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Tim Brodribb · Robert S. Hill

Light response characteristics of a morphologically diverse group of southern hemisphere conifers as measured by chlorophyll fluorescence

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Abstract Unlike northern hemisphere conifer families, the southern family, Podocarpaceae, produces a great variety of foliage forms ranging from functionally broad-, to needle-leaved. The production of broad photosynthetic surfaces in podocarps has been linked qualitatively to low-light-environments, and we undertook to assess the validity of this assumption by measuring the light response of a morphologically diverse group of podocarps. The light response, as apparent photochemical electron transport rate (ETR), was measured by modulated fluorescence in ten species of this family and six associated species (including five Cupressaceae and one functionally needle-leaved angiosperm) all grown under identical glasshouse conditions. In all species, ETR was found to increase as light intensity increased, reaching a peak value (ETR_{max}) at saturating quantum flux ($PPFD_{sat}$), and decreasing thereafter. ETR_{max} ranged from 217 μmol electrons · $m^{-2} \cdot s^{-1}$ at a $PPFD_{sat}$ of 1725 μmol photons · $m^{-2} \cdot s^{-1}$ in *Actinostrobus acuminatus* to an ETR of 60 μmol electrons · $m^{-2} \cdot s^{-1}$ at a $PPFD_{sat}$ of 745 μmol electrons · $m^{-2} \cdot s^{-1}$ in *Podocarpus dispermis*. Good correlations were observed between ETR_{max} and both $PPFD_{sat}$ and maximum assimilation rate measured by gas-exchange analysis. The effective quantum yield at light saturation remained constant in all species with an average value of 0.278 ± 0.0035 determined for all 16 species. Differences in the shapes of light response curves were related to differences in the response of non-photochemical quenching (q_n), with q_n saturating faster in species with low $PPFD_{sat}$. Amongst the species of Podocarpaceae, the log of average shoot width was well correlated with $PPFD_{sat}$, wider leaves saturating at lower light intensities. This suggests that broadly flattened shoots in the Podocarpaceae are an adaptation to low light intensity.

T. Brodribb (✉) · R.S. Hill
Department of Plant Science, University of Tasmania,
GPO Box 252C, Hobart, Tasmania 7001, Australia
fax: (002) 202698; e-mail: brodribb@postoffice.utas.edu.au

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Introduction

Conifer diversity in the southern hemisphere is dominated by the family Podocarpaceae, which has shown great flexibility in evolving a variety of foliage forms unrivalled by other conifer families. The genera of the Podocarpaceae exhibit foliar morphologies ranging from tightly imbricate shoots (analogous to needles) to bilaterally flattened foliage taking on the appearance and function of angiosperm broad leaves (Fig. 1) The production of bilaterally flattened foliage in podocarps has occurred in at least three ways (Hill 1995). In genera such as *Acmopyle, Dacrycarpus, Prumnopitys, Nageia, Retrophyllum* and *Afrocarpus*, the leaves on short shoots are oriented parallel to the shoot axis and arranged in a manner typical of the leaflets on angiosperm compound leaves. In *Sundacarpus* and some species of *Podocarpus*, leaves have become very long, but are still relatively narrow since they have only a single vein, and are often arranged two-dimensionally on the short shoot. In *Phyllocladus*, leaves have been replaced by a flattened phylloclade, which is multiveined and broad. *Nageia* has secondarily evolved multiple veins in the leaf, which enable the leaf width to expand, a response otherwise difficult in univeined leaves. In all of these genera, the evolution of flat photosynthetic foliage has been polyphyletic.

Podocarps are found in a wide variety of habitats from canopy dominant in dense rainforest, to understorey shrub in open woodland (Enright and Hill 1995), and it has been suggested that it is the ability to produce functional 'broad leaves' which has enabled them to compete with angiosperms in the low-light environment under forest canopies (Hill 1995). Relatively few northern hemisphere conifers produce two-dimensionally flattened foliage, and those that do generally inhabit dark, wet environments e.g. *Metasequoia*, *Taxodium* and

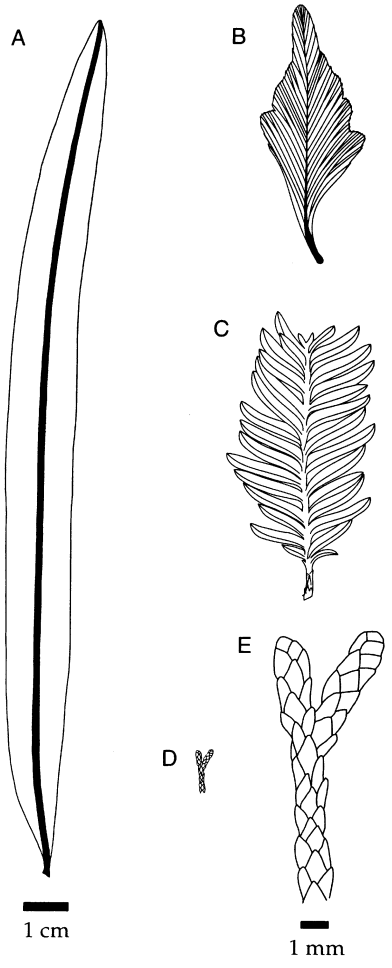

Fig. 1A–E Various leaf arrangements on short shoots of four species of Podocarpaceae. The 1-cm *scale bar* applies to **A–D** while **E** is shown with a 1-mm *scale bar*. Adapted from Hill (1995). **A** *Podocarpus* – large single-veined 'broad leaf'. **B** *Phyllocladus* – flattened shoot system. **C** *Acmopyle* – a single short shoot with leaves arranged parallel to the shoot axis, each short shoot taking the functional role of a single photosynthetic unit. **D** *Microstrobos* – an imbricate-leafed shoot, dimensionally and functionally acting as a needle leaf. **E** The leaf arrangement of *Microstrobos* in detail

