LEAF PHYSIOLOGY AND DROUGHT STRESS OF TWO *PANDANUS* SPECIES IN A HUMID LOWLAND TROPICAL CLIMATE

Thomas E. Marler, Robin A. DeMeo & Patrick D. Lawton

College of Agriculture and Life Sciences, University of Guam, UOG Station, Mangilao, Guam 96923, United States of America

MARLER, T.E., DEMEO, R.A. & LAWTON, P.D. 1996. **Leaf physiology and drought stress of two *Pandanus* species in a humid lowland tropical climate.** Water was withheld for eight weeks from *Pandanus dubius* and *Pandanus tectorius* trees to determine their physiological responses and adaptations to water deficits. When light was abruptly reduced as occurs when cumulus clouds block sunlight, stomata responded with a gradual decline in stomatal conductance to water (g_s). This response occurred in 2 to 3 min and increased water use efficiency by reducing transpiration. A slow increase in g_s occurred upon a return to high light, but this brief lag temporarily limited net CO_2 assimilation (A_{CO2}). Water deficits influenced this stomatal response by slowing down recovery of g_s after the return to high light following several minutes of low light. The dependence of A_{CO2} on irradiance conformed to an asymptotic exponential model. Trees experiencing water deficits exhibited a greater decrease in A_{CO2} in the lower levels of irradiance than did well-watered trees. The decrease in A_{CO2} caused by water deficits was due to direct inhibition of photosynthesis, since internal CO_2 concentration actually increased with the decrease in A_{CO2} and g_s. Carboxylation efficiency, photo-chemical efficiency, and relative leaf water content were reduced by drought stress. In contrast, leaf osmotic potential was not influenced by eight weeks of withholding water. Leaf tissue was fully re-hydrated following re-watering, but g_s and A_{CO2} did not return to pre-stress levels until after 11 days of re-watering.

Key words: Drought - net CO_2 assimilation - *Pandanus dubius* - *Pandanus tectorius*

MARLER, T.E., DEMEO, R.A. & LAWTON, P.D. 1996. **Fisiologi daun dan tekanan kemarau ke atas dua spesies *Pandanus* di pamah lembab beriklim tropika.** Kemasukan air pada pokok *Pandanus dubius* dan *Pandanus tectorius* ditahan selama lapan minggu untuk menentukan gerak balas fisiologi dan penyesuaian kedua-dua pokok tersebut terhadap kekurangan air. Bila cahaya dikurangkan secara mendadak seperti yang terjadi bila awan kumulus menghalang cahaya matahari, stomata bergerak balas secara pengurangan perlahan-lahan nilai konduksian stomata kepada air (g_s). Gerak balas ini berlaku selama 2 hingga 3 minit dan meningkatkan kecekapan peng-gunaan air melalui pengurangan transpirasi. Kenaikan secara perlahan g_s berlaku apabila cahaya ditinggikan, tetapi ketinggalan singkat ini secara sementara meng-hadkan asimilasi bersih CO_2 (A_{CO2}). Kekurangan air mempengaruhi gerak balas stomata dengan melambatkan pemulihan nilai g_s selepas cahaya yang tinggi dikembalikan setelah mengalami cahaya kurang selama beberapa minit. Pergantungan nilai A_{CO2} terhadap pancaran cahaya bersesuaian dengan model eksponen asimptotik. Pokok-pokok yang mengalami kekurangan air menunjukkan

penurunan nilai A_{CO_2} yang lebih besar pada sinaran cahaya yang rendah berbanding dengan pokok-pokok yang disiram dengan secukupnya. Penurunan nilai A_{CO_2} semasa kekurangan air disebabkan oleh penghalangan fotosintisis secara langsung. Memandangkan kepekatan CO_2 dalaman meningkat dengan berkurangnya nilai A_{CO_2} dan g_S. Kecekapan karboksilasi, kecekapan fotokimia dan kandungan relatif air daun menurun bila berlaku tekanan kemarau. Sebaliknya, potensi osmosis daun tidak dipengaruhi oleh penahanan air selama lapan minggu. Tisu daun dihidrat semula sepenuhnya bila pokok disiram semula, tetapi g_S dan A_{CO_2} hanya kembali ke tahap sebelum tekanan selepas 11 hari penyiraman semula.

Introduction

The climate of Guam is representative of humid lowland tropical regions characterised by a distinct dry season, a distinct rainy season, and short periods at each seasonal transition which may be wet or dry (National Oceanic and Atmospheric Administration 1993). On average, seven months per year are characterised by conditions where potential evapotranspiration exceeds rainfall (Young 1988). Drought stress of vegetation is a routine, temporary phenomenon especially toward the end of the dry season.

Highly variable light conditions are also characteristic of this climate (Tseng & Muniappan 1986). For example, during the average year on Guam only 18 days are classified as clear (National Oceanic and Atmospheric Administration 1993). The remaining days are cloudy or partly cloudy, mostly due to a broken cumulus cloud cover. Therefore, even plants which are growing in open habitats experience short-term high and low light periods (Knapp & Smith 1990). Photosynthesis of plants in these locations rarely obtains steady state conditions with respect to irradiance since leaves are constantly integrating the response to instantaneous irradiance with the most recent abrupt irradiance transitions.

