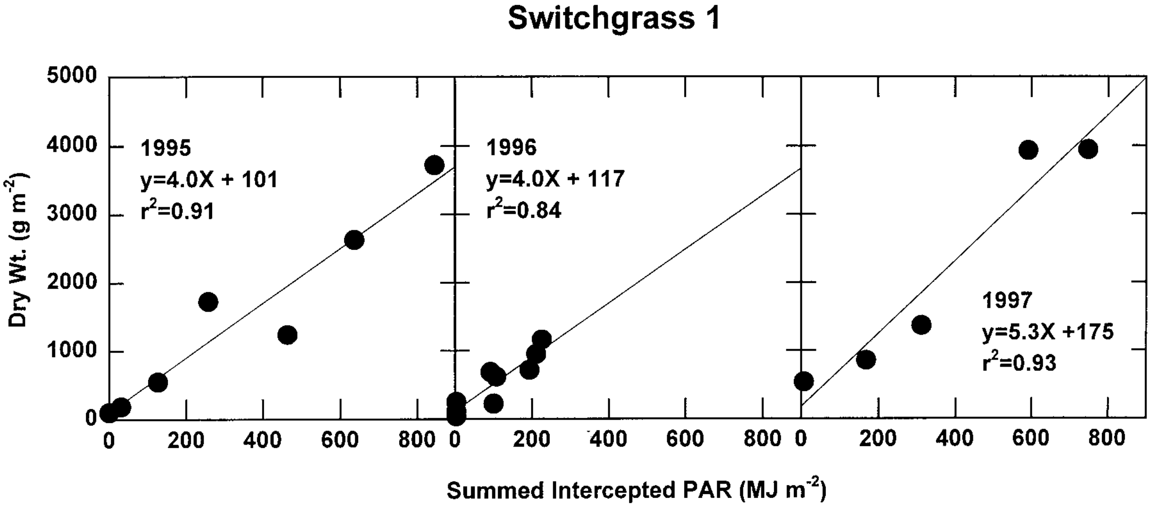

Fig. 7. For the first switchgrass plots, above-ground biomass and summed intercepted photosynthetically active radiation.

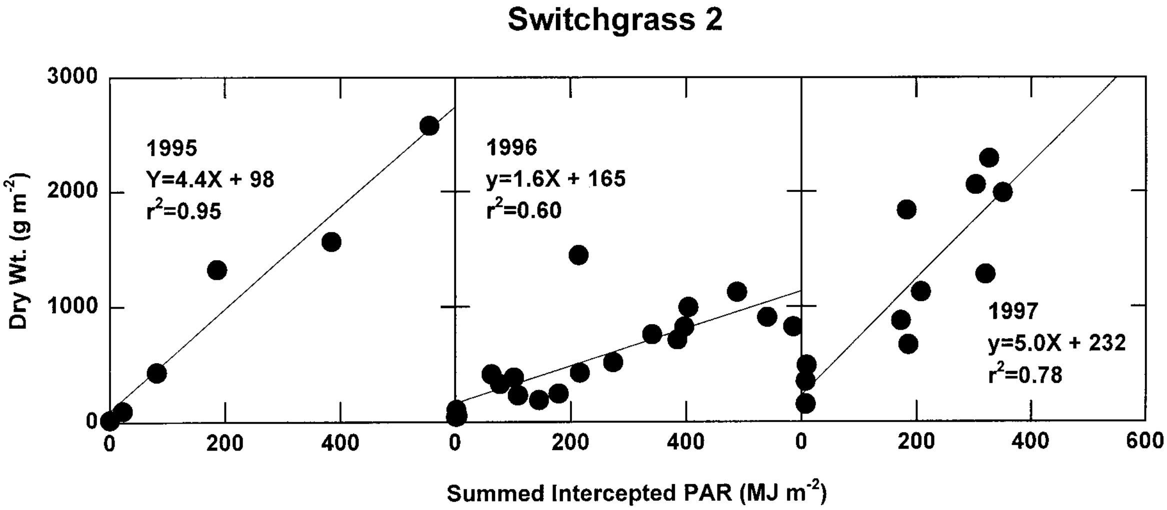

Fig. 8. For the second set of switchgrass plots, above-ground biomass and summed intercepted photosynthetically active radiation.

3.4. Leaf gas exchange

Sideoats grama had greatest CER values throughout most of the range of PAR in all years (Figs. 12 and 13). The eastern gamagrass CER data in 1997 was too limited to be useful. Big bluestem and switchgrass were similar in their responses to PAR. Values were greatest in 1996 and least in 1997 for sideoats grama, switchgrass, and big bluestem. Differences among years were not related to specific leaf nitrogen, as discussed below.

