Journal of Applied Ecology (1982), **19,** 647–657

WATER RELATIONS: A NEW DIMENSION FOR NICHE SEPARATION BETWEEN *BOUTELOUA GRACILIS* AND *AGROPYRON SMITHII* IN NORTH AMERICAN SEMI-ARID GRASSLANDS

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SUMMARY

(1) The dynamics of the leaf water status and stomatal behaviour in *Bouteloua gracilis* and *Agropyron smithii*, two of the dominant grasses of the semi-arid grasslands in North America were studied.

(2) The grasses showed remarkably different stomatal behaviour. While *A. smithii* showed a typical behaviour *B. gracilis* presented maximum values of conductance before dawn and then a slow decrease until reaching a stable status around mid-morning.

(3) Leaf water potential in *B. gracilis* was independent of leaf conductance and closely followed the pattern of atmospheric water demand. In the case of *A. smithii*, both leaf conductance and atmospheric water demand exerted control upon leaf water potential.

(4) It was concluded that the predawn opening of stomata represented an adaptive advantage for *B. gracilis* allowing this species to maximize carbon fixation during the early morning, the time of day when under the most frequent steppe conditions water deficit does not impair the photosynthesis process.

(5) It is proposed that *B. gracilis* and *A. smithii* have two different and complementary ecological strategies. *Bouteloua gracilis* is adapted to a scarce and highly variable water supply and to a precipitation pattern in which small rainfall events constitute a large portion of total water input. *Agropyron smithii* is adapted to a less variable water supply and to a water balance more favourable in which small precipitation events account for a smaller portion of the water input.

INTRODUCTION

Bouteloua gracilis and *Agropyron smithii* are two conspicuous grass components of the semi-arid grasslands in central North America. They have different physiological characteristics, as well as different phenological patterns (Dickinson & Dodd 1976). *Agropyron smithii* is a cool-season species, has the C_3 photosynthetic pathway (Williams & Markley 1973) and blooms in June–July. *Bouteloua gracilis* is a warm-season species, has the C_4 photosynthetic pathway and blooms in July–August.

Throughout the area where both grasses are distributed, water is the most frequent factor limiting primary productivity and reproduction. No other factor exerts as much influence in determining the structure and dynamics of semi-arid ecosystems as the availability of water (Lange, Kappen & Schulze 1976). Its influence occurs not only by way of its availability but also through the pattern of its distribution. Temporal distribution, frequency, distribution of different precipitation event sizes, as well as the total annual amount, shape the structure of these ecosystems, determining the life form

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0021–8901/82/0800–0647 $02.00

composition and the species composition. The pattern of distribution also influences the dynamics of the carbon, nitrogen, and phosphorus cycles. As a result of the high degree of control of system structure and dynamics exerted by water in semi-arid regions a thorough understanding of the water economy of the major plant species is a prerequisite to understanding the implications of perturbations, whether they be management strategies, altered land use or air pollution.

The ideas of ecological niche and niche overlap or amount of resource sharing have proven to be extremely useful in understanding competition, resource utilization spectra, and ultimately geographical distribution. Kemp & Williams (1980) presented a thorough study of the physiological responses of *A. smithii* and *B. gracilis* to environmental gradients of temperature and moisture. They reported several growth chamber experiments with both grasses grown in soil and hydroponically, in an attempt to characterize their ecological niches. They found a differential temperature response of photosynthesis and related metabolic processes but they did not find a niche separation along the moisture gradient.

