

Co-existence of a Perennial C₃ Bunchgrass in a C₄ Dominated Grassland: An Evaluation of Gas Exchange Characteristics*

R. A. HICKS**, D. D. BRISKE**,+ , C. A. CALL*** and R. J. ANSLEY++

Departments of Range Science, Texas A&M University, College Station, TX 77843–2126, U.S.A.**
Utah State University, Logan, UT 84322-5230, U.S.A.***

Texas Agricultural Experiment Station, Box 1658, Vernon, TX 76384, U.S.A.++

Abstract

Stipa leucotricha, a native C₃ perennial bunchgrass, represents an anomaly to the anticipated distributional patterns of C₃ species because it is restricted to grasslands below 35 °N latitude. We evaluated the seasonal patterns of gas exchange which potentially confer *S. leucotricha* with the ability to compete with a co-dominant C₄ bunchgrass, *Bouteloua curtipendula*, in an environment presumably most suitable for C₄ species. Gas exchange estimates and tiller water potentials (Ψ) were taken *in situ* for one diurnal period each month during the 1987 growing season. *S. leucotricha* displayed a maximum seasonal net photosynthetic rate (P_N) in March when sufficient leaf area had not yet developed for sampling in the C₄ species. Maximum daily P_N in *S. leucotricha* occurred at leaf temperatures comparable to those of the C₄ species, 30 – 40 °C, but water-use efficiencies conformed to those anticipated for C₃ species. Both species maintained low P_N at Ψ of –3.0 to –4.0 MPa, but *S. leucotricha* attained a greater percentage of its maximum seasonal P_N at more negative Ψ than did *B. curtipendula*. An estimate of seasonal carbon assimilation, derived by summing the mean monthly P_N , indicated that both species assimilated approximately 1.5 mol (CO₂) m⁻² of leaf area during the season. A prolonged period of carbon assimilation, over an uncharacteristically wide temperature range, confers this C₃ grass with the capability to co-exist with C₄ competitors in grasslands at relatively low latitudes.

Species within the *Poaceae* assimilate carbon *via* the Calvin-Benson (C₃) or Hatch-Slack (C₄) photosynthetic pathways. Each pathway possesses unique biochemical and anatomical features that confer adaptive value in specific environments. A single pathway is not optimally adapted to all environments because each encounters physiological limitations over a range of abiotic

* Received 23 May 1989.

+ Address for correspondence.

Acknowledgements: Research was supported by the Texas Agricultural Experiment Station and Texas Water Development Board. This manuscript is published with approval of the Experiment Station as technical publication 24818. The assistance of D. R. Black in generating graphics and editorial contributions of M. C. Drew and R. J. Ansley are gratefully acknowledged.

variables (*i.e.*, cost of the CO₂ pump in C₄ species or photorespiration in C₃ species; Ehleringer 1978, Ehleringer and Pearcy 1983). C₃ species are assumed to possess a physiological advantage in cool, moist, environments with relatively low irradiance, while C₄ species are assumed to perform nearer their physiological optimum in warm, dry environments with high irradiance. There is an increase in the percentage of C₃ species with increasing latitude or elevation substantiate the generalization (Teeri and Stowe 1976, Stowe and Teeri 1978, Boutton *et al.* 1980), but several exceptions have also been noted (see Pearcy and Ehleringer 1984).

Several C₄ species can conduct photosynthesis at temperatures substantially lower than anticipated for this pathway. *Atriplex confertifolia*, a C₄ shrub, exhibited maximum rates of photosynthesis in the cool spring months and an annual rate of carbon assimilation comparable to *Ceratoides lanata*, a co-existing C₃ shrub, in an environment presumably best suited to C₃ species in N. W. Utah (Caldwell *et al.* 1977). Similarly, *Spartina anglica*, a C₄ grass which grows in coastal salt marshes of N. W. Europe, photosynthesizes at rates comparable to C₃ species at temperatures of 5 – 10 °C (Long and Woolhouse 1978, Dunn *et al.* 1987). Temperature is also a predominate abiotic variable influencing growth initiation and minimizing competition between *Agropyron smithii* (C₃) and *Bouteloua gracilis* (C₄), which co-exist in the shortgrass prairie of eastern Colorado (Kemp and Williams 1980, Christie and Detling 1982, Monson *et al.* 1986). However, early season air temperatures above ambient in the microtopographic positions occupied by *B. gracilis* and frequent, drought-imposed restrictions on the length of growing season mirror the temporal separation of growth between these two species (Monson *et al.* 1986).