Whole canopy CER productivity was calculated taking into account the LAI of each species, the light penetration into the canopy of each species as described with the Beer–Lambert formula, and the light response functions described above. With this approach, the canopy CER/fraction of PAR intercepted by the whole canopy showed similar relative differences among

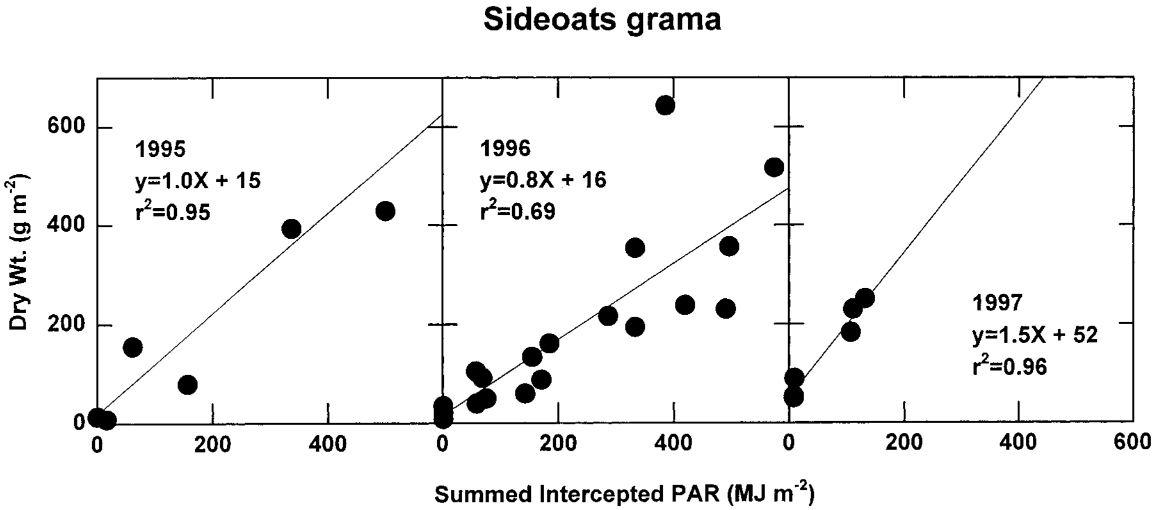

Fig. 9. For sideoats grama, above-ground biomass and summed intercepted photosynthetically active radiation.

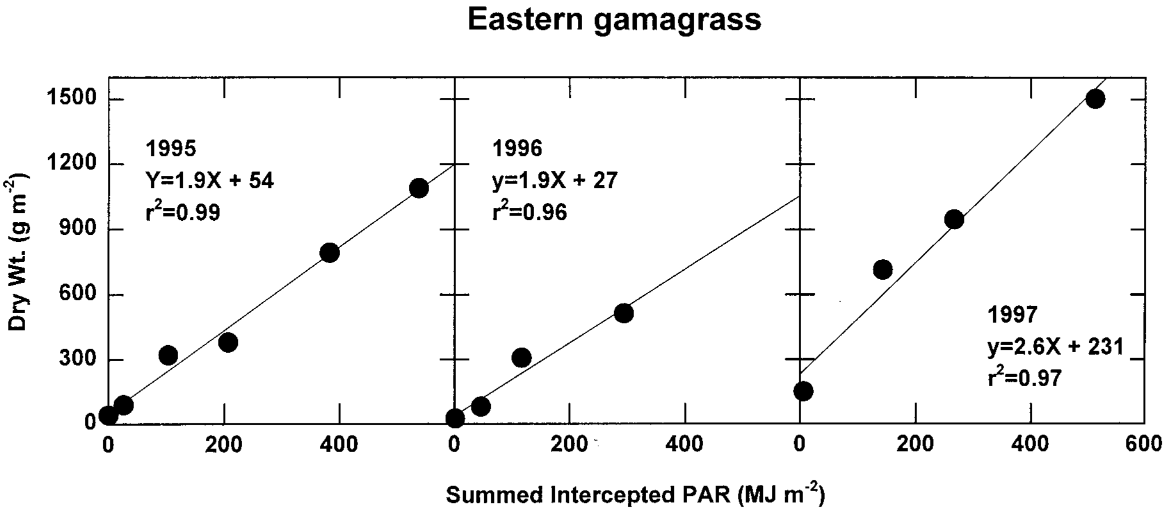

Fig. 10. For eastern gamagrass, above-ground biomass and summed intercepted photosynthetically active radiation.

species as did RUE (Table 3). Sideoats grama was 37% as great as Switch 1 for RUE over the 3 years. The value of CER/FIPAR for sideoats was 34% as great as for switchgrass. Big bluestem RUE, on average, was 47% as great as Switch 1 RUE while its CER/FIPAR value was 64% as great as for Switch 1. Finally, for 2 years with eastern gamagrass, RUE was 80% as great as Switch 1 while CER/FIPAR was 81% as great. Thus RUE values for these species showed similar relative values as these canopy-level CER values.

