

TECHNICAL REPORT

High temperature effects on gas exchange for the invasive buffel grass (*Pennisetum ciliare* [L.] Link)

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Buffel grass was introduced to the Sonoran Desert in the mid-twentieth century, where it has aggressively invaded new areas. Given its ecological success at a place where the air temperature can approach 50°C, the effects of high air temperatures on gas exchange were studied for this species. The carbon dioxide uptake and water use efficiency were maximal at day/night air temperatures of 30/20°C for potted plants, substantially decreasing at higher temperatures until the plants died at 45/35°C.

Keywords: acclimation, *Cenchrus ciliaris*, forage productivity, shade, Sonoran Desert, water use efficiency.

INTRODUCTION

Buffel grass (*Pennisetum ciliare* [L.] Link; syn. *Cenchrus ciliaris*) is a C₄ bunch grass from equatorial Africa that was introduced to the Sonoran Desert during the mid-twentieth century for forage production (Ibarra-F. *et al.* 1995). From this arid region of Mexico and the USA, it has since invaded new areas, posing a threat to native plant communities from what is considered to be the most biodiverse desert biome in the world (Saucedo-Monarque *et al.* 1997; Búrquez *et al.* 1999; Castellanos-V. *et al.* 2002; Jackson 2005). Indeed, various C₄ grasses have become invasive species of concern in the Americas (Williams & Baruch 2000). Their physiological characteristics confer them a tolerance of high temperatures and considerably high productivities that can result in competitive advantages over native vegetation, especially in warm, arid and semiarid environments (Lambers *et al.* 1998; Williams & Baruch 2000; Nobel 2005; Sage & McKown 2006). In particular, C₄ photosynthetic metab-

olism should enable *P. ciliare* to withstand higher temperatures than those tolerated by its C₃ counterparts because of a considerable reduction in photorespiration, while maintaining substantial productivity. The measurement of instantaneous rates of net carbon dioxide (CO₂) uptake can be an indicator of plant productivity under particular air temperatures. The CO₂-concentrating mechanism of C₄ plants, which comprise ≈ 3% of vascular plant species, also favors a reduced transpirational water loss (Nobel 2005). Therefore, *P. ciliare* can have a competitive advantage that favors its ecological success over native C₃ species, considering that water is a limiting environmental factor for arid environments like the Sonoran Desert (Cox *et al.* 1995).

While the mean air temperature in the Sonoran Desert oscillates between 12°C in January to 30°C in June, the maximum temperature can approach 50°C during summer (Cox *et al.* 1995; Ibarra-F. *et al.* 1995; Arriaga *et al.* 2004). The annual precipitation for this arid region of North America averages 450 mm (Cox *et al.* 1995). In this respect, the biological activity of *P. ciliare* is highest during the summer, when most of the precipitation occurs (Cox *et al.* 1995; Martín-R. *et al.* 1995). During the rainy season, a combination of reduced irradiation due to clouds and shade provided by annual herbs, perennial shrubs, and even standing dead grass biomass, can result in microenvironments that are favorable for *P. ciliare*. In particular, the photosynthetic photon flux (PPF; wavelengths of 400–700 nm) that reaches the ground can be reduced substantially during the rainy

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season, even under short canopies of grass (Jurik & Kliebenstein 2000; Nobel & De la Barrera 2004).

The net CO₂ uptake and transpiration rates were measured for *P. ciliare* under controlled environmental conditions in order to evaluate the effect of air temperature on gas exchange for this invasive species. In particular, a relatively low PPF was utilized, simulating the light environment prevalent within the dry matter canopy of *P. ciliare*, where most of the recruitment occurs for this species (Martín-R. *et al.* 1995; McIvor 2003). The grass was expected to tolerate high air temperatures, which in the Sonoran Desert approach 50°C during the summer (Ibarra-F. *et al.* 1995; Arriaga *et al.* 2004).

