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Seasonal and inter-annual photosynthetic response of representative C_4 species to soil water content and leaf nitrogen concentration across a tropical seasonal floodplain

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Abstract We examined the seasonal and inter-annual variation of leaf-level photosynthetic characteristics of three C_4 perennial species, *Cyperus articulatus, Panicum repens* and *Imperata cylindrica*, and their response to environmental variables, to determine comparative physiological responses of plants representing particular microhabitats within a seasonal tropical floodplain in the Okavango River Delta, Botswana. Five measurement campaigns were carried out over a period of 2 y which covered two early rainy seasons, two late rainy seasons and one dry season. For all three species, light-saturated net photosynthetic rates (A_{sat}) and stomatal conductance (g_{sat}) decreased with decreasing soil water content with a seasonal range for A_{sat} of approximately 5–45 μmol m^{-2} s^{-1}, and for g_{sat} of 0.03–0.35 mol m^{-2} s^{-1}. The species representing the wettest microhabitat (*Cyperus*) had the highest g_{sat} at low leaf-to-air vapour pressure deficits (D_l), the highest ratio of intercellular to ambient CO_2 concentration (C_i/C_a), as well as the highest degree of variation in C_i/C_a from season to season. We interpret this as being indicative of its adaptation to a moist growth environment allowing for non-conservative water use strategies as soil moisture is usually abundant. For all three species there was significant variation in photosynthetic fluxes from one year to another that was related to variation in leaf nitrogen and phosphorus. This study shows that when assessing the role of savanna stands in large-scale carbon balance models, the remarkable inter-annual variation in leaf photosynthesis reported in this study should be taken into account.

Key Words Africa, C_4 photosynthesis, C_i/C_a ratio, grassland, leaf nitrogen, leaf phosphorus, leaf-to-air vapour pressure deficit, savanna, stomatal conductance

INTRODUCTION

C_4 plants are most abundant in semi-arid tropical and subtropical regions. This is usually attributed to the C_4 pathway being competitive at high-light environments and allowing for higher temperature optimum of photosynthesis compared to C_3 plants (Edwards *et al.* 1985, Ehleringer *et al.* 1997). The CO_2 concentrating mechanism of C_4 plants allows them to attain high nitrogen and water use efficiencies (NUE and WUE respectively).

In (semi-)arid environments one benefit of having a high WUE should be a lengthening of the period of potential photosynthetic carbon gain during periods of water shortage. Only a few exceptions to the pattern of high WUE in C_4 species have been reported; this being for very highly productive stands of *Echinochloa polystachya*, *Paspalum repens* and *Paspalum fasciculatum* growing along river floodplains in tropical South America (Piedade *et al.*

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1991). C_4 plants also have a relatively low nitrogen requirement in order to sustain any given level of carbon uptake (Sage & Pearcy 1987). This may also be of benefit in savanna environments that are nutrient poor (Simioni *et al.* 2004).

Despite the fact that C_4 grasses account for 20–30% of global photosynthetic productivity (Lloyd & Farquhar 1994), there have been only a few studies on the photosynthetic properties, nutrient content and water relations and modulation of these factors by the environment for C_4 grasses growing in their natural environment (Anten *et al.* 1998, Baruch & Bilbao 1999, Simioni *et al.* 2004). Moreover, we still lack to date a comprehensive study of changes in photosynthetic characteristics of C_4 plants over a growing season or year in a tropical semi-arid environment, especially in relation to the underlying internal (physiological) or external (environmental) causes.

In order to help understand the underlying environmental and physiological controls of C_4 grass and sedge species we studied spatial and seasonal variation in photosynthetic capacities and stomatal conductances of C_4 species growing in the Okavango River Delta, Botswana. We studied three species, *Imperata cylindrica* (L.) P. Beauv., *Panicum repens* L. (grasses) and *Cyperus articulatus* L. var. *nodosus* (Humb. & Bonpl. ex Willd.) Kük. (sedge) that grow in distinct microhabitats characterized by markedly different hydrological regimes. We hypothesized that differences in leaf-level gas exchange properties between these species will vary across the period of measurements and this variation will be most pronounced during the dry season, reflecting different ecological traits of the studied species.

METHODS

Study site

The Okavango River Delta, situated in north-western Botswana, is one of the world's largest inland deltas with an estimated area of 40 000 km^2 (McCarthy & Ellery 1994). The area has a semi-arid climate. Rainfall occurs mainly in November to April, averages *c.* 500 mm y^{-1}, but is irregular both in spatial distribution and in intensity. Precipitation is greatly exceeded by potential evapotranspiration (1580 mm y^{-1}; McCarthy & Ellery 1994) but in many areas of the Delta rainfall is supplemented by annual floodwaters from the Angolan highlands that enter through the Okavango River. The work described here was undertaken at a seasonal floodplain located at the distal end of the Delta where the period of maximum inundation occurs during the climatically dry season, June–September (Ellery & McCarthy 1994). In this part of the Delta a mix of seasonal floodplains and of dry, rain-fed 'islands' at slightly higher elevations is typical.

Apart from clayey soils (Vertisols), extensive soil formations in northern Botswana, including the Okavango Delta, derive from Kalahari sands (Arenosols) with a low agronomic potential (Almendros *et al.* 2003). The vegetation cover of the Okavango Delta seasonal floodplains exhibits a marked zonation with different species occupying microhabitats characteristic of systematic variation in both frequency and length of inundation (Bonyongo *et al.* 2000). At the study location (S 19°36′33′ E 23°16′44′) a typical floodplain community occurred on low-lying ground where inundation lasts typically for several weeks to months during any given flood season. The dominant species in this area were a C_4 sedge, *Cyperus articulatus* var. *nodosus* growing alongside the C_3 sedge *Schoenoplectus corymbosus* (Roth ex Roem. & Schult.) Raynal. *Cyperus articulatus* is known to tolerate extended periods of standing water (Abd El-Ghani & Fahmy 2001). The soil material here is clay and, when wet, becomes blackish in colour. On the higher parts of the floodplain where plant water availability is almost always dependent on rainfall, and the soils are more sandy in character, sedges are all but absent and the perennial and rhizomatous grass *Imperata cylindrica* dominates. *Imperata cylindrica* belongs to the Nicotinamide-Adenine Dinucleotide Phosphate-malic enzyme (NADP-ME) photosynthetic subtype. This species is found throughout tropical regions, but has spread to warm temperate zones worldwide (Bryson & Carter 2004). It is one of the most intensively studied weed species worldwide but surprisingly limited data exists on its ecophysiological characteristics in its natural habitat. Few animals, other than hippopotami (*Hippopotamus amphibus* L.) will attempt to graze this plant (Thompson 1985). Lastly, what we refer to as the 'intermediate zone' (between the lower and upper floodplain) is characterized by a large year-to-year variation with respect to presence or absence, and height and duration of flooding. Here the pasture grass, *Panicum repens*, which belongs to the C_4 phosphoenolpyruvate carboxykinase (PCK) photosynthetic type, was the dominant species. Globally, *P. repens* is not confined to intermediate floodplains; its native range extends from terrestrial, wetland and aquatic environments of tropical and North Africa, Mediterranean, South America and Asia and it is considered a weed in Northern America (Gibbs Russell *et al.* 1991).