Stipa leucotricha Trin. & Rupr. represents somewhat of an anomaly to the anticipated latitudinal patterns of C₃ species because its range is confined within 25° and 35° N latitude in the south-central U.S. and northern Mexico (Fig. 1; Gould 1975, Waller and Lewis 1979). Strong correlations between the distribution of C₄ grasses and minimum daily temperatures during the warmest month of the growing season indicate that approximately 60% of the grassland of North America possesses the C₄ pathway at 33° N latitude (Teeri and Stowe 1976). *S. leucotricha* functions as a co-dominant with *Bouteloua curtipendula* (Michx.) Torr. (C₄) in the Rolling Plains of north-central Texas (Heitschmidt *et al.* 1982). The objective of this investigation was to evaluate the seasonal patterns of gas exchange and water potential which potentially confer *S. leucotricha* with the ability to successfully compete with a C₄ co-dominant in an environment presumably most suitable for C₄ species. Both species possess comparable growth forms and rooting habits prompting us to evaluate physiological processes as the most probable means of adaptation.

MATERIALS AND METHODS

The study site was located on the Wagon Creek Spade Ranch near Throckmorton, Texas (99° 14' W, 33° 20' N), in the Rolling Plains Resource region which comprises approximately six million ha of rolling to rough topography in north-central Texas (Fig. 1). Species associated with the two co-dominants include *Buchloe dactyloides* (C₄), *Aristida* spp. (C₄) and *Sporobolus cryptandrus* (C₄) (Waller and Lewis 1979, Heitschmidt *et al.* 1982). A sparse over story of *Prosopis glandulosa* var. *glandulosa* is common throughout much of the region.

Experimental plants were located in both weighing lysimeters and adjacent plots. Lysimeters were established by drilling a section of steel pipe (76 cm dia.) into the ground to a depth of 120 cm to enclose established monocultures of each species from native grassland. Six lysimeters, three per species, were established in a co-

tely randomized design. Three paired-plots of each species (1 m²), located within 15 m of the lysimeters on similar soils, were used to compare physiological and morphological responses of plants within the lysimeters to those on undisturbed sites. Hydrological data collected within the lysimeters will be reported separately.

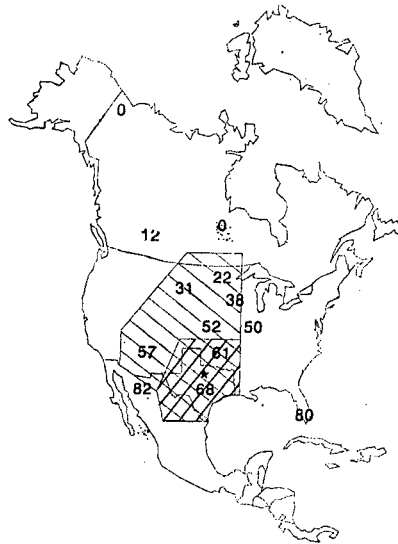


Fig. 1. Illustration of the percentage of C₄ grasses at various locations in North America, the distributional range of *S. leucotricha* (crosshatched lines) and *B. curtipendula* (diagonal lines), and location of the study site (star). (Illustration modified from Teeri and Stowe 1976.)

Although physiological responses of both species displayed similar seasonal trends within lysimeters and paired-plots, lysimeters significantly affected leaf temperature (T), net photosynthetic rate (P_N) and produced a significant species \times lysimeter interaction for stomatal conductance (g) ($p < 0.05$). Consequently, data could not be pooled between lysimeters and paired-plots. It is recognized, however, that lysimeter effects reflected changes in microclimate or resource-availability induced by lysimeter installation, *i.e.*, heat loading or plant density, rather than inherent physiological differences between plant populations.

Instantaneous measurements of transpiration (E), P_N and g were taken on leaf blades of one to four tillers *in situ* with a portable gas exchange system (*Li-Cor* model *LI-6000*). Gas exchange measurements were recorded for one diurnal period each month from mid-March to mid-October 1987. Diurnal gas-exchange measurements were initiated 1 h post-sunrise or as soon as dew accumulation had dried and repeated at 3 h intervals on the same leaf material until 1 h prior to sunset on each sampling date.

