

The photosynthetic characteristics of papyrus in a tropical swamp

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Summary. Photosynthesis and transpiration was measured in the large emergent C_4 sedge *Cyperus papyrus* (papyrus) which occupies wide areas of wetland on the African continent. The maximum observed value of net assimilation was $35 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at full sunlight but light saturation of photosynthesis did not occur. The quantum yield of photosynthesis obtained from the initial slope of the light response curves ($0.06 \text{ mol mol}^{-1}$ incident light) was relatively high and close to previously recorded values for some C_4 grasses. Measurements made over two days showed that stomatal conductance was sensitive to the ambient air vapour pressure deficit (VPD) and was consistently lower on the day when VPD's were higher. There was, however, no marked midday closure of the stomata. Photosynthesis was also reduced on the day when VPD's were higher. The relationship between net photosynthesis and stomatal conductance was close to linear over the range of measurement conditions, with the result that intercellular CO_2 concentrations (C_i) did not vary markedly. There was some evidence that C_i decreased at high VPD's. The regulation of stomatal movement in papyrus appears to minimise excessive water loss while not severely limiting photosynthesis. The significance of this strategy for a wetland species with plentiful supplies of water is discussed.

Key words: *Cyperus papyrus* – CO_2 -Assimilation – Stomatal response – Quantum yield – Humidity response

Permanent swamps occupy approximately 85,000 km² of the African continent (Thompson and Hamilton 1983) and in most of them the emergent sedge papyrus (*Cyperus papyrus* L.) is the dominant species. The most extensive papyrus swamps are found in the Lake Victoria and Nile basins where the altitudinal distribution is from sea level up to 2,000 m (Thompson 1976). The reasons for its success in African swamps is unclear but it does have a number of unusual characteristics which could influence competitive ability in a freshwater environment. It is probably amongst the largest of all herbaceous species with culms growing to a height of 5 m and an above ground standing biomass in excess of 30 t ha^{-1} (Jones and Muthuri 1985). The culms are topped by the main photosynthetic surface (the reproductive umbel) which is up to 50 cm in diameter and composed of several hundred rays, each of which extend into three to five flattened bracteoles (Jones and Muthuri 1985). Papyrus also has C_4 photosynthesis, which is not normally associated with waterlogged habitats but is most frequently found in plants under hot, arid and high light conditions (Björkman 1973). However, several species with C_4 photo-

synthesis are now known to occur in a wide range of other environments including low temperature (Long 1983) and deep shade (Pearcy and Calkin 1983) and this has led Pearcy and Ehleringer (1984) to argue that, while any physiological advantage of C_4 photosynthesis in cool and/or shaded environments is minimal, there is little evidence of any intrinsic disadvantage. The same reasoning may also apply to waterlogged compared with arid environments but there is little experimental evidence on which to base any discussion.

There are no previous reports of photosynthesis measurements in natural stands of papyrus. Laboratory measurements, using detached parts of the umbel collected from the field, showed light saturation at about one third full sunlight and a temperature optimum of about 32° C but a relatively flat response between 25° C and 37° C (Jones and Milburn 1978). Relatively few records of measurements of photosynthesis in other freshwater emergent wetland species have been published. The most notable exceptions are those of Gloser (1977) and Ondok and Gloser (1978) on *Phragmites australis* and McNaughton and Fullem (1970) and McNaughton (1973) on *Typha latifolia*; both C_3 species. In both species their photosynthetic potential was relatively high for C_3 plants and light saturation only occurred at levels close to full sunlight. Responses to the vapour pressure gradient between the air and leaf have not been considered.

The aim of this work was to characterise the response of photosynthesis in papyrus to the major aerial environmental factors and in particular, photosynthetic photon flux density (400–700 nm) (PPFD) and the leaf-to-air vapour pressure gradient.