Abies (Leverenz 1995). The relationship between shoot architecture and light environment is best demonstrated in *Abies*, where shoots that developed under high light are typically three-dimensional, while those that developed at lower irradiance show greater bilateral compression (increased silhouette area/total leaf area) (Sorrensen-Cothern et al. 1993).

Previous studies of northern hemisphere conifers have shown that maximum photosynthetic rate (per unit silhouette area) and quantum yield of CO_2 fixation in several genera of Pinaceae (*Pinus*, *Abies*, *Tsuga* and *Picea*) were related to the degree of shoot flattening (silhouette area/total leaf area), and that differences in physiology between flattened and non-flattened shoots were removed by illuminating stems from all directions during measurement (Carter and Smith 1985; Leverenz 1995). The variation in leaf and shoot morphology among species of Podocarpaceae is far more profound than the differences observed in the Pinaceae, and the aim of this study was to examine how these highly distinct morphologies are related to the light response characteristics of this unique group of conifers.

Instead of applying classical techniques whereby the potential of species to adapt to artificially imposed conditions of sun and shade is used to distinguish whether species are better suited to growth in high- or low-light environments all our plants were grown and measured under identical conditions of e.g. light, nutrient supply and temperature. To ensure that no species suffered from lethal extremes of light intensity, the light climate imposed was intermediate between sun and shade. The intention here was not to evaluate the short-term adaptive potential (morphological or physiological) of shoots to imposed extremes of sun or shade, but to indicate the relative light climate preferences of different shoot morphologies grown under uniform conditions to test the intuitive association between podocarp 'broad shoots' and low-light environments. Several species of the conifer family, Cupressaceae, and a needle-leaved angiosperm (*Allocasuarina verticellata*) were also included to determine whether relationships between morphology and light response were common to more distantly related species.

The light response of conifers was measured here using a modulated fluorometer (Schreiber et al. 1986) to determine the quantum yield of photosystem II ($Ø_{PSII}$) of individual leaves, or of a small part of a compound shoot (< 1.8 cm^2), avoiding the effects of self-shading. This allowed direct measurement of the leaf response without the complicating effects of leaf arrangement. The use of chlorophyll a fluorescence as a tool for measuring light response has been limited to date (e.g. McKiernan and Baker 1992; Bilger et al. 1995), despite its considerable potential for assaying both the rate of energy transfer through PSII and characteristics of the energy-dissipating processes such as the xanthophyll cycle (Demmig-Adams et al. 1995), which modulate the photochemistry response to light.

Rather than measuring the rate of CO_2 uptake at different light intensities, the response of the apparent electron transport rate (ETR) to photosynthetic photon flux density (PPFD) was determined here. ETR expresses the relative rate of electron transport through PSII for reduction of $NADP^+$, and is thus closely related to the rate of carboxylation (Edwards and Baker 1993). The calculation of ETR involves multiplying the $Ø_{PSII}$ as determined by fluorescence (Genty et al. 1989) by the quantum flux absorbed by PSII. Thus, measurement of ETR provides a means of probing the primary photochemical response and photochemical capacity of the leaf without confounding effects such as dark and light respiration rates.

Materials and Methods

Species

The following species were propagated in sand in Hobart: (1) podocarps – *Acmopyle pancheri* (Brongn. and Gris) Pilger, *Dacrycarpus dacrydioides* (Rich.) de Laubenfels, *Lagarostrobos franklinii* (Hook.) C.J.Quinn, *Microstrobos niphophilus* Garden and Johnson, *Phyllocladus aspleniifolius* (Labill.), *Podocarpus dispermis* White, *Podocarpus drouynianus* Mueller, *Podocarpus lawrencii* Hook.f., *Prumnopitys ferruginea* D.Don and *Retrophyllum comptonii* (Buchh.) C.N.Page; (2) and southern hemisphere Cupressaceae/Taxodiaceae – *Actinostrobus acuminatus* Parlatore, *Athrotaxis cupressoides* D.Don, *Athrotaxis selaginoides* D.Don, *Callitris rhomboidea* R.Br., and *Diselma archerii* Hook.f., and (3) the needle-leaved angiosperm *Allocasuarina verticellata* (Lam.) L. Johnson. Upon establishment, all plants were transferred to a pine bark potting mix in 3-l pots and grown under ambient light conditions in a well-irrigated, heated glasshouse near sea level in Hobart.