These grasses are the dominant species in different regions and also coexist in some others. *Agropyron smithii* is the most frequent dominant in the northern mixed prairie and its distribution extends into the shortgrass steppe and southern mixed prairie. *Bouteloua gracilis* dominates in the shortgrass steppe and its importance decreases at higher latitudes. The shortgrass steppe is characterized by a scarce and highly variable precipitation pattern in which small rainfall events account for a large portion of the water inputs (Sala & Lauenroth 1982). In the northern mixed prairie, although total precipitation is not significantly higher, soil water storage is higher (Rasmussen 1971), probably as a consequence of the fact that precipitation is slightly concentrated in early spring. This makes water supply less variable during the first part of the growing season. The swales in the northern portion of the shortgrass steppe, where *A. smithii* also dominates, possess a different soil profile from the upland sites and they receive other water inputs in addition to rainfall (R. G. Woodmansee, personal communication). The extra inputs, which are the consequence of run-on, decrease the temporal variability of soil water and result in a condition similar to that found on northern mixed prairie sites.

The objective for this research was to test the hypothesis that there are differences in the niches of *B. gracilis* and *A. smithii* in the dimension of water relations. This hypothesis is based upon the recognition of the differences in the water balance of the sites each species dominates and the crucial role of water in semi-arid regions.

MATERIALS AND METHODS

The experiment was conducted at a shortgrass steppe site (Central Plains Experimental Range administered by the USDA-ARS) located in the piedmont of north-central Colorado approximately 61 km northeast of Fort Collins and 40 km south of Cheyenne (40°49′ N latitude, 104°47′ W longitude). The topography of the area consists of gently rolling hills with broad tops separated by wide ephemeral stream courses (swales). The average elevation is 1650 m.

The major grass species on the study site are blue grama (*Bouteloua gracilis* (H.B.K.) Griffiths), buffalo grass (*Buchloe dactyloides* [Nutt.] Engelm.), western wheatgrass (*Agropyron smithii* Rydb.), and red three-awn (*Aristida longiseta* Steud.). Besides grasses, the perennial vegetation of the site is made up of suffrutescent shrubs like fringed sagewort

(*Artemisia frigida* Willd.), forbs including scarlet globemallow (*Sphaeralcea coccinea* [Pursh] Rydb.), and succulents such as plains prickly pear (*Opuntia polyacantha* Haw.).

Mean annual precipitation is 311 mm with a range of 110–580 mm recorded over the past 31 yr. Approximately 70% of the mean annual precipitation occurs during the April–September growing season. Mean monthly temperatures range from below 0 °C in December and January to 22 °C in July.

The daily course of the water status of *B. gracilis* and *A. smithii* was followed while simultaneously measuring the water status of the soil and the atmosphere surrounding the plants. The experiment was repeated twice, on 10 June and 27 August, in an attempt to avoid the masking effect of the different phenological patterns of the species. The water status of the plants was assessed by measuring leaf water potential and leaf conductance to water vapour. These variables were chosen to assess the differences in the ecological niches of *B. gracilis* and *A. smithii* because both are related to the major physiological processes of the plant. Leaf water potential is an important control of plant processes such as photosynthesis, respiration, translocation, and transpiration. Leaf water potential was measured using the pressure chamber technique (Scholander *et al.* 1965).

The largest part of the gaseous flux for most leaves is through the stomatal pore and consequently leaf conductance can generally be regarded as almost synonymous with stomatal conductance (Jarvis 1981). Stomatal aperture plays a major role in regulating transpiration water loss and also affects leaf conductance to CO_2. Stomatal behaviour is one of the major controls vascular plants have upon the compromise between water loss and carbon gain. Measurements of leaf conductance to water vapour in the field were by means of a diffusion porometer (Kanemasu, Thurtell & Tanner 1969).

Both variables were measured each day from before dawn until early afternoon since previous experience indicated that the status of these variables remained constant from shortly after midday until dusk. During the first trial, the readings were made quite frequently, nearly every hour, while in the second trial the frequency was decreased to only five readings a day because this proved to describe the daily pattern with sufficient accuracy. Both measurements were made utilizing the most recent fully expanded leaves. Ten replications were used in each case, maintaining the standard error below 10% of the mean for leaf water potential and around 12% for leaf conductance with this value only exceeded in the early morning.

The status of soil water was assessed by measuring the water content throughout the soil profile. Soil water content was determined by means of a neutron probe (Gardner & Kirkham 1952) and measurements were taken at depths of 15, 30, 45, 60, 75, and 90 cm in two access tubes. To describe the atmospheric water demand, calculations of vapour pressure deficit were made using data from a hygrothermograph.

