

Observations of the Photosynthetic Physiology of Tree Species within the C₃ Monocotyledon Genus *Pandanus*, and Comparison with Dicotyledon C₃ Tree Species

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Abstract

Photosynthetic characteristics of tree species from the tropical C₃ monocotyledon genus *Pandanus* were compared with C₃ dicotyledon species growing in similar environments. The *Pandanus* species had similar maximum photosynthetic rates (A_{\max}) to dicotyledon tree species in leaves from both sun and shaded environments when A_{\max} was expressed on an area basis. Because of the low specific leaf area of the sclerophyllous leaves of the *Pandanus* compared to the dicotyledon species, the similarity in A_{\max} was no longer evident when A_{\max} was expressed on a dry-weight basis. Leaf dark respiration rates of the *Pandanus* on a leaf area and weight basis were generally lower than the shade-intolerant dicotyledons and similar to the shade-tolerant dicotyledon species. Low dark respiration rates and low specific leaf area of the *Pandanus* may be important characteristics for growth and survival in environments where resource levels are low and the likelihood of tissue damage is high.

Introduction

Species from the monocotyledon family Pandanaceae are common throughout the coastal areas of the Indian and Pacific oceans. The growth form of the plants is highly distinctive, characterised by long, sclerophyllous, stiff-keeled leaves that form a spiral around the trunk, and the presence of prop-roots. On the archipelago of Papua New Guinea (PNG), where this study was done, the species' diversity of the family is extremely high, reaching some 123 species in three genera (Stone 1982), with 76 species within the genus *Pandanus* in PNG (M. Jebb, pers. comm.).

Some species of *Pandanus* appear to have specialised habitat requirements (Stone 1982; M. Jebb, pers. comm.). For example, there are some species that are predominantly found in the shaded understorey of tropical forest, as well as those that are more commonly found close to or on beaches and uplifted coral reefs in environments where they are exposed to high levels of solar radiation. C₃ dicotyledon species have been shown to exhibit plasticity in leaf morphology and physiology over large ranges in solar radiation levels that enable them to achieve a positive carbon balance necessary for growth (Björkman 1981). The aim of this study was to investigate how tree species of the monocotyledon genus *Pandanus*, with their thick, sclerophyllous leaves and distinctive plant architecture, acclimate their leaf morphology and photosynthetic physiology to a range of solar radiation levels. Preliminary observations on the photosynthetic physiology and leaf characteristics of three species of *Pandanus* were made and the results contrasted with three dicotyledon species inhabiting a similar range of environments. Where possible, the photosynthetic characteristics of plants growing in both full light and shade were measured to assess the extent of acclimation possible in each species.

Materials and Methods

Three species of *Pandanus* were used in the experiment (Table 1). All were growing in forest, or on beaches close to the Christensen Research Institute in Madang on the north coast of Papua New Guinea. *Pandanus krauelianus* (Section Maysops K.Schum.) is a species found commonly in the understorey,

Table 1. Habitat and habit descriptions of species

Species	Habitat	Habit when mature (m)	Leaf size (cm) (length × width)
<i>Pandanus tectorius</i> (Pandanaeae)	Sandy sea shores	tree, 15	150 × 15
<i>P. krauelianus</i>	Tropical forest understorey	treelet, 5–10	150–300 × 4–11
<i>P. dubius</i>	Rocky sea shores	tree, 20	150 × 15
<i>Terminalia catappa</i> (Combretaceae)	Sea shores and cultivated in gardens	tree, 20	20–30 × 10–20
<i>Endospermum</i> sp. (Euphorbiaceae)	Tropical forest edges and gaps	tree, 30	30 × 30
<i>Barringtonia</i> sp. (Lecythidaceae)	Tropical forest understorey	treelet, 5–10	10–40 × 5–10

and thus in low light environments of lowland coastal forests. *Pandanus tectorius* (Section *Pandanus* Parkinson) is widespread on the beaches in the Madang area and is generally found growing exposed to high levels of solar radiation. *Pandanus dubius* (Section *Hombronia* Spreng.) is a tall tree, found commonly on exposed coral and rocky shores. The habitat range of *P. tectorius* and *P. dubius* overlap.