All species were grown under identical light conditions, and only foliage which was directly exposed to the incident light was used in experimental work. Plants were grown in an opaque glasshouse with a uniform light intensity throughout, and in the sun where the maximum light intensity was only 900 μmol photons $\cdot\, m^{-2} \cdot s^{-1}$ at the leaf surface. Thus leaves developed under conditions intermediate between full sun (approximately 1600 μmol photons $\cdot\, m^{-2} \cdot s^{-1}$) and shade, avoiding leaf damage due to excessive or insufficient PPFD. Measurements were carried out during a 4 week period in mid-summer, ensuring maximum stability of light intensity and photoperiod while experimental work was being undertaken. All species were represented by at least five replicates (and in the case of the cuttings, from at least three parent trees), except for *A. pancheri, P. ferruginea* and *R. comptonii,* which could only be propagated from two cuttings each, due to a high mortality rate during propagation caused by extreme sensitivity to light and humidity conditions.

Fluorescence

Chlorophyll a fluorescence was measured using a PAM 2000 fluorometer (Waltz, Effeltrich, Germany). Leaves, or portions of shoot, which had been dark adapted for approximately 30 min were clamped into a leaf clip (Bilger et al. 1995), ensuring that no self-shading was occurring. Leaf temperature was maintained at approximately 20°C during fluorescence readings.

Initially F_o (minimum fluorescence with the electron chain fully reduced) was measured in the dark, after which a saturating pulse of light was applied to the foliage, allowing measurement of F_m (maximum fluorescence with electron acceptors fully oxidised) and F_v ($F_m - F_o$). An actinic light was then switched on, and light-adapted F_m' was measured by applying a saturating flash of light. F_o quenching was determined by illuminating the sample with far-red light for 3 s with the actinic light switched off, facilitating re-oxidation of the acceptor side of PSII while measuring F_o' (Schreiber et al. 1994). Actinic light intensities were stepped up gradually from 15 to around 2000 μmol photons $\cdot\, m^{-2} \cdot s^{-1}$, allowing a period of 20 min for acclimation at each light intensity. An external halogen lamp, with fibre optic light delivery was used during the acclimation period at PPFDs greater than 400 μmol photons $\cdot\, m^{-2} \cdot s^{-1}$, because continuous use of the PAM internal halogen caused excessive heating. The external light was switched off and the internal halogen used, only briefly, during measurement, thus avoiding drift in light intensity measurements produced by heating the apparatus. At light intensities above 1000 μmol photons $\cdot\, m^{-2} \cdot s^{-1}$, at least 30 min was allowed for acclimation. $Ø_{PSII}$, photochemical quenching (q_p), and non-photochemical quenching (q_n) of fluorescence were calculated at each light intensity using the equations of Schreiber and Bilger (1992). ETR was calculated as

$$ETR = Ø_{PSII} \cdot I \cdot \alpha/2$$

where I is the incident PPFD (in the waveband 400–700 nm), α is leaf absorbance, and the factor of 2 accounts for the fact that two photons are required per electron passed through PSII, assuming linear electron flow and even distribution of absorbed quanta between PSII and PSI. The average value of α for green leaves of 0.84 (Björkman and Demmig 1987) was used here, and it was assumed that the excitation energy was evenly distributed between PSII and PSI (Bilger et al. 1995; Loreto et al. 1995). The units of ETR are μmol electrons $\cdot\, m^{-2} \cdot s^{-1}$, although it should be noted that values of ETR will not be precise, because leaf absorbance was not measured. The use of the average α for leaves of 0.84 was considered a good approximation considering that all leaves were relatively thick and only healthy, green leaves were selected. The one podocarp measured in the survey by Björkman and Demmig (1987) was found to have an α of 0.835, very close to the average value used here.

All fluorescence measurements were carried out at approximately 20°C, and response curves were measured from five replicates of each species, except for *A. pancheri*, *P. ferruginea* and *R. comptonii*, where two replicates were used. Polynomial curves were used to fit the pooled data for each species, and saturating PPFD ($PPFD_{sat}$) and maximum ETR (at $PPFD_{sat}$) were read from these curves. $PPFD_{sat}$ was taken as the light intensity at the peak of the ETR versus PPFD response.

Gas exchange

Net CO_2 uptake was measured using an open-flow IRGA system (Hoddeson, UK) as described in Brodribb (1996). For all plants, the maximum rate of photosynthesis (A_{max}) was determined under approximately optimal conditions, with leaves at 20°C, leaf air vapour pressure deficit at 5–10 mmol $\cdot$ mol^{-1}, ambient CO_2 at 350 ± 5 μmol $\cdot$ mol^{-1}, and a saturating light intensity (generally 1400 μmol photons $\cdot\, m^{-2} \cdot s^{-1}$). A_{max} for each species was averaged from all replicates, and a standard error calculated. Where possible, the same leaves were used for both fluorescence and gas exchange analysis. In both cases, young, green foliage was selected.

The small volume of the cuvette (20 ml) and careful selection of foliage allowed leaves to be arranged such that no self-shading occurred during measurement of gas exchange. Following gas exchange analysis, the silhouette area of the shoot enclosed in the cuvette was determined using a digital camera (EDC-1000, Electrim Corp., Princeton, N.J.) after which, leaves were detached, oven dried at 70°C for 72 h, and leaf dry weight was measured. The assimilation rate was expressed in terms of leaf silhouette area rather than total leaf area.