Gas exchange measurements

Between December 2001 and March 2003 five field campaigns were conducted to study the response of plant gas exchange to seasonally varying environmental conditions. Light and CO_2 response curves were measured, between 08h00 and 13h00, on attached, fully expanded leaves randomly selected for each of the three species growing in their characteristic different microhabitats. We used a portable gas exchange system (Li-6400, Li-Cor Inc., Nebraska, USA) with one leaf from at least four plants or separate tillers sampled for each species. The leaf temperature inside the 6-cm^2 leaf chamber was not controlled, the only exception being in March 2003. This was to avoid temperatures in excess of 40 °C, the temperature above which C_4 net photosynthetic assimilation may become inhibited (Edwards & Walker 1983). The red/blue LED light source inside the chamber allowed for automatic changes of photon flux density (I).

For light response curves, measurements were made at $I = 2000, 1800, 1500, 1000, 700, 500, 300, 100$ and 0 μmol m^{-2} s^{-1} with the CO_2 mole fraction inside the chamber maintained at 370 μmol mol^{-1}. For the CO_2 response curves, measurements were made with $I = 1600$ μmol m^{-2} s^{-1}. Varying CO_2 concentrations were obtained from portable CO_2/air mixture tanks and automatically controlled by a CO_2 injector fitted onto the Li-6400 system. In situ CO_2 assimilation rates were measured at 370, 300, 200, 100, 50, 400 (twice), 500, 600 and 700 μmol mol^{-1}. During measurements both the leaf-to-air vapour pressure deficit, D_l, and leaf temperature, T_l, in the chamber did not always exactly match the ambient conditions because these two parameters are affected by leaf transpiration rate (Beale *et al.* 1999); T_l typically exceeded air temperature at time of measurements by not more than 1 to 2 °C.

For every leaf sampled, light and CO_2 response curves were fitted individually by a non-linear regression (SPSS 11.0 for Windows) to the hyperbolic function $y = a\,(1 - e^{b-cx})$, where y is the rate of CO_2 exchange, x is the independent variable (I or C_i), b and c are constants, with values set to 0.1 and 0.002, respectively (Causton & Dale 1990). In the case of light response curves, coefficient a gives the light-saturated rate of CO_2 exchange (A_{sat}), b/c gives the compensation point, $a(1 - e^b)$ gives the dark respiration, and apparent quantum yield (the slope, or derivative of the curve at the light compensation point) is given by ace^b. In the case of the A-C_i curve, a represents the light and CO_2-saturated rate of CO_2 exchange (A_{pot}), the CO_2 compensation point is again calculated from b/c, and the carboxylation efficiency (the slope, or the derivative of the curve at the CO_2 compensation point) is given by ace^b (for all see: Causton & Dale 1990). This simple equation has been widely used to analyse light and CO_2 response curves of a variety of species (Kgope 2004, Midgley *et al.* 1999, Wand *et al.* 2001) and fitted our data well ($r^2 \geq 0.9$). Light-saturated values of stomatal conductance (g_{sat}) and C_i/C_a values were obtained from the light response curves at $I > 1600$ μmol m^{-2} s^{-1}.

After completion of the gas exchange measurements the leaves were scanned and their area determined afterwards using WinFOLIA software (Regents Instruments Inc., Quebec, Canada). Leaf dry weight was obtained after oven-drying at 70 °C for 24 h and C and N concentration measured using a Vario EL (Elementar Americas, Inc. Mt. Laurel, New Jersey, USA). Leaf phosphorus concentration was measured after a nitric acid digestion using ICP-AES (Atomic Emission Spectrometry with Inductively Coupled Plasma, Perkin-Elmer, Norwalk, USA). Nitrogen use efficiencies (NUE) were determined by dividing A_{sat} by leaf N and expressed on a leaf area basis. Water use efficiency (WUE) is expressed here as A_{sat}/g_{sa}.

Meteorological variables and soil characteristics

Half-hourly rainfall, air temperature and water vapour saturation deficit at *c.* 3 m height were measured at a nearby eddy-covariance flux tower, using a tipping bucket rain gauge (Young; Model 52202, R.M. Young Company, Traverse City, USA), temperature probe (HMP45A, Vaisala, Helsinki, Finland) and RPT 410 Barometric Sensor (Druck, New Fairfield, CT, USA), respectively. Volumetric soil water content (θ) was measured at each microhabitat within the floodplain, at 0–5 cm, 5–10 cm and 10–15 cm soil-depth intervals using a battery-powered hand-held soil moisture sensor (Moisture Meter type HH2 with Theta probe, Delta T Devices, Cambridge, UK) for each measurement campaign.

For each microhabitat, four soil samples were randomly collected at intervals of 0–5, 5–10, 10–20, 20–30 and 30–50 cm. These were then oven dried at 40 °C before being analysed for nutrients using Vario MAX (Elementar Americas, Inc. Mt. Laurel, New Jersey, USA). Soil nutrient data reported here are for the upper 10 cm of the soil profile. Soil pH was measured, from similar depths as for soil nutrients, in mixtures of 10 g of soil with 25 ml of distilled water with a pH meter (pH 538 WTW, Germany).

RESULTS

The soils of this seasonal floodplain were alkaline, pH ranged from 7.7 to 9.8, being highest in the upper parts of the floodplain (Table 1). Bulk densities in the sandiest (upper) parts were somewhat higher (1.01 g cm^{-3}) compared with the flooded parts (*c.* 0.7–0.8 g cm^{-3}), but differences were not significant (ANOVA, n = 6 for each microhabitat, F = 5.29, df = 17, P = 0.097). Between the rainy and dry season December 2001 to June 2002, soil N, soil C and soil C:N remained almost constant within each microhabitat. In March 2003 soil C and N were higher (upper floodplain) and lower (intermediate floodplain) than during the previous campaigns but

Table 1 Mean (± SD) of soil N, soil C and soil C:N ratio, together with some soil physical characteristics of the three microhabitats at the seasonal floodplain. Soil pH and bulk density (BD) were determined in March 2003. Data shown represent the 0–10-cm soil layer, and were tested with ANOVA and grouped with the post hoc Tukey test. Different letters in a column indicate means are significantly different ($P < 0.05$) when testing for differences in each variable within each microhabitat.

