Plant Ecology **173:** 233–246, 2004.

Leaf gas exchange characteristics and water- and nitrogen-use efficiencies of dominant grass and tree species in a West African savanna

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Received 4 October 2002; accepted in revised form 6 June 2003

Key words: C_3 metabolism, C_4 metabolism, Lamto, Modelling, Photosynthesis, Stomatal conductance

Abstract

Whereas leaf gas exchange properties are important to assess carbon and water fluxes in ecosystems worldwide, information of this type is scarce for savanna species. In this study, gas exchange characteristics of 2 C_4 grass species (*Andropogon canaliculatus* and *Hyparrhenia diplandra*) and 2 C_3 tree species (*Crossopteryx febrifuga* and *Cussonia arborea*) from the West-African savanna of Lamto (Ivory Coast) were investigated in the field. Measurements were done in order to provide data to allow the parameterization of biochemically-based models of photosynthesis (for C_4 and C_3 plant metabolic types) and stomatal conductance ; and to compare gas exchange characteristics of coexisting species. No systematic difference was found between grass and tree species for reference stomatal conductance, under standard environmental conditions, or stomatal response to incident light or vapour pressure deficit at leaf surface. Conversely, grass species displayed higher water (1.5-2 fold) and nitrogen (2-5 fold) photosynthetic use efficiencies (WUE and NUE, ratio of net photosynthesis to transpiration and leaf nitrogen, respectively). These contrasts were attributed to the CO_2 concentrating mechanism of C_4 plants. When looking within plant life forms, no important difference was found between grass species. However, significant contrasts were found between tree species, *Cussonia* showing higher NUE and reference stomatal conductance than *Crossopteryx*. These results stress the need to account for functional diversity when estimating ecosystem carbon and water fluxes. In particular, our results suggest that the tree/grass ratio, and also the composition of the tree layer, could strongly affect WUE and NUE at the ecosystem scale in West African savannas.

Introduction

Information about photosynthetic characteristics and stomatal behaviour of plant species is required to predict carbon and water fluxes at the leaf, plant, ecosystem and biome levels (Schulze et al. 1994). In the last decades, photosynthesis and stomatal conductance have been intensively studied for a wide range of species belonging to various ecosystems worldwide. Particular attention has been paid to the light-saturated photosynthetic rate (A_{max}) and stomatal conductance (g_s) (Schulze et al. 1994; Kelliher et al. 1995; Woodward and Smith 1995) and to the relationships between A_{max}, g_s, and the amount of nitrogen per unit leaf area (Field and Mooney 1986; Ellsworth and Reich 1993; Reich et al. 1994; Schulze et al. 1994). Published work on photosynthesis for dominant plant species in a given ecosystem or biome has generally ignored the biochemically-based modelling approaches proposed by Farquhar et al. (1980) for the C_3 pathway, and by Collatz et al. (1992) for the C_4 pathway. This is surprising because those approaches can greatly improve the predictive capacity of photosynthesis models (Leuning 1990) and are frequently used in large-scale schemes representing land surface-atmosphere exchanges (Sellers et al. 1997).

Reviews on photosynthetic traits in the major terrestrial biomes show that no comprehensive data base is available for the dominant, coexisting species in savanna ecosystems (Schulze et al. 1994; Woodward and Smith 1994) despite the large area they cover (3×10^6 km^2 in West Africa, Menaut et al. 1991). These savannas often associate C_4 grass and C_3 tree species that are expected to exhibit contrasting photosynthetic traits (Ehleringer and Björkman 1977; Bolton and Brown 1980; Pearcy and Ehleringer 1984). Savanna ecosystems can also undergo rapid changes in their structure, particularly the tree/grass balance (Archer et al. 2001). Because C_4 species generally exhibit higher photosynthetic water- and nitrogen-use efficiencies (WUE and NUE) (Sage and Pearcy 1987), a shift from grass- to tree-dominated savanna areas would probably entail strong changes in WUE and NUE at the ecosystem scale.

A few field studies have quantified light-saturated net photosynthesis of grass species (Le Roux and Mordelet 1995, Anten et al. 1998, Baruch and Bilbao 1999) or tree species (Sobrado 1991 and 1996, Medina and Francisco 1994, Fordyce 1995, Prior et al. 1997) in humid savannas. Responses of g_s to air humidity have also been reported for a few humid savanna grass species (Baruch et al. 1985). However, no comprehensive approach allowing the comparison of the photosynthetic characteristics among major grass and tree species coexisting in a given humid savanna ecosystem (i.e., photosynthetic capacity, WUE and NUE) has been achieved to date. Furthermore, acclimation of leaf photosynthetic characteristics along light gradients within the canopy (i.e., variations between open areas or under tree clumps for grasses or intra tree crown variations) has not been documented for such species. This is essential for understanding and predicting surface-atmosphere exchanges in the humid savanna zone. This knowledge is also important for the understanding of the coexistence of plant life forms in humid savannas.

In this study, leaf photosynthesis and stomatal conductance were measured for two dominant perennial C_4 grass species (*Hyparrhenia diplandra* and *Andropogon canaliculatus*), and two dominant C_3 tree species (*Crossopteryx febrifuga* and *Cussonia arborea*) of the Lamto savannas (Ivory Coast). Our objectives were (1) to determine the photosynthetic capacities of the four species and parameterize biochemically-based models of photosynthesis for each, (2) to compare the stomatal responses to light and air humidity between the four species, and (3) to compare the photosynthetic water- and nitrogen-use efficiencies between these species. In particular, we tested whether differences in photosynthetic capacities, stomatal responses to environmental variables, and WUE and NUE were only explained by differences in the photosynthetic pathway and life forms (i.e., contrasts between C_3 trees and C_4 grasses), or whether significant differences could be observed between species sharing the same photosynthetic pathway and life form (i.e., importance of the species composition of the grass and tree layers).

Materials and methods

Study area

The Lamto ecological reserve is located 5°02' W and 6°13' N. It belongs to the guinean savanna type, characterised by a high annual rainfall (typically 1200 mm/year) following a bimodal seasonal distribution. A long dry period occurs from November to March, a long rainy season from March to July, a short dry season in August and a small rainy season from September to October. Vegetation at Lamto has been extensively described in Menaut and César (1979). It is a mosaic of gallery forests (following rivers and seasonal water streams) and savanna areas. The grass layer is dominated by C_4 perennial grasses, essentially from the genera *Hyparrhenia* and *Andropogon*. They belong to the Andropogoneae family (about 80% of grass phytomass, Le Roux 1995), among which are *Hyparrhenia diplandra* and *Andropogon canaliculatus*. The tree layer is dominated by four C_3 species among which are *Crossopteryx febrifuga* and *Cussonia arborea* (about 70% of the tree cover on the study site, Le Roux 1995).