Leaf characters

Because leaves were arranged to prevent any self-shading, methods of describing shoot morphology, such as silhouette leaf area/projected leaf area, were not necessary. In all species, short shoots were functionally and morphologically analogous to leaves; in imbricate species, shoot width was less than 2 mm, analogous to needle leaves, and in non-imbricate species, short shoots were analogous to single broad leaves (Fig. 1). For this reason, the width of the short shoot provided the easiest and best means of quantifying its morphological character in the various species. The width of short shoots was measured at their widest point with a set of digital callipers (with an accuracy of ± 0.01 mm), and for each species, averages were taken from 30–40 shoots (depending on the number of available plants).

The mass of foliage per unit area (LAI) was also calculated on a silhouette area basis, and values of LAI for each species represented averages from five shoots.

Results

ETR increased in response to increasing light intensity, to a well-defined maximum ETR (ETR_{max}) occurring at $PPFD_{sat}$, and declined thereafter. Figure 2 shows average values of ETR at each light intensity for three species with different morphological and light saturating characteristics (*A. acuminatus* and *D. archerii* both produce imbricate shoots, while *R. comptonii* produces broad, flat, short shoots). Fourth-order polynomials fitted the data reasonably well, and from these curves, ETR_{max} and $PPFD_{sat}$ were measured. The initial slope of the PPFD versus ETR response was virtually identical in all species regardless of ETR_{max} or $PPFD_{sat}$.

Photochemical quenching of fluorescence (q_p) decreased in a linear fashion as light intensity increased, with the rate of decrease inversely proportional to ETR_{max}: slope $q_p = 1.19 \times 10^{-6}$ $(ETR_{max})-4.5 \times 10^{-4}$ $r = 0.849$. Fig. 3a illustrates the increasing decay rate of q_p in species with lower $ETR_{max,}$ using the same three species shown in fig. 2. The relationship between non-photochemical quenching (q_n) and PPFD was more complex (Fig. 3b), with a hyperbolic increase in q_n as light intensity increased. The rate of q_n saturation in each species was related to its photochemical capacity, with a low ETR_{max} corresponding to rapid saturation. q_n saturation always occurred at light intensities higher than $PPFD_{sat}$, and in several species, q_n did not saturate at the maximum light intensity (approximately 2500 $\mu mol \cdot photons \cdot m^{-2} \cdot s^{-1}$).

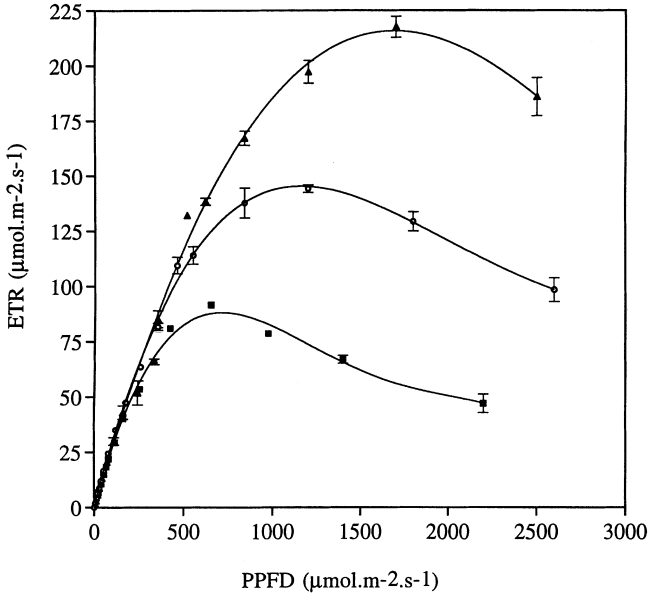

Fig. 2 The response of apparent of electron transport rate (*ETR*) to photosynthetic photon flux density (PPFD) in the conifers *Actinostrobus acuminatus* (▲, imbricate shoot), *Diselma archeri* (○, imbricate shoot) and *Retrophyllum comptonii* (■, broad shoot). Values shown represent averages from five plants (except *R. comptonii*, where only two plants were available). Curves fitted are fourth-order polynomials. Values of saturating PPFD ($PPFD_{sat}$) and maximum ETR (ETR_{max}) were taken from these light response curves

