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Photosynthetic gas exchange and water use in tropical and subtropical populations of the mangrove *Aegiceras corniculatum.*

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Abstract

Photosynthetic gas exchange and stomatal behaviour in the wet-dry tropical (Darwin: 12°25'S) and subtropical (Ballina: 28°50'S) populations of the mangrove *Aegiceras corniculatum* (L.) Blanco were compared at elevated air temperatures (>32°C) and leaf to air vapour pressure deficit (*vpd* >25 mbar) with a quantum flux at, or above, their light saturation capacity (>600 µmol m^{-2} s^{-1}). At the lower end of the tested aridity range, the tropical population followed a more conservative water use than the subtropical population. As aridity increased, both populations showed a reduction in stomatal conductance. However, transpiration rates remained higher in the tropical population at all times, reducing its water use efficiency from that under less arid conditions. At extreme aridity (temperature >37°C and vpd >35 mbar), the efficiency of the evaporative cooling of fully exposed leaves was evident in the leaf-to-air temperature differential which remained minimal in the tropical population while it increased

significantly in the subtropical population. Aridity-tolerance was more pronounced in individuals from the tropical site than from the subtropical site, as evidenced by a tighter stomatal control on water use in the tropical population. As the mangrove population of Darwin is likely to experience more severe arid conditions for longer periods than that of Ballina, these differences in stomatal behaviour and water use efficiency are possibly the result of differential genetic selection in the two populations.

Keywords

Carbon assimilation; stomatal behaviour; aridity; water use efficiency; mangrove leaves.

Introduction

Mangroves in the subtropical and tropical north of Australia experience prolonged periods of aridity when air temperature and relative humidity are at, or near, their environmental limits.

Leaf temperatures above 30°C appear to reduce the biochemical capacity of the mesophyll to fix carbon in mangrove leaves (Moore et al. 1973; Andrews et al. 1984; Andrews and Muller 1985). Similarly, high leaf to air vapour pressure deficit *(vpd),* typical of arid climates, has been shown to depress CO_2 assimilation both in the laboratory (Ball and Farquhar 1984a) and under field conditions (Andrews and Muller 1985). The combined effect of high leaf temperature and *vpd* could induce an increase in transpiration rate so as to maintain a favourable leaf temperature through evaporative cooling. Such a response, in turn, would cause a drastic increase in the cost of water per unit of carbon gain.

To avoid excessive salt loading of the shoot, which could reduce growth and inhibit other metabolic processes (Bradford and Hsiao 1982; Clough et al. 1982),

many mangrove species possess a conservative water-use strategy that is generally, however, at the expense of both carbon acquisition and light interception capacity of the leaf (Ball et al. 1988). *Aegiceras corniculatum* is one of the very few salt-secreting mangrove species that displays strong performance and growth across a wide range of environmental conditions, including the Australian tropics and subtropics. This paper explores the physiological adaptations which enable this species to exploit light and water resources in the field under high temperatures and low relative humidity, and whether or not these physiological adaptations differ between the tropical and subtropical populations of the same species.

Material and Methods

Gas exchange characteristics of tropical and subtropical populations of the mangrove *Aegiceras corniculatum* were studied in relation to temperature and relative humidity under field conditions. The wet-dry tropical population studied was located at Darwin (12°25'S) while the subtropical one was at Ballina (28°50'S) on the north coast of NSW (fig. 1). For the Darwin population, data were collected only at the end of the wet season (autumn - May, 1994) when substrate salinity was minimal but, for the subtropical population, data collection occurred throughout the year (1994).

Photosynthetic gas exchange of intact leaves was measured using a LI-6200 portable photosynthesis system equipped with a 1 L leaf chamber (LI-COR, Lincoln, Nebraska). Photosynthetic measurements were made around noon (1100 to 1400 hr local time) on at least two fully expanded sunlit leaves per tree (to ensure maximal photon flux densities and leaf temperatures were included). A total of 140 data points were collected regardless of the season to enable a comparison of the photosynthetic responses, water use strategies and quantum efficiencies of the two populations at similar temperatures, vapour pressure

deficits and quantum densities. Water-use efficiency was calculated from the ratio of CO_2 assimilated per amount of water transpired per mbar vapour pressure deficit [µmol CO2/(mmol H_2O. mbar)], a measure of CO_2 fixed per unit of leaf conductance (Pezeshki et al. 1990). Quantum efficiency was calculated as the amount of carbon fixed per quantum at incident light levels that exceeded saturation intensity.

Results & Discussion

Ranges of environmental parameters

Data presented in Table 1 show the upper and lower limits of each environmental parameter [air-temperature *(Ta),* leaf to air vapour pressure deficit *(vpd),* and quantum *(I)*] monitored during this study as well as the corresponding physiological responses of both tropical and subtropical populations. As measurements for the Darwin site were confined to only one season (end of the wet season), the aim behind monitoring the Ballina site over a full year was to locate the time (regardless of season) at which the ranges of the environmental parameters described above overlap during the measurement period. As shown in Table 1, the minimal photon flux density varied from 582 at Darwin to 677 µmol m^{-2} s^{-1} at Ballina, while the maximum reached 1620 to 1997 µmol m^{-2} s^{-1} respectively. Air temperature varied from 32.1 to 38.4°C at the Ballina site while at Darwin, it ranged from 34.3 to 36.7°C. Leaf to air *vpd* ranged from 26.3 to 48.2 mbar at Ballina, while at Darwin, it ranged from 35.6 to 49.1 mbar.

