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Changes in gas exchange characteristics and water use efficiency of mangroves in response to salinity and vapour pressure deficit*

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Summary. Measurements were made of the photosynthetic gas exchange properties and water use efficiency of 19 species of mangrove in 9 estuaries with different salinity and climatic regimes in north eastern Australia and Papua New Guinea. Stomatal conductance and CO_2 assimilation rates differed significantly between species at the same locality, with the salt-secreting species, *Avicennia marina*, consistently having the highest CO_2 assimilation rates and stomatal conductances. Proportional changes in stomatal conductance and CO_2 assimilation rate resulted in constant and similar intercellular CO_2 concentrations for leaves exposed to photon flux densities above 800 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in all species at a particular locality. In consequence, all species at the same locality had similar water use efficiencies. There were, however, significant differences in gas exchange properties between different localities. Stomatal conductance and CO_2 assimilation rate both decreased with increasing salinity and with increasing leaf to air vapour pressure deficit (VPD). Furthermore, the slope of the relationship between assimilation rate and stomatal conductance increased, while intercellular CO_2 concentration decreased, with increasing salinity and with decreasing ambient relative humidity. It is concluded from these results that the water use efficiency of mangroves increases with increasing environmental stress, in this case aridity, thereby maximising photosynthetic carbon fixation while minimising water loss.

Key words: Mangrove – Gas exchange – Water use efficiency – Environmental gradients

A close correlation between assimilation rate, A, and stomatal conductance, g, has been observed in a wide range of plants (e.g. Wong et al. 1979; Hall and Schulze 1980; Yoshie 1986), including mangroves (Ball and Farquhar 1984a; Andrews et al. 1984; Andrews and Muller 1985). In a review of stomatal responses in relation to water loss and CO_2 assimilation, Schulze and Hall (1982) suggested that the slope of the relationship between A and g might be steeper for plants adapted to arid environments than for those adapted to humid environments.

Mangroves are found in a diverse range of intertidal environments. They grow in climatic conditions which range from arid to humid, and in salinity regimes from close to zero to as high as 80 parts per thousand (ppt). High leaf to air VPD, typical of arid climates, has been shown to depress CO_2 assimilation in both the laboratory (Ball and Farquhar 1984a) and the field (Andrews and Muller 1985). CO_2 assimilation rate may also be reduced by high salinity (Ball and Farquhar 1984a, 1984b). These studies also showed that reduction in CO_2 assimilation in response to high salinity and high leaf to air VPD was accompanied by a reduction in stomatal conductance, resulting in most cases in a more or less constant intercellular CO_2 concentration (c_i). Water use efficiency was unusually high for a C_3 plant (Ball and Farquhar 1984a, 1984b; Andrews et al. 1984; Andrews and Muller 1985).

To the best of our knowledge, there has been no investigation of the effect of salinity on photosynthetic gas exchange and water use efficiency in mangroves under field conditions. The purpose of the present work was to test the hypothesis that salinity and leaf to air VPD are key factors influencing photosynthetic carbon fixation and water use efficiency in mangroves in their natural environment. The work was carried out on exposed sun leaves of 19 mangrove species at 9 sites spanning a broad spectrum of salinity and climatic regimes in northern Australia and Papua New Guinea.

Materials and methods

Experimental sites. Measurements of gas exchange were carried out in six estuaries in northern Australia and three in Papua New Guinea. In northern Australia these were: Norman R. (17°39′S, 141°05′E); MacArthur R. (16°26′S, 136°05′E); Daintree R. (16°16′S, 145°25′E); Trinity Inlet (16°58′S, 145°47′E); Murray R. (18°04′S, 146°02′E); and Missionary Bay, Hinchinbook Is. (18°16′S, 146°13′E). The sites in Papua New Guinea were: Era, Wapo and Ivi Rivers, Gulf of Papua (7°30′S, 144°38′E); Galley Reach (9°05′S, 146°54′E), 60 km north-west of Port Moresby; and Motupore Is. (9°31′S, 147°17′E), 20 km south-east of Port Moresby. These sites encompassed a broad range of salinity and climatic regimes (Table 1).

A total of 19 species representing 10 genera and 8 families (Table 2) were included in the study, although not all were present at each site.