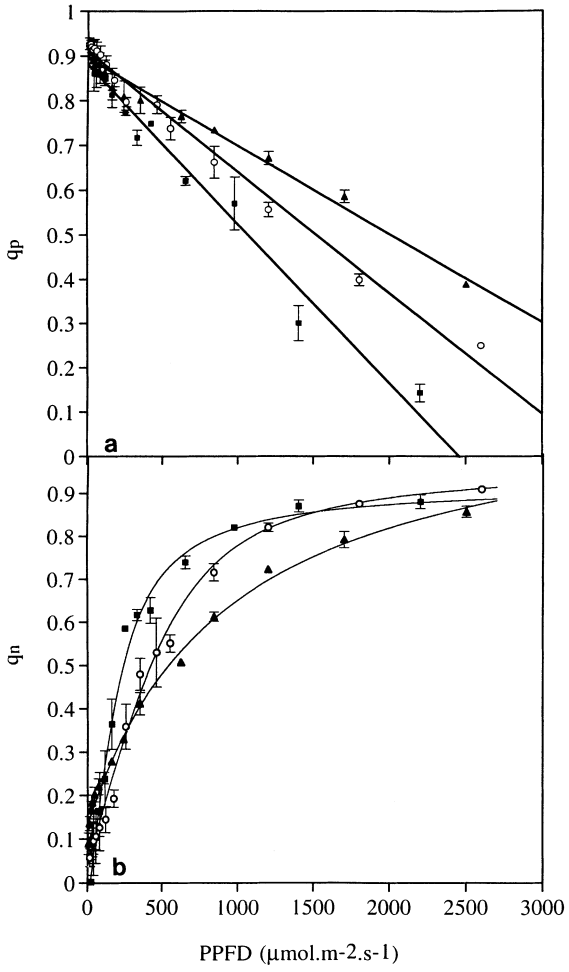

Fig. 3 Changes in photochemical (q_p; **a**) and non-photochemical (q_n; **b**) fluorescence quenching in response to increasing PPFD in the three species from Fig. 2. Linear regressions were used to fit the q_p data and rectangular hyperbolae were fitted to the q_n data. Symbols are as in Fig. 2

A linear relationship was observed between ETR_{max} and $PPFD_{sat}$ in the 16 species investigated (Fig. 4), with the maximum ETR_{max} of 217 µmol electrons $m^{-2} \cdot s^{-1}$ (*A. acuminatus*) occurring at a PPFD of 1725 µmol photons $\cdot m^{-2} \cdot s^{-1}$, and the minimum ETR_{max} of 60 µmol electrons $\cdot m^{-2} \cdot s^{-1}$ (*P. dispermis*) measured at a PPFD of 745 µmol photons $\cdot m^{-2} \cdot s^{-1}$ (Fig. 3). This linear relationship indicates that $Ø_{PSII}$ at $PPFD_{sat}$ was almost constant for each species. Measurement of the average $Ø_{PSII}$ at $PPFD_{sat}$ for each species indicated that quantum yield was conserved, with an average value of $Ø_{PSII} = 0.278 \pm 0.0035$ for all 16 species.

ETR_{max} was also linearly related to the maximum rate of CO_2 assimilation measured in each species by infrared gas analysis (Fig. 5), the maximum rate ETR of 217 µmol electrons $\cdot m^{-2} \cdot s^{-1}$ corresponding to an assimilation rate of 37.8 µmol electrons $m^{-2} \cdot s^{-1}$. This regression was not expected to pass through the origin due to the fact that A_{max} was a measure of net CO_2 flux, and hence would be negative (due to respiration) at an ETR of zero.

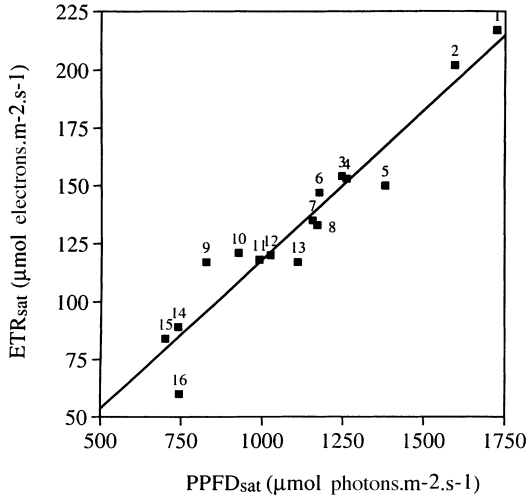

Fig. 4 A linear relationship was observed between light saturation intensity ($PPFD_{sat}$) and the maximum rate of electron transport through photosystem II as determined by fluorescence analysis. Among the 16 species shown are: 10 species of Podocarpaceae – *4 Podocarpus lawrencii*, *8 Microstrobos niphophilus*, *9 Phyllocladus aspleniifolius*, *10 Podocarpus drouynianus*, *11 Acmopyle pancheri*, *12 Dacrycarpus dacrydioides*, 13 *Lagarostrobos franklinii*, *14 Retrophyllum comptonii*, *15 Prumnopitys ferruginea*, *16 Podocarpus dispermis*; 5 species of Cupressaceae – *1 Actinostrobus acuminatus*, *3 Athrotaxis cupressoides*, *5 Callitris rhomboidea*, *6 Diselma archeri*, *7 Athrotaxis selaginoides*; one 'needle-leafed' angiosperm – *2 Allocasuarina verticellata*