Materials and methods

Measurements were made in a papyrus swamp which fringes the western shore of Lake Naivasha, Kenya (0° 45' S and 35° 20' E, altitude 1,900 m). Monthly mean air temperatures at the site range between 18° C in May and 15° C in July (Jones and Muthuri 1985). Structural characteristics of the canopy, which is a virtual papyrus monoculture, are given in Jones and Muthuri (1985). There appears to be little seasonal change in either the standing biomass or the area index of the major assimilatory organs, which are morphologically the reproductive umbels. These umbels in papyrus are composed of leaf-like bracteoles and cylindrical rays.

Measurements were made approximately 10 m from the lake shore where the papyrus rhizome and root system was stranded on the lake bottom but under water. An area of about 20 m² was cleared to give access and individual um-

bels were carefully pulled over and down from their normal height of about 4–5 m to about 2 m above ground level to allow measurements to be made.

Measurements of CO₂ assimilation and transpiration were made using a portable gas exchange system (the Analytical Development Co Ltd, Hoddesdon, Herts) consisting of an infrared gas analyser (LCA), a handheld clamp-on leaf cuvette and an air supply unit. The analyser was operated during these measurements in the differential mode with the sample gas alternating between the analysis and reference gas streams. The analyser was calibrated using aerosol cans of a standard gas (P.K. Morgan, Rainham, Kent). The cuvette was designed for use with grass-shaped leaves and enclosed an area measuring 2 × 5 cm. It contained a fan to ensure a high boundary layer conductance, a capacitance-type humidity sensor positioned in the exhaust air, and a thermistor to measure air temperature in the inlet port. A quantum sensor was positioned next to the cuvette top to measure incident PPFD. The air supply unit provided a measured flow of air to the leaf chamber and a supply of reference air to the analyser. When in use the air supply was drawn from a mast that extended above the plant canopy to minimise variations in ambient CO₂ concentration.

When the leaf cuvette was used to measure photosynthesis of papyrus bracteoles it was generally necessary to place three in parallel across the chamber to ensure a measurable depletion of CO₂ in the analysis air stream. Readings were taken under steady-state conditions which occurred 60 to 120 s after enclosure of the leaf material. The CO₂ partial pressure of the air entering the chamber was 275 ± 5 μ bar at the altitude of Lake Naivasha. The width of papyrus bracteoles used in the cuvette was determined after gas exchange measurements using a map-reading magnifying glass which was fitted with a graticule marked in 0.1 mm divisions. Gas exchange measurements were made at regular intervals throughout two consecutive days (17 and 18 July, 1984 and subsequently referred to as day 1 and 2 respectively) from dawn till dusk. Each set of data collected at a particular time consists of measurements made on five different sets of bracteoles with each set from a different umbel.

Net CO₂ assimilation rate (A), transpiration rate (E), stomatal conductance to water vapour (g_s), and the partial pressure of CO₂ in the intercellular air spaces (C_i) were calculated from the simultaneous measurements of CO₂ and water vapour exchange in the cuvette as described by Long and Hallgren (1985) using the equations of von Caemmerer and Farquhar (1981). Bracteole temperature in the cuvette was calculated using air temperature measurements and an energy balance equation (Parkinson 1985). All rates are expressed on a projected bracteole area basis.

Additional environmental observations consisted of regular measurements of incident PPFD on a horizontal surface, using a quantum sensor (Li-Cor Inc., Lincoln, Nebraska), and measurements of wet and dry bulb temperatures within the canopy, close to the umbels, using a whirling hygrometer (Brannan, Cleator Moor), to determine the vapour pressure deficit (VPD) of the air.

Results

The diurnal courses of net CO₂ assimilation, transpiration and stomatal conductance during the two days of measurements are shown in Fig. 1. The concurrent changes in incident PPFD, air temperature and VPD are also shown. The main difference in aerial environmental conditions between the two days was that the VPD of the air during the middle of the day reached double the level on day 2 compared with day 1. Levels of incident PPFD were also lower during the morning of day 1 due to cloud cover. The diurnal patterns of net assimilation were similar on both days, but there was a decline on day 2 in the early afternoon which did not occur until considerably later on day 1. Stomatal conductances during most of day 2 were markedly lower than day 1. When these conductances are used with the ambient values of VPD to calculate the transpiration rates of the bracteoles it is clear that the lower conductances on day 2 do not prevent transpiration rates rising to 30% more than on day 1. These calculations have ignored the contribution of any boundary layer conductance which is likely to be large because of the small dimensions of the bracteoles.