With the purpose of checking on some particular aspects of the leaf conductance pattern of *B. gracilis*, the experiment was repeated for this species under controlled environment conditions. Pots containing *B. gracilis* plants were placed in a Conviron (Model E-15) high light intensity growth chamber where they were maintained at a 14 h photoperiod with quantum flux density of 600 $\mu E\ m^{-2}\ s^{-1}$ (400–700 nm) and 25 °C/15 °C day/night temperatures. Pots were watered daily maintaining the soil near field capacity. All the other experimental conditions remained the same except that in this case leaf conductance was estimated by means of a null-balance porometer (Beardsell, Jarvis & Davidson 1972) and also the number of replications were increased to fifteen from twelve different plants. Three replications were used for the measurement of conductance at 16.00 hours.

RESULTS

The most striking difference between *B. gracilis* and *A. smithii* was observed in leaf conductance. *Agropyron smithii* showed a typical behaviour; leaf conductance was very low before dawn and slowly increased attaining a maximum value at 08.00 hours MST (Fig. 1(a) (b)). In contrast to this *B. gracilis* showed the maximum leaf conductance before dawn suggesting that the stomata were fully open at this time of the day. Changes in leaf conductances need not necessarily reflect a change in stomatal conductance. Assumptions that cuticular vapour loss is constant and negligible at all times and that the leaf air space is always 100% saturated with water vapour are not warranted (Meidner 1981). However, changes in leaf conductances as large as those observed in *B. gracilis* during the early morning can be accounted for only by changes in the stomatal aperture. The same pattern of predawn stomatal opening and then slow decrease of leaf conductance was observed in the early and late season (Fig. 1(a) (b)).