Light saturation capacity

Changes in the assimilation rate, *A,* in response to quantum, *I,* were plotted indiscriminately for all data points collected for both populations regardless of season (fig. 2). Light saturation capacity of this species was about 600 µmol m^{-2} s^{-1} and close to values reported for other species of mangroves under field

conditions (Clough and Sim 1989; Cheeseman et al. 1991). The scattering of data points is probably due to the oscillation in the stomatal behaviour during the period of the measurements (1100 to 1400 hr local time) as indicated by (Andrews and Muller 1985).

Water use efficiency

Water use efficiency, *(WUE)* of the Ballina population appears to decrease exponentially with increasing air temperature up to 38°C (fig. 3). A similar response was observed with increasing *vpd* to 50 mbar (fig. 4). However, due to the extremely arid conditions that prevailed in Darwin during the course of measurements, comparison between population responses to environmental parameters could only be made within the following ranges: quantum range >600 µmol m^{-2} s^{-1}, temperature range >32°C and leaf to air *vpd* range >25 mbar. Although the data (figs. 3 and 4) represent all measurements for both localities and no distinction has been made between seasons, subsequent data, however, relate to leaves exposed only to environmental range as described above and indicated by dotted lines in figs. 2, 3 and 4. Within this range, both populations showed a similar reduction in *WUE* with increasing *vpd* from 25 to 50 mbar (fig. 5a). As Ball and Farquhar (1984a) reported a decrease in the internal CO_2 concentration *(Ci)* with increasing the *vpd* in the range 6-24 mbar in *Avicennia* and *Aegiceras,* it was expected that within a *vpd* range of 25 to 50 mbar, the *Ci* would decrease even further. On the contrary, CO_2 tensions in the mesophyll were more or less constant (fig. 5b). Andrews and Muller (1985), on the other hand, found no change in *Ci* in *Rhizophora* in response to variation of *vpd* between 15-35, with a slight rise in *Ci* at *vpd* between 35 and 50 mbar. The stable *Ci* reported in this work is likely to be related to the proportional changes in stomatal conductance and CO_2 assimilation rate for leaves exposed to photon flux densities at their light saturation capacity (above 600 µmol m^{-2} s^{-1}). As these measurements were made at high leaf temperatures (i.e. >32°C), the reduction in

gas exchange rate is attributed to the decline in the biochemical capacity of the mesophyll to fix carbon. This is very evident from the effects of leaf temperatures above 32°C on quantum efficiency of both populations (fig. 6a), where the amounts of carbon fixed per every unit quantum within the light saturation capacity of the species dropped sharply with increasing leaf temperature, while internal CO_2 concentration remained more or less constant (fig. 6b and Table 1). These results are consistent with other studies on photosynthetic responses to temperature in mangroves from the tropics (Andrews et al. 1984; Andrews and Muller 1985) and subtropics (Moore et al. 1973).

Assimilation rate and stomatal conductance

Carbon gain must be accompanied by some water expenditure. Just how much water the plant can lose for a given carbon gain is dependent on both stomatal conductance and water vapour gradient between the leaf and air. Many authors have indicated a close correlation between the assimilation rate, *A*, and stomatal conductance, *g*, in a wide range of plants (eg. Wong et al. 1979; Hall and Schulze 1980; Yoshie 1986), including mangroves (Ball and Farquhar 1984a; Andrews et al. 1984; Andrews and Muller 1985). Such a close relationship between the assimilation rate and stomatal conductance has been associated with minimising water expenditure while maintaining assimilation rates at, or very close to, the capacity of the mesophyll for photosynthesis (Cowan and Farquhar 1977; Farquhar 1979; Cowan 1986). It has been also suggested that the slope of the relationship between *A* and *g* is steeper for plants adapted to arid environments than for the unadapted individuals (Schulze and Hall 1982; Clough and Sim 1989). Such a difference is evident (Fig. 7) between the subtropical and tropical populations of *A. corniculatum.* The slope of the linear regression between stomatal conductance and assimilation rate was significantly higher in the tropical population (51.19: r^2=0.645) than in the subtropical one (30.04: r^2=0.735).

Ball et al. (1988) indicated that the relation between *A* and *g* differs with specific differences in water-use characteristics which, in turn, are related to specific differences in salinity tolerance. However, as the present study investigates the difference in correlation between *A* and *g* of two populations of a single species, the data presented here indicate that the two populations are significantly different in their response to aridity.