Gas exchange measurements. Gas exchange measurements were made with a Licor LI-6000 portable photosynthesis

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Table 1. Climatic conditions and soil salinity for experimental localities in northern Australia and Papua New Guinea during the study periods. Climatic data for northern Australian sites were obtained from long term means for the nearest meteorological station (Australian Bureau of Meteorology). Climatic data for Papua New Guinea were extracted from McAlpine et al. (1983). Soil salinity (ppt = parts per thousand) is the mean for sites sampled at each locality or, where indicated by a footnote, interpolated from measurements of water salinity. *P* precipitation (mm per month); *E* pan evaporation (mm per month), *RH* relative humidity (%), *S* soil salinity (parts per thousand)

Locality	Month	*P*	*E*	Temperature (°C)		*RH*		*S*
				Max.	Min.	9 am	3 pm	
Norman R.	Aug	2	267	31.2	16.4	43.4	27.2	45
MacArthur R.	Aug	1	216	32.2	13.5	48.3	21.9	49
Missionary Bay	Nov	104	314	30.7	20.7	70.0	64.2	37
Motupore Is.	Jun	40	158	30.1	22.1	79.0	70.0	35[a]
Trinity Inlet	Feb	431	167	31.1	23.6	78.4	68.3	25
Galley Reach	Jun	40	158	30.1	22.1	79.0	70.0	20[a]
Murray R.	Jun	48	188	25.3	14.5	78.5	62.8	20
Daintree R.	Jun	47	143	25.1	17.7	76.7	71.0	11
Gulf of Papua	Jun	718	106	30.3[b]	n.a.	97.0	87.4[b]	10[a]

[a] Interpolated from measurements of estuarine water (see methods)
[b] Mean of measurements on 4 consecutive days

Table 2. Species (and their families) of mangroves on which gas exchange measurements were made

Family	Species
Acanthaceae	*Acanthus ilicifolius* L.
Avicenniaceae	*Avicennia marina* (Forsk.) Vierh. *Avicennia officinalis* L.
Euphorbiaceae	*Excoecaria agallocha* L.
Meliaceae	*Xylocarpus austalasicus* Ridl. *Xylocarpus granatum* Koen.
Myrsinaceae	*Aegiceras corniculatum* (L.) Blanco
Plumbaginaceae	*Aegialitis annulata* R. Br.
Rhizophoraceae	*Bruguiera exaristata* Ding Hou *Bruguiera gymnorhiza* (L.) Lam. *Bruguiera parviflora* (Roxb) W & A ex Griff *Bruguiera sexangula* (Lour.) Poir. *Ceriops decandra* (Griff.) Ding Hou *Ceriops tagal var australis* CT White *Ceriops tagal var tagal* (Perr.) CB Rob. *Rhizophora apiculata* Bl. *Rhizophora mucronata* Lam. *Rhizophora stylosa* Griff.
Sterculiaceae	*Heritiera littoralis* (Dryand.) Ait.

system (Li-Cor, Lincoln, Nebraska, USA) equipped with a leaf cuvette of our own design. Briefly, the cuvette was designed to clamp onto the leaf, enclosing an area of 5.7 cm^2 of the lower surface only, the upper surface of the leaf being exposed to ambient air. This arrangement was possible because the stomata of most mangrove species are restricted to the abaxial surface of the leaf. With this cuvette, leaf temperature rose by less than 0.3° C during measurements of leaves exposed to bright sunshine. The volume of the chamber was 275 cm^3. Air inside the chamber was circulated rapidly with a small fan, giving a boundary layer conductance of 1.32 $mol \cdot m^{-2} \cdot s^{-1}$. Leaf temperature was measured with a 36-SWG chromel-constantan thermocouple pressed to the abaxial surface of the leaf, and the relative humidity and air temperature inside the cuvette were measured with a Vaisala Humicap 6061 RH sensor (Vaisala Oy, Helsinki, Finland) and YSI-44202 (Yellow Springs Instrument Co., Yellow Springs, Ohio, USA) linearised thermistor, respectively. Magnesium perchlorate was used as a desiccant in the air line to the infrared gas analyser; the rate of flow of air through the desiccant was measured with a mass flow meter (Tylan Model FM-360; Tylan Corp., Torrance, California, USA). The infrared gas analyser (IRGA) of the LI-6000 was calibrated daily using a cylinder of air which had previously been intercalibrated against gas mixtures generated with Wosthoff pumps (H. Wosthoff oHG, Bochum, F.R. Germany). The IRGA zero was checked at approximately half-hourly intervals using CO_2-free air that had been passed through soda lime. The Vaisala humidity sensor was calibrated prior to each field trip using airstreams of known humidity. Barometric pressure was measured daily with an aneroid barometer.

Calculation of gas exchange parameters. Raw data accumulated by the LI-6000 were transferred to a computer for subsequent calculation of CO_2 assimilation rate (A), stomatal conductance to CO_2 (g), and intercellular CO_2 concentration (c_i). Corrections were made for the interaction of water vapour efflux and CO_2 influx (von Caemmerer and Farquhar 1981). The LI-6000 is a closed circuit gas exchange system in which the CO_2 concentration, relative humidity and other measured variables change with time. For this reason, linear regressions of measured and calculated variables against time were used to extrapolate to their initial values at the time that data collection on a particular leaf was begun. All data presented in this paper are these initial values, except for the photon flux densities, which are the arithmetic means of 10 replicate readings taken during a measurement on each leaf over a period 30–60 s.