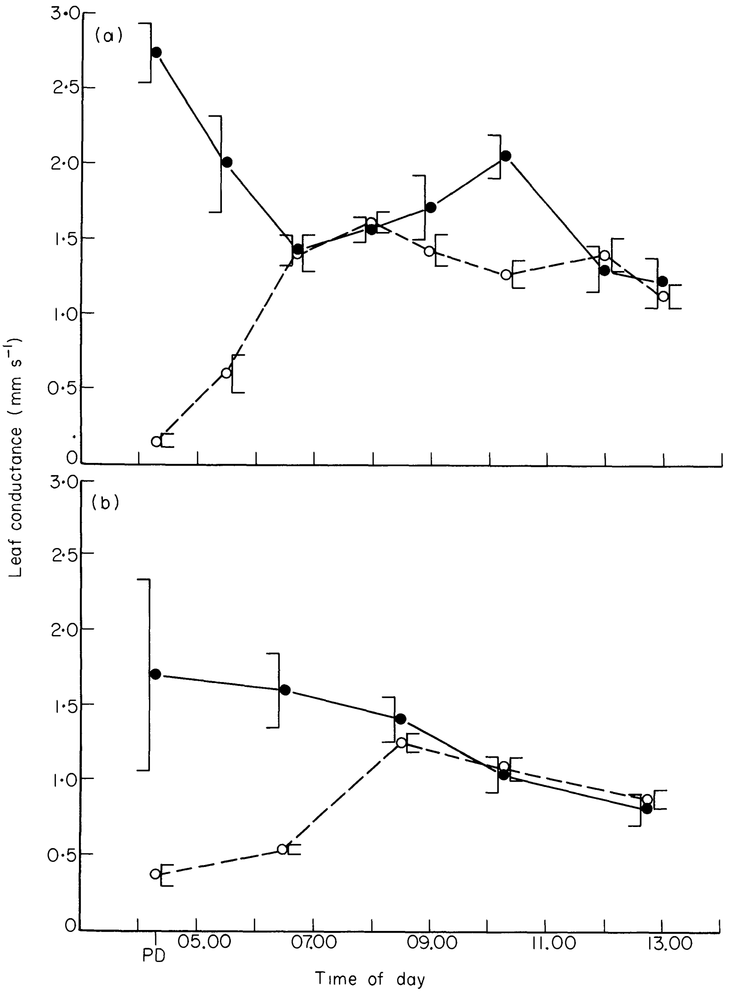

FIG. 1. Daily course of leaf conductance for *Bouteloua gracilis* (●——●) and *Agropyron smithii* (○---○). Each point represents the mean of ten leaves and vertical bars represent ±1 S.E. (a) on 10 June and (b) on 27 August. PD = pre-dawn.

In spite of the large differences observed before dawn and in the early morning, by 08.00 hours MST the values of leaf conductance were very similar for both grasses. The values observed at noon agreed with the ones previously reported for *B. gracilis* in the field at the same time of day and comparable water deficit (Sala *et al.* 1981). The values reported here also agreed very closely with the ones reported by Kemp & Williams (1980). They measured leaf conductance for *A. smithii* and *B. gracilis* in the laboratory under conditions of water availability similar to those in the present study (noon leaf water potential around −2·5 to −3·0 MPa).

The values of leaf conductance were lower on 27 August than 10 June. The differences between late and early growing season can be accounted for by the differences in the pattern of water availability. Although in both cases deeper layers of the soil contained more water than the top soil layers, in the early growing season the water availability in the deep layers was much higher than in the late growing season (Fig. 2). This pattern was a consequence of the relatively high precipitation of the winter and spring. The recharge of the profile in spring is a phenomenon which occurs infrequently in the shortgrass steppe but when it occurs it provides sufficient water to allow grasses to grow for more than a month without developing water-stress symptoms (Sala *et al.* 1981). Regardless of the pattern of water availability, in both cases the values of leaf conductance at noon very closely agree with a model which related leaf conductance with leaf water potential (Sala *et al.* 1981 and Fig. 3(a) (b)).

The values of leaf water potential were lower on 27 August than 10 June (Fig. 3). These differences also can be accounted for by the differences in the pattern of water availability.

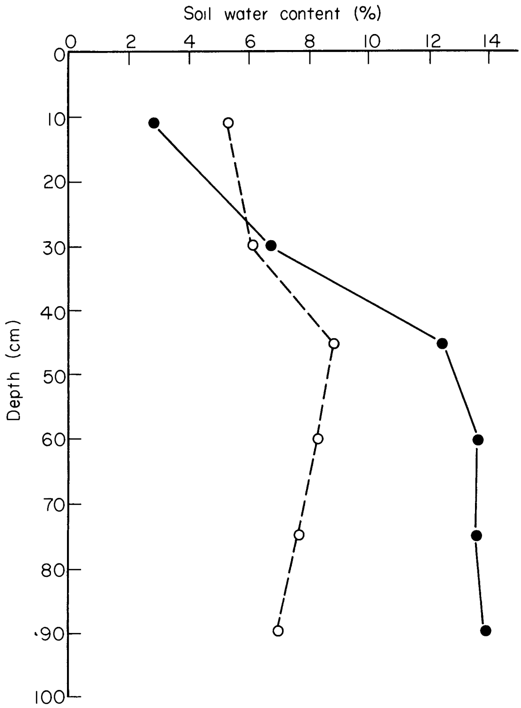

FIG. 2. Soil water content as a function of depth for the two experimental dates, 10 June (●——●) and 27 August (○---○).

The daily course of leaf water potential was different between *B. gracilis* and *A. smithii* and these differences were largely related with their stomatal behaviour. The maximum leaf water potential for both grasses occurred before dawn, then reaching a stable value around mid-morning. Leaf water potential in *B. gracilis* decreased almost steadily until mid-morning while *A. smithii* decreased very rapidly in the early morning and then stabilized (Fig. 3(a) (b)). *Bouteloua gracilis* apparently followed the atmospheric water demand, in this case represented by the vapour pressure deficit, closer than *A. smithii* (Fig. 3).