The individual measurements of net assimilation and

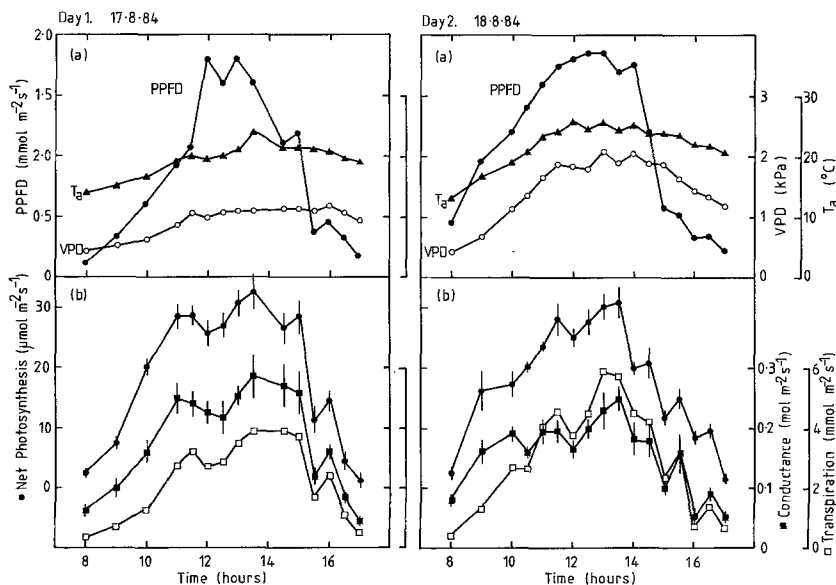


Fig. 1. Diurnal course of (a) PPFD above the papyrus canopy (●), air temperature (T_a) (▲) and air vapour pressure deficit (VPD) (○) within the canopy, and (b) net photosynthesis (●), stomatal conductance (■) and transpiration (□) of *Cyperus papyrus* on 17 and 18 July, 1984 (day 1 and 2 respectively) at Lake Naivasha, Kenya. Vertical bars are \pm S.E.M.

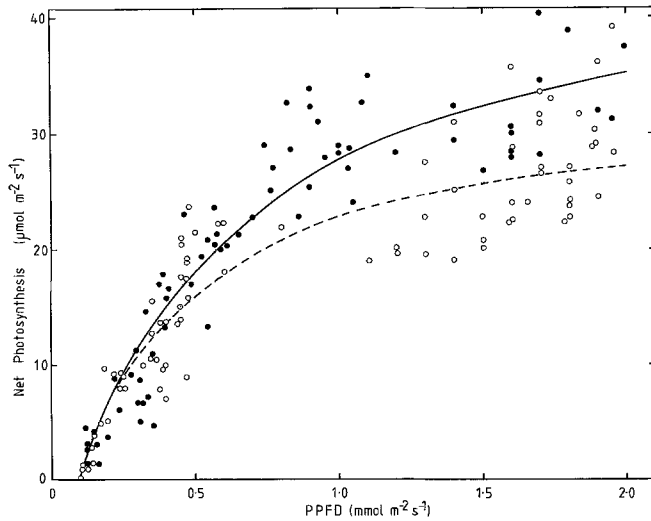


Fig. 2. The relationship between net photosynthesis of *Cyperus papyrus* bracteoles and PPFD on day 1 (●) and day 2 (○). The lines are fitted response curves (see text for details)

concurrent PPFD made on each day were used to construct irradiance response curves (Fig. 2). The curves can be described by the hyperbolic equation