The C_3 photosynthesis model

Two biochemical models were used to calculate photosynthetic characteristics. The model used to derive C_3 plant photosynthetic parameters corresponds to the version of Harley et al. (1992) of the model proposed by Farquhar et al. (1980), without including the potential limitation due to the use of triose phosphate.

Net CO_2 assimilation rate A_n (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) is expressed as:

$$A_n = \left(1 - \frac{0.5 \cdot O}{\tau \cdot C_i}\right) \cdot \min(W_c, W_j) - R_d \qquad (1)$$

where W_c (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) is the carboxylation rate limited by the amount, activation state or kinetic properties of Rubisco, W_j (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) is the carboxylation rate limited by the rate of RuP_2 regeneration, τ is the specitivity factor for Rubisco (Jordan and Ogren 1984), R_d (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) is the rate of CO_2 evolution in light that results from processes other than photorespiration, and O and C_i (Pa) are the partial pressures of O_2 and CO_2 in the intercellular air spaces, respectively.

W_c follows competitive Michaelis-Menten kinetics with respect to O_2 and CO_2:

$$W_c = V_{c\max} \cdot \frac{C_i}{C_i + K_c \cdot \left(1 + \frac{O}{K_O}\right)} \qquad (2)$$

where V_{cmax} (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) is the maximum rate of carboxylation, and K_c and K_O (Pa O_2 and Pa CO_2) are Michaelis constants for carboxylation and oxygenation, respectively.

W_j is controlled by the rate of electron transport J (μmol$\cdot m^{-2} \cdot s^{-1}$):

$$W_j = J \cdot \frac{C_i}{4 \cdot \left(C_i + \frac{O}{\tau}\right)} \qquad (3)$$

J depends on photosynthetically active photon flux density Q (μmol$\cdot m^{-2} \cdot s^{-1}$):

$$J = \alpha \cdot \frac{Q}{\sqrt{1 + \frac{\alpha^2 \cdot Q^2}{J_{\max}^2}}} \qquad (4)$$

where J_{max} (μmol$\cdot m^{-2} \cdot s^{-1}$) is the light-saturated rate of electron transport, and α is the apparent efficiency of light energy conversion on the basis of incident light (mol electrons per mol photons). The temperature dependence of R_d, τ, K_c, and K_O is described by:

$$(R_d, \tau, K_c, K_O) = e^{c - \frac{\Delta H_a}{R \cdot T_l}} \qquad (5)$$

where ΔH_a ($J \cdot mol^{-1}$) is the activation energy of the given parameter, R (8.3143 $J \cdot K^{-1} \cdot mol^{-1}$) is the gas constant, T_l (K) is leaf temperature, and c is the dimensionless, scaling constant of the given parameter. Similarly, the temperature dependence of V_{cmax} and J_{max} is described by:

$$(V_{c\max}, J_{\max}) = \frac{e^{c - \frac{\Delta H_a}{R \cdot T_l}}}{1 + e^{\frac{\Delta S \cdot T_l - \Delta H_d}{R \cdot T_l}}} \qquad (6)$$

where ΔS ($J \cdot K^{-1} \cdot mol^{-1}$) is an entropy term, and ΔH_d ($J \cdot mol^{-1}$) is the deactivation energy of the given parameter. To account for the linear relationships commonly observed between leaf photosynthetic capacities and the amount of nitrogen per unit leaf area N_a ($g\ N \cdot m^{-2}$), the scaling factors c for V_{cmax}, J_{max}, and R_d are linearly related to $\ln(N_a)$:

$$c = a_N + b_N \cdot \ln(N_a) \qquad (7)$$

where a_N and b_N are parameters.

The C_4 photosynthesis model

The model used to derive C_4 plant photosynthetic parameters corresponds to the simplified model of Collatz et al. (1992). Gross photosynthesis A is given as a function of Q, C_i, and T_l in the form of a pair of nested quadratic equations. The first equation is :

$$\theta \cdot M^2 - M \cdot (V_T + \alpha \cdot Q) + V_T \cdot \alpha \cdot Q = 0 \qquad (8)$$

where V_T (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) is the temperature-dependent, substrate saturated rubisco capacity, α (mol-.mol^{-1}) is the quantum efficiency (initial slope of the photosynthesis-light response), M (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) is the flux determined by the rubisco and light limited capacities, and θ is a curvature parameter that gives a gradual transition between Q and V_T limited fluxes. The limitation on the overall rate by M and the

CO_2 limited flux is expressed likewise :

$$\beta \cdot A^2 - A \cdot \left(M + k_T \cdot \frac{C_i}{P} \right) + M \cdot k_T \cdot \frac{C_i}{P} = 0 \qquad (9)$$

where k_T is the temperature-dependent pseudo-first order rate constant with respect with C_i, P is the atmospheric pressure (Pa), and β is analogous to θ and specifies the degree of co-limitation between M and the CO_2 limited flux. The smaller roots are the appropriate solutions for both quadratics. A_n is defined as:

$$A_n = A - R_T \qquad (10)$$

where R_T is the temperature-dependent rate of leaf respiration. Temperature dependencies follow:

$$V_T = \frac{V_{\max} \cdot Q_{10-V_{\max}}^{\frac{T_l - 25}{10}}}{(1 + e^{0.3 \cdot (13 - T_l)}) \cdot (1 + e^{0.3 \cdot (T_l - 36)})} \qquad (11)$$

$$R_T = \frac{R_d \cdot Q_{10-R_d}^{\frac{T_l - 25}{10}}}{1 + e^{1.3 \cdot (T_l - 55)}} \qquad (12)$$

$$k_T = k \cdot Q_{10-k}^{\frac{T_l - 25}{10}} \qquad (13)$$

where $Q_{10-(Vmax,\, Rd,\, k)}$ are proportional increases of V_T, R_T, and k_T respectively, with a 10 °C increase in temperature, T_l (°C) is leaf temperature, and V_{max}, k, and R_d are reference values for V_T, k_T, and R_T for 25 °C.

The stomatal conductance model

Stomatal conductance was parameterised according to the empirical model proposed by Jarvis (1976). The model assumes that stomatal conductance, g_s, is affected by non-synergistic interactions between plant and environmental variables. While the model is able to handle multiple environment effects, this study focused on Q and the vapour pressure deficit at leaf surface (VPD_l):

$$g_s = g_{sref} \cdot f(Q) \cdot f(VPD_l) \qquad (14)$$

where g_{sref} is the reference stomatal conductance, defined as measured stomatal conductance under standardized environmental conditions.

Determination of the parameters of the C_3 photosynthesis model

Gas exchange measurements were done during the beginning of the rainy season, in March-April 2000 and in May 2001, using a LI-COR 6400 infra-red gas analyser – leaf chamber system (LI-COR Inc., Lincoln, NE, USA) that allowed control of environmental conditions. A red light source was used during the 2000 period, while a blue-red light source was used for the 2001 measurements. Test samples showed that gas exchanges data were not affected by the type of light source used. Net CO_2 assimilation and transpiration rates, stomatal conductance, and CO_2 partial pressure in the substomatal spaces were calculated according to von Caemmerer and Farquhar (1981). Measurements were done on 12 *Crossopteryx* and 9 *Cussonia* leaves sampled on trees from various locations and of different sizes. Leaves were chosen to encompass full sunlight and shade conditions. All measurements were performed on fully expanded leaves.