The stomata of *A. smithii* were closed at dawn (Fig. 1(a) (b)) and by that time leaf water potential had reached its daily maximum (Fig. 3(a) (b)). When the leaf conductance began to increase, the leaf water potential decreased until both reached a stable condition around mid-morning. Under the particular conditions of constant soil water availability, for the trial in June, a multiple regression analysis showed that vapour pressure deficit (VPD) and

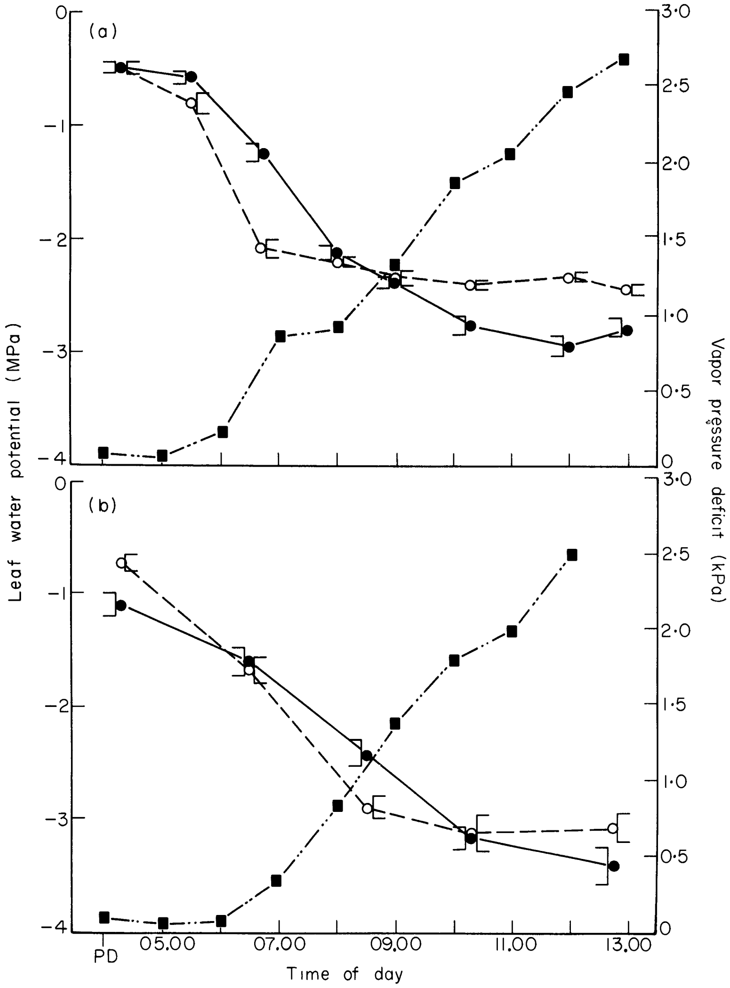

FIG. 3. Daily course of leaf water potential for *Bouteloua gracilis* (●——●) and *Agropyron smithii* (○– – –○) and daily course of vapour pressure deficit (■—·—■). Each point of the leaf water potential curves represent the mean of ten leaves and vertical bars represent ±1 S.E. (a) on 10 June and (b) on 27 August. PD = pre-dawn.

leaf conductance (LC) accounted for 97% of the variability throughout the day in leaf water potential. The addition of the variable LC given that VPD was already in the model significantly ($P < 0{\cdot}01$) contributed to the prediction of LWP and the addition of VPD given that LC was present was also significant ($P < 0{\cdot}01$). The regression for leaf water potential (LWP) was

$$\mathrm{LWP} = -0{\cdot}234 - 0{\cdot}330\ \mathrm{VPD} - 1{\cdot}10\ \mathrm{LC}$$

Under constant supply, the resistance to water vapour flow from the leaves to the atmosphere and the energy gradient between those two points are the factors controlling the leaf water potential in *A. smithii.* The pattern of these two variables can be expected to determine the daily pattern of leaf water potential.