MATERIALS AND METHODS

Pennisetum ciliare (L.) Link seeds were acquired from Agropecuaria y Servicios del Noroeste, Hermosillo, Mexico, and stored at an air temperature of 25°C and a relative humidity of 40% until they were utilized. The experiments were conducted at the Department of Scientific and Technological Investigations, University of Sonora, Hermosillo, Mexico. The seeds were planted in 3.8 L cylindrical plastic pots containing soil from a nearby site where *P. ciliare* has successfully invaded. This soil was a loamy sand with a pH of 7.3, organic matter content of 0.5% by mass, and total nitrogen content of 0.07% by mass (De la Barrera E., 2004, unpublished data). The pots were placed inside an environmental chamber (PGR-15; Conviron, Winnipeg, Canada) and watered as needed to maintain the soil near field capacity. The relative humidity inside the chamber was 50% and the PPF at the soil surface was 250 µmol m⁻² s⁻¹ for 13 h days that started at 06.00 hours. The day/night air temperatures were kept at 30/20°C during seed germination, which started at 3 days and peaked at 7 days after planting. At 10 days after planting, the temperatures inside the chamber were gradually adjusted (2–3°C per day) until reaching the desired setting. The plants were allowed to acclimate for 5 days at each temperature regime before conducting the gas exchange measurements. The CO₂ uptake and transpiration rates were measured at 10.00 hours for the plants kept at each temperature regime with a portable photosynthesis and transpiration measurement system (LCA-4; ADC, Hoddesdon, UK). The statistical analyses were performed with JMP v.4.0.3 (SAS Institute, Cary, NC). The data are presented as the mean ± 1 standard error.

RESULTS AND DISCUSSION

The highest rates of net CO₂ uptake for *P. ciliare* were achieved by plants kept at day/night air temperatures of

30/20°C, averaging $15.8 \pm 1.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 1a). The plants from the other temperature treatments had lower assimilation rates ($P < 0.05$ from a Tukey test following an ANOVA). Moreover, a temperature treatment of 45/35°C was lethal for *P. ciliare* (data not shown). With respect to transpiration, the water loss was reduced at the lower temperature treatments (Fig. 1b). Owing to a greater difference in vapor pressure between the air and the leaves (Fig. 1 inset), the plants kept at higher temperatures transpired more than those at the lower temperatures ($P < 0.05$) (Fig. 1b). The water use efficiency (WUE: net CO₂ uptake/transpiration) is an indicator of the water cost for photosynthesis, an issue of special importance in arid environments where water is a very limiting environmental factor of plant productivity. The WUE of 5.6 measured for *P. ciliare* at 30/20°C was higher than at the other temperature treatments ($P < 0.05$) (Fig. 1 inset) and comparable with those for other C₄ species (Lambers *et al.* 1998; Nobel 2005). Indeed, high WUEs confer C₄ plants an ecological advantage in warm regions, which might have contributed to the proliferation of *P. ciliare* in the Sonoran Desert (Williams & Baruch 2000; Castellanos-V. *et al.* 2002; Arriaga *et al.* 2004).

The substantially reduced net CO₂ uptake and WUE observed at temperatures > 30/20°C were not expected, considering that *P. ciliare* has been thriving for > 50 years in the Sonoran Desert, where high temperatures can approach 50°C during the summer growing season (Ibarra-F. *et al.* 1995; Martín-R. *et al.* 1995; Arriaga *et al.* 2004). Nevertheless, high temperatures in Kenya, in equatorial Africa, where *P. ciliare* is native and was originally collected, average 33°C, with an annual amplitude of only 5°C (Ibarra-F. *et al.* 1995). Indeed, the temperature environment of tropical regions is relatively stable, thus their native species tend to tolerate rather narrow temperature ranges (Lüttge 1997; Nobel & De la Barrera 2004).

If air temperatures in the Sonoran Desert can approach 50°C, why did substantially lower temperatures lead to reduced CO₂ uptake and even death for *P. ciliare*? First, constant air temperatures were utilized, while high temperature extremes occur in the field during only a few hours per day. Second, the biological activity of this grass coincides with the rainy season, when clouds and denser vegetation reduce the incident solar radiation, ameliorating the temperature microenvironment (Martín-R. *et al.* 1995; Nobel & De la Barrera 2004; Nobel 2005). Third, the individuals of *P. ciliare* studied here were young, at a stage when their survival in the field is reduced (McIvor 2003). The acquisition of temperature tolerance with age also occurs for *Opuntia ficus-indica*