A minimum of 6 cm² of leaf area is required within the cuvette for accurate esti-

mation of P_N . Typically, three to four tillers of *S. leucotricha* (each with two blades) and one to two tillers of *B. curtipendula* (each with three to five blades) were included in each sample to exceed the minimum area. Two separate groups of tillers were randomly selected for measurement within each lysimeter and paired-plot ($n =$ per species per date). A standardized leaf orientation within the cuvette, parallel to the soil surface, was employed during each measurement to standardize radiative microenvironments.

Initial CO_2 concentrations and relative humidity within the cuvette were maintained as near to ambient as possible at each sampling period during the season. Cuvette relative humidity, cuvette air temperature, T and photosynthetic photon flux density (I) outside the cuvette (perpendicular to the soil surface) were monitored during each sample period. Leaf area was harvested after the cuvette was removed on the final diurnal reading for each sampling date and estimated with a leaf area meter to compute gas exchange rates on an area basis. A pressure chamber was used to estimate xylem water potentials of individual tillers (Ψ). Three to five tillers were evaluated for each species, both in the lysimeters and in the paired-plots, at each sampling period. Ψ values were obtained predawn and 30 min preceding the second, third and fourth gas exchange measurements. Ψ during the first gas exchange measurement was assumed to be similar to the predawn measurement.

P_N , E , P_N/E , g and Ψ were subjected to analysis of variance procedures to test for date, species and lysimeter effects. A split-plot analysis was used to evaluate diurnal response when repeated measurements were taken on the same experimental unit. Seasonal responses were evaluated with procedures appropriate for a completely randomized design. Least squares means were used for mean separation when significant differences were indicated by analysis of variance.

RESULTS

Abiotic Variables

Total annual precipitation for 1987, 560 mm, approached the 30 year average of 624 mm, but the distribution was highly irregular (Fig. 2A, B). Precipitation was 21 % above average during the first six months of 1987 but decreased to 56 % of the 30 year average during the last six months. I ranged between 1170 to 1690 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the time of the second gas exchange measurement within a diurnal period (time of optimal I and Ψ approximately 4 to 5 h post-sunrise; Table 1). Mean ambient air temperatures for each sample date increased from a low in March, 6.5 °C, to a season high of 31.6 °C in June and then declined for the remainder of the season. The 1987 growing season for *S. leucotricha* began in early March and extended through October, while that of *B. curtipendula* extended from mid-April through October.

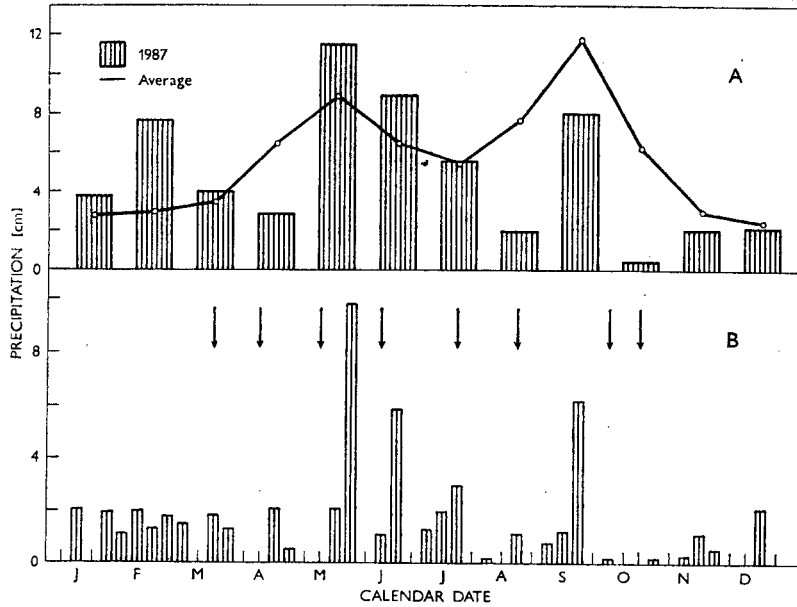


Fig. 2. (A) Cumulative monthly precipitation for 1987 and 30 year mean monthly precipitation and (B) cumulative weekly precipitation recorded at the study site during 1987. Arrows represent the times gas exchange measurements were taken.

Table 1

Mean photosynthetic photon flux densities [I ; $\mu\text{mol m}^{-2} \text{s}^{-1}$] at the time of the second diurnal gas exchange measurement, maximum, minimum and mean air temperatures [$^{\circ}\text{C}$] and mean relative humidity [RH; %] on each of eight dates that gas exchange measurements were taken for *S. leucotricha* and *B. curtipendula*.