Bouteloua gracilis presented a completely different pattern. The stomata were fully open before dawn and the leaf water potential showed the maximum daily value, the water stress was minimum (Fig. 1, 3). The leaf water potentials presented here are not indicative of a severe water stress in comparison with values previously reported (Sala *et al.* 1981). Leaf conductance decreased throughout the early morning but the values were always fairly high. Leaf water potential followed the atmospheric water demand (VPD) very closely. Multiple regression analysis showed that vapour pressure deficit in the atmosphere accounted for a significant ($P < 0{\cdot}01$) portion of the variability in leaf water potential ($r^2 = 0{\cdot}87$) throughout the day. Leaf conductance did not account for a significant ($P = 0{\cdot}795$) amount of the variability in leaf water potential. The equation was

$$\mathrm{LWP} = -0{\cdot}984 - 0{\cdot}892\ \mathrm{VPD} - 0{\cdot}114\ \mathrm{LC}$$

This indicated that under the range of water supply conditions explored here, leaf conductance did not control the status of leaf water potential. It is possible that the stomatal behaviour or even the leaf water potential pattern of the two grasses may change under conditions of severe water deficit.

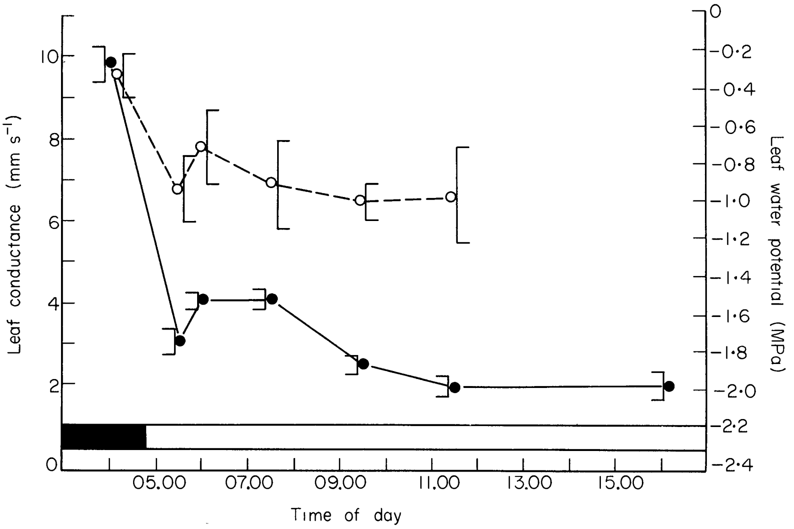

FIG. 4. Daily course of leaf water potential (○---○) and leaf conductance (●——●) for *Bouteloua gracilis* under controlled environmental conditions. Each point of the leaf water potential curve represents the mean of three leaves and each point of the leaf conductance curve represents the mean of fifteen leaves; vertical bars represent ±1 S.E.

When a similar trial was repeated in the laboratory for *B. gracilis* it was observed that during the dark period leaf conductances were the maximum values for the day (Fig. 4). Leaf conductance decreased rapidly at the start of the light period. The vapour pressure deficit was held constant and leaf water potential followed the conductance pattern. After a large reduction of leaf conductance in the early morning the leaf water potential only decreased from $-0{\cdot}3$ to $-0{\cdot}9$ MPa. Throughout the day the leaf water potential values were much higher than those recorded in the field (Fig. 3) and even higher than the values characteristic of minimum stress in the field (Sala *et al.* 1981). These higher leaf water potential values could be the result of the lower irradiance in the growth chamber. The leaf conductance values were also higher in the growth chamber than in the field experiment. In this case the differences are not only a function of the environmental conditions, because two different instruments were involved. In the field a diffusion porometer was used and in the growth chamber experiment a null-balance porometer which had a fan mixing the air and reducing the boundary layer resistance. The porometer was expected to give higher conductances since the boundary layer resistance is in series with the stomatal resistance. Hence, the instrument could be another factor which accounted for part of the difference between the results in the field and in the laboratory.