	Soil N (%)	Soil C (%)	Soil C:N	BD (g cm^{-3})	pH
Upper floodplain					
December 2001	0.04 ± 0.01*a*	0.62 ± 0.13*a*	14.7 ± 0.38*a*		
March 2002	0.04 ± 0.01*a*	0.68 ± 0.17*a*	16.2 ± 1.54*a*		
June 2002	0.06 ± 0.04*a*	0.84 ± 0.54*a*	14.6 ± 0.99*a*		
March 2003	0.12 ± 0.03*b*	1.58 ± 0.49*b*	13.5 ± 1.95*a*	1.01 ± 0.10	9.8 ± 0.33
Intermediate floodplain					
December 2001	0.10 ± 0.04*b*	1.47 ± 0.56*b*	14.5 ± 0.99*b*		
March 2002	0.12 ± 0.03*b*	1.65 ± 0.48*b*	14.1 ± 0.79*b*		
June 2002	0.11 ± 0.03*b*	1.48 ± 0.44*b*	13.7 ± 0.91*ab*		
March 2003	0.04 ± 0.01*a*	0.52 ± 0.06*a*	11.9 ± 0.98*a*	0.73 ± 0.06	9.1 ± 0.24
Floodplain					
December 2001	0.10 ± 0.06*a*	1.36 ± 0.91*a*	13.7 ± 0.92*b*		
March 2002	0.11 ± 0.09*a*	1.26 ± 0.32*a*	13.9 ± 0.77*b*		
June 2002	0.15 ± 0.07*a*	2.19 ± 0.91*ab*	14.6 ± 0.49*b*		
March 2003	0.10 ± 0.07*a*	1.16 ± 0.86*a*	11.1 ± 0.89*a*	0.78 ± 0.27	7.7 ± 0.59

remained unchanged in the floodplain. Overall, the sandy soils of the upper floodplain had lowest N and C content. With the exception of sulphur, the floodplain displayed the lowest concentrations of micronutrients (not shown).

Generally, air saturation deficit (D, Figure 1) was highest just before and at the onset of the rainy season. Towards the dry season T_a and air temperature (T_a)decreased, but even then average daily values were around 25 mbar and 25 °C, respectively. Cooler days with high cloud cover (not shown), particularly during the days when measurements were made, led to substantially lower chamber leaf-to-air vapour pressure deficit (D_l) during the December 2001 campaign when compared with the rest of the measurement periods. However, D_l remained similar across the rest of the measurement periods and also between species (Table 2).

During the periods of our measurements, it was only in December 2001 that the annual flood covered a substantial area of the floodplain, with standing water up to 0.8 m depth in the lowest parts. In these lower parts θ (0–10 cm depth) subsequently declined from 0.5 m^3 m^{-3} to 0.2 m^3 m^{-3} during the dry season (June 2002, Figure 2). In the rain-fed upper floodplain θ varied between 0.34 and 0.17 m^3 m^{-3} over the same period with the transitional *Panicum repens*-dominated area having soil water contents intermediate between the other two. In March and December 2003, all micro-habitats depended mostly on rainfall for their water supply as the flood

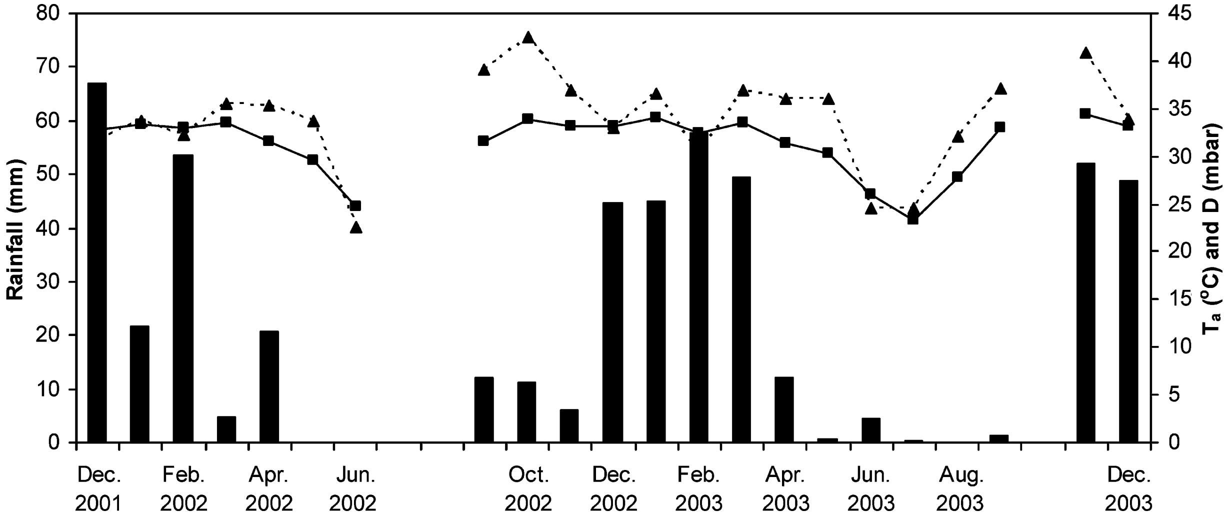

Figure 1. Monthly rainfall (bars), mean maximum monthly air temperature (solid line) and mean maximum vapour pressure deficit (dotted line) at the seasonal floodplain measurement site, located in the Okavango River Delta in north-western Botswana. Five measurement campaigns were conducted between December 2001 and December 2003.

Table 2 Leaf-to-air vapour pressure deficit (D_l), water use efficiency (WUE), nitrogen use efficiency (NUE) obtained from the A-c_i response and light response curves and specific leaf area (SLA). WUE and NUE were determined as A_{sat}/g_{sat} and A_{sat}/leaf N, respectively. Values are mean ±SD of at least four measurements on randomly selected leaves of each species. All data were tested with ANOVA and grouped with the post hoc Tukey test. Different letters in a column indicate means are significantly different ($P < 0.05$) when testing for differences in each variable within each microhabitat.