To provide a comparison with the species of the *Pandanus*, C_3 tree species from similar habitats were used. These were, *Terminalia catappa* L. (Combretaceae), commonly found in high solar radiation environments along the shores of the Pacific and Indian Oceans, *Endospermum formicarum* Becc. (Euphorbiaceae), a pioneer species of the tropical forest flora, and *Barringtonia calyptrocalyx* K.Schum. (Lecythidaceae), a representative of the commonly occurring understorey treelets of this genus.

In order to examine the photosynthetic characteristics of all six species (three *Pandanus* and three others), and also to assess the potential of the species for acclimation to both high and low levels of solar radiation, 10-cm² leaf discs were harvested from 3–6 individuals growing in both shaded and high solar radiation environments. Exceptions to this are for *P. tectorius*, where plants sufficiently shaded to facilitate comparison with other shade-growing plants were not found, and for *P. dubius*, where only one individual growing in full sunlight was sampled, because foliage from mature trees was inaccessible and juveniles in full sunlight with accessible foliage were rare. One leaf disc per plant was harvested from the most recently matured leaf. Where possible discs from *Pandanus* were cut so as to exclude as much of the central thickened mid-vein as possible. Plants of *P. krauelianus* growing in high solar radiation environments were obtained in areas that had been cleared for building gardens, and along roadsides. Whether leaves of these plants had developed under high solar radiation conditions could not be determined with absolute certainty, however discs were taken from the most recently matured leaf which was likely to have developed under the disturbed, high solar radiation conditions. Individuals of the three dicotyledon tree species growing in full sunlight and shaded environments were available within the Institute gardens (*Terminalia* and *Barringtonia* and *Endospermum*), at other adjacent shore-side areas (*Terminalia*), and in nearby forest (*Barringtonia* and *Endospermum*).

Maximum rates of photosynthetic O₂ evolution under saturating CO₂ concentrations and light levels (A_{max}) were obtained from 10-cm² leaf discs using a Hansatech Leaf Disc oxygen electrode system (model LD-2, Hansatech, Kings Lynn, UK) with a red LED light source. To obtain constant temperatures within the leaf disc chamber during measurements, the water jacket was attached to the water supply for the station which fluctuated between 26°C and 27°C. CO₂ was supplied using a fibre mat saturated with 1 M NaCO₃. Calibration of the system was obtained by using the average deflection of three 1 mL injections of air into the chamber. Leaf discs were first illuminated at 166 μ mol quanta m⁻² s⁻¹ to induce photosynthesis. After a constant oxygen evolution rate was obtained, the light levels were stepwise reduced to darkness to measure rates of dark respiration (*R*). Light levels were then

increased stepwise to $1650 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ to measure A_{max} . A_{max} presented are an average of four 1 min intervals once O_2 evolution was observed to be constant.

After measurements of A_{max} and R , leaf discs were dried in an oven until they reached a constant weight. Specific leaf area ($\text{m}^2 \text{kg}^{-1}$) was then calculated and A_{max} and R were calculated on a leaf area and dry weight basis.

Data were analysed using analysis of variance (ANOVA). Main effects were grouping (two classifications, *Pandanus* or other), species, and environment (sun or shade). Species (random effect) was nested within grouping (fixed effect). Environment was considered a fixed effect. Appropriateness of the models were assessed by examining residual plots. To satisfy the assumptions of the ANOVA model, data were logarithmically transformed prior to analysis.

Results

The specific leaf area (SLA) differed between species ($P \approx 0.0001$), and was also dependent on the environment in which leaves were grown ($P = 0.005$) (Fig. 1). Shade leaves had higher SLA than sun grown leaves. *Pandanus tectorius* and *P. dubius* had the lowest SLA of all species, ranging from $1 \text{ m}^2 \text{kg}^{-1}$ to $3 \text{ m}^2 \text{kg}^{-1}$.