3.5. Nitrogen concentration

Differences among species in RUE were not related to the N concentration per unit dry weight or per unit leaf area. Using the data for the 2 wet years, N per unit dry weight showed similar trends among species, decreasing nonlinearly

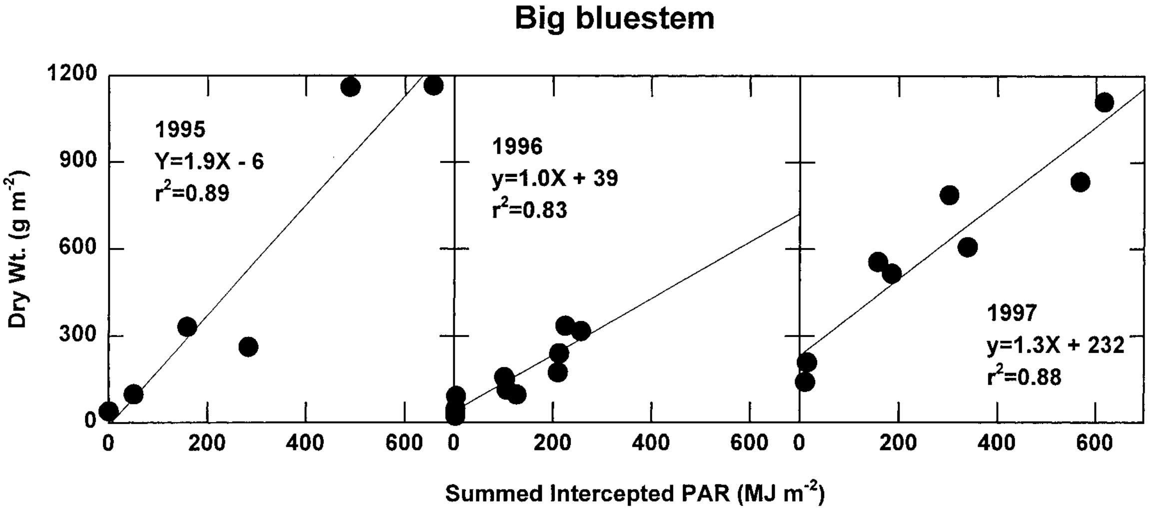

Fig. 11. For big bluestem, above-ground biomass and summed intercepted photosynthetically active radiation.