DISCUSSION

The partial or complete opening of stomata during the night or before dawn has been reported several times in the literature. Meidner & Mansfield (1968) reported a small opening in the absence of light for *Brassica oleracea* (L.) and also cited the early work of Loftfield (1921) with potato (*Solanum tuberosum* L.) who reported that stomatal closure occurred for a short period only, towards the end of the day. During the early part of the night, opening occurred again to full aperture and the stomata remained wide open until the following evening. Later, several authors (England 1963; Abdel-Aziz, Taylor & Ashcroft 1964; Van Bavel 1967; Rosenberg 1969) reported evapotranspiration losses during the night but they were not able to separate bare soil evaporation from transpiration. Hence, these works represented weak evidence of stomatal opening during the night. Conclusive evidence of the occurrence of the phenomenon in the field did not appear in the literature until modern techniques such as diffusion porometers were available. Sharpe (1973) observed that the adaxial stomata of cotton (*Gossypium hirsutum* L.) closed completely at sunset and opened at sunrise but the abaxial stomata remained at least partly open during the night. Turner *et al.* (1978) found for a soybean cultivar (*Glycine max* [L.] Merrill) values of leaf conductance in the dark of $1{\cdot}4$ mm s^{-1} which represented 10% of the values they observed during the day. Recently, Muchow *et al.* (1980), using diffusion porometry, observed partial stomatal opening for kenaf (*Hibiscus cannabinus* L.) during the night. Stomatal conductance of kenaf increased after 23.00 hours such that at dawn it was almost half the average daytime value.

Predawn stomatal opening in *B. gracilis* could be in response to environmental stimuli or the result of endogenous rhythm. The physiological mechanisms responsible for the phenomenon were not identified nor was a general description of the conditions under which it occurs. Furthermore there is evidence that the pattern of leaf conductance presented here is not the only one to be expected for *B. gracilis* (Sala & Lauenroth 1982). In an earlier experiment it was observed that leaf conductance was low before dawn and increased as quantum flux increased. Maximum leaf conductance was observed at 10.00 hours. These maximum mid-morning values were in some cases followed by decreased conductances at noon.

Throughout this study physiological characteristics of a C_4 plant, *B. gracilis*, and a C_3, *A. smithii* have been examined. These characteristics were related to the water status of leaves and their controls over the water loss and most of them, we believe, are characteristics of each species and not necessarily strongly associated with their photosynthetic pathway.

Some authors who observed the night opening of stomata have been concerned with the amount of water lost during the night as a result of this phenomenon. Muchow *et al.* (1980) estimated the night-time transpiration of irrigated kenaf to be up to 20% of total diurnal transpiration on nights of high advection. Rosenberg (1969) reported for an alfalfa (*Medicago sativa* L.) crop that from 7 to 21% of the total daily evaporation occurred at night during spring and 0–15% in summer. A characteristic of the continental climate of the shortgrass steppe is a large temperature difference between day and night. The remarkable drop in temperature at night results in low vapour pressure deficits. For a set of fifteen nights throughout the growing season vapour pressure deficit averaged 0·3 KPa. This indicated that the amount of water lost during the night because of the night opening of stomata could not be important for the water balance of the system. Parton, Lauenroth & Smith (1981) measured the daily course of evapotranspiration for the same site with a precision lysimeter and found that even under very wet conditions nocturnal losses were insignificant.