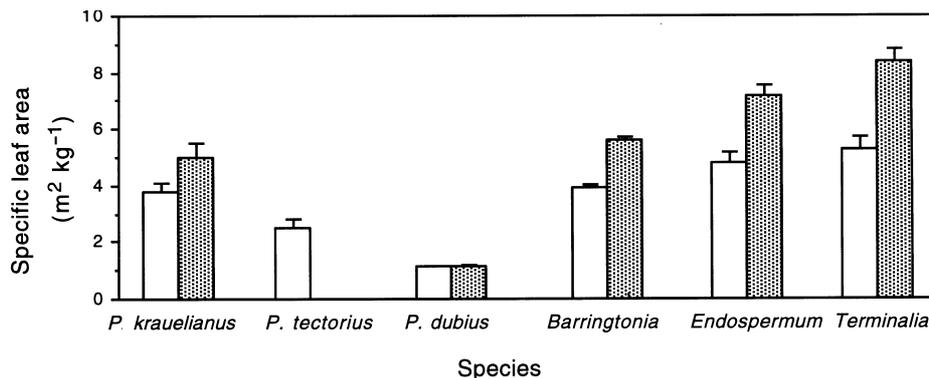


Fig. 1. Specific leaf area (SLA, $\text{m}^2 \text{kg}^{-1}$) of leaves grown in the sun (open bars) and shade (shaded bars) of three species of monocotyledon from the genus *Pandanus* (left) and three dicotyledon tree species (right).

A_{max} and R were expressed on both a leaf area ($A_{\text{max(Area)}}$, $R_{\text{(Area)}}$) and dry weight basis ($A_{\text{max(Wt)}}$, $R_{\text{(Wt)}}$). $A_{\text{max(Area)}}$ varied among species ($P = 0.001$), but no difference between the *Pandanus* and the dicotyledon species was observed ($P = 0.453$; Fig. 2a). Generally $A_{\text{max(Area)}}$ was higher in sun leaves than shade-grown leaves ($P = 0.051$), with the exception of *Barringtonia*, which had similar $A_{\text{max(Area)}}$ in both sun and shade leaves (Fig. 2a). In contrast, *P. krauelianus*, which also inhabits shaded environments, showed an increase in $A_{\text{max(Area)}}$ when growing under high levels of solar radiation, similar to species found most commonly in high solar radiation environments.

$A_{\text{max(Wt)}}$ of the *Pandanus* was low for sun leaves compared to the dicotyledon tree species *Terminalia* and *Endospermum*, and was comparable to the shade-tolerant treelet *Barringtonia* (Fig. 2b). A similar trend of higher $A_{\text{max(Wt)}}$ in sun leaves compared to shade leaves was evident ($P = 0.005$).