The intrinsic water use efficiency (W) of leaves was calculated from the ratio of the conductances to CO_2 in the gas phase and the total conductance as:

$$W = (c_a - c_i)/(c_a - \Gamma)$$

where c_a and c_i are the CO_2 concentrations ($\mu l \cdot l^{-1}$) of ambient air and the intercellular spaces, respectively, and Γ is the CO_2 compensation point ($\mu l \cdot l^{-1}$) (Fischer and Turner 1978; Andrews and Muller 1985). It was not feasible in this study to determine Γ in the usual way from the relationship between CO_2 assimilation rate, A, and intercellular CO_2 concentration, c_i. Several workers have reported temperature dependent values of Γ in mangroves ranging from 50 to 90 $\mu l \cdot l^{-1}$ (Moore et al. 1972; Andrews et al. 1984; Ball and Critchley 1982; Ball and Farquhar 1984a). In this paper a mean value for Γ of 70 $\mu l \cdot l^{-1}$ was used in calculating W.

Environmental variables. For the measurement of soil salinity, interstitial (pore) water from between the soil particles was allowed to drain into a 0.45 m-deep core hole. The salinity of a sample of water withdrawn from the hole was measured with a conductivity type salinometer (TPS Model

81C, TPS, Springwood, Queensland, Australia). Corrections were made for the temperature of the sample. The salinity of estuarine water was measured with the same salinometer or with a refractometer. Soil salinity measurements were not made at sites in Galley Reach, Motupore Is. or the Gulf of Papua. For these sites estimates of soil salinity were derived by interpolation from the salinity of estuarine water, based on local experience and our own experience from Australian mangrove environments.

Ambient relative humidity was measured with an aspirated wet and dry bulb thermometer.

Results

Assimilation rate

Analyses of the photosynthetic characteristics of leaves exposed to different average light levels at various positions in the canopy have shown that assimilation rate (A) reached a plateau at photon flux densities of about 800 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Clough and Sim, unpublished data). The data presented in this paper relate to leaves exposed to irradiances above 800 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

Mean rates of CO_2 assimilation ranged from a low of 2.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for *X. australasicus* in the Norman River to a high of 22 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for *A. marina* in Galley Reach (Table 3). The latter species, which has salt-secreting glands in its leaves, consistently had the highest A at those sites where it was present. Another species with salt-secreting glands, *A. corniculatum*, also had higher than average rates of assimilation at less arid sites but not at the Norman River, a highly saline and arid site. There were only small differences in A between the three *Rhizophora* species, which lay in the middle to upper part of the range of A for a particular locality (Table 3). Of the other more common species, *B. gymnorhiza*, *B. parviflora* and *X. granatum* tended to have lower than average rates of assimilation in a given locality. Overall, there were highly significant differences in the mean for A between sites ($F_{8,330} = 7.45$; $P < 0.001$). Rates of assimilation were greater at localities with low soil salinity and low VPD (e.g. Daintree River and Gulf of Papua), and least in localities with high soil salinity and high VPD, such as the MacArthur and Norman Rivers (Table 3). The exception to this was Galley Reach, where the rates of assimilation for three species, *A. marina*, *A. corniculatum* and *R. apiculata*, were higher than at any other locality. While the locality means for A (i.e. including

Table 3. CO_2 assimilation rate (A, $\mu mol \cdot m^{-2} \cdot s^{-1}$), stomatal conductance (g, $mol \cdot m^{-2} \cdot s^{-1}$), intercellular CO_2 concentration (c_i, $\mu l \cdot l^{-1}$) and intrinsic water use efficiency (W) of 19 species of mangroves at 9 localities in northern Australia and Papua New Guinea. Each value is the mean of n leaves (± s.e.) exposed to an irradiance greater than 800 μmol (photons) $\cdot m^{-2} \cdot s^{-1}$