	D_l (kPa)	WUE (μmol CO_2 mol^{-1} H_2O)	NUE (CO_2 mol (N)$^{-1}$ s^{-1})	SLA (cm^{-1} g^{-1})
Upper floodplain				
Imperata cylindrica				
December 2001	1.7 ± 0.1*a*	156 ± 14.9*a*	671 ± 146*c*	176 ± 11.1*b*
March 2002	4.9 ± 1.1*b*	173 ± 12.3*a*	340 ± 22.9*a*	188 ± 14.8*b*
June 2002	4.2 ± 1.4*b*	180 ± 21.7*a*	365 ± 37.3*a*	158 ± 17.6*b*
March 2003	4.8 ± 0.2*b*	178 ± 24.5*a*	522 ± 69.8*bc*	116 ± 13.2*a*
December 2003	4.4 ± 0.4*b*	159 ± 20.1*a*	482 ± 65.8*bc*	181 ± 10.3*b*
Intermediate floodplain				
Panicum repens				
December 2001	2.3 ± 0.2*a*	151 ± 28.2*a*	745 ± 64.5*c*	156 ± 13.6*ab*
March 2002	3.8 ± 0.4*b*	163 ± 5.2*a*	391 ± 35.4*a*	162 ± 21.0*ab*
June 2002	3.9 ± 1.3*b*	176 ± 12.3*a*	625 ± 27.2*b*	167 ± 11.7*ab*
March 2003	5.1 ± 0.8*b*	183 ± 11.6*ab*	479 ± 26.3*b*	132 ± 18.1*a*
December 2003	4.1 ± 0.9*b*	170 ± 29.7*a*	489 ± 48.9*b*	171 ± 12.4*ab*
Floodplain				
Cyperus articulatus				
December 2001	2.5 ± 0.2*a*	113 ± 38.7*a*	900 ± 91.9*b*	156 ± 9.6*ab*
March 2002	5.3 ± 1.3*b*	94.9 ± 15.5*a*	443 ± 68.9*a*	155 ± 13.0*ab*
June 2002	5.1 ± 0.8*b*	106 ± 26.9*a*	455 ± 78.7*a*	158 ± 15.6*ab*
March 2003	3.9 ± 0.5*b*	142 ± 26.1*ab*	1053 ± 35.5*c*	126 ± 15.1*a*
December 2003	5.1 ± 0.6*b*	122 ± 25.3*a*	505 ± 153*a*	168 ± 10.8*b*

had either already receded and was limited to a very narrow strip only (March 2003), or had not reached this floodplain at all (December 2003). Such inter-annual variation in flooding is a characteristic feature of the Okavango Delta. Nonetheless, during these two later campaigns, θ still consistently increased towards the lowest parts of the floodplain (Figure 2).

For all three species, light-saturated stomatal conductances, g_{sat}, were highest during the wet season (December and March) with mean values ranging from 0.15 and 0.23 mol m^{-2} s^{-1} (Figure 2), and in each campaign increasing from the driest microhabitat to the wettest microhabitat. For all three species g_{sat} were lowest during the June 2002 campaign when θ was the lowest.

Figure 2 shows reductions in C_i/C_a in all microhabitats towards the end of the rainy season (December 2001 vs. March 2002). However, as the dry season progressed mean C_i/C_a of the sedge, *C. articulatus*, increased substantially (June 2002). By contrast, the mean C_i/C_a of the grass species continued to decline. Overall, differences in C_i/C_a across the floodplain were most pronounced in the absence of surface flooding, i.e. in June 2002, March 2003 and December 2003 (Figure 2). During these periods, C_i/C_a in *C. articulatus* was consistently higher than those measured at the drier microhabitats (ANOVA, $n = 6$ for each microhabitat; June 2002: $F = 27.\ 2$, $df = 17$, $P < 0.001$; March 2003: $F = 7.08$, $df = 17$, $P = 0.008$; December 2003: $F = 9.36$, $df = 17$, $P = 0.001$).

With the exception of March 2003, which showed a tendency of low specific leaf area (SLA), no significant differences were found in the values of mean SLA within each microhabitat (ANOVA; *I. cylindrica:* $n = 26$, $F = 22.2$, $df = 25$, $P > 0.05$; *P. repens:* $n = 25$, $F = 29.2$, $df = 24$, $P > 0.05$; *C. articulatus*: $n = 22$, $F = 19.1$, $df = 21$, $P > 0.05$) and across the species (ANOVA, $n = 15$, $F = 0.366$, $df = 14$, $P = 0.701$) (Table 2). Foliar N of the grass species was highest in the wet season just after the onset of the annual rains and declined progressively towards the dry season, reaching their lowest values in June (Figure 3). Values measured in December 2003 were in all species significantly higher (t-test, *I. cylindrica*: $t = 13.4$, $n = 13$, $df = 12$, $P < 0.05$; *P. repens*: $t = 9.2$, $n = 11$, $df = 10$, $P < 0.05$; *C. articulatus*: $t = 9.2$, $n = 11$, $df = 10$, $P < 0.05$) than in December 2001. With the exception of the dry season, mean leaf N values in *P. repens* were always higher than those of the other species, but the difference was not always statistically significant. Moreover, leaf N values of *P. repens* varied seasonally by a factor of three (67 to 22 mmol N m^{-2}) contrasting with a much lower variation in leaf N for *C. articulatus*. Leaf phosphorus data were available only for the last two wet-season measurement campaigns, March and December 2003. No species showed significant differences (t-test; *I. cylindrica:* $t = 15.3$, $n = 8$, $df = 7$, $P = 0.074$; *P. repens:* $t = 25.7$, $n = 8$, $df = 7$, $P = 0.46$; *C. articulatus:* $t = 7.62$, $n = 8$, $df = 7$, $P = 0.065$) in mean