Month	I	Temperature			RH
		max	min	mean	
March	1692 ± 89	14.0	2.1	6.5	48.3
April	1842 ± 52	30.5	16.2	24.3	21.3
May	1596 ± 88	22.4	16.2	19.7	59.6
June	1492 ± 98	37.1	20.3	31.6	20.1
July	1330 ± 98	34.4	19.5	25.9	19.0
August	1534 ± 110	—	—	—	—
September	1171 ± 83	30.6	14.0	21.7	18.2
October	1490 ± 79	25.9	11.0	15.2	20.3

Mean Seasonal Responses

B. curtipendula exhibited P_N equal to or greater than that of *S. leucotricha* throughout most of the season, but a significant species \times date interaction was ob

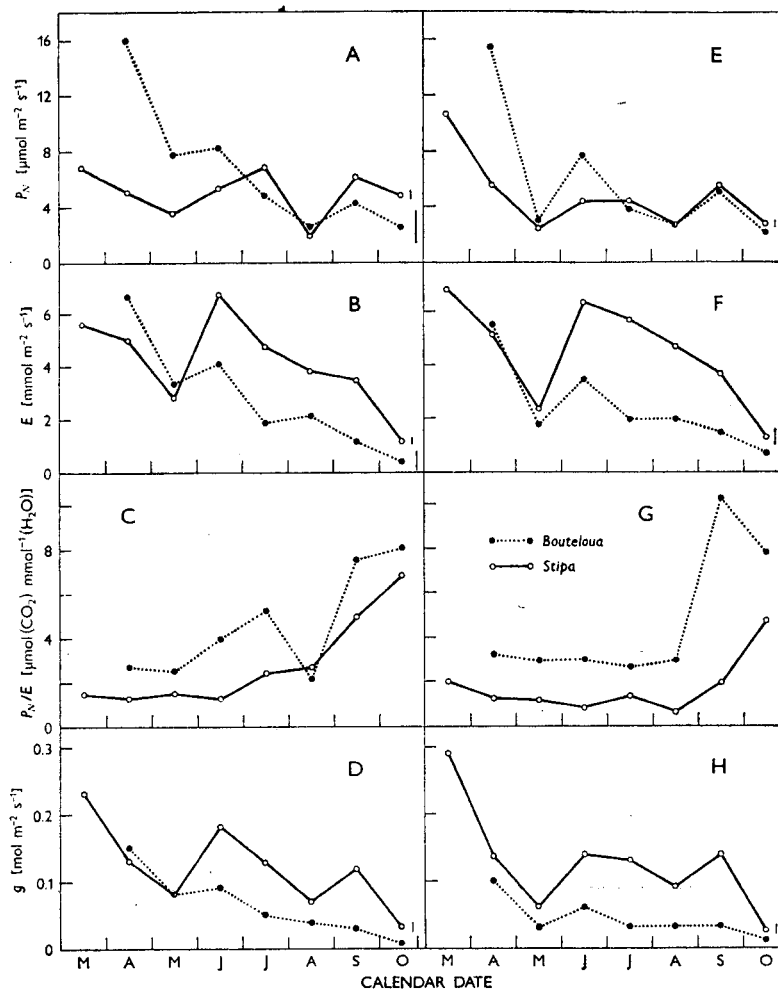


Fig. 3. Mean diurnal estimates of net apparent photosynthesis P_N , transpiration (E), P_N/E and stomatal conductance (g) for *S. leucotricha* and *B. curtipendula* within lysimeters and adjacent paired-plots for eight dates during 1987.

served ($p < 0.01$; Fig. 3A, E). P_N of *B. curtipendula* exceeded that of *S. leucotricha* by 2-fold inside the lysimeters and 2.5-fold within the paired-plots early in the growing season ($p < 0.01$). In July, *S. leucotricha* exhibited a significantly higher P_N than

did *B. curtipendula* ($p < 0.05$). From August through October, the two species demonstrated similar P_N . P_N inside the lysimeters was higher than within the paired-plots throughout the season ($p < 0.05$).

E of *S. leucotricha* was equal to or greater than that of *B. curtipendula* throughout most of the season, but a significant species \times date interaction was observed ($p < 0.01$; Fig. 3B, F). E of *B. curtipendula* was significantly higher than that of *S. leucotricha* during April ($p < 0.05$), but significantly lower during June through September ($p < 0.01$). The magnitude of these differences decreased as the season progressed.