For each leaf, an A-C_i response curve at high irradiance (1000 to 1200 μmol·m^{-2}·s^{-1}) was used to infer the best fit V_{cmax} value by non-linear least square regression. Only data collected for C_i values below 20 Pa were used. Measurements for which carboxylation was not limiting (i.e., values below those predicted by Equation (1) and (2) were used to estimate J_{max}. Typically, for each response curve, the order of measurements was: 1) a reference value at ambient CO_2 (350-360 ppm), 2) a measurement at high CO_2 (1800 ppm), 3) several measurements while decreasing CO_2 down to 50-100 ppm, and 4) a respiration measurement at ambient CO_2 and in darkness. At least three measurements were taken for each CO_2 level. Given the high sensitivity of stomatal conductance to high atmospheric CO_2 concentrations, this scheme was not always respected and shifts between high and low CO_2 were often necessary to keep the stomata open, and to prevent hysteresis during the procedure. All measurements were done at leaf temperatures ranging from 28 to 33 °C. Parameter values were corrected to avoid temperature effects, to a reference temperature of 31 °C, using temperature dependence Equations 5 and 6 with parameters proposed by Harley et al. (1992) (Table 1).

Table 1. Parameter values used to derive photosynthetic parameters from field measurements, according to Harley et al. (1992) for the C_3 model, and according to Collatz (pers. com.) for the C_4 model

parameter	value	Unit
C_3 model		
α	0.24	$mol.mol^{-1}$
c_{Kc}	35.79	–
c_{Ko}	9.59	–
c_{τ}	− 3.9489	–
$\Delta H_{a\text{-}Kc}$	80470	$J.mol^{-1}$
$\Delta H_{a\text{-}Ko}$	14510	$J.mol^{-1}$
$\Delta H_{a\text{-}\tau}$	− 28990	$J.mol^{-1}$
$\Delta H_{a\text{-}Rd}$	84450	$J.mol^{-1}$
$\Delta H_{a\text{-}Vcmax}$	116300	$J.mol^{-1}$
$\Delta H_{a\text{-}Jmax}$	79500	$J.mol^{-1}$
$\Delta H_{d\text{-}Vcmax}$	202900	$J.mol^{-1}$
$\Delta H_{d\text{-}Jmax}$	201000	$J.mol^{-1}$
ΔS_{Vcmax}	650	$J.K^{-1}.mol^{-1}$
ΔS_{Jmax}	650	$J.K^{-1}.mol^{-1}$
C_4 model		
$Q_{10\text{-}k}$	1.8	–
$Q_{10\text{-}Vmax}$	2.1	–
$Q_{10\text{-}Rd}$	2	–

Determination of the parameters of the C_4 photosynthesis model

A-C_i response curves were made as for C_3 plants on 11 leaves for *Andropogon*, and 6 leaves for *Hyparrhenia*. Leaves were chosen to encompass full sunlight and shade conditions (i.e., for grasses in open areas or under tree clumps). α and θ were derived from A-Q response curves (same as g_s-Q curves, see below). No significant difference was found between the two grass species ($P > 0.05$), thus mean values were used ($\alpha = 0.0657$ mol·mol^{-1}, $\theta = 0.7617$). The parameters β, V_T, and k_T were computed from each A-C_i curve by fitting Equations 8 and 9 to measured data. No significant difference was found between species for β ($P > 0.05$), thus equations were re-fitted to A-C_i curves with a mean value for β of 0.915. R_T was estimated as for C_3 plants. Measurements were done at leaf temperatures from 29 °C to 35 °C.

Parameter values were corrected to account for temperature effects. Equation 11-13 and Q_{10} parameters presented in Table 1 were used to estimate reference values at 31 °C.

Figure 1 presents typical A-C_i response curves obtained for the four species.

Determination of the parameters of the stomatal conductance model

g_s-Q and g_s-VPD_l response curves were obtained under ambient CO_2 (350-360 ppm) and for leaf temperatures ranging from 28 to 34°C. For each g_s-Q curve, measurements were acquired at Q = 1800, 1600, 1400, 1200, 1000, 800, 600, 400, 200, 100, 50, and 0 μmol·m^{-2}·s^{-1}, under VPD_l around 1 kPa. Each curve had a particular reference stomatal conductance, $g_{sref\text{-}Q}$, defined as the mean measured g_s at Q = 1000-1200 μmol·m^{-2}·s^{-1}. $g_{sref\text{-}Q}$ allowed to compare variations of the $g_s/g_{sref\text{-}Q}$ ratio with light for the different curves. For each g_s-VPD_l curve, measurements were acquired at VPD_l values ranging from 1 or below, to as high as environmental conditions allowed (3 to 5 kPa). Q was maintained between 1000-1200 μmol·m^{-2}·s^{-1}. $g_{sref\text{-}VPD}$ was defined as mean g_s at VPD_l values of 1.4-1.6 kPa. A total of 8, 5, 5, and 4 g_s-Q and 5, 4, 6, and 5 g_s-VPD_l curves were done for *Crossopteryx*, *Cussonia*, *Andropogon*, and *Hyparrhenia* respectively.

For each species, a reference stomatal conductance g_{sref} was computed as the stomatal conductance measured at Q = 1000-1200 μmol·m^{-2}·s^{-1}, VPD_l = 1-1.6 kPa, T_l = 29-34 °C, and air CO_2 = 350-360 ppm. Values for g_{sref} from all response curves (A-C_i, g_s-Q, and g_s-VPD_l) corresponding to these conditions were used to compute g_{sref}. Measured g_{sref} was corrected for VPD_l effects using species specific g_s-VPD_l relations described above.

Leaf analysis

All leaves on which gas exchange measurements were done were collected. Tree leaves were copied fresh to have a print of the fresh leaf surface. Tree leaf surfaces were then measured using a leaf area meter (Delta T Devices, Hoddeston, U.K.) on leaf copies. Tree leaves were dried 3 days at 70 °C and weighed. For each grass leaf, leaf exchange surface was calculated with measured leaf dimensions inside the LI-COR leaf chamber. A larger part of the leaf was collected to provide sufficient matter for nitrogen analysis. Each grass leaf was dried 3 days at 70 °C and the leaf part corresponding to the leaf exchange surface was weighed. All leaves were crushed using a 0.08 mm filter and leaf N concentration was measured using an elemental analyser (NA 1500 series 2, Fisons).