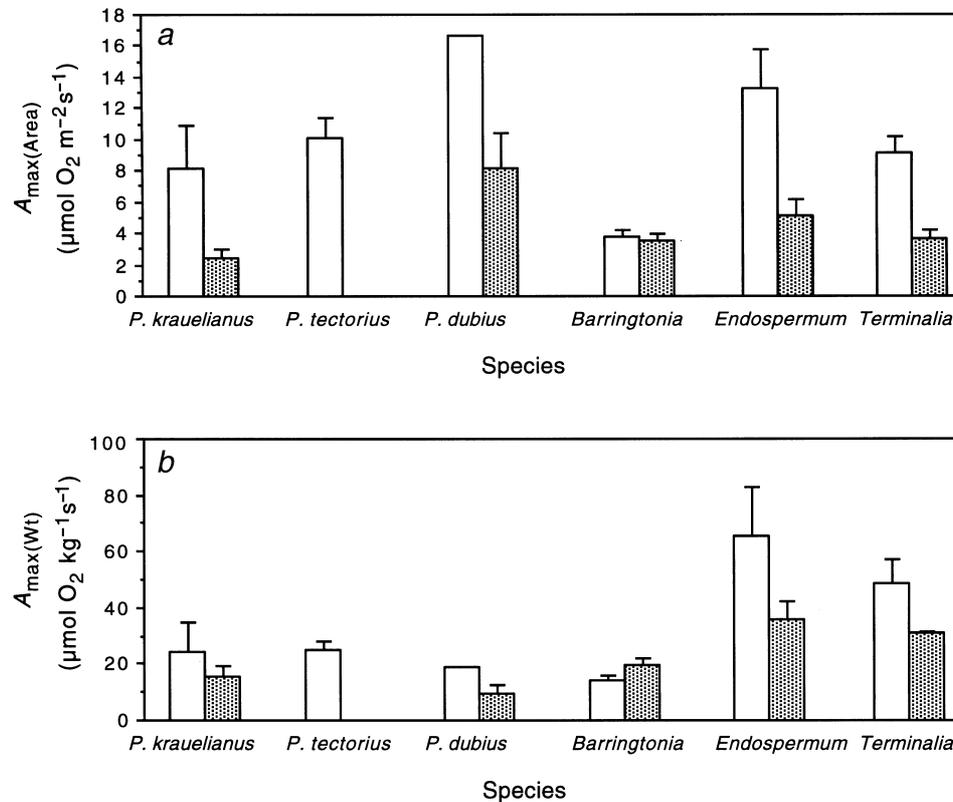


Fig. 2. Maximum rate of photosynthesis (A_{\max}) under saturating light and CO_2 concentrations of leaves grown in the sun (open bars) and shade (shaded bars) of three species from the monocotyledon genus *Pandanus* (left) and three dicotyledon tree species (right), expressed on a leaf-area (a) and dry-weight (b) basis.

$R_{(\text{Area})}$ was generally lower in the *Pandanus* than in the dicotyledon tree species ($P = 0.011$; Fig. 3a). The shade-tolerant *Barringtonia* had similarly low rates of $R_{(\text{Area})}$ as the *Pandanus*. In *Barringtonia* and the *Pandanus* there was no difference in $R_{(\text{Area})}$ between leaves grown in the shade or the sun, while there was a large difference in *Terminalia* and *Endospermum*. Similarly to $R_{(\text{Area})}$, $R_{(\text{Wt})}$ was lower in the *Pandanus* than the dicotyledon tree species ($P = 0.039$). There appeared to be no trend in the way light environment affected $R_{(\text{Wt})}$ ($P = 0.972$), with only *Terminalia* showing a reduction in $R_{(\text{Wt})}$ in shade-grown leaves.

Discussion

The *Pandanus* appear to be similar to two of the dicotyledon tree species studied (*Terminalia* and *Endospermum*) with respect to their $A_{\max(\text{Area})}$ and their ability to acclimate photosynthesis to both high and low solar radiation levels (Fig. 2). Shade leaves had generally lower A_{\max} than sun leaves, with this trend being particularly evident in $A_{\max(\text{Area})}$ (Fig. 2). Lower $A_{\max(\text{Area})}$ in shade-grown leaves compared to sun-grown leaves has been