$$A = \frac{\Phi_i(I - C)}{1 - B(I - C)}$$

where A is the net assimilation rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$), I is the incident PPFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$), Φ_i is the initial slope of the irradiance response curve (mol mol^{-1}), B is a constant ($\text{m}^2 \text{s} \mu\text{mol}^{-1}$) and C is the light compensation point ($\mu\text{mol m}^{-2} \text{s}^{-1}$). The parameters derived from the fitted curves are presented in Table 1. The maximum value of net assimilation (A_{max}) was taken as the rate achieved at a PPFD of $2.0 \text{ mmol m}^{-2} \text{s}^{-1}$, which is approximately full sunlight. The fitted response curves were not light saturated at full sunlight but A_{max} on day 2 was reduced by 25% compared with day 1. The initial slope of the response curve at very low light levels (Φ_i) is an estimate of the maximum efficiency for harvesting of incident light in the assimilation of CO_2 (the quantum yield of photosynthesis). The values of Φ_i for the two days of measurements were similar.

When values of leaf conductance, obtained at PPFD's above light saturation for stomatal opening (approximately $1.0 \text{ mmol m}^{-2} \text{s}^{-1}$) were plotted against the prevailing VPD of the air there was clear evidence of a partial closure of the stomata as VPD increased (Fig. 3). In order to extend the range of VPD's over which conductances have been measured Fig. 3 includes values obtained on a previous occasion at the same site (Jones and Muthuri 1984) when the VPD in the middle of the day was higher. The values of conductance on this earlier occasion were obtained using a steady-state porometer (LI-1600, Li-Cor Inc., Lincoln, Nebraska). Air temperatures during these measurements varied between 20°C and 26°C .

The relationship between net assimilation (A) and stomatal conductance (g_s) for all of the individual measurements over both days is shown in Fig. 4. The close to proportional relationship between A and g_s implies an approximately constant intercellular partial pressure of CO_2 (C_i) of about 75 to 85 μbar . However, because the stomata were

Table 1. Parameters of the fitted net assimilation-light response curves for the two days of measurement. A_{max} is A at $2.0 \text{ mmol m}^{-2} \text{s}^{-1}$ PPFD, and C is the light compensation point

	Φ_i (mol mol^{-1})	A_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	C ($\text{mmol m}^{-2} \text{s}^{-1}$)
Day 1	0.060	35.3	0.10
Day 2	0.055	27.1	0.10

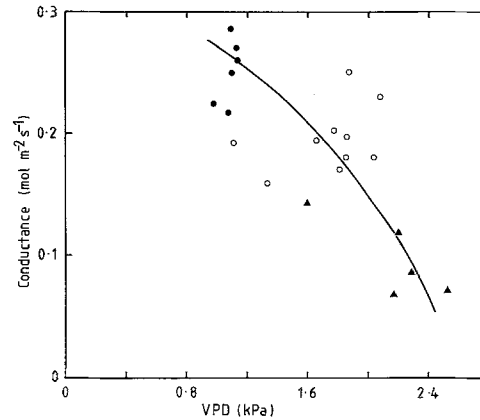


Fig. 3. The relationship between stomatal conductance of *Cyperus papyrus* bracteoles and VPD of the air on day 1 (●) and day 2 (○) and 16 March 1982 (▲) when incident PPFD exceeded $1.0 \text{ mmol m}^{-2} \text{s}^{-1}$. Each point is the mean of five measurements

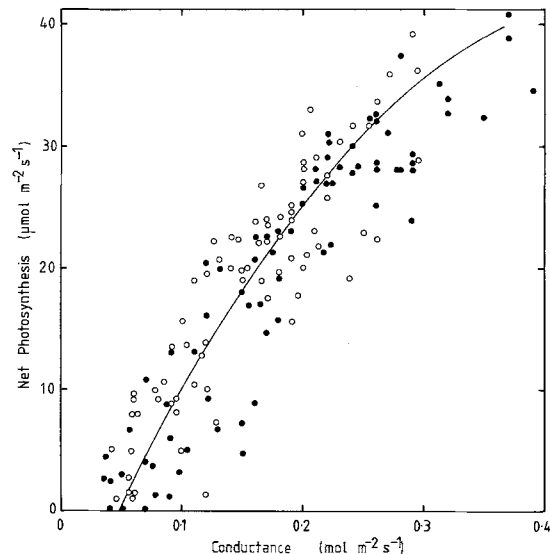


Fig. 4. The relationship between net photosynthesis and concurrent stomatal conductance of *Cyperus papyrus* bracteoles on day 1 (●) and day 2 (○)