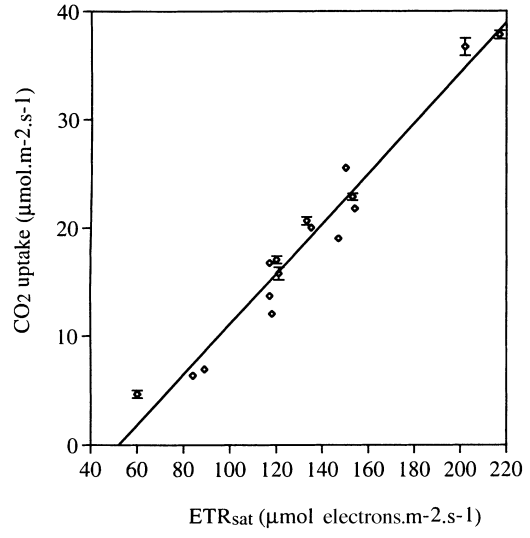

Fig. 5 The relationship between electron transport rate as determined by fluorescence analysis and the maximum rate of CO_2 uptake in all 16 species. A highly significant linear regression is shown ($P < 0.001$). The relationship is not expected to go through the origin, because CO_2 uptake at 0 ETR will be negative due to respiration. Values of CO_2 uptake are average maximum rates from five individuals, except for *P. ferruginea*, *R. comptonii*, and *P. dispermis*, all represented by two individuals

$PPFD_{sat}$ was significantly correlated [$PPFD_{sat} = -241.\log(\text{shoot width}) + 1209$; $P < 0.001$] with the log of the width of short shoots in the 10 species of Podocarpaceae used here (Fig. 6). In narrow (imbricate)

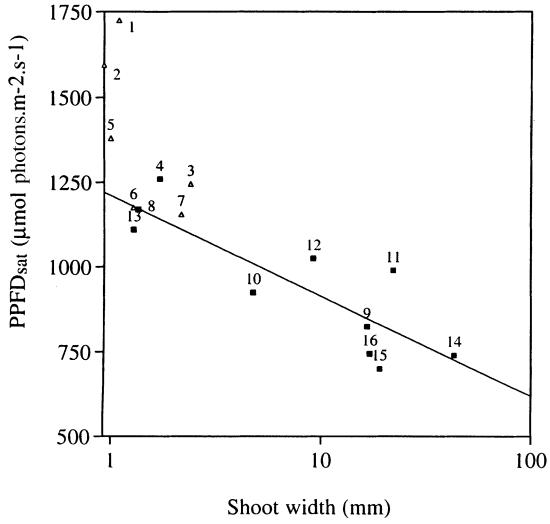

Fig. 6 The relationship between light saturation intensity and average width of short shoots in 10 species of Podocarpaceae (■). A highly significant log regression ($P < 0.001$) is shown. The 6 species of non-podocraps also shown (▲) did not fit this regression. Species are as in Fig. 4

shoots, ETR was found to saturate at higher light intensities than in broader, flattened shoots (Table 1). Among the 5 species of Cupressaceae/Taxodiaceae and *Allocasuarina* included in the study, there was no significant degree of shoot flattening, and thus there was no relationship between shoot width and light saturation characteristics in these non-podocarp species (Fig. 6).

A weak but significant positive linear relationship was present between LAI and $PPFD_{sat}$ ($r = 0.50$; $P < 0.05$).

Discussion

Fluorescence technique

Analysis of chlorophyll a fluorescence provides a useful means to compare light response characteristics among species. The utilisation of fibre optics to deliver light to a small portion of the leaf means that high light intensities can be used without concomitant leaf-heating problems. This allows the photochemical response curve to be extended above saturating light intensities until a combination of high q_n and photoinhibition cause a decline in ETR. The advantage of this is that the maximum rate of ETR appears as a well-defined peak, from which $PPFD_{sat}$ can be determined precisely. In a previous field study (Bilger et al. 1995), high light intensities were associated with decreased accuracy in the measurement of ETR; this effect was not observed in the data here, and was probably associated with the use of ambient light in the field rather than artificial illumination.

The relationship between Φ_{PSII}, and Φ_{CO2} has been shown to be linear across a range of conditions in maize leaves (Edwards and Baker 1993); however, the rela-

Table 1 Average maximum width of shoots, saturating photosynthetic photon flux density ($PPFD_{sat}$) and maximum electron transport (ETR_{max}) in 10 species of Podocarpaceae, 5 species of Cupressaceae, and a single needle-leaved angiosperm

Species	Average shoot Width (mm)	$PPFD_{sat}$ (μmol photons · $m^{-2} \cdot s^{-1}$)	ETR_{max} (μmol electrons · $m^{-2} \cdot s^{-1}$)
Podocarpaceae			
Acmopyle pancheri	22.2	990	118
Dacrycarpus dacrydioides	9.16	1025	120
Lagarostrobos franklinii	1.27	1110	117
Microstrobos niphophilus	1.34	1170	133
Podocarpus lawrencii	1.7	1260	153
Podocarpus drouynianus	4.74	925	121
Podocarpus dispermis	17.2	745	60
Retrophyllum comptonii	43.4	740	89
Prumnopitys ferruginea	19.18	700	84
Phyllocladus aspleniifolius	16.7	825	117
Cupressaceae			
Actinostrobus acuminatus	1.08	1725	217
Athrotaxis selaginoides	2.15	1155	135
Athrotaxis cupressoides	2.38	1245	154
Callitris rhomboidea	0.99	1380	150
Diselma archeri	1.27	1175	147
Angiospermae			
Allocasuarina verticellata	0.92	1595	202

tionship for C_3 plants has yet to be determined precisely, largely because of the complicating effects of photorespiration. The data presented here indicate a close correlation between ETR_{max} and A_{max} (Fig. 5), suggesting that photorespiration was not causing any significant variation in the relationship between $Ø_{PSII}$ and $Ø_{CO2}$ under the standard measurement conditions for ETR_{max} and A_{max} applied here. The probable reason for this is that only a relatively small variation in the leaf internal CO_2 concentration (between approximately 205 and 250 μmol · mol^{-1}) occurs in these species under the conditions which A_{max} was measured (unpublished data). This amount of variation in internal CO_2 concentration would only be expected to produce a maximum variation of approximately 8% (using the stoichiometry of Farquhar et al. 1980) across the range of A_{max}, due to the effects of differing Rubisco oxygenase/carboxylase activities.