The general appearance of the vegetation on Guam is correlated with the seasons, and many species are unsightly toward the end of each dry season. However, *Pandanus dubius* Spreng. and *P. tectorius* Sol. ex. Park. trees are widespread throughout the island and always look healthy even at the end of the dry season. These members of the Pandanaceae are woody perennial monocots, and are pervasive on Guam in natural forest stands and in cultivated urban forestry (Stone 1970). Their use in urban landscapes has increased in recent years because of their distinctive look, low maintenance requirements, and year-round healthy appearance.

We found no published information pertaining to drought tolerance of *Pandanus* species. Moreover, we found no reports which presented any facet of leaf physiology for these species. As a result, this study was conducted to determine the photosynthetic and water relations responses of *P. dubius* and *P. tectorius* trees to water deficits under the conditions of a humid, lowland tropical climate. Included are the responses to highly variable light conditions and dynamics of recovery following re-watering.

Materials and methods

The experimental site for this study was in northern Guam (13.5° N latitude) where the soil type is classified as clayey, gibbsitic, nonacid, isohyperthermic Lithic Ustorthents (Young 1988). We selected *P. dubius* and *P. tectorius* trees of uniform size within natural stands to include in the study. The trees ranged in height from 60 to 85 cm. Rain exclusion shelters were built on 15 October 1993 by stretching polypropylene sheets on frames that were built over the seedlings. The end of the rainy season was selected as the time to begin this study to ensure that all of the plants were well-watered for an extended period before withholding water. We also maintained an accompanying group of well-watered seedlings adjacent to the shelters by irrigating to ensure at least 26-mm of water per week whenever rainfall was inadequate. The air temperature within the shelters was not different from outside the shelters throughout most days; however, it was $c.1°C$ higher than outside for a few hours during midday on mostly sunny days. The polypropylene sheets also reduced irradiance by 9% from ambient conditions. These methods provided at least six trees which remained well-watered and six trees which experienced a progressive increase in water deficits for each of the species.

Leaf gas-exchange responses to natural abrupt transitions from full sun conditions to cumulus cloud cover were measured during the morning hours from 26 November 1993 until 3 December 1993. Gas-exchange was measured on 2.5 cm^2 of leaf surface using an open gas exchange system (CIRAS-1, PP Systems, Stotfield, Hitchin, Herts, U.K.). However, we were unable to combine data from any two irradiance transitional periods because of the high variability in time lapse and incident photosynthetic photon flux (PPF) during and between cumulus cloud blockage of sunlight.

In order to standardise the PPF and duration of the light-limiting phase to allow combining data from the replicates, we used an illumination unit supplied by the manufacturer of the gas-exchange system. The illumination unit used a halogen lamp to provide PPF at the leaf surface of 1900-2000 $\mu mol\ m^{-2}\ s^{-1}$. A period of 10 min at this irradiance was provided after inserting a leaf into the cuvette. Following this period of homogeneous high irradiance, a neutral density filter was placed between the lamp and leaf surface for 3 min to provide irradiance at the leaf surface of 280 to 300 $\mu mol\ m^{-2}\ s^{-1}$. The neutral density filter was removed at the end of 3 min, and the entire procedure allowed repeated measurements with pre-determined high-low-high irradiance transitions.

Mean initial values of gas-exchange (after 10 min of homogeneous high irradiance) were determined from two records on each leaf. Placement of the neutral density filter was designated as time zero, and leaf gas-exchange was recorded at 15 s intervals. After removing the filter, recovery of gas-exchange characteristics following the low-to-high irradiance transition was recorded for another 3 min.

Six sets of measurements were made for each species and drought treatment from 0830 h until 1000 h on 2 and 3 December 1993. Conditions during the measurement periods were 345 to 355 μl liter^{-1} ambient CO_2, 31 to 33 °C, and

1.7 to 1.9 kPa vapor pressure deficit (VPD). Stomatal conductance to water (g_s), net CO_2 assimilation (A_{CO2}) and water use efficiency (WUE, defined as A_{CO2}/transpiration) data were combined from the six replicates.

Following these measurements of gas-exchange responses to variable light conditions, we determined the influence of water deficits on other gas-exchange and water relations variables. These measurements were made from 4 until 11 December 1993.

A photosynthetic light response curve was determined for six replicates of each treatment combination during early to mid-morning on 4 December 1993 by measuring the dependence of A_{CO2} on PPF. The previously described gas-exchange system was used, and a period of 5 min at each level of irradiance was allowed before gas exchange was recorded. Sunlight was used as the light source, and various layers of neutral density polyethylene fabric were placed over the cuvette to provide a range of PPF from 150 to 2200 μmol m^{-2} s^{-1}. The conditions during these measurements were 350 to 365 μl liter^{-1} ambient CO_2, 26 to 31°C, and 1.8 to 2.2 kPa VPD.