partly open at zero A the relationship does not pass through the origin and the value of C_i cannot be constant. Also, there is some evidence that C_i decreases as the ambient VPD increases. In Fig. 5 the ratios of C_i/C_o (where C_o is the ambient CO_2 concentration), calculated for periods when incident PPFD was above $1.0 \text{ mmol m}^{-2} \text{s}^{-1}$, are plotted against ambient VPD. At small VPD's the C_i/C_o ratio was close to 0.4 but it fell to 0.2 as the VPD increased. This ratio is generally between 0.6–0.8 for C_3 species and 0.2–0.4 for C_4 species (Berry and Downton 1982).

Discussion

The relatively high maximum rates of net assimilation previously reported for emergent wetland species (McNaughton and Fullem 1970; Gloser 1977; Jones 1986) are translated into high levels of net productivity for these plants (Bradbury and Grace 1983). However, the difficulty of using conventional harvesting techniques in communities which can maintain more than 50% of their biomass underground (Sharma and Gopal 1977; Hejný et al. 1981) means that it is still not possible to determine precisely the range of primary productivity which might be observed in freshwater wetland systems (Bradbury and Grace 1983). An alternative to the measurement of changes in biomass with time is to construct a carbon budget for the community and to investigate those characteristics which may influence carbon flux in photosynthesis, respiration and translocation and therefore regulate productivity. The aim of the work reported here was to quantify the photosynthetic characteristics of papyrus in its natural environment and to characterise the response of net assimilation to changes in the aerial environment. In the longer term the aim is to gather enough information to allow us to construct a detailed carbon budget for the ecosystem.

The method of gas exchange used here involved clamping the leaf cuvette onto the photosynthetic material for a short period of time (up to 2–3 min) and recording conditions as soon as they became stable. The aim was to determine CO_2 and H_2O exchange under conditions which were as close as possible to the natural environment. The obvious short-coming of this approach is that the correlation of environmental factors in the natural environment can make the interpretation of some of these responses difficult. However, the measurements reported here, made during two days when VPD's were quite different, have made it possible to investigate the effect of VPD on gaseous exchange of papyrus.

The response of net assimilation in papyrus to incident PPFD shows characteristics which are typical of many C_4 species, with relatively high values of A at full sunlight (A_{max}) and a failure to light saturate the response. The maximum value of A achieved was $35.3 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, which is only half the maximum values observed in several other C_4 species; although much lower rates of light saturated net assimilation have been reported for several other C_4 plants (Winter et al. 1982; Robichaux and Pearcy 1984; Pearcy and Ehleringer 1984). There was a marked difference between the response curves at high PPFD's on the two days and this was associated with the smaller stomatal opening on day 2. The initial slopes of the light response curves (Φ_i) on both days gave values of quantum yield close to $0.06 \text{ mol CO}_2 \text{ mol}^{-1}$ incident radiation. Ehleringer and Pearcy (1983) found that C_4 grasses with NADP-malic enzyme as the major decarboxylating enzyme had the highest quantum yields of up to $0.07 \text{ mol mol}^{-1}$ of absorbed radiation when they surveyed a large number of C_4 species from different sub-groups. Papyrus is also a NADP-malic enzyme sub-group species and it would appear that this sedge can be classed with grasses having the same photosynthetic pathway and which primarily occupy mesic grasslands or savanna communities with high leaf area indices (Osmond et al. 1982; Pearcy and Ehleringer 1984).