It is proposed that the ecological significance of the predawn opening of stomata for a species adapted to a semi-arid environment must be related not with water loss but with the carbon gain process. Detling, Parton & Hunt (1978) constructed a photosynthesis model for *B. gracilis* which closely agreed with field data. This model predicted that under conditions of soil water potentials at 10 cm from −2·1 to −3·2 MPa, which are not extremely dry for this ecosystem (Sala *et al.* 1981), the photosynthetic rate reached its maximum value around 08.00–09.00 hours and then rapidly decreased. The rate of photosynthesis did not follow the irradiance pattern because other factors, in this case water availability, were limiting the process. Hanson & Dye (1980) reported for *Prosopis glandulosa* Torr. in semi-arid west Texas that maximum net photosynthesis shifted from 12.00 to 08.00 hours in response to increased water stress. Combining the photosynthesis data reported for *B. gracilis* and *A. smithii* by Kemp & Williams (1980) with the observed daily pattern of leaf water potential (Fig. 3), similar conclusions were arrived at. The occurrence of a peak in photosynthesis very early in the day is even clearer if the severe water stress conditions reported by Sala & Lauenroth (1982) are used. High conductance and high leaf water potential throughout the first hours of the morning represent an adaptation which allows *B. gracilis* to maximize carbon fixation under the environmental conditions of the shortgrass steppe. Stomata are open at those times of the day when conditions are favourable for CO_2 uptake with minimal associated water loss. Tenhunen *et al.* (1980) arrived at a similar conclusion when they analysed the behaviour of the Mediterranean evergreen shrub *Arbutus unedo*.

The stomatal behaviour and the related water relations are visualized as an important dimension of the niches of the shortgrass steppe grasses. It is proposed that *B. gracilis* and *A. smithii* have different and complementary strategies. *Bouteloua gracilis* is adapted to a scarce and highly variable water supply, and to a precipitation pattern in which small rainfall events constitute a large portion of total water input. Sala & Lauenroth (1982) reported the extremely rapid response of this species to a 5 mm rainfall event. They concluded that this characteristic allowed *B. gracilis* to utilize this kind of event, which accounted for 70% of the events in the shortgrass steppe. In this experiment it was found that leaf water potential closely followed the highly variable conditions of atmospheric water demand. Stomata did not follow the highly predictable quantum flux pattern and they were fully open before dawn and in the early hours of the morning. These features allowed *B. gracilis* to be more closely coupled with its hydrologic environment and to cope with the high variability of water availability, the most frequently limiting resource. It is understood that the shift of the photosynthesis peak toward the early morning is an adaptation to water scarcity and that it is a consequence of physiological characteristics such as high conductance and high leaf water potential in the early morning. There are other possibilities for the daily pattern of leaf conductance and water potential (Sala & Lauenroth 1982). While we have speculated about the significance of pre-dawn stomatal opening to *B. gracilis* it has not resulted in an explanation why both a typical diurnal and the pre-dawn opening behaviours are observed for this species. On the other hand, it is proposed that *A. smithii* is adapted to a frequent recharge of the soil profile, a less variable, more predictable water supply and to a water balance more favourable in which small precipitation events account for a smaller portion of the water input. *Agropyron smithii* has a typical stomatal behaviour (Meidner & Mansfield 1968), closed during the night and open in response to the quantum flux after sunrise. Taking this view of the ecological strategy of *A. smithii*, one would not expect it to be able to respond to a small rainfall event.

It is recognized that many other aspects of the ecophysiology of *B. gracilis* and *A. smithii* can be studied and used as new niche dimensions. However, a knowledge of just a few of them will be useful in understanding competition, dominance, or even spatial distribution of a couple or more species. Pianka (1981), when presenting ideas about niche and competition pointed out that niche overlap is a necessary but not sufficient condition for exploitation competition. Two populations with partially overlapping niches will compete only if that resource is in short supply. Therefore, niche dimensions related to the water absorption, loss, and status of plants will dictate competition since water availability is the most frequent limiting resource in the shortgrass steppe region.

ACKNOWLEDGMENTS

We would like to thank D. G. Milchunas and R. Hays for their assistance during data collection and J. K. Detling and W. J. Parton for many helpful discussions. This work was supported by USDA-SEA Science and Education Administration grant No. 58-9AHZ-8-332, National Science Foundation grants No. DEB-7906009, DEB-8004193-01 and Consejo Nacional de Investigaciones Científicas y Técnicas, República Argentina.

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(*Received* 19 *January* 1982)