Species	n	A	g	c_i	W
Norman R.					
A. annulata	6	9.40±1.36	0.062±0.008	162±5	0.65±0.02
A. corniculatum	3	5.64±0.87	0.040±0.007	176±5	0.59±0.02
A. ilicifolius	2	7.82±0.03	0.068±0.001	201±1	0.50±0.00
A. marina	8	10.28±1.17	0.084±0.010	188±1	0.55±0.02
E. agallocha	3	5.07±1.18	0.031±0.004	160±22	0.65±0.08
R. stylosa	6	7.71±0.74	0.049±0.005	159±8	0.66±0.03
X. granatum	5	2.54±0.36	0.018±0.001	185±18	0.56±0.07
MacArthur R.					
A. marina	8	19.07±7.77	0.098±0.016	173±7	0.60±0.03
B. exaristata	2	5.77±2.84	0.045±0.029	170±28	0.62±0.11
C. tagal var australis	9	4.50±0.89	0.036±0.008	187±12	0.55±0.05
R. stylosa	3	8.28±0.35	0.056±0.008	163±16	0.64±0.06
Hinchinbrook Is.					
C. tagal var australis	3	9.10±0.57	0.078±0.001	201±7	0.50±0.03
R. apiculata	19	8.65±0.30	0.073±0.003	196±4	0.52±0.02
R. stylosa	13	11.12±0.79	0.093±0.008	191±3	0.53±0.01
Motupore Is.					
R. apiculata	3	13.57±0.36	0.111±0.016	187±15	0.55±0.06
R. stylosa	7	13.19±1.11	0.131±0.007	211±9	0.46±0.04
Trinity Inlet					
B. gymnorhiza	5	4.30±1.07	0.037±0.011	200±13	0.50±0.05
R. apiculata	27	11.00±0.41	0.107±0.005	207±4	0.47±0.01
R. mucronata	9	11.11±0.92	0.139±0.007	233±7	0.37±0.03
Galley Reach					
A. corniculatum	4	18.57±1.48	0.266±0.024	236±5	0.36±0.02
A. marina	9	22.04±1.02	0.270±0.017	217±4	0.43±0.02
B. gymnorhiza	3	9.53±0.94	0.115±0.018	231±18	0.38±0.07
C. decandra	12	7.91±0.56	0.105±0.004	242±7	0.34±0.03
H. littoralis	6	8.78±0.51	0.092±0.010	217±11	0.44±0.04
R. apiculata	12	13.77±1.06	0.194±0.011	240±7	0.35±0.03
X. granatum	6	6.45±0.46	0.075±0.021	205±21	0.48±0.08
Murray R.					
B. gymnorhiza	10	7.14±0.92	0.093±0.014	241±4	0.34±0.02
B. parviflora	8	9.03±0.50	0.121±0.010	242±4	0.34±0.01
C. decandra	12	9.44±0.44	0.129±0.006	242±3	0.34±0.01
R. mucronata	7	11.70±1.25	0.165±0.022	240±7	0.35±0.03
X. granatum	10	13.43±0.56	0.188±0.008	239±5	0.35±0.02
Daintree R.					
A. corniculatum	6	11.66±1.20	0.135±0.002	228±10	0.39±0.04
A. ilicifolius	9	9.86±1.00	0.164±0.023	253±4	0.30±0.02
B. gymnorhiza	7	8.42±0.59	0.149±0.009	262±4	0.26±0.02
B. parviflora	3	7.87±0.23	0.158±0.010	269±2	0.24±0.01
B. sexangula	7	6.70±0.24	0.104±0.010	253±4	0.30±0.02
R. stylosa	18	9.92±0.59	0.161±0.013	251±4	0.30±0.01
R. mucronata	10	10.82±1.06	0.184±0.007	256±7	0.29±0.03
Gulf of Papua					
A. officinalis	5	13.19±1.25	0.217±0.027	249±8	0.31±0.03
B. gymnorhiza	7	8.91±0.85	0.117±0.018	239±6	0.36±0.02
B. sexangula	2	5.78±1.33	0.079±0.007	250±12	0.31±0.05
H. littoralis	2	8.57±0.14	0.113±0.018	241±11	0.34±0.04
R. apiculata	3	9.84±0.60	0.159±0.009	255±1	0.29±0.00
R. mucronata	8	11.26±0.22	0.186±0.010	253±4	0.30±0.02
R. stylosa	3	19.13±1.24	0.271±0.005	234±7	0.37±0.03
X. granatum	6	9.94±1.15	0.196±0.016	264±9	0.25±0.03