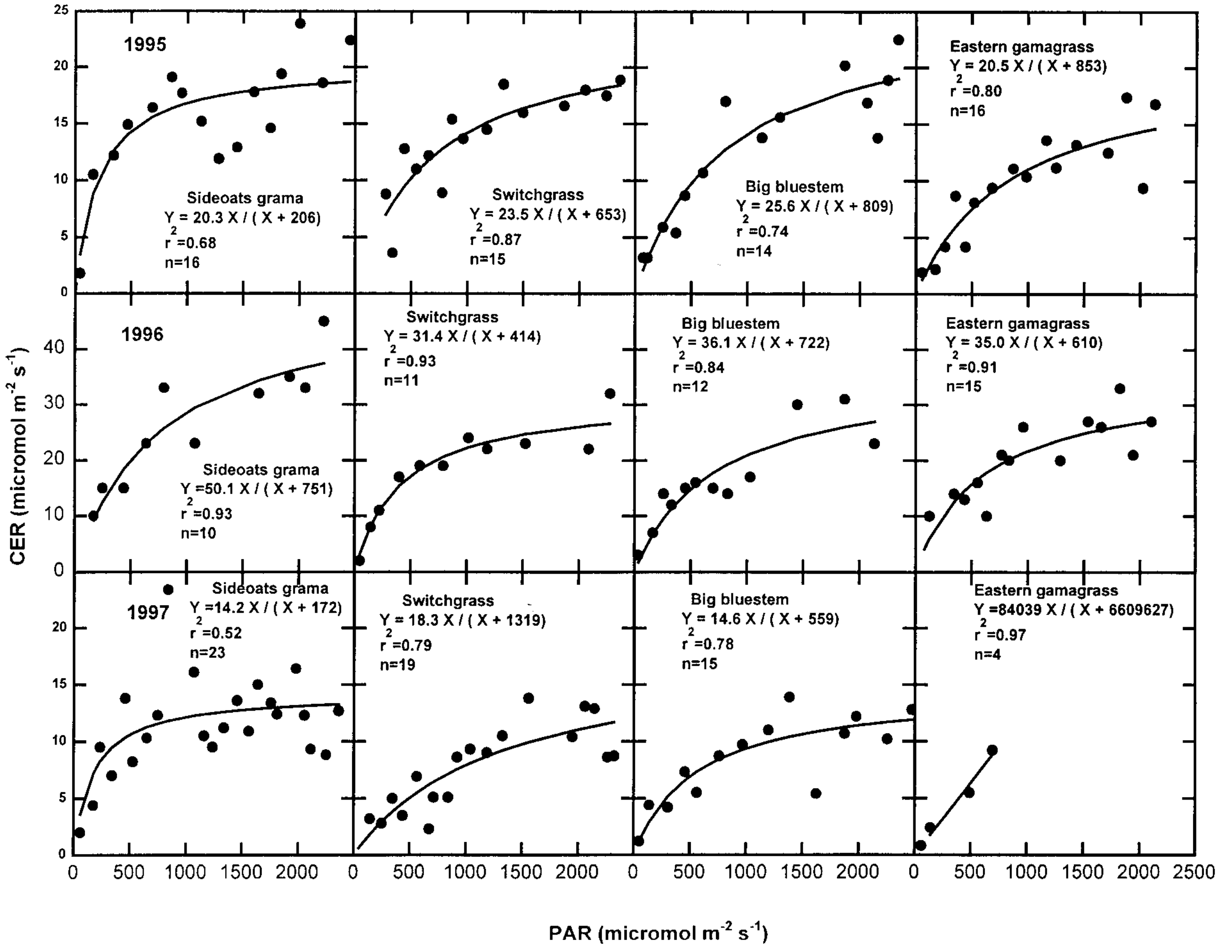

Fig. 12. Leaf carbon exchange rates for the periods of active vegetative growth. The y-axis in 1996 was larger due to the greater value for CER that year.

during the season (Fig. 14). Leaf plus stem area per unit dry weight also decreased nonlinearly during the season, with big bluestem having the greatest values early and sideoats having the lowest (Fig. 15). The resulting N concentration per unit leaf plus stem area did not show any trends of changing during the season (Fig. 16). Means for concentration per unit leaf plus stem area were greatest for sideoats grama and least for Switch 2 and big bluestem. Thus, sideoats grama, with the lowest RUE, had the greatest N concentration per unit leaf plus stem area due to its low values for leaf plus stem area per unit dry weight. Likewise, switchgrass, with the greatest RUE, did not have the greatest N concentration per unit leaf plus stem area.

Table 3
Mean radiation use efficiency (RUE) of shoots and mean canopy-level carbon exchange rates divided by fraction of PAR intercepted (CER/FIPAR; C/F), both relative to switchgrass

	1995		1996		1997		Mean	
	RUE	C/F	RUE	C/F	RUE	C/F	RUE	C/F
Sideoats grama	0.23	0.26	0.47	0.43	0.42	0.32	0.37	0.34
Big bluestem	0.43	0.71	0.60	0.32	0.38	0.90	0.47	0.64
Eastern gamagrass	0.43	0.61	1.18	1.01	–	–	0.80	0.81

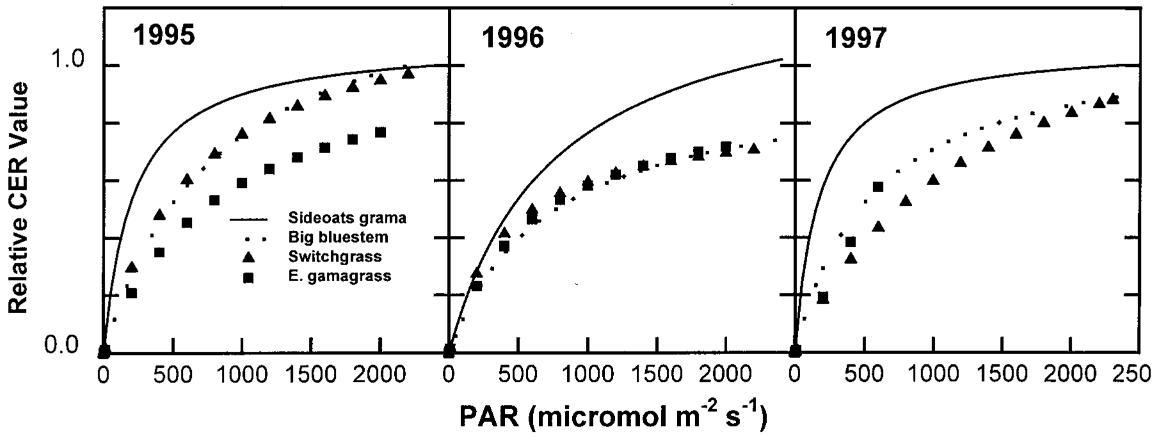

Fig. 13. Comparison of leaf carbon exchange rate functions for the four grasses. Values are relative to the predicted rate for sideoats grama at 2500 micromol m^{-2} s^{-1} of PAR. Sideoats grama is given as a line to facilitate comparisons.