Net CO_2 assimilation was measured as a function of CO_2 concentration by varying the CO_2 supplied to the leaf cuvette with the internal air supply unit from the previously described gas-exchange system. Response curves on two replicates per treatment combination were measured on 8, 9, and 10 December 1993, for a total of six response curves for each treatment and species combination. The CO_2 dose levels varied from 200 to 800 μl CO_2 liter^{-1}. Incident PPF during these measurements ranged from 1350 to 1700 μmol m^{-2} s^{-1}, air temperature ranged from 31 to 34 °C, and VPD was 1.9 to 2.4 kPa.

Chlorophyll fluorescence induction was measured with a Morgan CF-1000 fluorescence system (P.K. Morgan Instruments, Andover, Mass.) on one leaf per replication on 9 and 10 December 1993. Measurements were made at ambient temperature on the adaxial surface of each leaf following 30 min of dark adaptation, provided by the system cuvettes. These cuvettes were placed on the leaves at 1300 h on each of the days. Photosynthetic photon flux of excitation light for fluorescence induction was 800 μmol m^{-2} s^{-1}.

Leaf water status was measured as relative water content (RWC) from 2.5 cm^2 sections from one leaf per replication. Sections were sampled on 2,4,9, and 11 December 1993. Fresh mass, turgid mass following 24 h of floating in a bath of deionised water, and mass after drying to a constant weight at 70 °C were measured. Calculation of RWC was based on [(fresh mass - dry mass) / (turgid mass - dry mass)] * 100.

The osmotic potential of leaves at full turgor was measured from a 2 cm^2 leaf section from each replication on 11 December 1993. These sections were soaked in deionised water for 24 h to ensure they were at full turgor before freezing. Osmotic potential (ψ_π) was measured (model 5500 vapor pressure osmometer, Wescor, Inc., Logan, Utah) on expressed sap after thawing each leaf section (Markhart & Lin 1985).

Soil moisture status was determined on each day of measurements as mass wetness (w) from fresh soil samples taken from 10 to 15 cm deep. Each sample size was 60 to 70 g, and w was defined as mass of water / mass of dry soil (Hillel 1982).

Immediately before re-wetting the soil surrounding the drought-stressed trees, dark respiration (R_d) and light-saturated gas-exchange at ambient CO_2 were measured on 11 December 1993. This was initiated by measuring CO_2 efflux on one leaf from each replication with the previously described gas-exchange system from 0500 h to 0530 h in order to determine R_d during pre-dawn conditions. Conditions during these measurements were 347 to 356 μl CO_2 liter^{-1}, 25 to 26 °C, and 0.3 to 0.4 kPa VPD. Then light-saturated gas-exchange was measured between 0900 h and 1030 h, and the conditions for these measurements were 349 to 354 μl CO_2 liter^{-1}, 29 to 31°C, and 1.8 to 2.1 kPa VPD.

The drought-stressed plants were re-watered immediately after these measurements. Recovery of light-saturated gas-exchange following re-wetting was measured on 15 December 1993 (day 4 of recovery), 18 December 1993 (day 7), and 21 December 1993 (day 11). Measurements were made from 0900 h to 1030 h on each of these days, when conditions were external CO_2: 350 to 355 μl CO_2 liter^{-1}; PPF: 1500 to 1750 μ mol m^{-2} s^{-1}; temperature: 29 to 33 °C; and VPD: 1.8 to 2.3 kPa. In addition, RWC and w were determined on 15 December 1993 as previously described.

Statistics

The statistical analyses were executed separately for each species. The relationship between A_{CO2} and PPF for each drought treatment was determined using nonlinear regression. The response curves were defined by the equation

$$A_{CO2} = a(1-e^{-b \cdot PPF}),$$

and were fitted by the modified Gauss-Newton method (SAS Institute 1988). The dependence of A_{CO2} on external CO_2 or internal CO_2 concentration was determined for each drought treatment with linear and non-linear regression analysis. Three days of data were analysed with day defined as block, then the data were combined after the day was determined to be a non-significant source of variation. The two days of chlorophyll fluorescence data were subjected to analysis of variance with day defined as block. All remaining response variables were subjected to analysis of variance.

Results

Rapid fluctuations in irradiance

Well-watered *P. dubius* trees exhibited A_{CO2} of c.11 μmol m^{-2} s^{-1} and g$_s$ of c. 280 μmol m^{-2} s^{-1} after 10 min of acclimating to a homogeneous PPF of 2000 μmol m^{-2} s^{-1} (Figure 1b). Within 30 s of the transition from high to low irradiance, g$_s$ was unchanged but A_{CO2} was abruptly reduced by almost 50%. Following this short lag time, g$_s$ began gradually declining for the remainder of the 3 min period of low irradiance. Following 3 min of low irradiance, g$_s$ was 64% of the original value. Stomatal conductance began increasing immediately after the low-to-high irradiance transition, and was back to the original value within 1.25 min. The increase in

A_{CO2} following the return to high irradiance was slower than the decline which followed the high-to-low irradiance transition. There was a close synchrony between the increase in A_{CO2} and that of g_s.