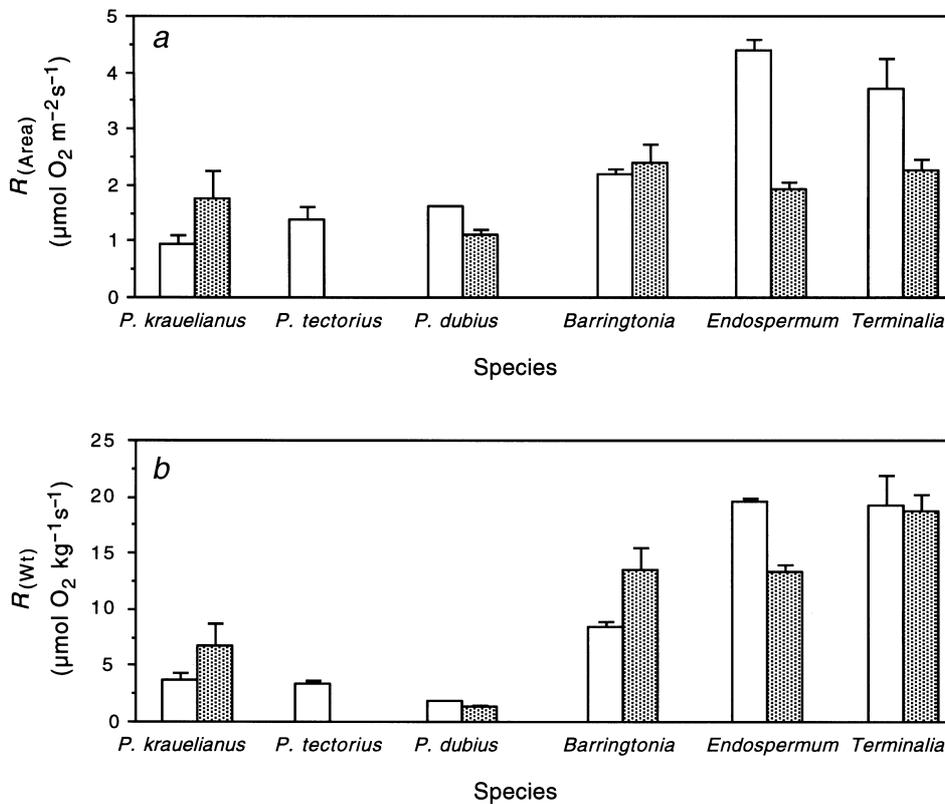


Fig. 3. Dark respiration rates (R) of leaves expressed on a leaf-area, $R_{(Area)}$ (a), and dry-weight basis, $R_{(Wt)}$ (b) of three species of monocotyledon from the genus *Pandanus* (left) and three dicotyledon tree species (right). Leaves were grown either in the sun (open bars) or in shaded (shaded bars) environments.

commonly observed (Boardman 1977; Björkman 1981). This is in contrast to the shade-tolerant treelet species, *Barringtonia*, which did not increase $A_{\text{max}(Area)}$ or $A_{\text{max}(Wt)}$ when grown in high-light environments, or when it was transferred from shaded conditions to full sunlight (Lovelock *et al.* 1994). In species from the New World tropics, it has also been observed that some highly shade-tolerant species fail to increase their photosynthetic rates when grown in full sunlight (Mulkey 1986; Strauss-Debenedetti and Bazzaz 1991; Kitajima 1994). *Pandanus krauelianus*, the shade-tolerant *Pandanus*, appeared to acclimate to higher levels of sunlight, possibly indicating a greater physiological plasticity than *Barringtonia*.

Although both the *Pandanus* species and *Terminalia* and *Endospermum* acclimated to high solar radiation environments by increasing their $A_{\text{max}(Area)}$ they appeared to achieve this in different ways. The *Pandanus* increased their $A_{\text{max}(Area)}$ in the sun by decreasing their specific leaf area (Fig. 1 and Fig. 2). That is, differences in A_{max} between sun and shade leaves in the *Pandanus* are reduced when A_{max} is expressed on a dry-weight basis. In contrast, the shade-intolerant dicotyledons *Terminalia* and *Endospermum* increased their photosynthetic capacity on both a dry-weight and area basis (Fig. 2).