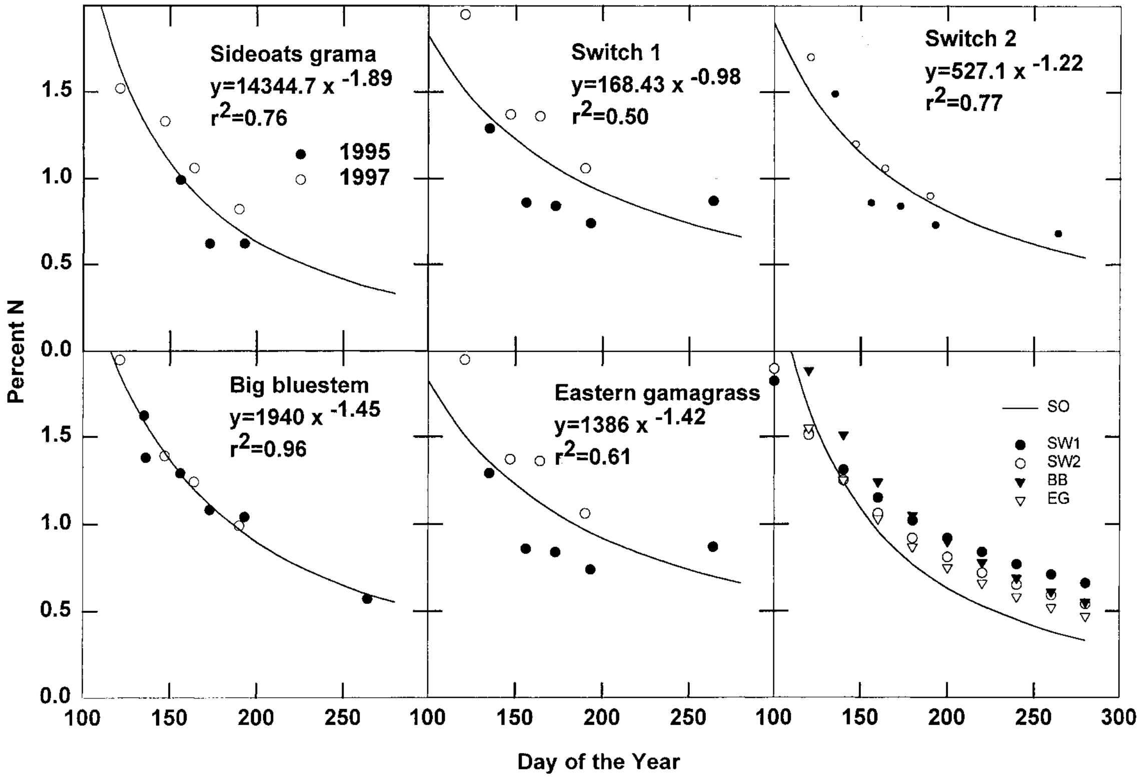

Fig. 14. Nitrogen concentration per unit dry weight of above-ground biomass for the different grasses in the two wettest years. The lower right figure compares the fitted curves for individual species. Sideoats grama is given as a line in the lower right figure to facilitate comparisons.