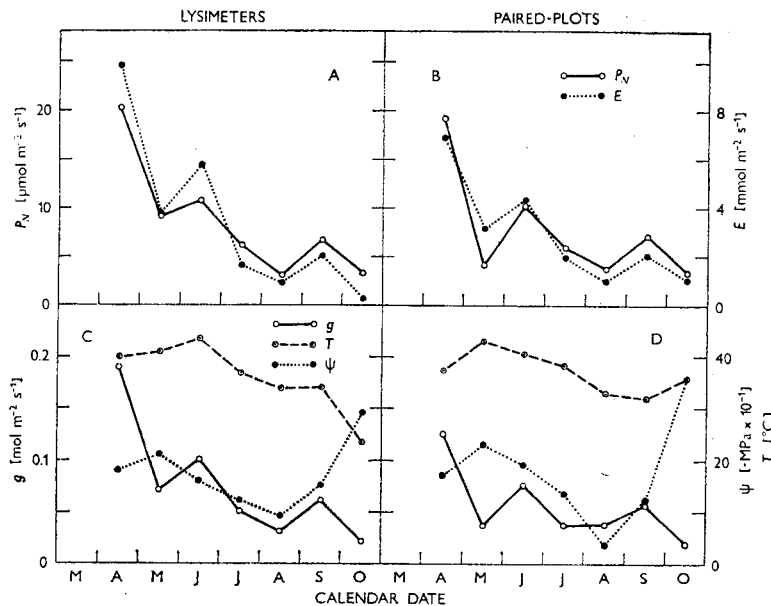


Fig. 4. Maximum net apparent photosynthesis P_N recorded within eight diurnal periods and associated values for transpiration (E), stomatal conductance (g), leaf temperature (T) and tiller water potential (Ψ) for *B. curtipendula* within lysimeters and adjacent paired-plots during 1987.

P_N/E of *B. curtipendula* was equal to or greater than that of *S. leucotricha* throughout the season, but a significant species \times date interaction was observed ($p < 0.05$; Fig. 3C, G). P_N/E of *B. curtipendula* was significantly greater than that of *S. leucotricha* in June, July, September and October within the lysimeters and in September and October within the paired-plots ($p < 0.05$). P_N/E of *S. leucotricha* within the lysimeters was 2-fold greater than within the paired-plots ($p < 0.05$). A significant species \times lysimeter interaction was not observed, indicating that both species were responding in a similar manner even though absolute differences occurred between the lysimeters and paired-plots.

S. leucotricha generally displayed greater g than did *B. curtipendula* throughout

the season, but a significant species \times date interaction was observed ($p < 0.05$, Fig. 3D, H). Early in the season, g was similar for both species. However, g of *leucotricha* increased to two to four times that of *B. curtispindula* in June and remained at this level through September ($p < 0.01$). No significant lysimeter \times date effect occurred for g . A significant species \times lysimeter interaction was observed indicating that g of *S. leucotricha* within the paired-plots was higher than within the lysimeters, while g of *B. curtispindula* within the paired-plots was lower than within the lysimeters ($p < 0.05$).

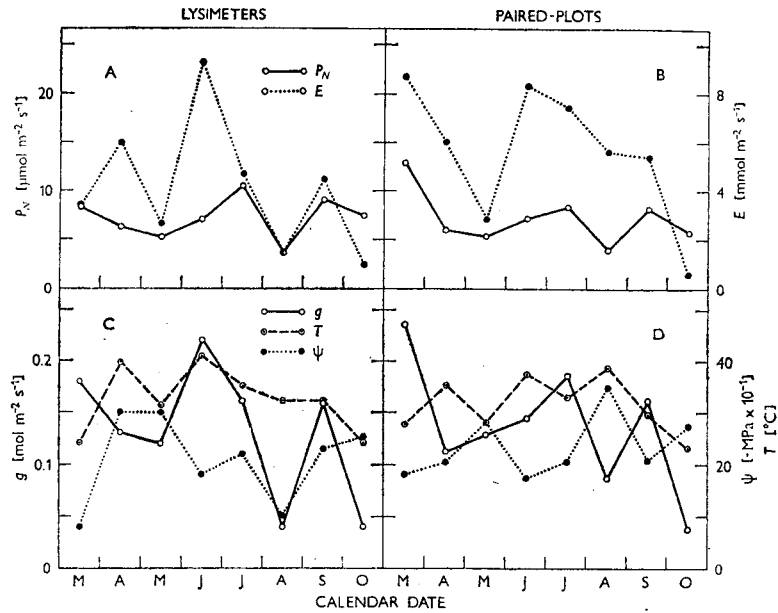


Fig. 5. Maximum net apparent photosynthesis P_N recorded within eight diurnal periods and associated values for transpiration (E), stomatal conductance (g), leaf temperature (T) and turgor potential (Ψ) for *S. leucotricha* within lysimeters and adjacent paired-plots during 1981.