Other potential problems such as uneven distribution of absorbed quanta between PSII and PSI and non-cyclic electron flow may have been present, but their effects did not alter the linear relationship observed between ETR and A.

Light response characteristics

The photochemical capacity (ETR_{max}) of foliage here was found to be proportional to the light intensity which just saturated photochemistry (Fig. 4). This indicates that the light reactions in all plants were initially maximal, and saturated in a standard fashion (see Bordman 1977) resulting in a constant $Ø_{PSII}$ at ETR_{max} of 0.278 ± 0.0035 in all species investigated. This figure represents the quantum yield at light saturation prior to the saturation of q_n and the production of photoinhibitory effects which occur at supersaturating quantum fluxes. From this it is clear that all species were unstressed prior to measurement and thus that differences in the light response of the various species reflected functional characteristics of the photochemistry and were not an artifact of stressful light conditions during growth. Conventional techniques of quantifying sun or shade adaptation potential generally involve subjecting foliage to extremes of sun or shade during the 'acclimation period' prior to measurement, and this has the potential to cause photochemical damage to the leaves, thus affecting the quantum yield at all light intensities.

The differences in light response observed between species here appear to be related to differences in the characteristics of q_n (Fig. 3b). In species with a low light requirement for $PPFD_{sat}$, q_n was found to become saturated at light intensities around 1000–1500 μmol photons · $m^{-2} \cdot s^{-1}$, whereas q_n in species with high $PPFD_{sat}$ did not saturate even at the maximum light intensity used (2500 μmol photons · $m^{-2} \cdot s^{-1}$). This variation in the characteristics of q_n is most probably due to differences in the size and characteristics of the xanthophyll pool. The xanthophyll cycle pigments are responsible for regulating the bulk of non-fluorescent energy dissipation from the photosystems, channelling excess excitation energy away from reaction centres to prevent the formation of toxic oxygen radicals. The size and composition of this xanthophyll pool has been correlated with the photosynthetic capacity of leaves of species occupying different light environments in tropical forest (Königer et al. 1995), with species adapted to growth in high-light conditions found to possess larger, more dynamic xanthophyll pools (Demmig-Adams et al. 1995). A relatively large xanthophyll pool allows plants

to rapidly respond to increasing light intensity (Demmig-Adams et al. 1995), while species adapted to low-light environments have no need for efficient energy dissipation. This is consistent with the different saturating characteristics of q_n shown in Fig. 3b, the rapid saturation of q_n in *R. comptonii* illustrating a high sensitivity to low – medium light intensity, but a low capacity for responding to light intensities over 1000 μmol photons $\cdot m^{-2} \cdot s^{-1}$. In contrast, q_n in *A. acuminatus* was able to respond to increasing light intensity even at values of PPFD greater than full sun.

Evolutionary implications of increased shoot width

The relationship between shoot width and light response illustrated here (Fig. 6) has implications for the evolution of conifers in terms of their competitive interaction with angiosperms. One of the explanations used to account for the near complete replacement of conifers by angiosperms is that conifers only have slow rates of foliage production, especially during establishment, making them unable to compete for light with fast-growing broad-leaved angiosperms, particularly in more productive temperate-tropical forest (Bond 1989). The production of bilaterally compressed short shoots resembling broadleaves in several genera of the Podocarpaceae provides a mechanism for rapidly increasing foliar area for light capture, and the presence of these genera in temperate and tropical broad-leaf forest suggests that this morphological adaptation has contributed to the success of these genera.

The palaeohistory of conifers in the southern hemisphere suggests that the evolution of a broad, flat photosynthetic unit in the Podocarpaceae did not occur until diverse, broad-leaved angiosperm forests with a closed canopy had developed. In Australia, this had begun by the Late Palaeocene, where a macroflora from south-eastern Australia contains diverse broad-leaved angiosperms and conifers that include *Acmopyle* (Taylor et al. 1990; Hill and Carpenter 1991). Complex rainforest associations on the west coast of Tasmania in the Early Eocene contain *Dacrycarpus* and broad-leaved *Podocarpus*, and other extant and extinct genera of podocarps with similar adaptations are present by the Middle Eocene across southern Australia (Hill and Pole 1992; Hill 1995, unpublished data). However, Cretaceous forests in southern Australia and adjacent Antarctica were apparently more open, in response to low sun angles at the prevailing very high latitudes (Truswell 1991; Hill and Scriven 1995), and there is no evidence of podocarps with a broad photosynthetic unit.