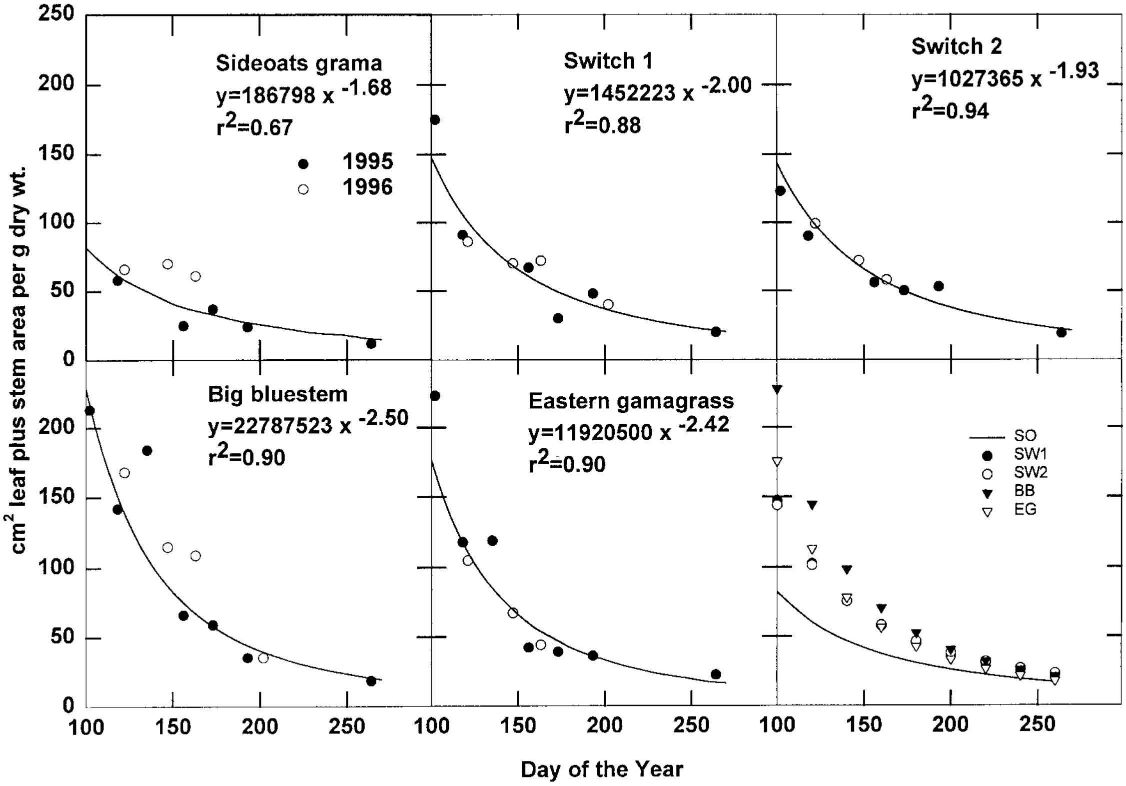

Fig. 15. Leaf area per unit dry weight for the different grasses in the two wettest years. The lower right figure compares the fitted curves for individual species. Sideoats grama is given as a line in the lower right figure to facilitate comparisons.

3.6. Root mass and soil carbon

Root biomass was measured to see how species differences in above-ground biomass production were related to the fraction of total biomass in the roots. Root biomass of these species had similar patterns of depth distribution, with sideoats grama being the shallowest rooting (Figs. 17 and 18). In 1995 and 1996, sideoats grama had 61–68% of its total root biomass in the top 0.25 m of soil and 84–85% in the top 0.5 m. By comparison, the other species had 45–54% in the top 0.25 m in 1995 and 34–65% at that depth in 1996. For the top 0.50 m the other species had 67–77% in 1995 and 50–84% in 1996.

The fraction of total plant biomass in the roots was similar between switchgrass and sideoats grama, about 0.34 in 1995 and 0.63 in 1996 (Table 4). In 1995, the root:total biomass ratio of sideoats grama was between that for Switch 1 and Switch 2. Eastern gamagrass and big bluestem had ratios greater than 0.50 in this year. Root values were generally greater in the drier, 1996 season than in 1995. The root:total mass ratios were sometimes doubled relative to the

Table 4
Ratio of root biomass divided by total biomass for the end of the growing seasons in 2 years

	1995	1996
Sideoats grama	0.35 (390)[a]	0.60 (635)
Switchgrass 1	0.37 (2142)	0.73 (1384)
Switchgrass 2	0.30 (978)	0.60 (1853)
Eastern gamagrass	0.62 (1473)	0.81 (2290)
Big bluestem	0.53 (1134)	0.83 (1654)

[a] Values in paranthesis are the amount of root biomass per unit ground area (g m^{-2}).