Pandanus dubius trees which experienced seven weeks of withholding water exhibited light-saturated A_{CO2} of 7.3 μmol m^{-2} s^{-1} and g_s of 190 μmol m^{-2} s^{-1} (Figure 1a). The decline in A_{CO2} following the high-to-low transition in irradiance was not as fast as that of the well-watered trees. Within 30 s of this transition A_{CO2} declined 30%. However, the ultimate level of A_{CO2} during the 3 min of low irradiance was about 50% of the initial value. The response of g_s to the abrupt transition from high to low irradiance was similar to that of the well-watered trees. By the end of 3 min of low irradiance, g_s was 68% of the original value. Stomatal conductance began a slow and consistent increase after the return to high irradiance, but did not return to the original value by the end of the 3 min of measurements in high irradiance. As a result, A_{CO2} did not return to the original value until almost 3 min after the low-to-high irradiance transition.
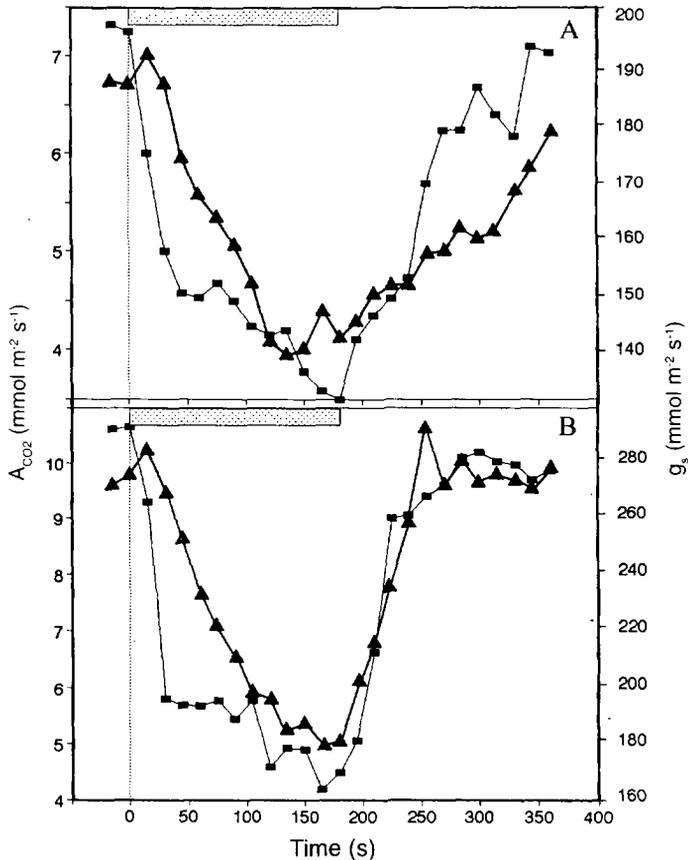
Figure 1. Net CO$_2$ assimilation (A_{CO2}, ■) and stomatal conductance (g_s, ▲) of *Pandanus dubius* leaves on drought-stressed (A) and well-watered (B) trees to variations in irradiance. The shaded bar indicates 3 min of low irradiance (photosynthetic photon flux = 280 - 300 μmol m^{-2} s^{-1}). Time intervals without the shaded bar indicate high irradiance (photosynthetic photon flux = 1900 - 2000 μmol m^{-2} s^{-1}). Notice the difference in scale. Symbols are means of 12 measurements for initial data point and 6 for remaining data points.

The dynamics of *P. tectorius* leaf gas-exchange responses to rapid changes in irradiance were similar to those of *P. dubius*. Following the transition from high to low irradiance, A_{CO2} of leaves from well-watered trees declined from 11 to $c.6.5$ μmol m^{-2} s^{-1} and that of drought-stressed trees declined from 5.7 to $c.3.5$ μmol m^{-2} s^{-1} (Figure 2). Stomatal conductance slowly declined for both sets of trees after a brief time lag which followed the abrupt change from high to low irradiance. The gradual increase in g_s which followed the return to high irradiance was much delayed by drought stress. Stomatal conductance of well-watered trees returned to the original value by 1 min after the return to high irradiance, but that of drought-stressed trees required 3 min at high irradiance for this to happen.
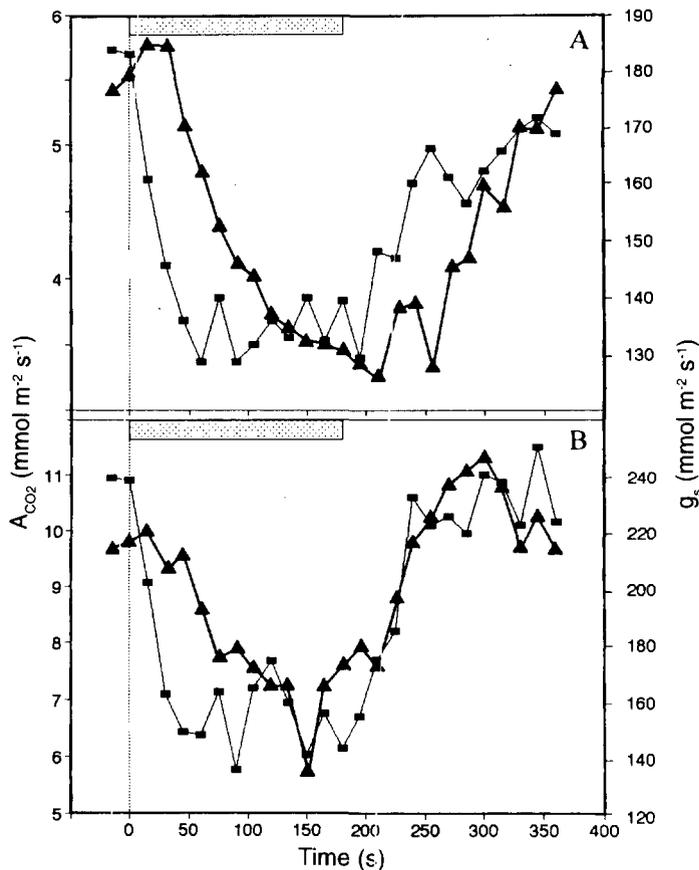
Figure 2. Net CO_2 assimilation (A_{CO2}, ■) and stomatal conductance (g_s, ▲) of *Pandanus tectorius* leaves on drought-stressed (A) and well-watered (B) trees to variations in irradiance. The shaded bar indicates 3 min of low irradiance (photosynthetic photon flux = 280 - 300 μmol m^{-2} s^{-1}). Time intervals without the shaded bar indicate high irradiance (photosynthetic photon flux = 1900 - 2000 μmol m^{-2} s^{-1}). Notice the difference in scale. Symbols are means of 12 measurements for initial data point and 6 for remaining data points.