Figure 7 shows that, at any given stomatal conductance above 0.1 mmol m^{-2} s^{-1}, the carbon assimilation rate is higher in the tropical population than in the subtropical one. At the same stomatal conductance range (0.1 mmol m^{-2} s^{-1}), transpiration rate was also higher in the tropical population (Fig. 8). Changes in assimilation and transpiration rates at a given stomatal conductance are not parallel. For example, at a stomatal conductance of 0.20 mmol m^{-2} s^{-1}, in the subtropical population, assimilation rate was 9.97 µmol m^{-2} s^{-1} while transpiration was 5.95 mmol m^{-2} s^{-1}. In the tropical population, assimilation was 11.80 µmol m^{-2} s^{-1} while transpiration of rate was 8.25 mmol m^{-2} s^{-1} (calculated from the regression equation given in figs. 7 and 8). Accordingly, at this particular stomatal conductance value, *WUE* of the tropical population is higher than the subtropical one (0.699 and 0.596 respectively). However, at extremely low stomatal conductance, the difference between the two population became reversed. As these lower values of stomatal conductance reflect that both leaf temperature and *vpd* are at the very top end of the measured aridity range, it appears that the tropical population has responded by increasing its evaporative cooling more than the subtropical population (see below) which, in turn, has reduced the *WUE* of the tropical population from that under less extreme conditions.

Leaf-to-air temperature differentials

The better correlation between *A* and *g*, shown by the individuals in the tropical site (r^2=0.961) over the subtropical site (r^2=0.790), suggests tighter stomatal control of water use in the tropical population. Such control of the evaporative cooling by stomata is reflected in the leaf-to-air temperature differential which is minimal in the tropical population at air temperatures up to 38°C (Fig. 9). For example, at an air temperature of 37°C the tropical population maintained the temperature of its fully exposed leaves only 0.19°C higher than air temperature (calculated from the regression equation given in Fig. 9: r^2=0.538) while the fully exposed leaves of the subtropical one were higher by more than 1.4°C (r^2=0.559). As air temperature decreased towards 30°C (optimal leaf temperature for both populations) the leaf-to-air temperature differentials were reduced.

Ecological implications

Many mangroves such as *Aegiceras corniculatum, Avicennia marina* and *Rhizophora stylosa,* reportedly display a conservative water use strategy under both field and laboratory conditions (Ball 1981; Andrews et al. 1984; Ball and Farquhar 1984a; b; Andrews and Muller 1985), with a stomatal conductance considerably lower than that of typically well-watered C3 plants. The benefit of having a high water use efficiency in these halophytes is related to the necessity to regulate the salt balance in the tissues while minimising energy loss in eliminating accumulated salt.

Under arid conditions, maintenance of favourable leaf temperatures can be managed in several ways including changes in leaf inclination, area and succulence, which help to minimise the need for evaporative cooling (Ball et al. 1988). The present study was designed, therefore, to eliminate the possible effect of substrate salinity and leaf inclination factors. As described in the methodology section, comparisons in the present study were deliberately made at the end of the wet season, around noon and on fully exposed leaves. With these criteria,

data points represent, more or less, the physiological response to aridity by the two populations, regardless of their physical adaptations. For these fully exposed leaves, aridity requires leaves to operate at higher rates of water loss in order to maintain favourable leaf temperatures. It seems logical that when leaves operate with high evaporation rates they normally take advantage of both maximum light interception and CO_2 acquisition to maintain high rates of photosynthesis, and thereby offsetting the effects of their normal conservative water use i.e. optimising carbon gain in relation to water loss (Clough and Sim 1989). However, at excessively high leaf temperatures, reduction of the biochemical capacity of the mesophyll to fix CO_2, not only results in less efficient water use but also lowers the quantum efficiency.

The present study shows that in quantum flux at, or above, the light saturation capacity of the mangrove species *Aegiceras corniculatum,* the tropical and subtropical populations respond differently to aridity (elevated air temperature and leaf to air *vpd*). At the lower end of the recorded aridity range, the tropical population follows a more conservative water use than the subtropical one. At the upper end of the recorded aridity range, however, the tropical population responded by increasing evaporative cooling more than the subtropical one which, in turn, reversed their respective *WUE* from that under less extreme conditions. At this end of the scale, the efficiency of evaporative cooling of fully exposed leaves was evident on the leaf-to-air temperature difference which remained minimal in the tropical population when compared with the subtropical one. Aridity tolerance was also more pronounced in individuals at the tropical site (r^2=0.961) than those of the subtropical site (r^2=0.790), indicating a tighter stomatal control of water use in the more aridity-tolerant, tropical population.

These conclusions seem logical in the sense that the Darwin population is likely to experience more severe arid conditions for longer periods than that of Ballina. In addition, as has been noted with other halophytes (Dudley 1996a; b), it seems likely that the differences in stomatal behaviour and water use efficiency between these mangrove populations are a reflection of a lengthy genetic selection process under differing climatic conditions by widely separated populations.

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Fig. 3. Correlation between water use efficiency and air temperature in two populations of the mangrove *Aegiceras corniculatum.* The fitted curve represents the equation $y = 2205135.232x-4.326$ $r^2 = 0.738$, $P<0.001$.

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