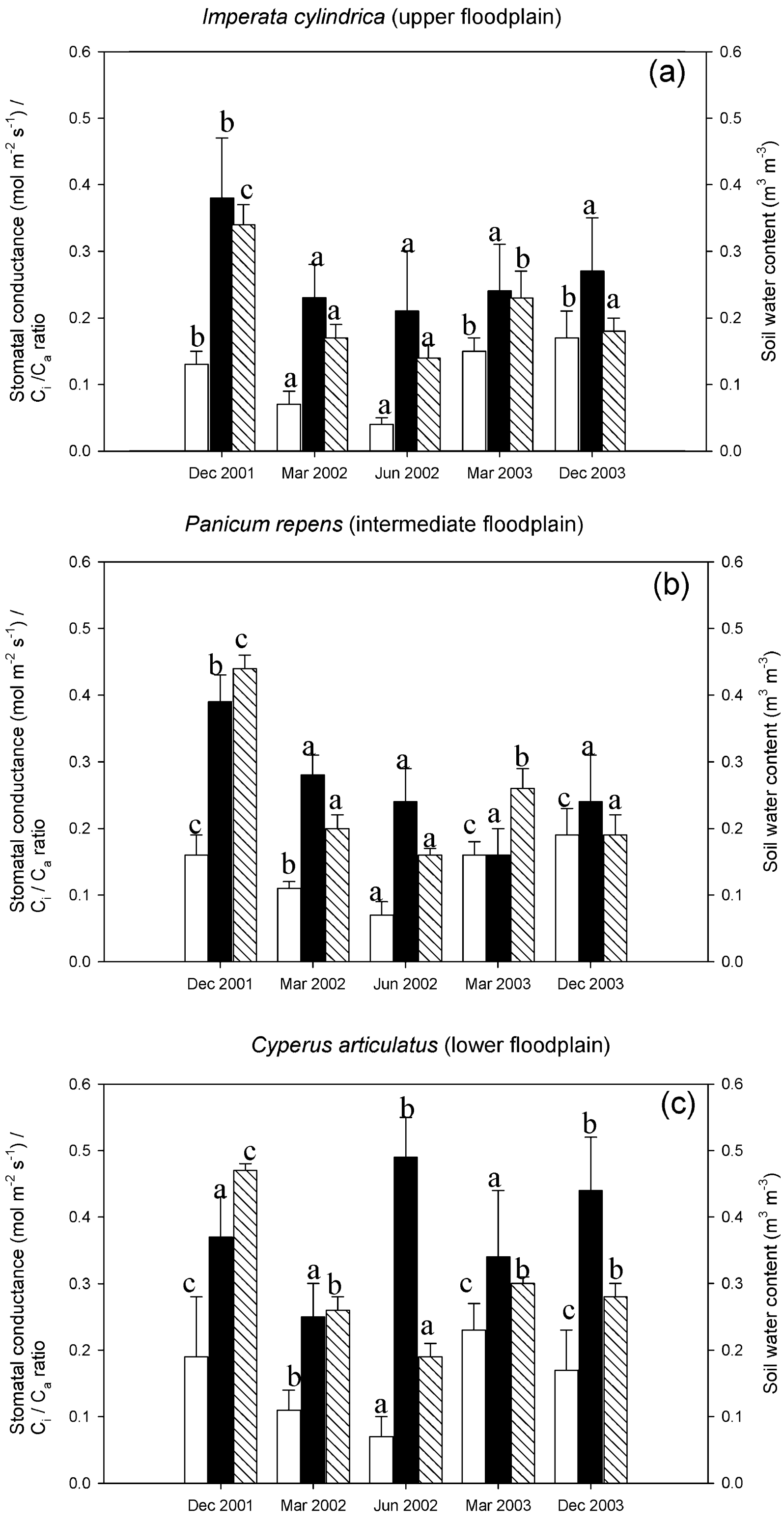

Figure 2. Stomatal conductance (white), C_i/C_a ratio (black) and soil water content (shaded) of the three species during the measurement periods. Data are mean (± SD) and were tested with ANOVA and grouped with the post hoc Tukey test. Different letters indicate means are significantly different ($P < 0.05$) when testing for between-season differences in each variable within each microhabitat. *Imperata cylindrica* (a) grows on the driest parts in the floodplain, *Panicum repens* (b) grows on the intermediate part of the floodplain, while *Cyperus articulatus* (c) grows on the (lower) wettest parts in the floodplain.

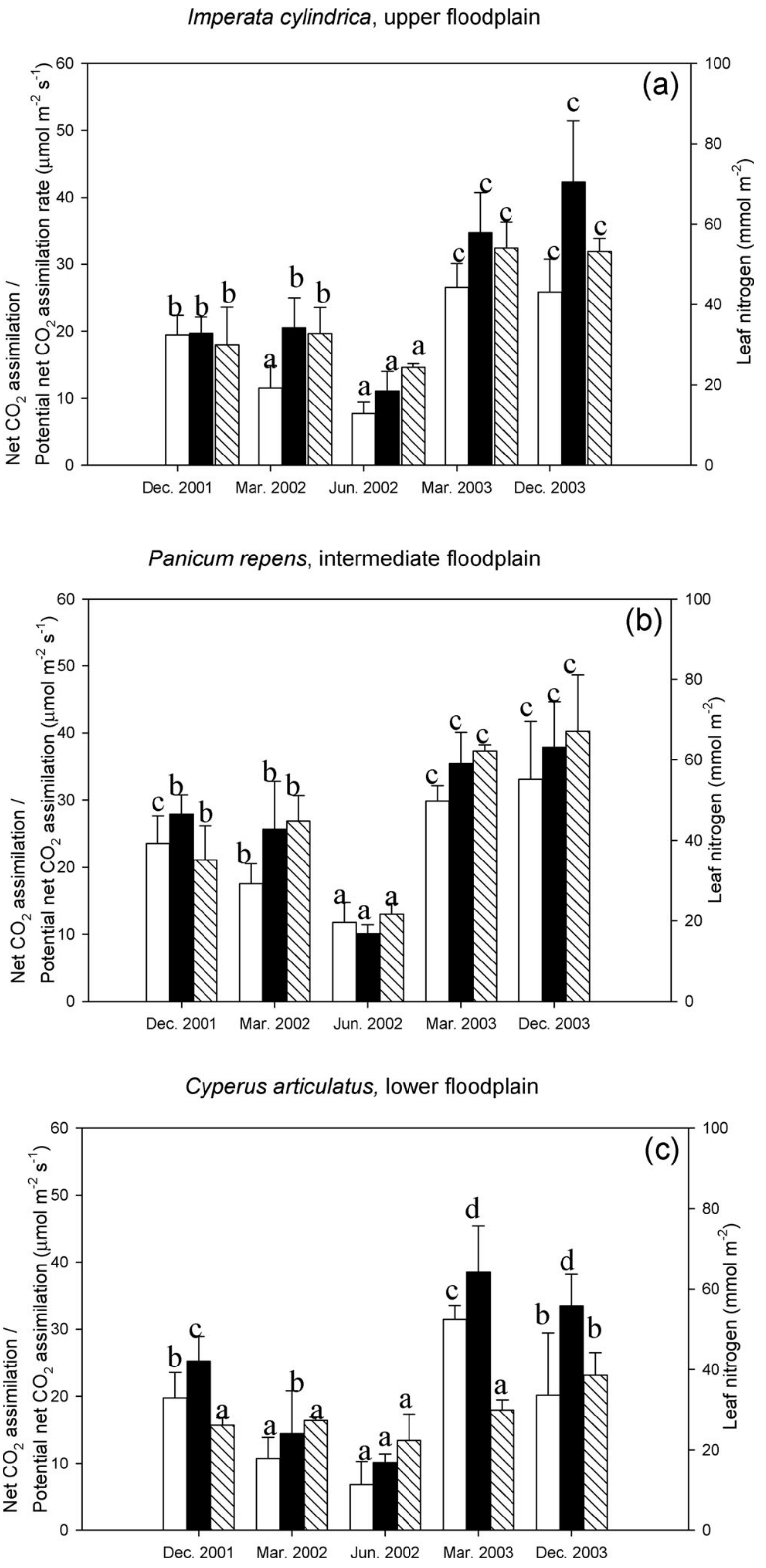

Figure 3. Light-saturated net CO_2 assimilation (white), potential net CO_2 assimilation rate (black) and leaf nitrogen content (shaded) for *Imperata cylindrica* (a), *Panicum repens* (b) and *Cyperus articulatus* (c) during the measurement periods. Data are mean (± SD) and were tested with ANOVA and grouped with the post hoc Tukey test. Different letters indicate means are significantly different ($P < 0.05$) when testing for between-season differences in each variable within each microhabitat.

leaf P between March 2003, ranging from 1.04 to 1.84 mmol m^{-2}, and December 2003, ranging 1.49–1.86 mmol m^{-2}. During both periods, the two grasses had higher mean leaf P than the sedge, although this difference was significant (ANOVA, $n = 4$ for each species, $F = 29.1$, $df = 11$, $P < 0.05$) only in March 2003.