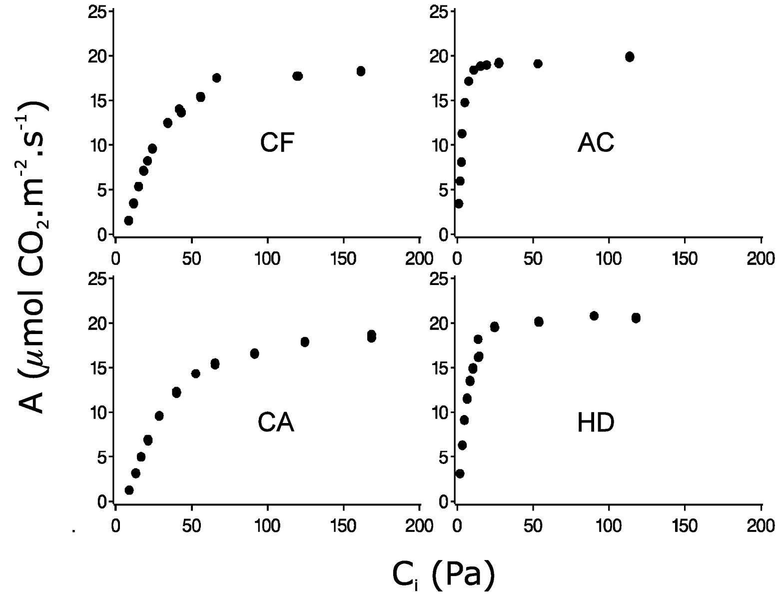

Figure 1. Examples of the response of net assimilation rate to variations in internal CO_2 partial pressure (A-C_i response curves) for the two C_3 trees, *Crossopteryx febrifuga* (CA), and *Cussonia arborea* (CA), and the two C_4 grasses, *Andropogon canaliculatus* (AC), and *Hyparrhenia diplandra* (HD).

Calculation of water- and nitrogen-use efficiencies

Measurements from all response curves from which g_{sref} were computed were used to calculate photosynthetic WUE (ratio A_n/transpiration, in µmol CO_2·mmol H_2O^{-1}) and NUE (A_n/N_a ratio, in µmol CO_2·s^{-1}·g N^{-1}). Only a few leaves were suitable for g_{sref} computation for *Hyparrhenia*, thus all grass g_{sref}, WUE and NUE data were pooled.

Statistical analyses

All variance and covariance analyses were performed with the SAS proc GLM procedure (SAS inst., Cary, USA). All regression analyses were performed using the SAS proc REG procedure.

Results

Photosynthesis parameters

For tree species, V_{cmax} and J_{max} were linearly correlated to N_a (Figure 2). Assuming similar intercepts between the two tree species for the V_{cmax}-N_a relationship, a significantly higher slope was found for *Cussonia* (covariance analysis, $P < 0.05$). Similarly, assuming similar slopes between the two species for the J_{max}-N_a relationship, a significantly higher intercept was found for *Cussonia* (covariance analysis, $P < 0.05$). R_d was not significantly correlated with N_a and was not found to be different between tree species (covariance analysis, $P > 0.05$).

For grass species, no species effect was found for any parameter, and no nitrogen effect was detected for R_d (analysis of covariance, $P > 0.05$). A weak relation suggests an increase of V_{max} with N_a ($P = 0.08$), while k increased significantly with N_a ($P < 0.05$) (Figure 2).

Stomatal conductance

g_{sref} increased with N_a for *Crossopteryx* and grasses, while no significant relationship was found for *Cussonia*. Analysis of covariance showed no significant difference between grasses and *Cussonia*, while *Crossopteryx* exhibited lower g_{sref} values (Figure 3).

Stomatal conductance decreased with decreasing Q for all species (Figure 4). Data were fitted using a logarithmic relationship, that gave the most accurate fit for the pooled four species. This common relation allowed to test for a species effect. Analysis of covariance showed no difference between *Andropogon*, *Hyparrhenia*, and *Crossopteryx*, but the *Cussonia* fit

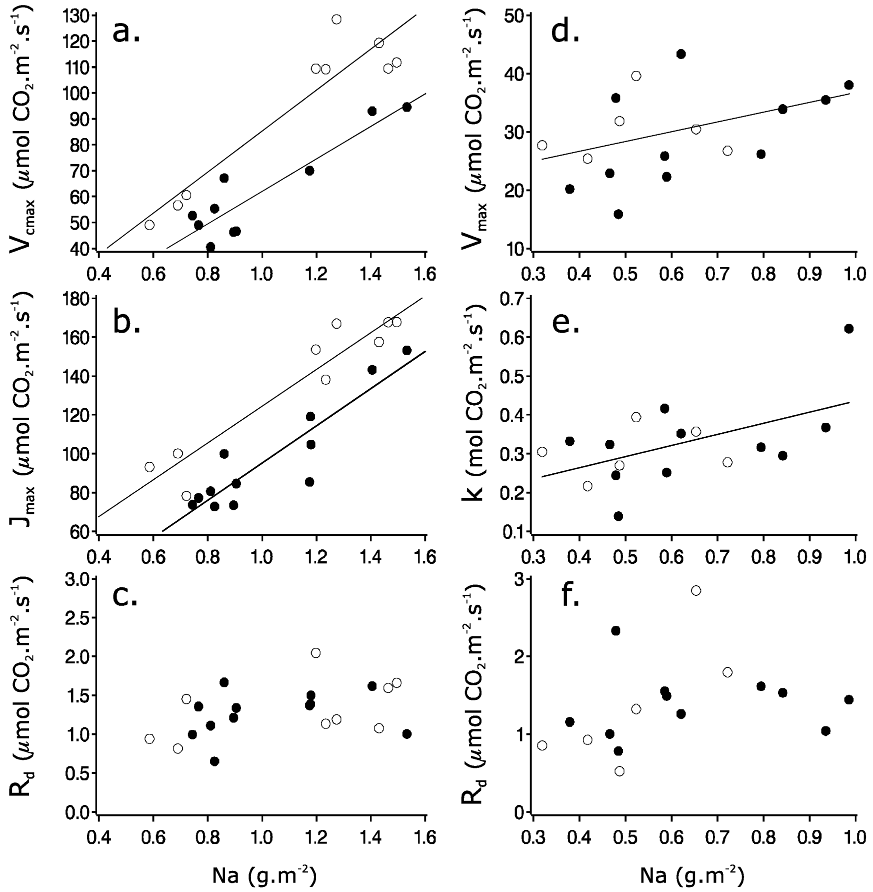

Figure 2. Variations of the C_3 photosynthesis model parameters (a., b., and c.) for *Crossopteryx febrifuga* (CF, ●) and *Cussonia arborea* (CA, ○), and of the C_4 photosynthesis model parameters (d., e. and f.) for *Andropogon canaliculatus* (AC, ●) and *Hyparrhenia diplandra* (HD, ○), with nitrogen per unit leaf area (N_a). Values were corrected to a reference temperature of 31°C for all species. Lines represent significant ($P < 0.05$) regression fits per species for C_3 plants, and for pooled species for C_4 plants (except for V_{max}-N_a: P = 0.08). Regression coefficients are for V_{cmax}-N_a: 0.83 for CF and 0.88 for CA; for J_{max}-N_a: 0.82 for CF and 0.90 for CA; for V_{max}-N_a: 0.18; and for k-N_a: 0.29

had a significantly different slope and origin ($P < 0.05$). *Cussonia* maintained a higher g_s than other species at low irradiance, but the difference was small.