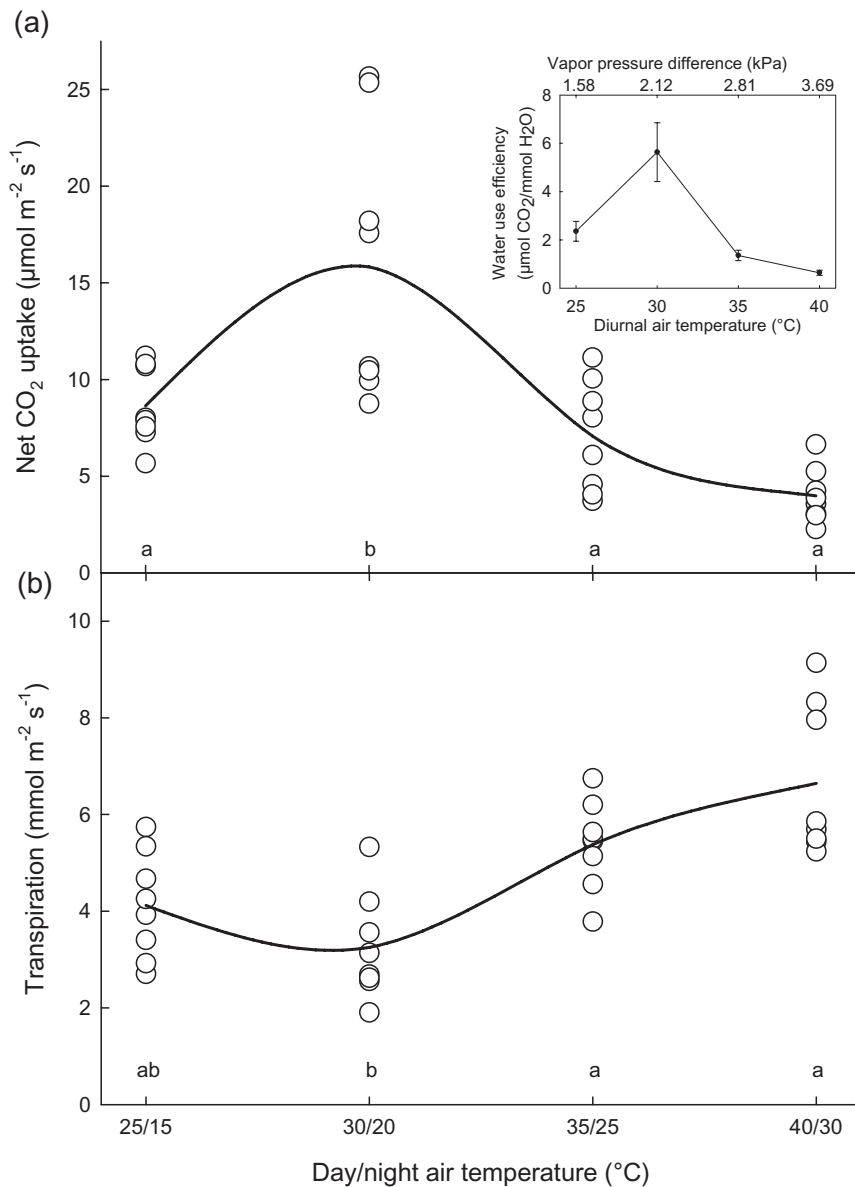


Fig. 1. Gas exchange rates for *Pennisetum ciliare* at the indicated day/night air temperatures. (a) The net carbon dioxide (CO₂) uptake and (b) the transpiration rates for young plants kept at the indicated day/night air temperatures, with a photosynthetic photon flux of 250 μmol m⁻² s⁻¹ and a relative humidity of 50%. (○), the values of the actual measurements ($n = 8$); the solid lines intercept the average rates. For each panel, the different lower-case letters near the bottom abscissa indicate significant differences between the temperature treatments ($P < 0.05$). Inset: The effect of diurnal air temperature and the corresponding difference in water vapor pressure between the plant and the air on the water (H₂O) use efficiency (net CO₂ uptake/transpiration) for *P. ciliare*.

(Nobel & De la Barrera 2003). Despite being unrelated to *P. ciliare*, this cactus also can be found in arid environments. For *Pennisetum setaceum*, an invasive grass of importance in Hawaii, USA, the productivity and CO₂ uptake are favored at warmer temperatures that generally do not exceed 35°C (Williams *et al.* 1995). However, an air temperature pulse of 36°C, simulating a heat wave, causes a substantial decrease in photosynthesis for eight grass species in ≈ 4 days of exposure and can lead to the extinction of gas exchange if the treatment is prolonged (Milbau *et al.* 2005).

The present study confirmed that *P. ciliare* has a high WUE, typical of C₄ grasses, but that this invasive grass has a rather low tolerance of high temperatures, at least

at a young age. Future research should characterize the field microenvironments where young plants actually survive and determine how plant age affects the temperature tolerance of *P. ciliare*.

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