T of the two species remained within 1.5°C of each other throughout the season but T of *B. curtispindula* was significantly greater than that of *S. leucotricha* in April, June, July and September ($p < 0.05$) (not shown). T was significantly warmer within the paired-plots than within the lysimeters ($p < 0.05$), but a significant species \times lysimeter effect was not observed. Mid-day Ψ of *S. leucotricha* was approximately 1.0 MPa lower than that of *B. curtispindula* on all dates except April, June and October when Ψ of the two species were equal ($p < 0.05$). Pre-dawn Ψ did not vary significantly between species. Ψ decreased significantly as the season progressed ($p < 0.05$). No significant lysimeter, lysimeter \times date or species \times date interactions were observed for Ψ . T and Ψ values associated with the occurrence of maximum I for each of the diurnal periods are presented in Figs. 4 and 5.

Maximum Photosynthesis and Associated Variables

Maximum daily P_N of *B. curtipendula*, $20 \mu\text{mol m}^{-2} \text{s}^{-1}$, occurred in April, decreased dramatically in May and stabilized at approximately $5 \mu\text{mol m}^{-2} \text{s}^{-1}$ during July through October (Fig. 4A, B). T at the time of maximum daily P_N ranged from $23 - 43^\circ\text{C}$ (Fig. 4C, D). Associated daily maximum E and g values paralleled P_N as anticipated. Associated Ψ ranged between -0.9 and -3.0 MPa within the lysimeters and -0.4 and -2.3 MPa within the paired-plots. An increase in Ψ to -0.4 MPa in August (paired-plots), following a 20 mm precipitation event, did not appreciably increase P_N . Conversely, P_N of approximately $4 \mu\text{mol m}^{-2} \text{s}^{-1}$ was observed when Ψ ranged between -3.0 and -4.0 MPa. Seasonal maximum P_N of *B. curtipendula* was attained at a T of 38°C and Ψ of -2.0 MPa (Fig. 4A–D).

Maximum daily P_N of *S. leucotricha* occurred in July within the lysimeters ($11 \mu\text{mol m}^{-2} \text{s}^{-1}$) and in March within the paired-plots ($13 \mu\text{mol m}^{-2} \text{s}^{-1}$) at a T of 35 and 31°C , respectively (Fig. 5A, B). The three subsequent seasonal maxima (July and September) occurred at a T of 32 , 36 and 33°C (Fig. 5C, D). Associated daily maximum E and g values were erratic and less closely coupled to P_N than those of *B. curtipendula*. Three to four-fold increases in E were associated with only modest increases in P_N as the season progressed. Ψ at the time daily maximum P_N was attained ranged between -0.9 and -4.3 MPa (Fig. 5C, D). Low P_N values, $5 \mu\text{mol m}^{-2} \text{s}^{-1}$, were observed at Ψ between -3.0 and -4.0 MPa. Seasonal maximum P_N of *S. leucotricha* was attained at a T of 30°C and Ψ of -1.9 MPa (Fig. 5A–D).

Both species attained maximum daily P_N at similar times during the diurnal period within the lysimeters and the paired-plots (not shown). In instances where the times of absolute maxima differed, they did not significantly differ from secondary or tertiary diurnal seasonal maxima with only one exception; *B. curtipendula* attained maximum daily P_N 3 h later than did *S. leucotricha* within the paired-plots in April. Ψ of *S. leucotricha* was lower than that of *B. curtipendula* at the time of maximum daily P_N within both the lysimeters and paired-plots on all dates except June and October (Figs. 4A–D and 5A–D).

