

The diurnal course of plant water potential, stomatal conductance and transpiration in a papyrus (*Cyperus papyrus* L.) canopy

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Summary. The diurnal course of water potential, stomatal conductance and transpiration was measured on mature umbels (the major evaporating surface) of papyrus (*Cyperus papyrus* L.) growing in a fringing swamp on Lake Naivasha, Kenya.

Umbel water potential declined only slightly during the morning but fell rapidly after midday to a minimum value of -1.5 MPa in early afternoon. The two main structures forming the umbels, the bracteoles and rays, showed similar patterns of change of stomatal conductance throughout the day. The values of conductance indicate major stomatal opening during the morning, partial midday closure and some recovery of opening during the afternoon.

It appears that the increase in water vapour pressure deficit of the air is the major cause of the midday closure of the stomata and that plant water potential has little effect. The reason why transpiration is reduced at high vapour pressure deficits when water is freely available to the roots is not clear. However, it is speculated that the restricted water movement into the plant from the anaerobic root environment has the effect of reducing the uptake of toxic ferrous iron.

The daily total of canopy transpiration is estimated to be 12.5 mm, twice the value previously reported for papyrus but similar to daily values determined for other wetland communities.

tanks and Rijks (1969) who used micrometeorological measurements and the Bowen ratio method to calculate rates of evaporation from a papyrus swamp at Namulonge, Uganda. Rijks estimated that the evaporation from an 'old' stand of papyrus was $60 \pm 15\%$ of the Penman estimates of evaporation from open water, *i.e.* evaporation was significantly less than potential evaporation and the presence of the papyrus vegetation conserved water. However, Penman (1963) analysed the rates of evaporation measured by Migahid (1952) and found that water evaporation and swamp vegetation evaporation were almost equal. Rijks (1969) suggested that these differences in the amount of evaporation from papyrus swamps were due to differences in the nature of the stand; the papyrus used by Magahid being much more 'luxuriant' than that at Namulonge.

There appear to be no other reports concerning the water relations of papyrus either in a natural or controlled environment. In fact the water relations of swamp plants have been largely ignored even though it would appear that a study of such plants which have a plentiful supply of water, but experience 'atmospheric drought' in the form of large air to leaf water vapour concentration gradients, may help to uncouple the often close correlation between soil drought and atmospheric drought under natural conditions. The water relations of papyrus are also of interest because it is a C4 plant (Jones and Milburn 1978) growing in swamp conditions and is therefore unlike most other C4 species which seem to be adapted to some extent to growth under conditions where soil moisture deficits are likely to develop (Ludlow 1976). The reason why the C4 papyrus is so successful as a swamp species may be answered by a better understanding of its water relations under natural conditions.

In another publication (Jones and Muthuri in press) we report on some of the important structural features of the canopies of two papyrus swamps. In the present study measurements were made of a diurnal cycle of the water relations of papyrus in one of these swamps at Lake Naivasha, Kenya. The objective was to investigate the effects of environmental variables on transpiration from papyrus umbels, which are the main evaporating surface of the plant. Also, a knowledge of canopy structure (Jones and Muthuri in press) allowed us to estimate canopy transpiration rates and compare them with the previous measurements made by Migahid (1952) and Rijks (1969).

Introduction

The magnitude of evaporation from the papyrus (*Cyperus papyrus* L.) swamps of East and Central Africa has been a topic of interest for many years, largely because the swamps occupy vast areas and therefore have a significant influence on their hydrology (Linacre 1976). The papyrus swamps are associated mainly with the headwaters of the river Nile (Thompson 1976) and a knowledge of water loss from these swamps by evaporation is important in constructing a hydrological balance for one of the largest river systems in the world. It is surprising therefore that there appear to be few reports of measurements of evaporation from papyrus swamps; the most notable exceptions being the work of Migahid (1952) using papyrus grown in 10 m^2