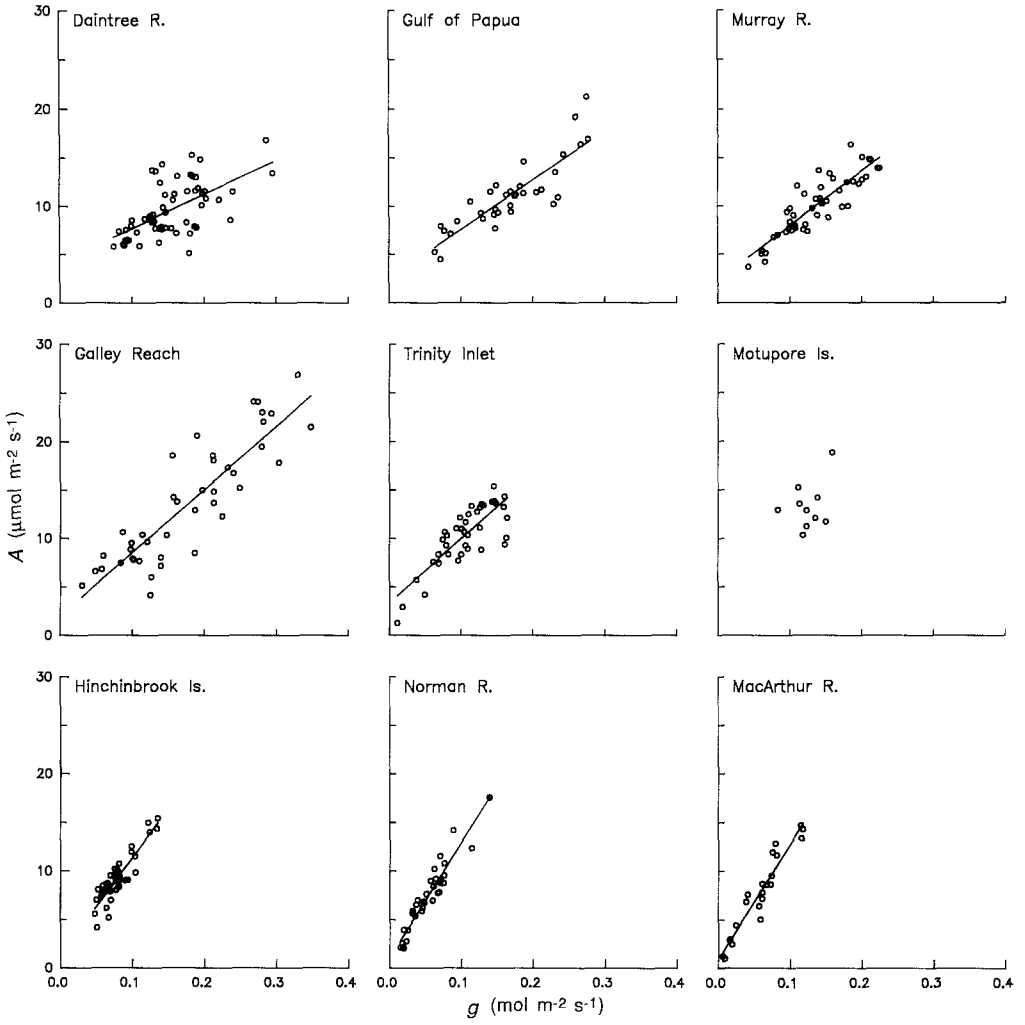

Fig. 1. Correlation between CO_2 assimilation rate (A, $\mu mol \cdot m^{-2} \cdot s^{-1}$) and stomatal conductance (g, $mol \cdot m^{-2} \cdot s^{-1}$) at each locality. Each data set includes only those leaves from all species that were exposed to irradiances above 800 μmol photons $\cdot m^{-2} \cdot s^{-1}$. Coefficients for the straight lines of best fit are given in Table 4

Table 4. Coefficients for the linear regression of CO_2 assimilation rate on stomatal conductance for all leaves sampled at each locality. n, number of leaves sampled; R^2, coefficient of determination; $SE(Y)$, standard error of the CO_2 assimilation estimate

Locality	n	Intercept	Slope	R^2	$SE(Y)$
Gulf of Papua	34	2.45	51.16	0.74	1.85
Daintree R.	60	4.12	35.35	0.36	2.25
Murray R.	47	2.24	56.79	0.78	1.48
Galley Reach	52	2.01	65.06	0.78	2.86
Trinity Inlet	40	3.35	66.23	0.66	1.84
Motupore Is.		Regression not fitted			
Hinchinbrook Is.	38	1.24	101.43	0.81	1.13
MacArthur R.	22	0.87	118.71	0.91	1.30
Norman R.	33	1.06	118.91	0.90	1.14

all species at a given site) were significantly different, the highest A observed at all sites was 15–20 $\mu mol \cdot m^{-2} \cdot s^{-1}$, except for Galley Reach and the Gulf of Papua where rates as high as 27 $\mu mol \cdot m^{-2} \cdot s^{-1}$ were recorded (Fig. 1).

Relationship between assimilation rate and stomatal conductance

Variation in A, both within and between species, at a given locality was matched by corresponding differences in g, resulting in a close correlation between A and g at all localities (Fig. 1). The data points shown in each graph of Fig. 1 represent all the data for that particular locality, no distinction having been made between the individual species present. The regression coefficients, correlation coefficient and standard error of the assimilation estimate for each locality are given in Table 4. An analysis of covariance showed that the slope of the relationship of A vs g differed significantly between sites ($F_{1,251} = 116.49$; $P < 0.001$). A further interesting feature of the data presented in Fig. 1 (and also shown by the regression R^2 in Table 4) is the much tighter fit of the data to the regression line for those localities with high salinity and high VPD, compared with localities having relatively low salinities and low VPD, where the variance is greater.

Intercellular CO_2 concentration and water use efficiency

All species at the same locality had remarkably similar intercellular CO_2 concentrations (Table 3), consistent with the linear relationship between A and g (Fig. 1). When averaged across all species at each locality, differences in mean c_i between localities were highly significant ($F_{8,330} = 65.94$; $P < 0.001$). Similarly, W differed significantly between localities ($F_{8,330} = 65.85$; $P < 0.001$), ranging from almost 0.6 at the Norman and MacArthur River sites down to 0.3 at the Daintree River and the Gulf of Papua (Table 3).