The consequence of reduced g_s during the 3 min of low irradiance was to provide more favorable WUE while A_{CO2} was light-limited (data not shown). Water use efficiency following 10 min of high irradiance was 3.01 μmol CO_2 : μmol H_2O for well-watered *P. dubius* trees, and 3.15 μmol CO_2: μmol H_2O for well-watered *P. tectorius* trees. As A_{CO2} rapidly declined while g_s lagged for a brief time following the high-to-low irradiance transition, WUE declined to a minimum for both species and drought treatments. However, WUE began increasing in concert with the gradual decline in g_s during the 3 min of low irradiance. Due to this partial recovery during the period of low irradiance, full recovery of WUE after the return to high irradiance was more rapid than that of A_{CO2} or g_s.

Coincident with these gas-exchange measurements, soil w was 0.28 for the substrate around the drought-stressed plants, and 0.52 for that of the well-watered plants. Leaf RWC was reduced from 91% for well-watered *P. dubius* trees to 84% for drought-stressed trees, and from 91% for well-watered *P. tectorius* trees to 85% for drought-stressed trees.

Dependence of A_{CO2} on irradiance

The dependence of A_{CO2} on PPF conformed to an asymptotic exponential model for *P. dubius* leaves (Figure 3). The A_{CO2} of well-watered trees was more limited than that of drought-stressed trees as PPF became more important as the limiting factor. As a result, A_{CO2} of drought-stressed trees was *c.* 70% of well-watered trees at PPF of 150 μmol m^{-2} s^{-1}, but 50% of well-watered trees at PPF of 2200 μmol m^{-2} s^{-1}. The photosynthetic light response curves for well-watered and drought-stressed *P. tectorius* trees were similar to those in Figure 3 (data not shown). The response curve for well-watered trees was characterized by the equation

A_{CO2} = 12.04 $(1 - e^{-0.0015x})$, $(r^2 = 0.78)$; and that of drought-stressed trees was A_{CO2} = 6.92 $(1 - e^{-0.0024x})$, $(r^2 = 0.65)$. Net CO_2 assimilation at PPF of 2200 μmol m^{-2} s^{-1} was 11.64 μmol m^{-2} s^{-1} for well-watered and 6.89 μmol m^{-2} s^{-1} for drought-stressed trees.

Coinciding with these measurements was a soil w of 0.28 for drought-stressed trees and 0.49 for the well-watered trees. Leaf RWC was 90% or 84% for well-watered or drought-stressed *P. dubius* trees, and 91% or 87% for well-watered or drought-stressed *P. tectorius* trees.

Dependence of A_{CO2} on CO_2

Increasing external CO_2 from ambient to 800 μl CO_2 liter^{-1} enhanced A_{CO2} of drought-stressed trees more so than well-watered trees. Net CO_2 assimilation of the well-watered trees at 800 μl CO_2 liter^{-1} was 74% greater than at ambient CO_2, and A_{CO2} of drought-stressed trees at 800 μl CO_2 liter^{-1} was 105% greater than at ambient CO_2 (combined data from both species). The methods of Farquhar *et al.* (1980) were used to determine the relative efficiency of carboxylation. Drought stress decreased this response variable to about 50% below the level of the well-watered trees for both species (Table 1).