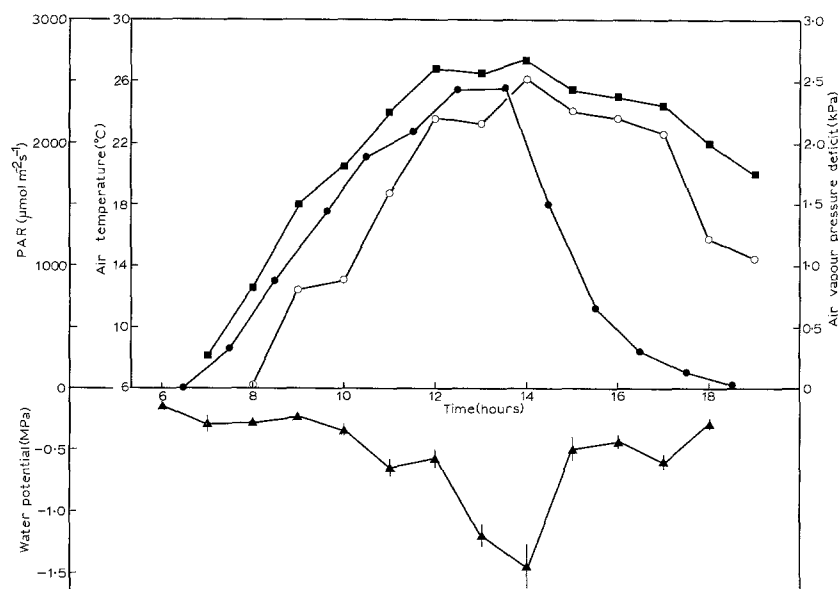


Fig. 1. Diurnal course of photosynthetically active radiation (PAR) above the papyrus canopy (\bullet), air temperature (\blacksquare) and air vapour pressure deficit (\circ) within the canopy, and plant (ray) water potential (\blacktriangle) on 16 March, 1982. Vertical bars are \pm S.E.M.

Materials and methods

Measurements were made throughout a single day (March 16, 1982) on a papyrus swamp fringing the western shore of Lake Naivasha, Kenya ($0^{\circ}45'S$ and $35^{\circ}20'E$). An area of papyrus about 20 m from the shore was used for measurements and access to this site was along a path cleared through the papyrus. Structural characteristics of this papyrus community are given in Jones and Muthuri in press. The rhizome of papyrus bears green stems (culms) which are terminated by a crown of inflorescence (umbel). Measurements were made on the structures forming the umbel which is the plants main photosynthetic surface. These structures are the leaf-like bracteoles and the cylindrical rays (for further details of umbels structure, see Jones and Muthuri in press).

Plant water potential was estimated from xylem pressure potential measured with a pressure chamber (PMS Instruments, Corvallis, Oregon) located on the lake shore. The chamber interior was humidified with moist paper tissue and plant material was carried to the instrument in a sealed and humidified polythene bag to reduce errors due to loss of water subsequent to detachment from the plant. Measurements were made on rays detached from the umbel of papyrus as it was more convenient to observe the end point using rays rather than bracteoles. At least five rays from different umbels were used for water potential determinations at any time. Some preliminary measurements indicated that there were no differences in the water potentials of these structures if sampled at the same time.

Measurements of bracteole and ray conductance to water vapour and rates of transpiration from these structures were made with a Lambda Instruments ventilated steady-state porometer (LI-1600, Li-Cor, Inc., Lincoln, Nebraska). The porometer was used on the upper surface of the grass-like bracteoles which are hyperstomatous. Bracteoles and rays from at least five different mature umbels were used for replicate determinations at any time. The umbels were at the top of culms which are up to 5 m long when mature but they could be pulled down with care to the level of the operator without damaging the culm.

Wet and dry bulb temperatures within the papyrus canopy, determined with a whirling hygrometer, and the photosynthetically active radiation (PAR) incident on the canopy, determined with a Lambda Instruments quantum sensor, were measured immediately prior to pressure chamber and porometer measurements.

Results

During the day of measurements the sky was clear until early afternoon when it became overcast for the rest of the day. Levels of PAR incident on the canopy rose to almost $2,500 \mu\text{mol m}^{-2} \text{s}^{-1}$ by midday and the air temperature within the canopy reached a maximum of almost 28°C in the early afternoon (Fig. 1). At this time the saturation deficit of the air within the canopy reached a maximum of 2.45 kPa, rising from zero early in the morning and falling to 1.50 kPa at nightfall (Fig. 1).

The water potential of the papyrus rays fell slowly during the morning and only reached -0.6 MPa by midday (Fig. 1). During the following two hours it fell rapidly to -1.5 MPa and then recovered over the next hour to -0.5 MPa ; following this it remained steady for the rest of the day.