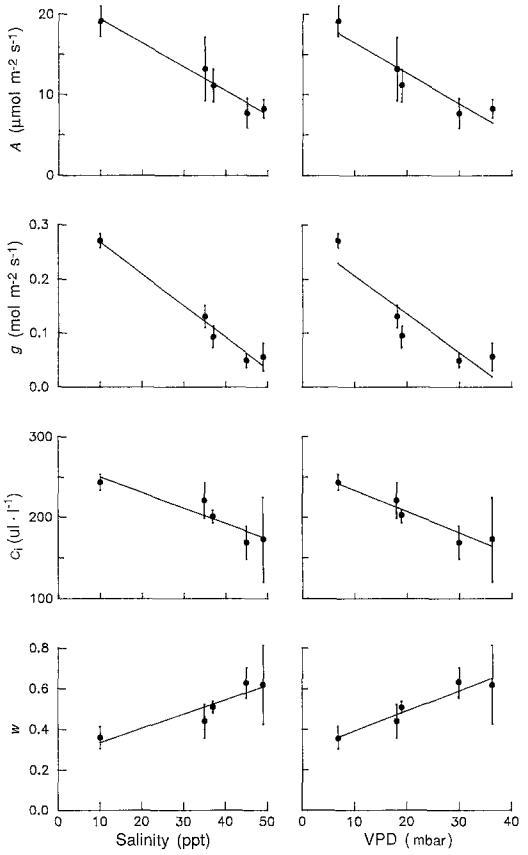

Fig. 2. Changes in CO_2 assimilation rate (A, $\mu mol \cdot m^{-2} \cdot s^{-1}$), stomatal conductance (g, $mol \cdot m^{-2} \cdot s^{-1}$), intercellular CO_2 concentration (c_i, $\mu l \cdot l^{-1}$) and intrinsic water use efficiency (W, non-dimensional) in *Rhizophora stylosa* along natural gradients of salinity and leaf to air VPD. Data points are means for each locality; error bars are the standard error of the mean. Coefficients for the straight lines of best fit are given in Table 5

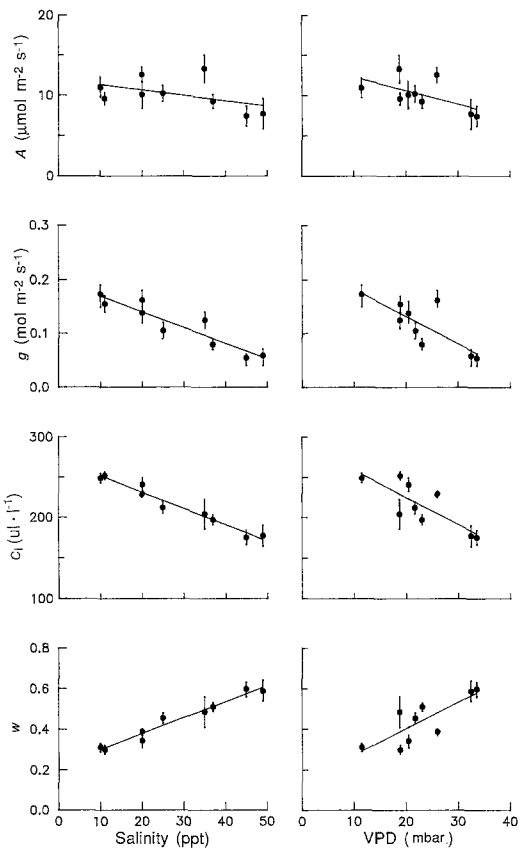

Fig. 3. Changes in CO_2 assimilation rate (A, $\mu mol \cdot m^{-2} \cdot s^{-1}$), stomatal conductance (g, $mol \cdot m^{-2} \cdot s^{-1}$), intercellular CO_2 concentration (c_i, $\mu l \cdot l^{-1}$) and intrinsic water use efficiency (W, non-dimensional) for all species investigated along natural gradients of salinity and leaf to air VPD. Data points are means for each locality; error bars are the standard error of the mean. Coefficients for the straight lines of best fit are given in Table 5

Changes in gas exchange characteristics with salinity and VPD

As shown in Table 1, there were significant differences in salinity and climatic conditions between localities. *Rhizophora stylosa* was one species that occured over a wide range of environmental conditions. In this species, locality means for A, g and c_i decreased more or less linearly with increasing salinity and increasing leaf to air VPD (Fig. 2, Table 5). As expected from changes in c_i, locality means for W increased linearly with both salinity and leaf to air VPD (Fig. 2, Table 5). Regression analysis using all available data (i.e. not means) for *R. stylosa* showed that salinity was a better predictor ($R^2 = 0.54$–0.56) than VPD ($R^2 = 0.34$–0.52) for g, c_i and W, while VPD ($R^2 = 0.43$) was a better predictor than salinity ($R^2 = 0.33$) for A. In all cases addition of the other independent variable (salinity or VPD) in a multiple stepwise regression analysis yielded only a small improvement in R^2.