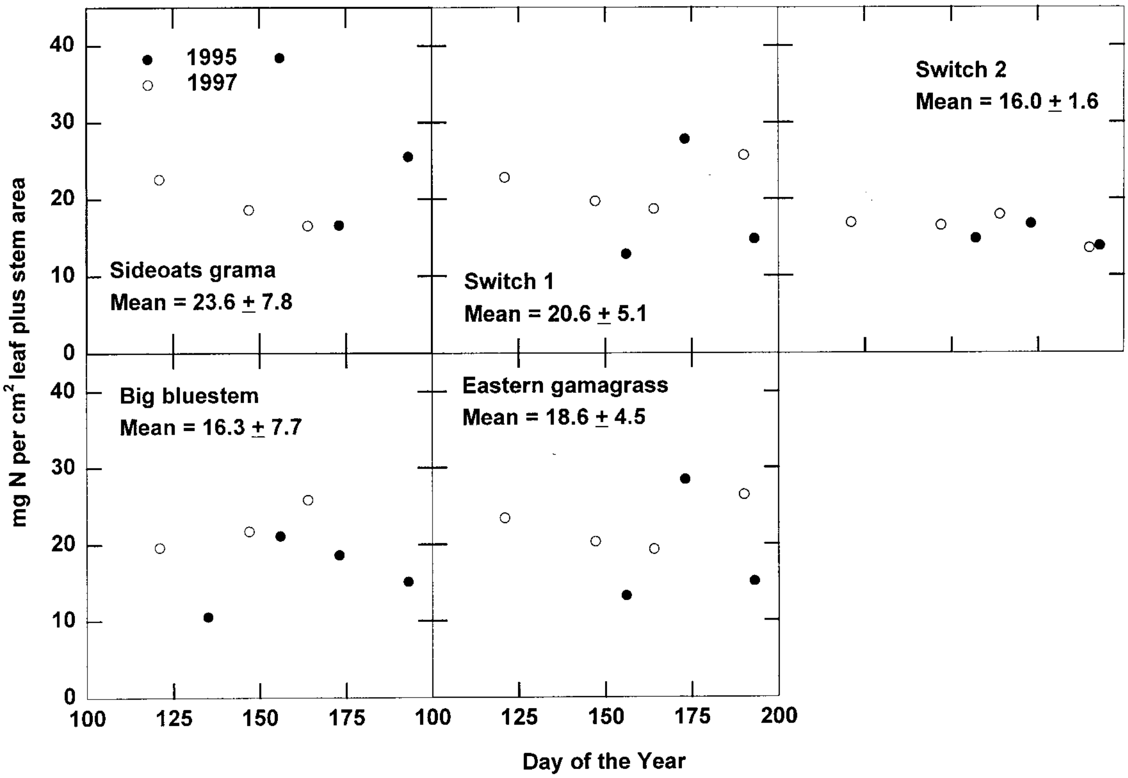

Fig. 16. Nitrogen per unit leaf plus stem area for the different grasses in the two wettest years.

ratio in 1995. Mean root mass increased in all cases except for Switch 1.

Soil carbon is a possible site where carbon losses could differ among grass species. While soil carbon often must build up for several years to see differences, we wanted to look for any obvious trends among species. Organic carbon lost to the soil for sideoats grama was not greater than for switchgrass (Table 5). The mean for sideoats was intermediate to the two switchgrass plots in 1995 and lower than the two switchgrass plots in 1996. In 1995, all grass plots means were greater than the mean for an adjacent area that had been in continuous cultivation with row crops. The nearby native prairie had the highest organic carbon.

4. Conclusions

With the exception of switchgrass, the RUE values of the grasses we studied were similar to values reported in the literature for other grasses. RUE values similar to our results for switchgrass have been reported for maize and sunflower [6]. Differences among species in RUE were not related to N concentrations, partitioning between roots and shoots, or soil organic carbon.

Single leaf CER measurements alone were of no value for describing biomass productivity in absolute terms or per unit of intercepted PAR. However, stratifying the canopy into layers, using the Beer–Lambert formula to determine mean incident PAR in each layer, and using the CER:PAR curves provided realistic estimates for