Soil w was 0.27 for the trees experiencing drought stress, and 0.49 for the well watered-trees. Leaf RWC during these measurements was 89% or 83% for well-watered or drought-stressed *P. dubius* trees, and 91% or 86% for well-watered or drought-stressed *P. tectorius* trees.
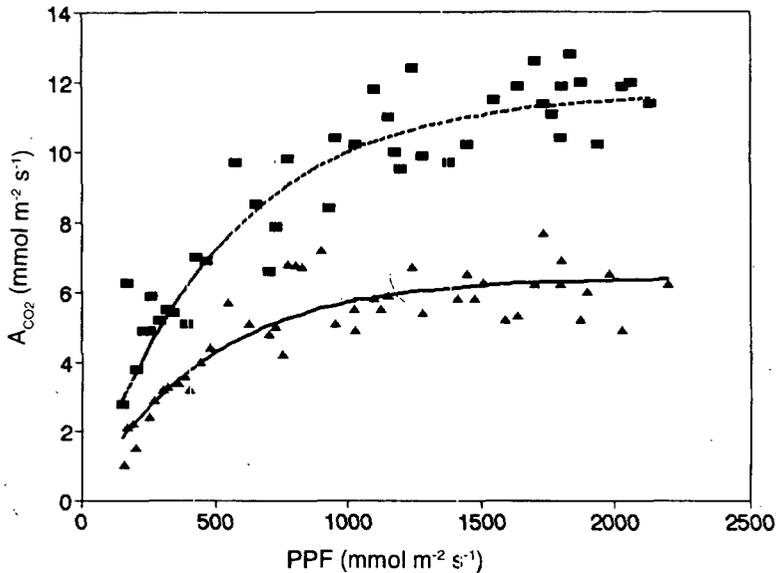
Figure 3. Net CO_2 assimilation (A_{CO2}) of leaves from well-watered (■) or drought-stressed (▲) *Pandanus dubius* seedlings at ambient CO_2 as influenced by photosynthetic photon flux (PPF). Data were obtained on 4 December 1993. Response equations were:
$A_{CO2} = 11.75 \ (1 - e^{-0.0019x})$, $(r^2 = 0.88$, well-watered) and $A_{CO2} = 6.42 \ (1 - e^{-0.0022x})$ $(r^2 = 0.80$, drought-stressed).

**Table 1.** Net CO_2 assimilation (A_{CO2}), stomatal conductance (g_s), transpiration (E), dark respiration (R_d), the ratio of internal to ambient CO_2 $(c_i : c_a)$, efficiency of carboxylation $(dA_{CO2}:dc_i)$, osmotic potential of leaves at full turgor (ψ_π), and relative leaf water content (RWC) of *Pandanus dubius* and *Pandanus tectorius* trees as influenced by drought stress

Variable	*Pandanus dubius*			*Pandanus tectorius*		
	Drought-stressed	Well-watered	p ≤	Drought-stressed	Well-watered	p ≤
A_{CO2} (μmol CO_2 m^{-2} s^{-1})	4.6	11.3	0.0001	5.3	11.2	0.0001
g_s (mmol H_2O $m^{-2}s^{-1}$)	175	243	0.0007	168	231	0.0001
E (mmol H_2O m^{-2} s^{-1})	2.0	3.1	0.0014	2.1	2.9	0.0015
R_d (μmol CO_2 m^{-2} s^{-1})	0.71	0.45	ns	0.67	0.41	ns
$c_i : c_a$	0.76	0.57	0.0145	0.74	0.59	0.0242
$dA_{CO2}: dc_i$	0.09	0.05	0.0001	0.08	0.04	0.0001
ψ_π (MPa)	- 1.45	- 1.46	ns	- 1.60	- 1.62	ns
RWC (%)	83	91	0.0214	86	89	0.0416

Note: n = 6; ns = not significant at p< 0.05.

Final measurements

Drought stress decreased A_{CO_2} relative to that of the well-watered trees to a greater degree (52 to 59%) than g_s or E (27 to 35%) (Table 1). Dark respiration was not influenced by water deficits, and values ranged from 0.41 to 0.71. The ratio of internal to ambient CO_2 increased for drought-stressed trees above that of well-watered trees. Following eight weeks of withholding water, the ψ_π of rehydrated leaf tissue was not different from that of leaves from trees which were well-watered throughout the study. The ratio of variable to maximal fluorescence measured during early afternoon was reduced by drought stress to about 20% below that of well-watered trees (Figure 4). The leaf RWC on the last morning of the drying cycle was 83% for *P. dubius* trees and 86% for *P. tectorius* trees, compared with 90 to 91% for the well-watered trees (Table 1). Soil *w* just prior to re-watering was 0.26.
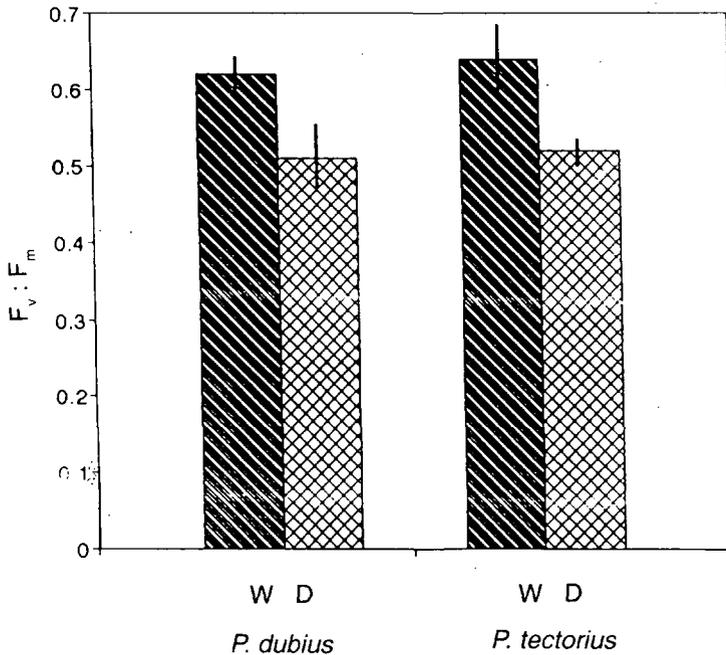