DISCUSSION

Seasonal mean and maximum diurnal P_N values indicate that *B. curtipendula* conforms to the published norm for a C₄ species with regard to temperature optima and P_N/E . *S. leucotricha* displayed daily maximum P_N comparable to that of *B. curtipendula* at T of $30 - 40^\circ\text{C}$ and P_N/E values 2- to 4-fold less than *B. curtipendula* (Fig. 3C, G; Fig. 5A–D). These temperatures are above the established temperature optimum for photosynthetic activity in the C₃ pathway, while the relative ranking of P_N/E between the two species conform to the published norm (Percy *et al.* 1981, Percy and Ehleringer 1984). Photosynthetic activity at T in excess of 30°C suggests

that RuBP-carboxylase is active over an uncharacteristically wide temperature range in this species. P_N values of *S. leucotricha* were comparable to those of the C_3 species throughout much of the season in spite of the inherent inefficiencies associated with C_3 photosynthesis at high temperatures (a reduction in the $CO_2 : O_2$ ratio which increases photorespiration and decreases quantum yield; Ehleringer and Pearcy 1983). This response is analogous to the adjustment in temperature optima displayed by two C_4 species, *Spartina anglica* and *Atriplex confertifolia*, which were associated with C_3 species in cool temperate environments (Caldwell *et al.* 1977, Long and Woolhouse 1978).

Although, maximum seasonal P_N displayed the anticipated order between species the rates were quite low in comparison with those of other native grasses, even in the early portion of the year when precipitation exceeded the long-term mean (Fig. 2A, B; Monson *et al.* 1986). Ψ in excess of -1.0 MPa on all but two sampling dates for both species undoubtedly reduced maximum P_N (Fig. 4A–D; Fig. 5A–D Brown and Trlica 1977, Kemp and Williams 1980). P_N of *S. leucotricha* appeared more responsive to intermittent increases in Ψ associated with small rainfall events than that of *B. curtipendula* (*e.g.*, Sala and Lauenroth 1982). Since both species experienced similar levels of water deficit and no new leaf production was observed this response is assumed to have been physiological in origin. Both species were capable of maintaining low P_N at Ψ values between -3.0 to -4.0 MPa, but *S. leucotricha* attained a greater percentage of its seasonal maximum P_N at more negative Ψ than did *B. curtipendula* (Fig. 4A–D; Fig. 5A–D). This suggests that *S. leucotricha* may be capable of partially compensating for low P_N/E with greater drought tolerance. Brown and Trlica (1977) suggested that P_N of *Agropyron smithii* (C_3) was more tolerant of water stress than that of *Bouteloua gracilis* (C_4) (but see Kemp and Williams 1980). This difference is presumably secondary to temperature and soil water availability in regulating the growth dynamics of *S. leucotricha* and *B. curtipendula*.

Although maximum P_N of *S. leucotricha* was lower than that of *B. curtipendula*, photosynthesis can potentially be maintained for a greater portion of the year. For example, *S. leucotricha* exhibited seasonal maximum P_N in March when *B. curtipendula* still had not developed sufficient leaf area for sampling. Abnormally cool temperatures and high precipitation in May and early June undoubtedly allowed *S. leucotricha* to maintain a large amount of live leaf area and continue photosynthesis for a greater portion of the summer than usual (Table 1, Fig. 2A, B). This species usually senesces and becomes quiescent in early summer. In addition, if precipitation had been available in the autumn, *S. leucotricha* could have potentially continued to assimilate carbon through November and December as temperatures and vapor pressure deficits decreased. Alternatively, *B. curtipendula* employed a strategy of rapid carbon assimilation over a relatively short portion of the year when temperature and soil water availability were most favorable. Temporal separation of growth between species with contrasting photosynthetic pathways appears to be

of greater significance to resource partitioning in this grassland than in the shortgrass prairie (Monson *et al.* 1986) or cold-desert shrub communities (Caldwell *et al.* 1977) referenced previously. The potential growing season in the two latter communities is constrained to a greater extent by the availability of soil water during the portion of the year when temperature is favorable for growth than in the Rolling Plains Resource region.

An estimate of seasonal carbon assimilation, derived by summing mean monthly P_N and assuming a standardized photoperiod of 10 h, indicates that both species assimilated approximately $1.5 \text{ mol}(\text{CO}_2) \text{ m}^{-2}$ of leaf area within the undisturbed paired-plots. Comparable rates of seasonal carbon assimilation would establish the basis for co-dominance between these two species. However, the stochastic nature of the abiotic environment makes it difficult to assess competitive superiority on a seasonal or annual basis. Seasonal variation in precipitation, in conjunction with temperature, may periodically confer competitive superiority to one species over the other by influencing the extent of photosynthetic surfaces and the rate of photosynthesis realized. Over the long-term, the prolonged period of carbon assimilation displayed by *S. leucotricha*, albeit at a low rate with a relatively inefficient use of water, appears to confer this C₃ species with the capacity to co-exist with C₄ competitors in grasslands at relatively low latitudes.