The *Pandanus* had similar $A_{\max(\text{Area})}$ to the dicotyledon species but generally had lower $R_{(\text{Area})}$, indicating that the *Pandanus* have lower gross rates of photosynthesis on an area basis than the dicotyledon species (gross rate of photosynthesis is the sum of A_{\max} and R). Lower gross rates of photosynthesis in the *Pandanus* compared to the dicot species may be due to lower concentrations of photosynthetic enzymes and correspondingly lower concentrations of nitrogen per unit leaf area (Evans 1989), however this remains to be assessed. Lower rates of $A_{\max(\text{Area})}$ of the *Pandanus* compared to dicot species may also reflect lower levels of light absorbed by the chloroplasts, possibly because some chloroplasts are imbedded more deeply within the tissue of the sclerophyllous leaves of *Pandanus* than those of dicot species. This has been proposed as a cause of variation in photosynthetic rate of cotyledons with varying thicknesses (Kitajima 1992).

Similar rates of photosynthetic carbon gain on a leaf-area basis in the *Pandanus* and dicotyledon species in conjunction with lower dark respiration rates in the *Pandanus* may indicate that net carbon gain on a leaf area basis over a 24 h period could be as good or better in *Pandanus* than in the dicotyledon species, in both shaded and high-light environments. In the understorey, high efficiency of 24 h carbon gain per unit leaf area is beneficial because light availability limits photosynthetic carbon gain (Pearcy 1987). In high solar radiation, shoreline environments, leaves that are highly efficient with respect to carbon gained per unit leaf area over day–night cycles may be important if photosynthetic carbon gain is daily limited by drought.

High efficiency of 24 h carbon gain in the *Pandanus* may also be important in partially compensating for low leaf-area ratio (leaf area, or assimilatory area as a proportion of the total plant biomass) and low specific leaf area of the *Pandanus* species. Ash (1987) found that the dry weight of leaves accounted for approximately 50% of the plant dry weight of *P. tectorius*. This is a commonly found proportion in tropical dicotyledon tree species (Osunkoya and Ash 1991; Kitajima 1994). However, given leaves of the *Pandanus* may have lower specific leaf area than those of dicotyledon tree species (Fig. 1), and that they have a thickened central keel to their leaves, the leaf-area ratio may be substantially less in *Pandanus* than for dicotyledon tree species. Low leaf-area ratio and low specific leaf area have been shown to limit growth rates and competitive ability (Lambers and Poorter 1992; Walters *et al.* 1993; Kitajima 1994; but see Osunkoya and Ash 1991). In a recent study of Australian flora, specific leaf area was shown to underlie phylogenetic differences in growth rates among orders and families, and also be responsible for more recent divergences in growth rate among species and genera within families (Saverimuttu and Westoby 1996).

Pandanus thrive over a range of environments, despite their low specific leaf area and probable low growth rates. The long leaf-lifetimes recorded for the *Pandanus* (approximately 5 years in *P. tectorius* growing at 23° S on One Tree Island, Great Barrier Reef, Australia (Heatwole *et al.* 1981)) may be an important factor in compensating for the effects of low specific leaf area on growth rates, as has been shown in other species (Reich *et al.* 1991; Reich 1993). Additionally, while dicot species have to invest carbon in stem tissue to support their leaves, species of the *Pandanus* have lower construction costs because of the self-supporting structure of the leaves. Plasticity in allocation of carbon to leaves or wood has been suggested to be an important component in determining growth rates of tree species (King 1991). Thus, reduced construction cost of *Pandanus* compared to that of dicots may increase growth rates and the competitive ability of *Pandanus*.

Low specific leaf area of the *Pandanus* compared to dicot species may also enhance survival of *Pandanus* where the probability of leaf damage due to herbivory or physical agents is high, and the cost of leaf replacement is high. For example, *Pandanus krauelianus* grows in the the rainforest understorey where herbivory (Coley 1985) and physical damage due to falling debris (Clarke and Clarke 1989) have been shown to be factors limiting plant survival and growth. *Pandanus tectorius* and *P. dubius* inhabit environments that are often

saline, nutrient-poor and prone to wind damage and salt spray. In these environments the probability of tissue damage is likely to be high, as is the cost of replacing damaged tissue. Thus, the benefits of resistance to herbivores and physical damage in *Pandanus* may also contribute to balancing the effect of low specific leaf area on growth rates.

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