As was the case with leaf N and g_{sat}, A_{sat} and A_{pot} were highest during the wet season when mean values ranged between 20 and 31 μmol m^{-2} s^{-1} and 19 and 42 μmol m^{-2} s^{-1}, respectively (Figure 3). The species dominating the intermediate floodplain, *P. repens*, had the highest mean A_{sat} overall (except for March 2003) and highest mean A_{pot} values from December 2001 to June 2001. However, these differences in A_{sat} and A_{pot} were not always significantly different. From December 2001 to June 2002, both A_{sat} as well as g_{sat} (Figure 2 and Figure 3) decreased by approximately 60–70% across the entire floodplain, while A_{pot} was less affected. The seasonal decline of A_{sat} was smallest in *I. cylindrica* and largest in *C. articulatus*. Over a broad range of D_l and during the drying sequence December 2001–June 2002, the C_4 sedge (in the wettest microhabitat) consistently had lower A_{sat} at similar or higher g_{sat} when compared to the grasses (representing the drier microhabitats). Thus the slope of the linear A_{sat} versus g_{sat} relationship was considerably lower (data not shown). As a consequence, mean water use efficiency (WUE) was lowest in *C. articulatus*, ranging from 95 to 142 μmol CO_2 mol^{-1} H_2O (Table 2), whereas WUE of *I. cylindrica* and *P. repens* were similar, ranging between 152 and 183 μmol CO_2 mol^{-1} H_2O. Largest and significant differences between the mean WUE of the grass species and those of sedge species were found during the late rainy (ANOVA; March 2002: $n = 19$, $F = 34.9$, $df = 18$, $P < 0.01$), and dry season (ANOVA; June 2002: $n = 27$, $F = 34.0$, $df = 26$, $P < 0.01$).

All species showed the typical curvilinear decline of g_{sat} with D_l at non-limiting light conditions (Figure 4) which can be described by using for instance, the logarithmic 'Lohammar-type' relationship $gs = -m \ln D_l + b$; where m is the slope and b the intercept. There was some scatter in the data, but in general g_{sat} at a given D_l in the wettest microhabitat (*C. articulatus*) was higher than in the driest microhabitat (*I. cylindrica*) irrespective of time of year. *Cyperus articulatus* also showed the highest stomatal sensitivity, indicated by the highest initial decline of g_{sat} with D_l.

For the two grasses, a strong positive relationship between leaf N and A_{pot}, was discernible across all experimental campaigns as can be seen for instance when comparing the response found for *I. cylindrica* in March 2002 vs. June 2002 (Figure 5a). When merging data from all measurement periods there was an overall increase of A_{pot} with N in *P. repens* and *I. cylindrica*, which was notably steeper for the latter. By contrast, no significant relationship existed between A_{pot} and leaf N in *C. articulatus*, except for the December 2003 campaign. These patterns were similar in A_{sat} (not shown).

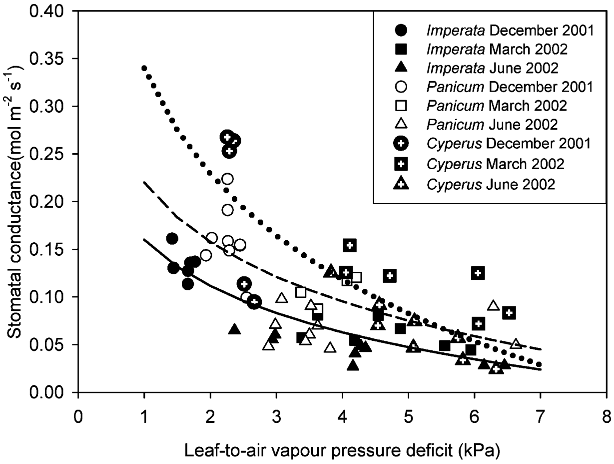

Figure 4. Relationship between leaf-to-air vapour pressure deficit and stomatal conductance of *Imperata cylindrica*, *Panicum repens* and *Cyperus articulatus*. Data shown were obtained during the soil drying cycle (December 2001 to June 2002). Each datum point represents measurements taken from an individual leaf. All data points were obtained at high light ($\geq$1600 μmol m^{-2} s^{-1}) and at ambient CO_2 concentration (370 μmol mol^{-1}). Lines were fitted using the logarithmic Lohammar-type relationship.

Leaf N in the sedge was at the lower end of the range observed in the floodplain, and varied seasonally only little between *c.* 20–40 mmol N m^{-2}. This translated into higher mean NUE in the wet season when compared to the plants in the other microhabitats (Table 2). Across the entire floodplain, NUE values were higher, but not significantly different (ANOVA, $n = 30$, $F = 0.931$, $df = 29$, $P = 0.76$), during the rainy season December 2001, when compared to the dry season, June 2002. The species and seasonal response of g_{sat} to leaf N was similar to that of A_{pot} and A_{sat} to leaf N (data not shown).

For the two periods where leaf phosphorus data were available, all three species expressed a strong linear relationship of leaf P with A_{pot} with greatly lessened difference between species and microhabitats than was the case for N (Figure 5d). Values obtained for *C. articulatus* in March 2003 were however exceptional, as A_{pot} of a similar magnitude to those observed in another species were obtained at much lower foliar phosphorus concentrations.