Similarly, approximately linear relationships were obtained when the mean values of A, g, c_i and W for all species at each locality were plotted against salinity and leaf to air VPD (Fig. 3). The locality means for A and g are somewhat scattered owing to the variation in these two parameters within and between species (Table 3). However, locality means for c_i and W were both strongly correlated

Table 5. Coefficients for the linear regression of locality means for CO_2 assimilation rate (A), stomatal conductance (g), intercellular CO_2 concentration (c_i) and intrinsic water use efficiency (W) on leaf to air VPD and salinity. Data points are shown in Figs. 2 and 3. R^2, coefficient of determination; $SE(Y)$, standard error of the estimate of the dependent variable

Type	Intercept	Slope	R^2	$SE(Y)$
Rhizophora stylosa				
A vs VPD	20.24	−0.378	0.88	1.84
g vs VPD	0.278	−0.0071	0.82	0.044
c_i vs VPD	260	−2.65	0.91	11
W vs VPD	0.295	0.0098	0.91	0.041
A vs Salinity	22.36	−0.287	0.96	1.07
g vs Salinity	0.327	−0.0059	0.98	0.016
c_i vs Salinity	269	−1.92	0.84	14
W vs Salinity	0.262	0.0071	0.84	0.015
All species at each site				
A vs VPD	13.96	−0.167	0.35	1.69
g vs VPD	0.233	−0.0050	0.62	0.030
c_i vs VPD	292	−3.37	0.64	19
W vs VPD	0.144	0.0130	0.64	0.073
A vs Salinity	11.98	−0.0665	0.23	1.84
g vs Salinity	0.199	−0.0029	0.87	0.018
c_i vs Salinity	272	−2.03	0.96	6
W vs Salinity	0.223	0.0078	0.96	0.024

with salinity and, to a lesser extent, with leaf to air VPD (Fig. 3, Table 5). As in the case of *R. stylosa*, regression analysis using all available data (i.e. not means) for all species showed that salinity was a better predictor ($R^2 = 0.40$–0.61) than VPD ($R^2 = 0.23$–0.33) for g, c_i and W, while VPD ($R^2 = 0.19$) was a better predictor than salinity ($R^2 = 0.06$) for A. Again addition of the other variable in a multiple stepwise regression analysis yielded only a small improvement in R^2 for each parameter.

Discussion

Previous studies of the gas exchange of mangroves in the field have all been carried out at sites with salinities close to that of seawater (30–35 ppt) (e.g. Golley et al. 1962; Miller 1972; Moore et al. 1972, 1973; Attiwill and Clough 1980; Andrews et al. 1984; Andrews and Muller 1985). The CO_2 assimilation rates, stomatal conductances and intercellular CO_2 concentrations reported here for sites with a comparable salinity (i.e. 30–35 ppt) are consistent with these previous studies. Our data for *R. apiculata* and *R. stylosa* at Hinchinbrook Island, for example, are very similar to those obtained by Andrews et al. (1984) and Andrews and Muller (1985) for the same species at this site, even though they were collected some years apart.

The highest CO_2 assimilation rates observed in this study, obtained at sites with low to moderate salinities and high ambient humidities, are almost twice those reported previously for mangroves in the field (e.g. Moore et al. 1972, 1973; Attiwill and Clough 1980; Andrews et al. 1984; Andrews and Muller 1985) or in the laboratory (Ball and Critchley 1982; Ball and Farquhar 1984a, 1984b). They lie near the upper end of the range for assimilation rate found in other trees (Larcher 1975; Schaedle 1975). This shows clearly that under favourable conditions mangroves have a photosynthetic capacity comparable with that of other trees.

The similarity of the gas exchange characteristics and intrinsic water use efficiencies of all species under a particular set of environmental conditions (i.e. at a given locality) was striking, especially in view of their broad phyllogenetic origins (Table 2). This is illustrated by the fact that all species at a given locality were observed to fit a single consistent relationship between A and g (Fig. 1), and by the similarity of the intercellular CO_2 concentrations and intrinsic water use efficiencies of all species at the same locality (Table 3, Fig. 3). A similar result was obtained by Yoshie (1986) for a wide range of temperate genotypes in Japan.