REFERENCES

- Boutton, T. W., Harrison, A. T., Smith, B. N.: Distribution of biomass of species differing in photosynthetic pathway along an altitudinal transect in southeastern Wyoming grassland. — *Oecologia* **45**: 287–298, 1980.
- Brown, L. F., Trlica, M. J.: Interacting effects of soil water, temperature and irradiance on CO₂ exchange rates of two dominant grasses of the shortgrass prairie. — *J. appl. Ecol.* **14**: 197–204, 1977.
- Caldwell, M. M., White, R. S., Moore, R. T., Camp, L. B.: Carbon balance, productivity, and water use of cold-winter desert shrub communities dominated by C₃ and C₄ species. — *Oecologia* **29**: 275–300, 1977.
- Christie, E. K., Detling, J. K.: Analysis of interference between C₃ and C₄ grasses in relation to temperature and soil nitrogen supply. — *Ecology* **63**: 1277–1284, 1982.
- Dunn, R., Thomas, S. M., Keys, A. J., Long, S. P.: A comparison of the growth of the C₄ grass *Spartina anglica* with the C₃ grass *Lolium perenne* at different temperatures. — *J. exp. Bot.* **38**: 433–441, 1987.
- Ehleringer, J. R.: Implications of quantum yield differences on the distribution of C₃ and C₄ grasses. — *Oecologia* **31**: 255–267, 1978.
- Ehleringer, J., Pearcy, R. W.: Variation in quantum yield for CO₂ uptake among C₃ and C₄ plants. — *Plant Physiol.* **73**: 555–559, 1983.
- Gould, F. W.: *The Grasses of Texas*. — Texas A&M University Press, College Station 1975.
- Heitschmidt, R. K., Price, D. L., Gordon, R. A., Frasure, J. R.: Short duration grazing at the Texas Experimental Ranch: Effects on aboveground net primary production and seasonal growth dynamics. — *J. Range Manage.* **35**: 367–372, 1982.
- Kemp, P. R., Williams, G. J., III: A physiological basis for niche separation between *Agropyron smithii* (C₃) and *Bouteloua gracilis* (C₄). — *Ecology* **61**: 846–858, 1980.

- Long, S. P., Woolhouse, H. W.: The responses of net photosynthesis to light and temperature in *Spartina townsendii* (*sensu lato*), a C₄ species from a cool temperate climate. — *J. exp. Bot.* **29**: 803–814, 1978.
- Monson, R. K., Littlejohn, R. O. Jr., Williams, G. J., III: Photosynthetic adaptation to temperature in four species from the Colorado shortgrass steppe: a physiological model for coexistence. — *Oecologia* **58**: 43–51, 1983.
- Monson, R. K., Sackschewsky, M. R., Williams, G. J., III: Field measurements of photosynthesis water-use efficiency, and growth in *Agropyron smithii* (C₃) and *Bouteloua gracilis* (C₄) in Colorado shortgrass steppe. — *Oecologia* **68**: 400–409, 1986.
- Pearcy, R. W., Tumosa, N., Williams, K.: Relationships between growth, photosynthesis competitive interactions for a C₃ and a C₄ plant. — *Oecologia* **48**: 371–376, 1981.
- Pearcy, R. W., Ehleringer, J.: Comparative ecophysiology of C₃ and C₄ plants. — *Plant Environ.* **7**: 1–13, 1984.
- Sala, O. E., Lauenroth, W. K.: Small rainfall events: An ecological role in semiarid regions. — *Oecologia* **53**: 301–304, 1982.
- Stowe, L. G., Teeri, J. A.: The geographic distribution of C₄ species of the Dicotyledonae relation to climate. — *Amer. Naturalist* **112**: 609–623, 1978.
- Teeri, J. A., Stowe, L. G.: Climatic patterns and the distribution of C₄ grasses in North America. — *Oecologia* **23**: 1–12, 1976.
- Waller, S. S., Lewis, J. K.: Occurrence of C₃ and C₄ photosynthetic pathways in North American grasses. — *J. Range Manage.* **32**: 12–28, 1979.