DISCUSSION

On islands and dry floodplain areas of the Okavango Delta soil pH values above 9, as found in this study, frequently indicate the development of sodic soils that turn hard and crusted when dry (Bonyongo & Mubyana 2004, McCarthy & Ellery 1994, Tooth & McCarthy 2007). The range of A_{sat} (20–45 μmol m^{-2} s^{-1}) observed when soil moisture levels were high is similar to values reported for

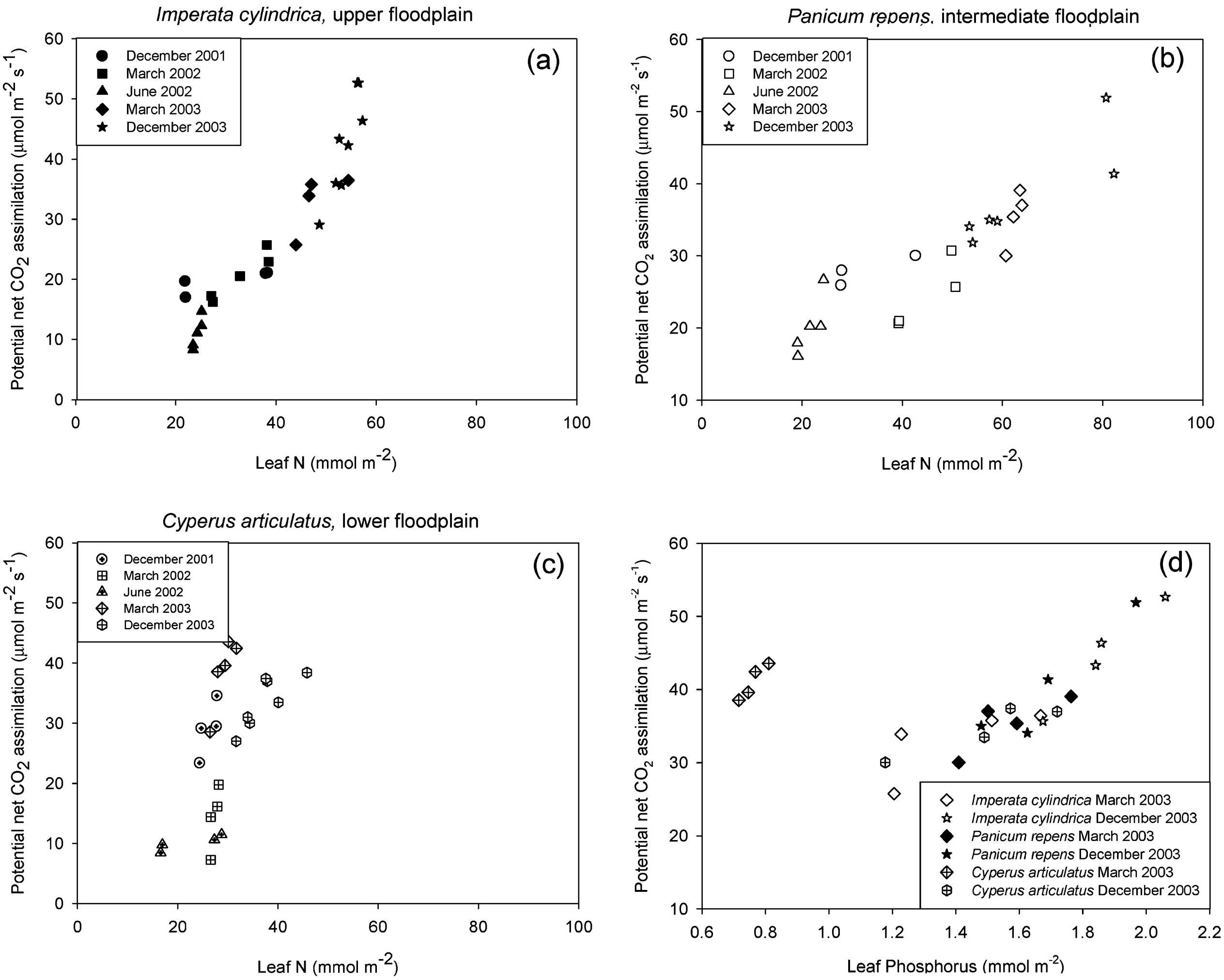

Figure 5. The relationship between leaf nitrogen and potential net CO_2 assimilation for *Imperata cylindrica* (a), *Panicum repens* (b) and *Cyperus articulatus* (c) throughout the entire measurement periods. Figure 5(d) shows the relationship between leaf phosphorus and potential net CO_2 assimilation at the three microhabitats species during the rainy season campaigns of March and December 2003.

C_4 species elsewhere under well-watered field conditions (15–60 μmol m^{-2} s^{-1}; Long 1985). Values for rainy season g_{sat}, however, were at the lower end of the spectrum (0.14–0.23 mol m^{-2} s^{-1} versus 0.2–0.7 mol m^{-2} s^{-1}; Lawlor 2001, Long 1985), and as such the C_i/C_a ratios were also relatively low (0.16–0.49), with the highest values generally found in the sedge. Mean WUE of *C. articulatus* (95–142 μmol CO_2 mol^{-1} H_2O) was comparable to that found in two *Cyperus* species, 100 μmol CO_2 mol^{-1} H_2O, in a tropical wetland at Kahawa Swamp, Kenya (Jones 1988), while mean WUE of the two grasses (151–183 μmol CO_2 mol^{-1} H_2O) was higher than that found in the C_4 grasses of a tallgrass prairie, 96 μmol CO_2 mol^{-1} H_2O, in Kansas, USA (Knapp 1993). In the grass species a more efficient stomatal function relative to that of the sedge allowed carbon uptake at minimal loss of water but structural differences between the grass and sedge species may also have played a role in the observed gas exchange differences. It is likely that the root system of the sedge is deeper and larger than that of the grass species, so as to provide support during periods of inundation and more importantly giving it access to larger amounts of water to support its relatively high water demand even in the dry season.

The range of leaf N observed in the sedge and the two grasses when soil water content was not limiting was comparable to that found in a range of C_4 sedge and grass species in South American and African ecosystems (Anten *et al.* 1998, Le Roux & Mordelet 1995, Olivares *et al.* 2002) with the exception of a cerrado of Brazil where leaf N was considerably lower (Miranda *et al.* 1997; 2–6 mg g^{-1}). The range of mean leaf P during the wet-season measurement periods (1.02–1.62 mg g^{-1}) at this seasonal floodplain was only a little lower than reported for *Echinochloa polystachya*, 1.5–1.9 mg g^{-1}, growing in a flooded area of the Amazon River (Piedade *et al.* 1997) and higher than that found in South African C_4 savanna grasses (0.4–0.9 mg g^{-1}; Scholes & Walker 1993) and native and alien grasses of Venezuela savannas (0.5–1.4 mg g^{-1}; Baruch *et al.* 1985).

Different responses of the plants to their environment during the 2001–2002 rainy and subsequent dry season were observed when compared with the 2003 data. Most notably, our results showed significantly higher leaf N, A_{sat}, A_{pot}, g_{sat} in March 2003 and December 2003 when compared with December 2001. In the December 2001 campaign measurements had been conducted after a high annual flood, and an early onset of the annual rains (P. Wolski, unpubl. data). By contrast, the onset of the rainy season proper was delayed in 2002–2003 and there was no surface flooding in either March or December 2003. The campaigns differed also with respect to air temperatures and water vapour saturation deficits, which were to some extent lower in December 2001 while soil moisture levels were higher.