It has been shown here that increasing shoot width is associated with a photosynthetic preference for lower light intensity, expressed as a low $PPFD_{sat}$ and a low maximum photosynthetic capacity. This, in combination with ecological and palaeobotanical evidence, suggests that the production of broad short shoots in the Podocarpaceae is an adaptation to low light intensity.

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References

Bilger W, Schreiber U, Brock M (1995) Determination of the quantum efficiency of photosystem II and of non-photochemical quenching of chlorophyll fluorescence in the field. Oecologia 102: 425–432

Björkman O, Demmig B (1987) Photon yield of O_2 evolution and chlorophyll fluorescence characteristics at 77 K among vascular plants of diverse origins. Planta 170: 489–504

Bond WJ (1989) The tortoise and the hare: ecology of angiosperm dominance and gymnosperm persistence. Biol J Linn Soc 36: 227–249

Bordman N (1977) Comparative photosynthesis of sun and shade plants. Annu Rev Plant Physiol 28: 355–377

Brodribb T (1996) Dynamics of changing intercellular CO_2 concentration during drought and determination of minimum functional c_i. Plant Physiol 111: 179–185

Carter GA, Smith WK (1985) Influence of shoot structure on light interception and photosynthesis in conifers. Plant Physiol 79: 1038–1043

Demmig-Adams B, Adams W, Logan B, Verhoeven A (1995) Xanthophyll cycle dependant energy dissipation and flexible photosystem II efficiency in plants acclimated to light stress. Aust J Plant Physiol 22: 249–260

Edwards GE, Baker NR (1993) Can assimilation in maize leaves be predicted accurately from chlorophyll fluorescence analysis? Photosynth Res 37: 89–102

Enright NJ, Hill RS (eds) (1995) Ecology of the southern conifers. Melbourne University Press, Melbourne

Farquhar GD, Caemmerer S von, Berry JA (1980) A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. Planta 149: 78–90

Genty B, Briantais J, Baker NR (1989) The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. Biochim Biophys Acta 990: 87–92

Hill RS (1995) Conifer origin, evolution and diversification in the southern hemisphere. In: Enright NJ, Hill RS (eds) Ecology of the southern conifers. Melbourne University Press, Melbourne pp 10–29

Hill RS, Carpenter RJ (1991) Evolution of *Acmopyle* and *Dacrycarpus* (Podocarpaceae) foliage as inferred from macrofossils in south-eastern Australia. Aust Sys Bot 4: 449–479

Hill RS, Pole MS (1992) Leaf and shoot morphology of extant *Afrocarpus*, *Nageia* and *Retrophyllum* (Podocarpaceae) species, and species with similar leaf arrangement from Tertiary sediments in Australasia. Aust Syst Bot 5: 337–358

Hill RS, Scriven LJ (1995) The angiosperm-dominated woody vegetation of Antarctica: a review. Rev of Palaeobot Palynol 86: 175–198

Leverenz JW (1995) Shade shoot structure of conifers and the photosynthetic response to light at two CO_2 partial pressures. Funct Ecol 9: 413–421

Loreto F, Domenico T, Di Marco G (1995) On the relationship between electron transport rate and photosynthesis in leaves of the C_4 plant *Sorghum bicolor* exposed to water stress, temperature changes and carbon metabolism inhibition. Aust J Plant Physiol 22: 885–892

Königer M, Harris GC, Virgo A, Winter K (1995) Xanthophyll-cycle pigments and photosynthetic capacity in tropical forest species: a comparative field study on canopy gap and understorey plants. Oecologia 104: 280–290

McKiernan M, Baker NR (1992) A method for the rapid monitoring of photosynthetic shade adaptation in leaves. Funct Ecol 6: 405–410

Schreiber U, Bilger W (1992) Progress in chlorophyll fluorescence research: major developments during the past years in retrospect. Prog Bot 54: 151–173

Schreiber U, Schlewa U, Bilger W (1986) Continuous recording of photochemical and non–photochemical chlorophyll fluorescence quenching with a new type of modulation fluorometer. Photosynth Res 10: 51–62

Schreiber U, Bilger W, Neubauer C (1994) Chlorophyll fluorescence as a non-intrusive indicator for rapid assessment of in vivo photosynthesis. In: Schulze ED, Caldwell MM (eds) Ecophysiology of photosynthesis. Springer, Berlin Heidelberg New york, pp 49–70

Sorrensen-Cothern KA, Ford ED, Sprugel DG (1993) A model of competition incorporating plasticity through modular foliage and crown development. Ecol Monogr 63: 277–304

Taylor G, Truswell EM, McQueen KG, Brown MC (1990) Early Tertiary palaeogeography, landform evolution and palaeoclimates of the Southern Monaro, NSW, Australia. Palaeogeogr Palaeoclimatol Palaeoecol 78: 109–134

Truswell EM (1991) Antarctica: a history of terrestrial vegetation. In: Tingey RJ (ed) The geology of Antarctica. Clarendon, Oxford. pp 499–537

Yun JI, Taylor SE (1986) Adaptive implications of leaf thickness for sun- and shade-grown *Abutilon theophrasti*. Ecology 67: 1314–1318