The conductances of the bracteoles and rays followed the same general pattern through the day although values for the rays were more variable, as reflected by the larger standard errors (Figs. 2a, b). Measurements started at 8.30 h (GMT-3) for the bracteoles and 9.30 h for the rays, after all dew had evaporated from the tissue surfaces. The conductance of both bracteoles and rays increased rapidly during the morning to reach peaks of 0.42 cm s^{-1} and 0.59 cm s^{-1} respectively by 10.30 h. Following these maximum conductances the value for the bracteoles fell during the next two hours to 0.20 cm s^{-1} and for the rays it fell more rapidly to 0.13 cm s^{-1} within one hour. In both the bracteoles and rays the conductance increased during mid-afternoon and finally declined with falling levels of irradiance at the end of the day. The marked fall in conductance of both the bracteoles and rays around midday corresponds with the time when maximum saturation deficit of the air

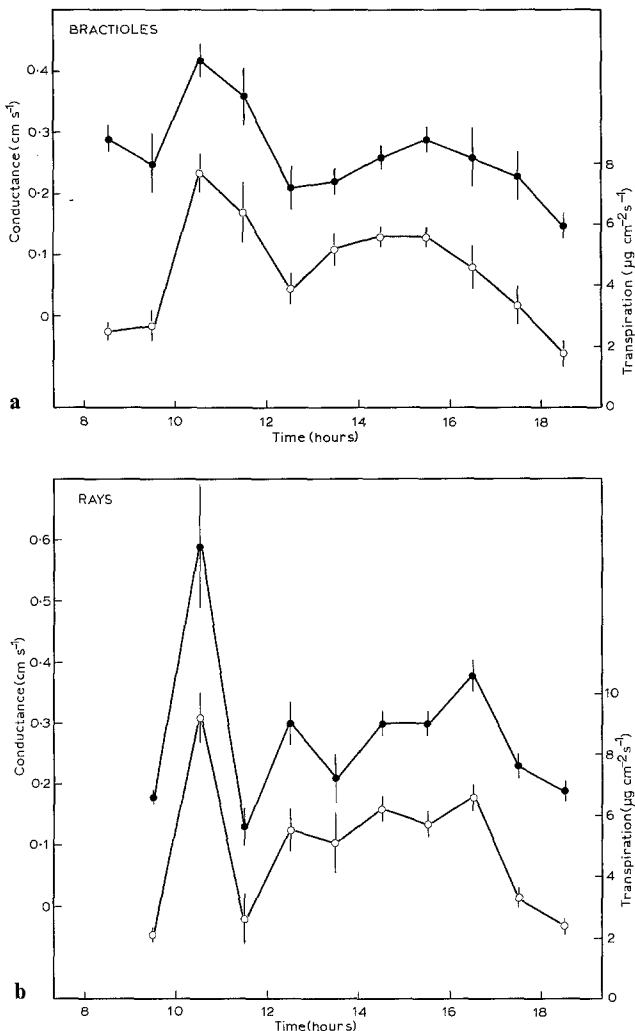


Fig. 2a, b. Diurnal course of conductance (●) and transpiration (○) for (a) bracteoles and (b) rays on 16 March, 1982. Vertical bars are \pm S.E.M.

within the canopy was recorded. However there is no clear relationship between conductance and saturation deficit as increase in conductance occurred during the afternoon while saturation deficit of the air declined only slightly. Similarly, there is no obvious relationship between plant water potential and conductance because the water potential did not start to decline significantly until the recovery of conductance was underway in the early afternoon.

As expected, transpiration rates for bracteoles and rays (Figs. 2a, b) followed the same pattern as conductances but the higher saturation deficits during the middle of the day resulted in higher transpiration rates for any given level of conductance. Transpiration rates for the papyrus canopy (Fig. 3) were calculated from a knowledge of mean bracteole and ray area per mature umbel and the number of mature umbels per unit ground area (Jones and Muthuri in press) so that canopy transpiration = (bracteole transpiration \times bracteole area index) + (ray transpiration \times ray area index). This assumes that no bracteoles and rays were sufficiently shaded to reduce transpiration through stomatal closure and it does not include the contribution to evaporation made by senescent and juvenile umbels and the culms. It also ignores the effect of aerodynamic resistance,

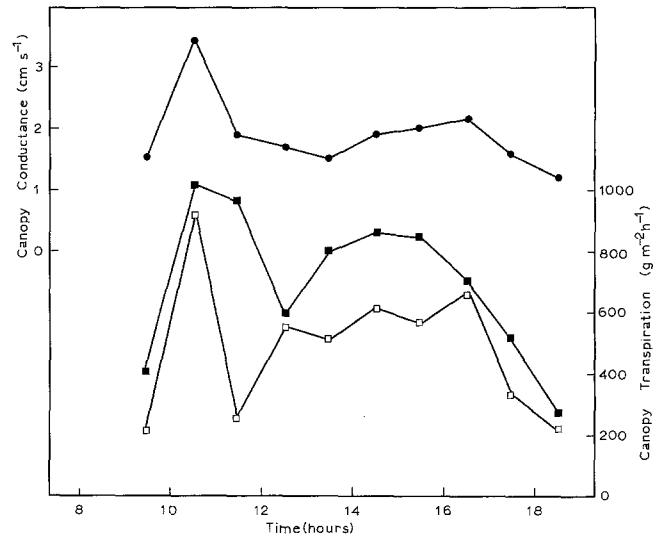


Fig. 3. Diurnal course of papyrus canopy conductance (●) and the contribution made by rays (□) and bracteoles (■) to canopy transpiration on 16 March, 1982. Calculated using ray area index = 2.8, and bracteole area index = 4.2