Figure 4. The ratio of variable to maximal fluorescence ($F_v:F_m$) from leaves of well-watered (W) or drought-stressed (D) *Pandanus dubius* and *Pandanus tectorius* seedlings. Data were obtained at 1300 h on 9 and 10 December 1993. Vertical bars indicate standard errors of means, n = 12.

Recovery after re-watering

Soil *w* was 0.50 to 0.52, and RWC was 89 to 91% by four days after rewatering, and there were no differences among the treatments. In contrast, A_{CO_2} of plants

previously exposed to water deficits had recovered slightly by day 4, but did not return to the level of well-watered plants until day 11 for either species (Figure 5). Stomatal conductance also exhibited a delay in full recovery, similar to that of A_{CO2} (data not shown).
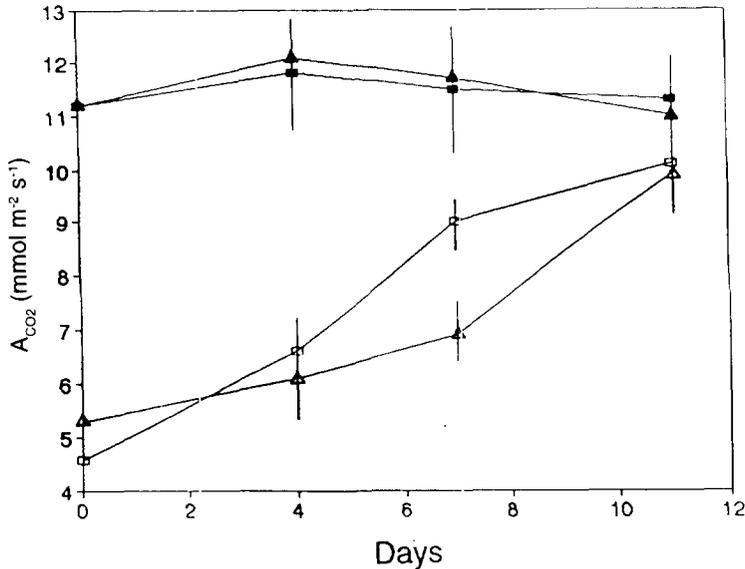
Figure 5. Net CO_2 assimilation (A_{CO2}) of *Pandanus dubius* (■) and *Pandanus tectorius* (▲) leaves following re-watering of drought-stressed trees. Filled symbols are well-watered trees, and open symbols are trees which experienced eight weeks of withholding water prior to rewatering on 11 December 1993 (day 0). Symbols are means ± standard errors of the means, n = 6.

Discussion

The gas-exchange characteristics of *P. dubius* and *P. tectorius* trees were similar in every regard. The range of values for leaf gas-exchange characteristics of these trees was within the confines expected for evergreen woody plants (Körner *et al.* 1979). As a group, herbaceous plants exhibit values of g_s and A_{CO2} that are about twice those of woody plants (Körner *et al.* 1979).

Pandanus dubius and *P. tectorius* trees experiencing water deficits were efficient at limiting transpiration through stomatal closure. This degree of limitation was not sufficient to maintain stable RWC during the two months of withholding water. Leaf RWC of species which are more efficient at tissue dehydration postponement may remain unchanged during water deficits until gas-exchange is greatly reduced. For instance, papaya leaves retain stable RWC during water deficits until g_s is less than 10% of well-watered plants (Marler *et al.* 1994), indicating a high degree of regulation for maintaining tissue hydration. Leaf RWC of *Pandanus* trees in this study was reduced by drought stress even though g_s remained functioning at levels of about 70% of well-watered trees.

Integrated acquisition of carbon for these trees was diminished by water deficits through a limitation of A_{CO2} and a relative increase of R_d. The ratio R_d : A_{CO2} increased from 4% for well-watered trees to 13% for *P. tectorius* and 15% for *P. dubius* trees (calculated from Table 1). The limitation of A_{CO2} by water deficits was not via stomatal or other gas phase limitations. Stresses which reduce A_{CO2} via partial stomatal limitation invariably exhibit decreased c_i (Long & Hallgren 1985). The drought-stressed *Pandanus* trees exhibited an increase in c_i when compared with well-watered trees, as indicated by the increase in c_i:c_a (Table 1). A closer look at the recovery of gas-exchange following rewatering also supports that drought stress directly inhibited photosynthesis rather than inhibiting the gas phase limitations. Although g_s recovered slowly as did A_{CO2}, there was no difference in c_i among the treatments. As a result, g_s was correlated with, but not causally related to A_{CO2}. Moreover, the causal agent for this delay in recovery of stomatal and photosynthetic capacity after re-watering was not directly tied to tissue hydration, as RWC fully recovered shortly after re-watering.