The effect of leaf to air VPD on c_i and the carbon gain/water loss ratio (water use efficiency) in mangroves is not clear cut. As in the present study, Ball and Farquhar (1984a) observed a decrease in c_i with increasing leaf to air VPD in the range 6–24 mbar in seedlings of *Avicennia marina* and *Aegiceras corniculatum*. Andrews and Muller (1985), on the other hand, found no change in c_i for *Rhizophora stylosa* in response to natural variations in VPD over a range of 15–35 mbar, with a slight rise in c_i at VPDs between 35 and 50 mbar. The effect of salinity is equally unclear. Ball and Farquhar (1984a) observed a rise in c_i with increasing salinity in seedlings of *Aegiceras corniculatum* exposed to long term salinity treatments, but no such effect in *Avicennia marina*. On the other hand, Ball and Farquhar (1984b) found that c_i decreased in response to increasing transient salinity treatments (step changes of two day duration) in *Avicennia marina*. In our study, c_i likewise decreased with increasing salinity (Figs. 2 and 3), but in this case to long term salinity regimes; an examination of weather records for each locality for a period of several months prior to measurements revealed no unusual rainfall patterns that might have lead to transient changes in soil salinity.

Because of the strong linear correlation between salinity and leaf to air VPD across localities ($R^2 = 0.90$), it was not clear whether the observed differences in gas exchange properties between localities were a response to salinity, or to the leaf to air VPD. While there is no *a priori* reason to expect a linear relationship between any of the measured gas exchange parameters and either salinity or leaf to air VPD, our data show that stomatal conductance, intercellular CO_2 concentration and intrinsic water use efficiency were all better correlated with salinity than with leaf to air VPD. CO_2 assimilation rate, on the other hand, was better correlated with leaf to air VPD. On balance, it appears that salinity, rather than leaf to air VPD, was the more important environmental factor leading to the observed differences in gas exchange properties between the different localities. The effects of these two factors on stomatal conductance, CO_2 assimilation rate and water loss are not independent, however. Apart from possible effects directly on photosynthetic capacity (Ball and Farquhar 1984a, 1984b), salinity plays a major role in determining leaf water status because the upper limit to diurnal fluctuations in leaf water potential is set largely by the osmotic potential of the soil solution (Clough et al. 1982). In this sense high salinities are analogous to drought in terrestrial plant systems, and the changes in CO_2 assimilation, stomatal conductance and water use efficiency observed here in response to increasing salinity were similar to those reported for terrestrial plants experiencing drought (e.g. Schulze et al. 1980).

The relative constancy of c_i and the linearity of the relationship between A and g at each locality implies tight control of the carbon gain/water loss ratio by all the mangrove species investigated. Furthermore, the better correlation between A and g, shown in Fig. 1 and Table 4, for the localities with high salinities and high leaf to air VPD could be an indication of much tighter stomatal control of water use efficiency in these more arid environments.

In many natural environments, seasonal variations in rainfall and flooding with freshwater result in wide fluctuations in soil salinity. Similarly, variations in ambient humidity and leaf temperature, both of which are influenced by the degree of cloudiness, may lead to substantial seasonal differences in leaf to air VPD. These seasonal variations in environmental conditions may induce corresponding seasonal shifts in water use efficiency and other gas exchange characteristics, as has been observed in short-term laboratory studies with seedlings of *Avicennia marina* (Ball and Farquhar 1984b). In consequence, measurements made at only one time of the year, such as those carried out in this study, are unlikely to provide a reliable estimate of water use efficiency integrated over all seasons of the year. A better estimate of integrated long-term water use efficiency is likely to be obtained from an analysis of the $\delta^{13}C$ ratio, which has been shown to shift to a more positive value with lower c_i and higher water use efficiency in C_3 plants (Farquhar et al. 1982) and in C_3 halophytes exposed to high salinity

(Guy and Reid 1986). This might explain differences in $\delta^{13}C$ values reported by Andrews et al. (1984).

An increase in intrinsic water use efficiency with increasing environmental aridity appears to have great adapative significance for mangroves growing at or near their environmental limits. There is some evidence that the flux of salt to leaves is proportional to both salinity and the rate of water loss from the leaves (Clough, unpublished data). In consequence, minimisation of water loss is likely to be an important strategy for avoiding excessive salt loading in the shoot. Minimisation of water loss, particularly in areas with high salinity, is also likely to be important in avoiding the development of severe water deficits, which could reduce growth and inhibit other metabolic processes (Bradford and Hsiao 1982; Clough et al. 1982). However, minimisation of water loss through stomatal regulation is accompanied by the penalty of reduced photosynthesis to an extent that depends amongst other things on water use efficiency. In an integrated sense, the water use efficiency and the operational range for stomatal regulation of photosynthesis and water loss in mangroves represent a compromise for achieving a balance between the acquisition of carbon for growth and maintenance on one hand and, on the other, the cost of salt overloading and severe water deficits in terms of reduced growth (e.g. Downton 1982; Burchett et al. 1984; Clough 1984) and/or excessive maintenance requirements (Clough et al. 1982).

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