although this should be small for the long and narrow transpiring surfaces. Despite these limitations, which on balance could lead to an underestimate of canopy transpiration, the concentration of the major evaporating surfaces into what is effectively one uniform layer at the top of the canopy (Jones and Muthuri in press) allows us to estimate relatively easily the evaporation from the papyrus swamp. Canopy conductance (Fig. 3) was calculated in a similar fashion to canopy transpiration. Insufficient data is available to calculate potential evaporation from open water surfaces at the same time as these measurements. The maximum canopy transpiration rate obtained in these measurements was $2,098 \text{ g m}^{-2} \text{ h}^{-1}$ while the summing of hourly rates gives a daily transpiration of 12.05 mm.

Discussion

The most striking feature of the diurnal cycle of conductance to water vapour in papyrus is the partial midday closure of stomata (Fig. 2a, b). This brings about a marked decline in the rate of transpiration and will also, of course, reduce the rate of photosynthesis. However, because net photosynthesis in C4 species is less sensitive to partial stomatal closure than transpiration (Bunce 1982), the rate of photosynthesis in the C4 papyrus will decline less than transpiration. Further work is required to confirm this pattern of photosynthesis response in papyrus but it will clearly have important consequences for the total amount of carbon assimilation by the papyrus canopy if it is the normal cycle of daily carbon fixation.

The cause of the (partial) midday closure of the stomata in papyrus appears to be more closely associated with the increase in vapour pressure deficit of the air, and therefore the high leaf to air water vapour pressure difference, than a decline in bulk tissue water potential. The mechanism by which stomata respond to the vapour pressure deficit of the air is poorly understood but it has been pointed out that the feed-forward nature of the response prevents deleterious deficits from developing in the bulk tissue and reduces the possibility of permanent injury (Ludlow 1980).

Where soil water availability is restricted this clearly has the effect of conserving soil water supplies and maximises daily photosynthesis for a given level of transpiration, in line with the model of optimum stomatal function proposed by Cowan (1977). However, in the case of papyrus which has water freely available at its roots, the explanation for a reduced water loss through transpiration at times of high vapour pressure deficit of the air are not so obvious.

It has been pointed out that a feature common to many wetland plants is the xeromorphic nature of their leaves and stems (Armstrong 1982), and it is suggested that the primary function of xeromorphism in these plants is not water conservation *per se* but reduced water flux into the roots which allows time for oxidation and exclusion of iron compounds which would be toxic if taken up by the plants (Jones 1971). The source of oxygen which brings about this oxidation is from the atmosphere *via* the system of aerenchyma common in wetland plants. We therefore propose that in papyrus the control of water loss through partial stomatal closure at high atmospheric demand is directed at decreasing the amount of toxic ferrous iron which reaches the roots from the strongly anaerobic and reducing root environment (Jones and Muthuri in press). This need to restrict water uptake, and therefore loss in transpiration, in papyrus will have the effect of reducing evaporation from the canopy more than might have been expected of considered solely from the point of view of maximising CO₂ uptake in photosynthesis. Indeed, it may also help to explain why a C4 species is suited to this environment even though water supply is not limiting. The higher water use efficiency of C4 plants (Fischer and Turner 1978) means that papyrus can achieve high rates of photosynthesis and therefore production while restricting the possibly harmful effects of high rates of water uptake.

Despite the partial midday closure of stomata observed in these measurements the estimates of daily canopy transpiration at 12.05 mm are twice the highest daily values determined by Rijks (1969). The difference could be due to the fact that the papyrus stand used by Rijks was 'old' and contained much senescent material while the Naivasha swamp has a high standing biomass with a high proportion of mature and young plant units (Jones and Muthuri in press). Similar daily transpiration rates have been recorded for other stand of wetland vegetation including *Phragmites communis* L. in central Europe during summer (Smid 1975). Clearly, longer term measurements on a range of papyrus canopies of differing density are required to determine those factors which regulate transpiration but these preliminary

results indicate the usefulness of this technique based on the use of the steady-state porometer.

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