For all species, the stomatal conductance decreased with increasing VPD_l (Figure 5). To test for significant differences between species, an analysis of covariance was conducted using a logarithmic relationship for all species (that gave the best fit for the pooled four species). The slope and the intercept obtained for *Crossopteryx* were significantly different from those obtained for the other species. *Andropogon* had a significantly different slope from *Hyparrhenia* and from *Cussonia*, but these three species had similar intercepts. *Hyparrhenia* and *Cussonia* slopes and intercepts were not significantly different. These results, along with graphical comparison of the fits (Figure 5) suggest that for *Crossopteryx*, g_s decreased more at high VPD_l than for all other species (about 75% decrease at 3-4 kPa). Stomatal conductance of *Andropogon* exhibited the lowest decrease (less than 50% decrease at more than 4 kPa), and g_s of *Hyparrhenia* and *Cussonia* exhibited an intermediate decrease (about 60% decrease at 4 kPa).

Water and nitrogen use efficiencies

Crossopteryx WUE decreased with increasing N_a, while no relation was found for all other species (Figure 6). Analysis of variance showed that *Crossopteryx* and *Cussonia* WUE were not significantly different (average values of 5.84 and 5.45 μmol

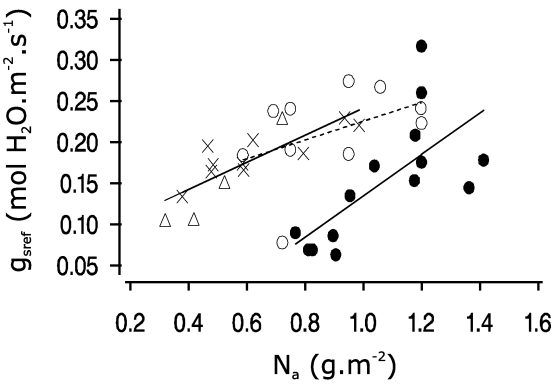

Figure 3. Reference stomatal conductances (g_{sref}) of *Crossopteryx febrifuga* (●),*Cussonia arborea* (○), *Andropogon canaliculatus* (×), and *Hyparrhenia diplandra* (Δ), as a function of leaf nitrogen per unit leaf area (N_a). Solid lines represent significant regression fits for *Crossopteryx* and for grasses. The dashed line represents a non significant regression fit for *Cussonia.*

CO_2·mmol H_2O^{-1}, respectively), but were lower than that of grasses (9.15 μmol CO_2·mmol H_2O^{-1}).

Grass NUE decreased with increasing N_a, and was much higher than tree NUE (ANOVA, $P < 0.05$). *Cussonia* NUE (average value of 12.95 μmol $CO_2 \cdot s^{-1} \cdot$ g N^{-1}) was higher than that of *Crossopteryx* (8.7 μmol $CO_2 \cdot s^{-1} \cdot$g N^{-1}). Tree NUE was not correlated with N_a ($P > 0.05$).

Discussion

Differences in gas exchange characteristics between C_4 grass and C_3 tree species of the Lamto savannas

Stomatal behaviour

g_{sref} values reported for the two tree species (i.e., from 100 to 300 mmol $H_2O \cdot m^{-2} \cdot s^{-1}$) were close to maximal stomatal conductance values reported for tropical trees (145-270 mmol $H_2O \cdot m^{-2} \cdot s^{-1}$; Schulze et al. 1994), savanna trees from central Venezuela (from 100 to 500 mmol $H_2O \cdot m^{-2} \cdot s^{-1}$; Medina and Francisco 1994), lowland rainforest trees (around 300 mmol $H_2O \cdot m^{-2} \cdot s^{-1}$; Koch et al. 1994), amazonian rain forest trees from the upper canopy layer (around 260 mmol $H_2O \cdot m^{-2} \cdot s^{-1}$; Roberts et al. 1990), and Kenyan savanna tree species (about 330 mmol $H_2O \cdot m^{-2} \cdot s^{-1}$; Hesla et al. 1985). Higher values have been reported for *Tectona grandis* and *Gmelina arborea* in Nigeria (around 500 mmol $H_2O \cdot m^{-2} \cdot s^{-1}$; Grace et al. 1982), and *Eucalyptus tetrodonta* in savannas of northern Australia (around 1000 mmol $H_2O \cdot m^{-2} \cdot s^{-1}$; Prior et al. 1997). g_{sref} obtained for the grasses *Andropogon* and *Hyparrhenia* were lower than maximum stomatal conductance reported for temperate grasslands, tropical savannas or tropical pasture (from 210 to 500 mmol $H_2O \cdot m^{-2} \cdot s^{-1}$; Schulze et al. 1994), and maximum g_s values measured on potted individuals of *Hyparrhenia rufa* grown in a controlled environment and with fertilisation (around 600 mmol $H_2O \cdot m^{-2} \cdot s^{-1}$; Baruch et al. 1985, Baruch 1994, and about 450 mmol $H_2O \cdot m^{-2} \cdot s^{-1}$; Baruch and Fernandez 1993). Our results are in the range of values reported for Kenyan savanna grass species (about 250 mmol $H_2O \cdot m^{-2} \cdot s^{-1}$; Hesla et al. 1985). No systematic difference in g_{sref} was observed between C_4 grasses and C_3 tree species. In particular, g_{sref} of *Cussonia* was close to values obtained for the grass species. This is consistent with the close values for g_{smax} reported for coniferous tree species versus grassland species of temperate regions (Kelliher et al. 1993).

The response of g_{sref} to Q was roughly similar between grass and tree species. A typical non-linear response to Q (e.g., Leverenz 1995) was obtained. Stomatal conductance decreased linearly with increasing VPD_l over the 1 to 3.5 kPa range for *Cussonia*, whereas a non-linear response was observed for the other species. A linear decrease of g_s with increasing VPD_l has been reported for several herbaceous species (Aphalo and Jarvis 1991; Bunce 1996) and tree species (e.g., Dang et al. 1997; Le Roux et al. 1999). However, non-linear relationships are also common for trees (e.g., Dang et al. 1997) and have been reported for *Hyparrhenia rufa* (Baruch et al. 1985). Differences in the g_s-VPD_l response (either in the shape or in the extent of the decrease of g_s with VPD_l) were observed between species, but not between grasses and trees. This can be explained because the four species are all shallow rooted (Le Roux et al. 1995). Such a decrease of g_s with VPD_l can thus be explained evolutionarily because all the species have to restrict water loss during dry spells to a certain extent.