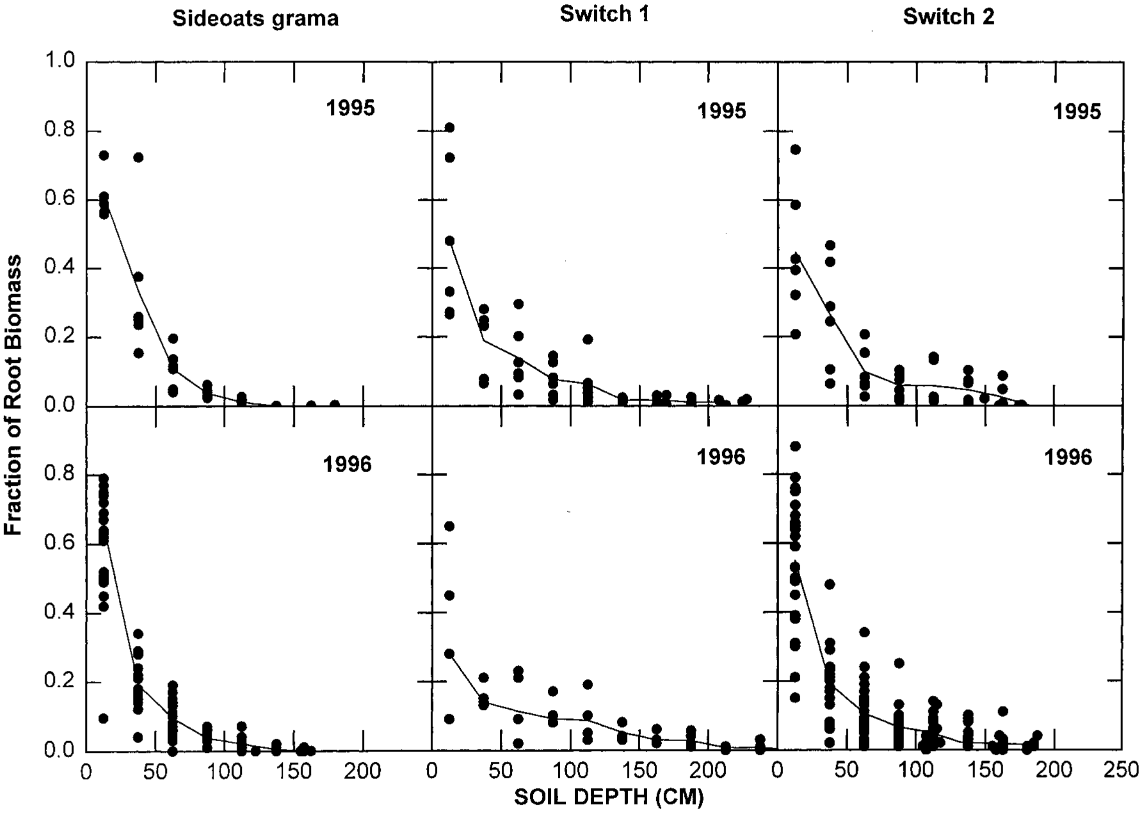

Fig. 17. Fraction of total root mass at different soil depths for sideoats grama and two plots of switchgrass. Samples were taken at the end of the 1995 and 1996 growing seasons. ines connect the mean values for each depth.

the productivity differences among species. Sideoats grama was 37% as productive as switchgrass in terms of RUE and 34% as productive in terms of canopy CER/FIPAR. Relative to switchgrass, eastern gamagrass was, on average, 80% as productive in terms of RUE and 81% as productive in terms of CER/FIPAR. For big bluestem, these values were 47 and 64%, respectively. Such a stratification technique could be used to predict productivity of a grass based on its LAI, its light extinction coefficient, and its CER:PAR curve. This could aid in the simulation modelling of grass biomass based on canopy characteristics.

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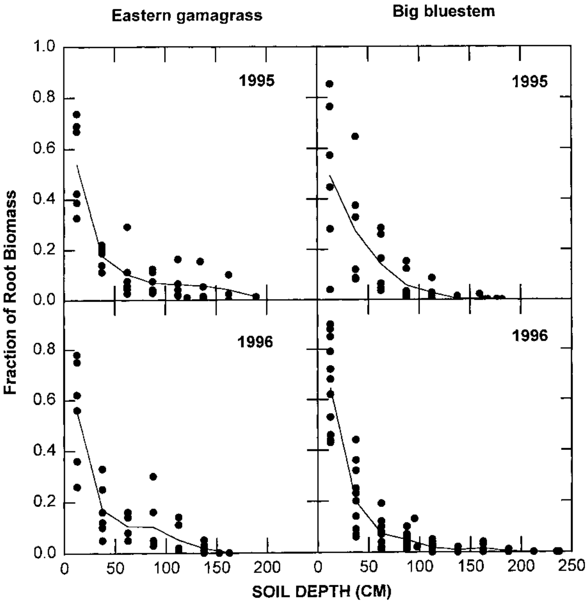

Fig. 18. Fraction of total root mass at different soil depths for big bluestem and eastern gamagrass. Samples were taken at the end of the 1995 and 1996 growing seasons. Lines connect the mean values for each depth.

Table 5
Soil organic carbon concentration (by weight). Values are for four cores per replication, with 13 to 14 July samplings in 1995 and 15 July samplings in 1996. Soil cores were taken to 1.0 m in 1995 and to 1.5 m in 1996. No SE is shown when only one replication was sampled. Switch 1 and Switch 2 are different plots of switchgrass

	Mean ± SE %	Mean/sideoats mean
1995		
Sideoats grama	1.10	1.00
Switch 1	1.15	1.04
Switch 2	1.03	0.94
Eastern gamagrass	1.04	0.95
Big bluestem	0.95	0.86
Cultivated field	0.83	0.76
1996		
Sideoats grama	0.72 ± 0.04	1.00
Switch 1	1.15	1.60
Switch 2	0.79 ± 0.06	1.10
Eastern gamagrass	0.73	1.01
Big bluestem	0.79 ± 0.05	1.10
Cultivated field	0.90	1.25
Native prairie	1.22	1.69

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