The marked seasonality of leaf N in grasses together with the lower leaf P in the sedge species did not match the constant values in soil N during the soil drying period and the similar levels of soil P across this seasonal floodplain. Across a range of species from different biomes, those with higher SLA generally have a higher A_{sat} per unit leaf N and also vary more in A_{sat} per unit variation in leaf N than those with lower SLA (Reich *et al.* 1998, 2003). Our results showed little variation in SLA both within and across the species. The data suggest that year-to-year variation in foliar N was responsible for inter-annual variation in leaf gas exchange characteristics. One possibility for variation in leaf N might be the timing of the initiation of new leaf growth and the measured leaves may have differed in age. In seasonally variable environments it is normal to encounter leaves of different age during field measurements even within one plant (e.g. at our site due to grazing). Yet this seems unlikely as a main factor as in March 2003 leaves would have been as old, if not older that those grown in December 2001, but they had A_{sat}, g_{sat}, and leaf N that were similar or higher. Likewise, leaf N did not vary much between leaves measured in December 2001 and March 2002 although the leaves sampled were probably of different age.

A linear increase of A_{sat} and A_{pot} with leaf N is typical for many plants because of the large amount of leaf N fixed in Rubisco (Field & Mooney 1986, von Caemmerer 2000). In C_4 plants, phosphoenol pyruvate carboxylase (PEP-C) activity, which is assumed to control the C_4-cycle, affects primarily carboxylation efficiency while A_{pot} reflects the level of Rubisco activity (von Caemmerer 2000). High A_{pot} can also be associated with good soil water and nutrient supply (De Lucia *et al.* 2003, Sage *et al.* 1987). Over the period of our measurements A_{pot} of the two grasses showed the clearest relationship with leaf N. Moreover, leaf N of measured leaves varied most in the grass-dominated floodplain, particularly at the driest, rain-fed microhabitat where a tripling of leaf N was accompanied by a five-fold increase in A_{pot}. In terms of their C_4 sub-type (*I. cylindrica* belongs to NADP-ME and *P. repens* to PCK) differences in the physiological characteristics that have been observed under controlled conditions, e.g. nitrogen requirements (Taub & Lerdau 2000), the initial slope of the A-C_i response curve (von Caemmerer 2000) and quantum yields (Edwards *et al.* 1985), were not found in this study. This was not surprising when considering the inherent scatter in field data and the limited number of species.

In the wet, sedge-dominated parts, the seasonal variation leaf N was small and there was no clear effect of leaf N on A_{pot} (and A_{sat}) in *C. articulatus* although A_{pot} varied by a factor of five, and maximum rates were well within what had been observed at the other parts of the floodplain. As a result the NUE of the sedge was most often the highest of the three species, and varied seasonally by a factor of two to three. The pattern of high g_{sat}, and high C_i/C_a ratio may have contributed to its high NUE since at high C_i less photosynthetic enzyme is needed to achieve high rates of photosynthesis (Hikosaka 2004). These results corroborate observations from the seasonal floodplains in central Venezuela (Anten *et al.* 1998) where highest NUE was also typical for (C_3 as well as C_4) species that grow on the flooded sites.

Obviously maximum assimilation rates were constrained by other resources, perhaps other nutrients, other than N, particularly so in the sedge but probably also in the two grass species. One plausible candidate would be phosphorus which has been shown to be an important limiting soil nutrient to C_4 productivity (Mott *et al.* 1985). During plant growth, leaf P modulates the influence of leaf N on photosynthetic capacity (Jia & Gray 2004). At our floodplain site, the use of only three species limits making general conclusions. Our results do suggest, however, that across the grass-dominated microhabitats, the effects of leaf P on assimilation capacity were at least as strong if not stronger than leaf N, and much more uniform than in the sedge-dominated microhabitat, where during the March 2003 campaign high rates of assimilation were observed at very low levels of phosphorus.

Seasonal re-translocation of leaf N similar to what we found in the grasses at our study site has also been observed in grasses at the infertile lowland savannas of Venezuela (Baruch 1996). The authors of this Venezuelan study suggested that an accumulation of reserves underground contributes to their preservation from fire volatilization, thus constituting an important conservation strategy. Indeed, the roots and rhizomes of *I. cylindrica* have been reported to be remarkably resistant to fire (MacDonald 2004). A recent study on the fire history for southern Okavango Delta, using satellite imagery, identified the seasonal floodplains as the regions with the highest fire frequency and serving as a source of fires spreading into drylands (Heinl *et al.* 2007). In addition, storage of a large fraction of nutrients, biomass and meristems underground protects savanna species also from herbivory (Archer *et al.* 1996).

The seasonality in environmental conditions covered by the measurement campaigns, including the dry-season data set from June 2002 allowed us to investigate the extent of stomatal vs. mesophyll constraints on leaf gas exchange in *C. articulatus* vs. the two grasses. The initial response across the floodplain as D_l increased and soil water became sparser during the dry season was a decrease in g_{sat} and A_{sat}, while leaf N remained nearly constant or even increased. In unison with a wide range of plants, g_s decreased with increasing D in a curvilinear fashion (Bunce 1998, Maroco *et al.* 2000, Morison & Gifford 1983). The largest differences between the species were found at low D_l. Under these conditions, species that had higher g_{sat} showed the fastest decline with increasing D_l. Such high stomatal sensitivity is typical for species with relatively high g_{sat} (Bunce 1998, Comstock & Ehleringer 1993, Maherali *et al.* 2003, Oren *et al.* 1999). However, daytime D_l below 2 kPa are untypical for semi-arid environments and within the range of commonly occurring D, 3–6 kPa, the rate of decline of g_{sat} with D converged in the three species. Nevertheless, *C. articulatus* maintained the highest g_{sat} of the three species examined throughout the year.

In conclusion, the three different C_4 species showed pronounced seasonal and inter-annual variation in their leaf physiological characteristics. Since these species were compared in their own growth environment it is difficult to judge whether the observed differences are genotypic or the result of plasticity, although the observed relationships of gs with D indicate intrinsically different WUE strategies. Largest differences in gas exchange characteristics of the three species were found during the dry season, reflecting differences between stomatal and mesophyl regulation under limiting soil water conditions. An efficient use of CO_2 at low C_i/C_a was associated with strong stomatal control and a strong dependence of biochemical components of photosynthesis on leaf N. In two of the three species, the effect of leaf P on assimilation was as high, if not higher than that of leaf N with photosynthesis-P relationships tending to be more uniform across the floodplain than was the case for N.

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