Photosynthetic water- and nitrogen-use efficiency

In accordance with the literature (Pearcy and Ehleringer 1984), WUE was higher for C_4 than C_3 plants. WUE values obtained for *Crossopteryx* and *Cussonia* (from 4 to 8 μmol CO_2·mmol H_2O^{-1}) were close to values reported for acacia species invading the Fynbos (around 4 μmol CO_2·mmol H_2O^{-1}; Kraaij and Cramer 1999) and for the C_3 herb species *Chenopodium album* and *Festuca arundinacea* (5

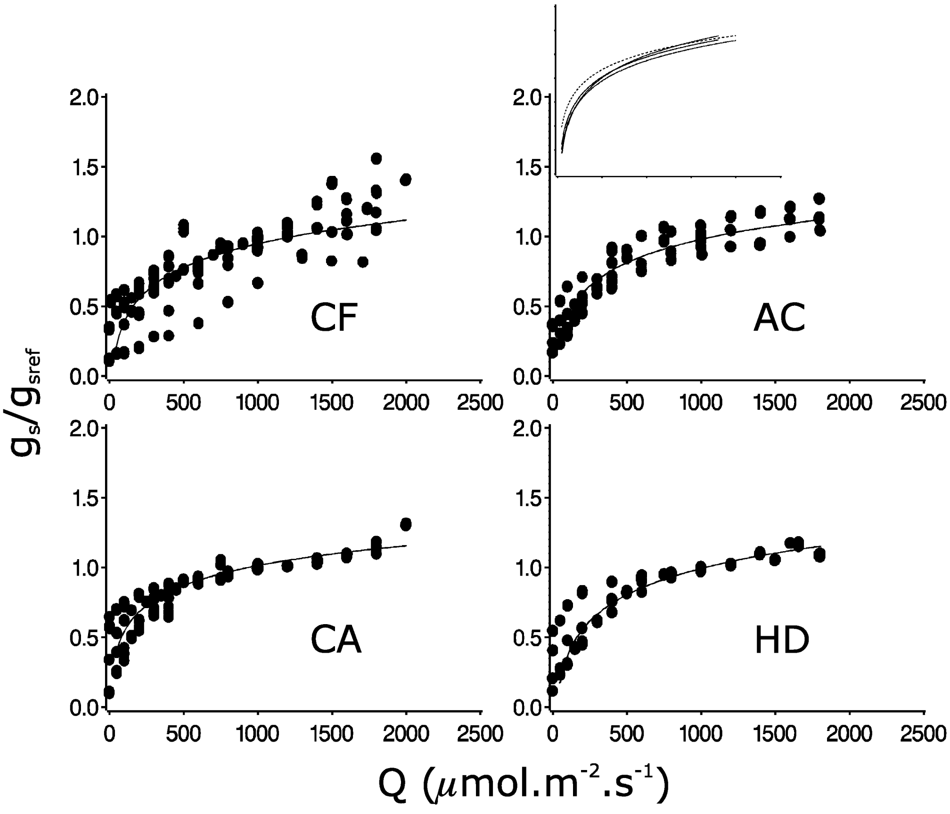

Figure 4. The response of stomatal conductance to incident photosynthetically active radiation (*Q*) for *Crossopteryx febrifuga* (CF), *Cussonia arborea* (CA), *Andropogon canaliculatus* (AC), and *Hyparrhenia diplandra* (HD). Stomatal conductance is represented as the ratio of actual (g_s) to reference stomatal conductance (g_{sref}). Lines represent regression fits using a common relation for all species. Regression coefficients are 0.66, 0.83, 0.86 and 0.88 for CF, CA, AC, and HD, respectively. The inset graph represents regression fits for all species. No difference was found between species except for CA, represented with a dashed line.

μmol CO_2·mmol H_2O^{-1}; Sage and Pearcy 1987; Bolton and Brown 1980). Lower values have been reported for the evergreen savanna tree *Curatella americana* in Venezuela (from 1.0 to 1.4 μmol CO_2·mmol H_2O^{-1}; Sobrado 1996). Similarly, the ratio of light-saturated net photosynthesis under ambient CO_2 to g_{sref}, i.e., another index of WUE, was higher for *Cussonia* and *Crossopteryx* (about 64 μmol CO_2·mmol H_2O^{-1}) than for two savanna tree species of central Venezuela (from 36 to 46 μmol CO_2·mmol H_2O^{-1}; Medina and Francisco 1994). This could reveal a difference between deep rooted evergreen species exhibiting low photosynthetic activity and WUE (as in Neotropical savannas) and shallow rooted deciduous tree species exhibiting higher photosynthetic activity and WUE (as found in Lamto). However, more data are needed for tropical savanna trees before such a conclusion can be generalized. WUE values obtained for *Andropogon* and *Hyparrhenia* (from 6 to 12 μmol CO_2·mmol H_2O^{-1}) were in the range of those reported for potted *Hyparrhenia rufa* individuals growing under controlled conditions (6.35 μmol CO_2·mmol H_2O^{-1}; Baruch et al. 1985) and for the C_4 herb species *Amaranthus retroflexus* (8 μmol CO_2·mmol H_2O^{-1}; Sage and Pearcy 1987) and *Panicum maximum* (10 μmol CO_2·mmol H_2O^{-1}; Bolton and Brown 1980). Given the similar g_{sref} values obtained for grass and tree species (see above), such high grass WUE values were explained by high photosynthetic capacities allowed by the C_4 pathway under a high-light, hot climate (Pearcy and Ehleringer 1984).

The difference between the higher NUE values obtained for grass species and the lower values for the tree species were also in accordance with the literature comparing C_4 and C_3 species (Bolton and Brown 1980; Sage and Pearcy 1987; Anten et al. 1998). NUE values obtained for *Crossopteryx* and *Cussonia* (from