The ability of stomata of a large number of species to respond directly to changes in ambient humidity has been

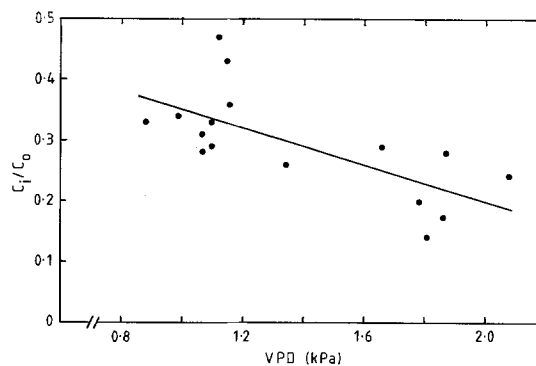


Fig. 5. The relationship between the C_i/C_o ratio of *Cyperus papyrus* bracteoles and VPD of the air, when incident PPFD exceeded $1.0 \text{ mmol m}^{-2} \text{ s}^{-1}$

widely documented (Lösch and Tenhunen 1981). As a consequence of this response, the increase in VPD of the air in the middle of the day can lead to marked midday depressions of photosynthesis and transpiration (Tenhunen et al. 1984; Roessler and Monson 1985). The stomata of papyrus also appear to respond to VPD of the atmosphere (Fig. 3) but on neither of the days was the effect of VPD sufficient to cause a clear midday depression of photosynthesis or transpiration. Nevertheless, the total amount of assimilation during the middle of day 2 was considerably reduced compared with day 1 and this might be attributed to a direct effect of VPD on stomatal opening. Furthermore, the decrease in the intercellular space CO_2 concentration (C_i) at high VPD's (Fig. 5) also indicates that the reduction in A on day 2 is due partly to a lower stomatal conductance. However, the degree of stomatal limitation of photosynthesis may not be sufficient to account for all of the reduction in A . This is because, as Fig. 4 shows, across the range of measurement conditions, there is an almost linear relationship between A and g_s , which if maintained would result in a constant C_i . This observation suggests the possible influence of some non-stomatal effects of VPD on photosynthesis; similar to those observed by Forseth and Ehleringer (1983), Bunce (1984) and Lange et al. (1985). It also supports the increasing number of reports which suggest that plants are operating to maintain over extensive periods of time a more or less constant intercellular CO_2 concentration (Farquhar and Sharkey 1982), but the underlying mechanism involved is still unknown.

The amount of water loss in transpiration is determined both by the stomatal conductance and the leaf to air vapour pressure gradient. Our observations show that the reduced stomatal conductance on day 2 is insufficient to prevent transpiration rates being considerably higher than on day 1 because of the higher VPD of the air. Nevertheless, papyrus does appear to have a strategy to conserve water loss which probably occurs even at the expense of a reduction in photosynthesis. The reasons for this type of strategy in a freshwater wetland plant with a plentiful supply of water for its roots is unclear. Furthermore, the higher water use efficiency which the possession of C_4 photosynthesis confers would also seem to be of no particular advantage. It is possible that the C_4 pathway, while not conferring any clear advantage in this environment, nevertheless imposes no disadvantage. Conversely, two other characteristics of C_4 photosynthesis might be considered as advantageous in this environment. The first is the high quantum yield at low

PPFD's observed here, which is associated with the NADP-malic enzyme sub-group of C_4 photosynthesis (Ehleringer and Pearcy 1983), and could be advantageous because of the intense shading of some of the papyrus umbels in the dense canopy (Jones and Muthuri 1985). Secondly, C_4 species have frequently been demonstrated to possess a higher nitrogen use efficiency than C_3 plants (Wilson 1975; Bolton and Brown 1980). Freshwater wetlands are often nutrient, and in particular nitrogen, limited (Gaudet and Muthuri 1981). The papyrus bracteoles at the Naivasha site contained 2% N and Muthuri (1985), using plants grown in nutrient solution, found that A increased linearly up to 4% N. Net assimilation in papyrus was therefore likely to be limited by available N, but because it has C_4 photosynthesis it can use this N more efficiently, achieving a higher rate of net assimilation at a given N content than a C_3 species in the same situation. Under these circumstances a C_4 species like papyrus would be expected to achieve a higher net productivity in freshwater wetlands and therefore be more competitive than C_3 species.

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