Drought stress decreased carboxylation efficiency, as indicated by the slope of the initial phase of A_{CO2} dependence on c_i; and photochemical efficiency, as indicated by the reduction in F_v:F_m. Chlorophyll fluorescence affords a rapid and sensitive examination of the effects of stresses on the photosynthetic apparatus. When leaves are exposed to direct sunlight, the fraction of this light which is excessive for the leaves is increased by environmental stress (Demmig-Adams & Adams 1992). Water stress may predispose the photosynthetic system to damage by excessive light, and this high light damage may be an important component of the damage field plants incur when exposed to drought (Bjorkman & Powles 1984).

Many plants experiencing water deficits use leaf movement to minimise exposure to incident sunlight, thereby decreasing the chance of damage to the photosynthetic system by excessive light (Turner 1986). Leaf movement may be active, as occurs with species possessing assimilatory organs equipped with pulvini (e.g. Marler & Lawton 1995); or passive, as occurs with leaf wilting. Reducing incident radiation during periods of water deficits is important for species which adapt to drought through dehydration postponement mechanisms (Turner 1986). The *Pandanus* trees in this study exhibited no leaf movement due to the distinctive form and rigidity of the leaves, so there was no possibility of reducing potentially damaging incident light via leaf movement.

Mechanical strengthening of leaves with abundant sclerenchyma and a high volume: surface area ratio are common features which are considered xeromorphic (Esau 1977). As a result, the rigid and relatively thick leaves of *Pandanus* trees are characteristic xeromorphic features. So sclerified are the leaves of *Pandanus* that they are used to make durable woven mats for roofing, flooring, and sails for canoes (Rickard & Cox 1984, Whistler 1987, Raulerson & Rinehart 1991).

With rapid reductions in irradiance, photosynthesis invariably declines due to rapid biochemical adjustments. However, the response of g_s to abrupt irradiance transitions is under more genetic control, and is quite variable among species. Plants have been classified into two broad groups with respect to stomatal responses to irradiance transitions (Knapp & Smith 1990). Some species exhibit partial

stomatal closure after a decrease in irradiance, then re-opening of stomata after return to high irradiance. This closing and re-opening has a short time delay, and this lag in g_s recovery may limit A_{CO_2} for a short time following the return to high irradiance. In contrast, the stomata of other species are relatively unaffected by abrupt changes in irradiance, and A_{CO_2} recovers as quickly following the return to high light as it declines following the transition from high to low light.

The *Pandanus* trees in this study exhibited a tracking response, whereby g_s declined slowly after an abrupt decrease in PPF. This tracking response produced an increase in WUE during the periods of low irradiance. Moreover, WUE returned to maximum almost immediately after the return to high light, even though A_{CO_2} exhibited a short time delay for recovery. These results indicate that the rapid response of g_s allows *Pandanus* trees to maximise WUE throughout the typical day of the lowland tropical climate which is characterised by direct sunlight chronically interrupted by the passage of cumulus clouds.

A consequence of maximising WUE by minimising water loss during episodes of low irradiance is that carbon gain is not maximised because of temporary stomatal limitation of A_{CO_2} during the recovery phase. Water conservation at the expense of carbon acquisition is probably adaptive in nature (Cowan 1982). A slower depletion of soil moisture by stomatal tracking would lower the possibility of prolonged plant moisture stress between rainfall events. This may afford *Pandanus* trees a competitive advantage during episodes of drought in situations where neighboring plants are non-tracking species, even though carbon gain is not maximised.

Water stress may alter the gas-exchange response to rapid changes in irradiance for many species (Davies & Kozlowski 1975, Knapp & Smith 1989). Knapp and Smith (1990) reported that some species even switch from a non-tracking stomatal behavior under well-watered conditions to a tracking stomatal behavior under conditions of water stress. The most striking manifestation of drought stress in this regard was a slowing of the recovery phase of g_s (Figures 1 & 2). For example, g_s of well-watered *P. dubius* trees exhibited full recovery by about 1 min after the return to high light, but that of drought-stressed trees had not fully recovered by the end of our 3 min of measurements in high light.

In summary, water deficits directly and independently decreased A_{CO_2} and g_s of *P. dubius* and *P. tectorius* trees. Carboxylation efficiency, photochemical efficiency, and relative leaf water content were also reduced by drought stress. Leaf osmotic potential was not influenced by drought stress for either species. Leaves of these trees are able to physiologically track sunlight such that stomatal limitation of water loss occurs within minutes of an abrupt transition from high light to low light which is limiting to A_{CO_2}. This ability allows *Pandanus* trees to maximise water use efficiency throughout the photoperiod where sunlight is periodically interrupted by cumulus clouds. Recovery of gas-exchange after re-wetting the drought-stressed trees was delayed for 11 days.

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