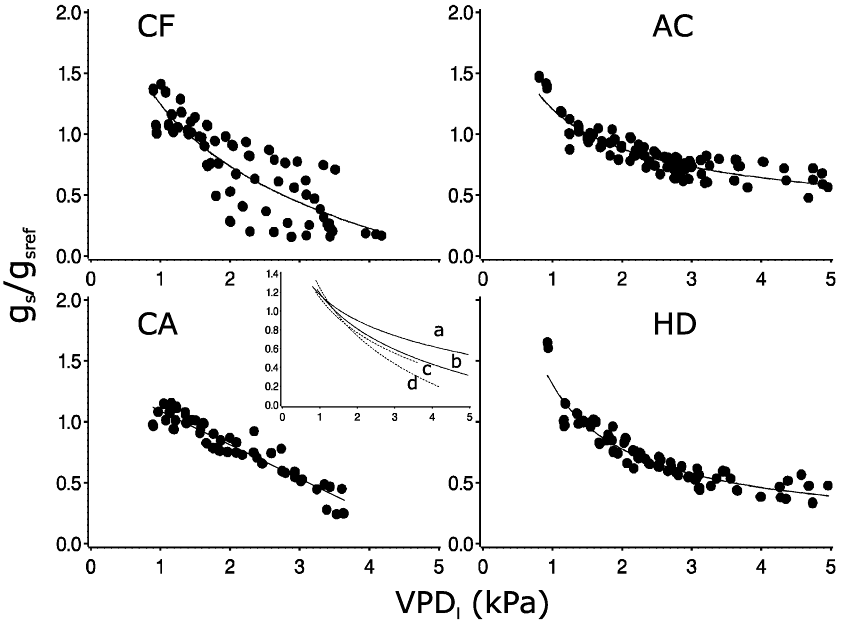

Figure 5. The response of stomatal conductance to vapour pressure deficit at leaf surface (*VPD_l*) of *Crossopteryx febrifuga* (CF), *Cussonia arborea* (CA), *Andropogon canaliculatus* (AC), and *Hyparrhenia diplandra* (HD). Stomatal conductance is represented as the ratio of actual (g_s) to reference stomatal conductance (g_{sref}). Lines represent best regression fits. Regression coefficients are 0.72, 0.89, 0.80 and 0.88 for CF, CA, AC, and HD, respectively. The inset graph represents logarithmic fits for AC (a), HD (b), CA (c), and CF (d), that were used for statistical comparison between species.

5 to 14 μmol $CO_2 \cdot g\ N^{-1}.s^{-1}$) were slightly higher than values measured for savanna tree species of central Venezuela (from 4.1 to 4.7 μmol $CO_2 \cdot g\ N^{-1}.s^{-1}$; Medina and Francisco 1994), and lower than values reported for Fynbos acacia species (from 20 to 54 μmol $CO_2 \cdot g\ N^{-1}.s^{-1}$; Kraaij and Cramer 1999) and the evergreen savanna tree *Curatella americana* of Venezuela (from 32 to 98 μmol $CO_2 \cdot g\ N^{-1} \cdot s^{-1}$; Sobrado 1996). The NUE values computed for *Andropogon* and *Hyparrhenia* (from 25 to 50 μmol $CO_2 \cdot g\ N^{-1} \cdot s^{-1}$) were higher than NUE measured on the C_4 annual *Amaranthus retroflexus* (about 18 μmol $CO_2 \cdot g\ N^{-1} \cdot s^{-1}$; Sage and Pearcy 1987), but in the range of values measured for potted *Hyparrhenia rufa* individuals growing under controlled conditions (40 μmol $CO_2 \cdot g\ N^{-1} \cdot s^{-1}$; Baruch et al. 1985), *H. rufa* growing in a seasonal savanna of central Venezuela (from 25 to 34 μmol $CO_2 \cdot g\ N^{-1} \cdot s^{-1}$; Anten et al. 1998; 38.8 μmol $CO_2 \cdot g\ N^{-1} \cdot s^{-1}$; Baruch and Bilbao 1999), and *Hyparrhenia* individuals growing in the field in Lamto (25.1 μmol $CO_2 \cdot g\ N^{-1} \cdot s^{-1}$; Le Roux and Mordelet 1995). These contrasts in NUE between C_4 and C_3 pathways are explained by the CO_2-concentrating mechanism allowed by the C_4 pathway (Edwards and Huber 1981; Pearcy and Ehleringer 1984). These results show that the C_4 savanna grasses exhibit a remarkably high leaf photosynthetic capacity at low leaf nitrogen levels. As anticipated by Le Roux and Mordelet (1995), this feature is a key attribute for understanding the productivity of the grass layer in humid savanna environments.

Differences in gas exchange characteristics within C_4 grass and C_3 tree life forms of the Lamto savannas

Homogeneity among grass species

No difference in V_{max}, k, R_d, WUE nor NUE were found between *Andropogon* and *Hyparrhenia*. This homogeneity of grass photosynthetic characteristics is in accordance with the homogeneity of production patterns observed for perennial grasses at Lamto (César 1992; Mordelet 1993; Le Roux 1995; Simioni 2001). k was related to N_a, but only a weak relation was found for V_{max}. Nonetheless, this relation is physiologically relevant, as photosynthetic capacity, for a number of C_4 species, has been related with N_a (Bolton and Brown 1980; Sage and Pearcy 1987; Anten et al. 1995; Anten et al. 1998). Most studied species had higher N_a values than *Hyparrhenia* and

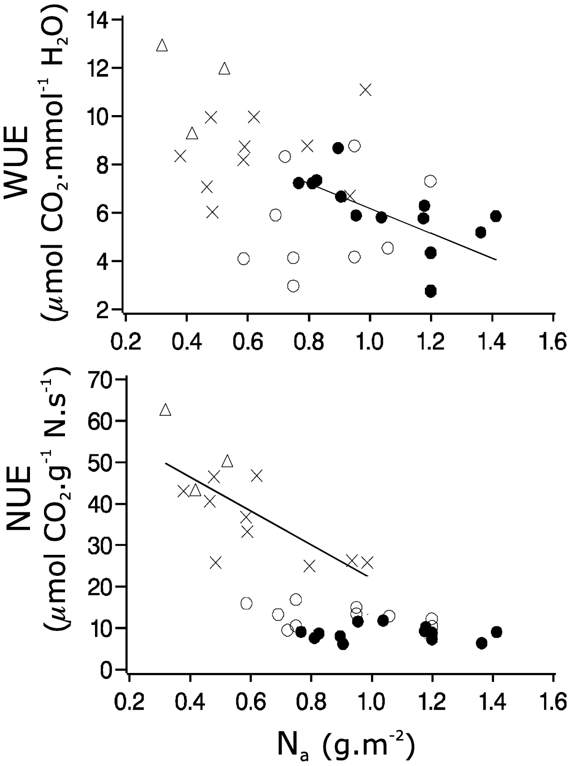

Figure 6. Variations of water use efficiency (*WUE*), and nitrogen use efficiency (*NUE*) of *Crossopteryx febrifuga* (●), *Cussonia arborea* (○), *Andropogon canaliculatus* (×), and *Hyparrhenia diplandra* (Δ), with the amount of nitrogen per unit leaf area (N_a). Solid lines represent significant regression fits ($P < 0.05$) for *WUE* of *Crossopteryx*, and for *NUE* of grasses (*Andropogon* and *Hyparrhenia*.)

Andropogon, partly because several studies were carried out on greenhouse-grown and fertilized plants. R_d is generally correlated with N_a (Boot and den Bubbelden 1990; Anten et al. 1995), but no R_d-N_a relationship was observed in our study. This was probably due to measurement precision, as CO_2 fluxes associated with respiration were very low compared to fluxes associated with photosynthesis, and difficult to measure under field conditions.

Only a few g_{sref} values could be derived from field measurements for *Hyparrhenia*, and the similarity of g_{sref} between *Andropogon* and *Hyparrhenia* has thus to be confirmed. While the responses of g_s to Q were identical for the two grasses, the response of stomatal conductance to VPD_l slightly differed. This difference occurred mainly at high VPD_l. Nonetheless, it is likely that in case of water stress (usually, high VPD_l values are observed during the heart of the dry season at Lamto) g_s will be more affected by plant water status than by VPD_l. Thus the difference of response to VPD_l does probably not entail large differences in g_s between *Andropogon* and *Hyparrhenia* in the field.

Contrasts between tree species

Crossopteryx and *Cussonia* exhibited contrasting photosynthetic characteristics. *Cussonia* exhibited higher V_{cmax} and J_{max} with similar R_d at a given N_a, and thus a higher NUE, than *Crossopteryx*. V_{cmax} and J_{max} values were high given the low N_a values, when compared to other studies (Harley et al. 1992; Le Roux et al. 1999a; Le Roux et al. 2001). But this is at least partly due to the high reference temperature (31 °C), as optimal temperatures for V_{cmax} and J_{max} are generally higher than 30 °C, even for temperate trees (Dreyer et al. 2001). At a given N_a value, *Cussonia* also displayed a higher g_{sref} than *Crossopteryx.* Such a higher photosynthetic capacity at a given N_a level can be explained at the physiological level, e.g., by differences in leaf internal resistance to CO_2 transport (Epron et al. 1995), and should be analysed at the ecological level in terms of growing strategy and leaf construction costs (Sobrado 1991).

Similar to *Crossopteryx*, *Cussonia* mainly uses water from the top soil layer (0-60 cm) during the rainy periods (Le Roux et al. 1995; Le Roux and Bariac 1998). However, it has access to deeper soil layers and thus probably benefits from better water conditions than *Crossopteryx*, especially during dry periods (Le Roux and Bariac 1998). This may account for the slower decrease in g_{sref} for *Cussonia* than for *Crossopteryx* with increasing VPD_l, because *Cussonia* could sustain higher transpiration rates than *Crossopteryx* during dry spells.

The lower stomatal closure with decreasing incident Q of *Cussonia* compared to *Crossopteryx* may be linked with plant growth strategies. At Lamto, only *Crossopteryx* seedlings can grow in open areas, while *Cussonia* seedlings grow under tree clumps (Gignoux 1994). *Cussonia* could thus be more adapted to shade conditions. Differences in the g_s-Q response between light adapted and shade tolerant species have already been reported for savanna grass species (Amundson et al. 1995). However, the difference in response to Q between *Crossopteryx* and *Cussonia* was weak, and its importance on plant performance has yet to be tested.

Importance of species functional diversity on savanna ecosystem WUE and NUE

Gas exchange characteristics measured at one time during the growing season cannot be directly used to infer patterns of transpiration and carbon gain at the ecosystem level over the entire year. A documenting of the seasonal courses of both photosynthetic capacity and leaf area is required to predict plant-atmosphere exchanges. Furthermore, photosynthesis is only one of the many characteristics that contribute to plant production and ecological success in a given environment. However, our results can be used to infer the importance of plant species composition on some aspects of the functioning of savannas.

Dominant C_4 grasses and C_3 trees at Lamto did not exhibit similar resource use efficiencies. Thus the tree/grass ratio may be a critical aspect for savanna WUE and NUE. This problem is of importance when regarding the tree encroachment phenomenon observed worldwide (Archer et al. 2001), including Lamto savannas (Gautier 1989). To our knowledge, no attempt has been made to test the impact of varying tree/grass ratios on savanna resource use efficiency. The two tree species exhibited significant differences in gas exchange characteristics. Hence, the respective abundances of each species may also affect ecosystem performance. Documenting the seasonal dynamics of leaf area and N_a during an entire year would be required to scale the contribution of both species at the ecosystem level. In addition, given that only two species were used for each photosynthetic pathway, the generalizations infered above should be verified by measurements on additional species.

Acknowledgements

This study was funded by the Programme National de Recherche en Hydrologie (PNRH, France) and the Programme Environnement, Vie et Société, France. The writing of the paper was partially funded by the Cooperative Research Centre for Greenhouse Accounting, Australia. The authors are also thankful to three anonymous reviewers for their suggestions to improve the manuscript.

Appendix 1 – Equations of the significant relationships obtained

Photosynthesis relationships

Crossopteryx:

$$c_{V_{c\max}} = 50.226 + 0.996 \cdot \ln(N_a) \quad R^2 = 0.75$$

$$c_{J_{\max}} = 36.224 + 0.942 \cdot \ln(N_a) \quad R^2 = 0.78$$

Cussonia:

$$c_{V_{c\max}} = 50.546 + 0.988 \cdot \ln(N_a) \quad R^2 = 0.94$$

$$c_{J_{\max}} = 36.507 + 0.758 \cdot \ln(N_a) \quad R^2 = 0.88$$

grasses (25ºC):

$$V_{\max} = 15.64 + 13.28 \cdot N_a \quad R^2 = 0.18; P = 0.08$$

$$k = 0.1044 + 0.2013 \cdot N_a \quad R^2 = 0.29$$

g_{sref}-N_a *relationships*

grasses:

$$g_{sref} = 0.0755 + 0.1655 \cdot N_a \quad R^2 = 0.68$$

Crossopteryx:

$$g_{sref} = -0.1176 + 0.2519 \cdot N_a \quad R^2 = 0.52$$

Cussonia:

$$g_{sref} = 0.1106 + 0.1143 \cdot N_a \quad R^2 = 0.19; P = 0.21$$

g_{sref}-Q *relationships*

Andropogon:

$$g_s / g_{sref} = -0.6927 + 0.2416 \cdot \ln(Q) \quad R^2 = 0.86$$

Hyparrhenia:

$$g_s / g_{sref} = -0.6943 + 0.2436 \cdot \ln(Q) \quad R^2 = 0.88$$

Crossopteryx:

$$g_s / g_{sref} = -0.7438 + 0.2445 \cdot \ln(Q) \quad R^2 = 0.66$$

Cussonia:

$$g_s / g_{sref} = -0.4103 + 0.2060 \cdot \ln(Q) \quad R^2 = 0.83$$

g_{sref}-VPD_l *relationships*

Andropogon:

$$g_s / g_{sref} = e^{0.1852 - 0.4548 \cdot \ln(VPD_l)} \quad R^2 = 0.80$$

Hyparrhenia:

$$g_s / g_{sref} = e^{0.2670 - 0.7512 \cdot \ln(VPD_l)} \quad R^2 = 0.88$$

Crossopteryx:

$$g_s \big/ g_{sref} = 1.2469 - 0.7367 \cdot \ln(VPD_l) \quad R^2 = 0.72$$

Cussonia:

$$g_s \big/ g_{sref} = 1.3666 - 0.2774 \cdot VPD_l \quad R^2 = 0.89$$

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