

Ecophysiology of the Soft Tree Fern, *Dicksonia antarctica* Labill

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Abstract Environmental constraints on gas exchange, stomatal conductance and water relations were investigated in the Soft Tree Fern, *Dicksonia antarctica*, at sites across its natural distribution and in the glasshouse. *Dicksonia antarctica* exhibited strong stomatal response down to a vapour pressure deficit (VPD) of 0.25 kPa, an unusual characteristic when compared with other ground fern species. Net photosynthetic rate may be a response of the microenvironment prevalent during frond development, reflecting acclimatory capacity. Both these ecophysiological characteristics are consistent with the ecological niche of *D. antarctica*, a long-lived, fire-resistant species that, during its lifetime, may be exposed to: (i) a humid environment beneath a rainforest canopy; and (ii) an exposed environment following wildfire. Maximum net photosynthesis and quantum yield of photosynthesis correlated strongly with VPD and the maximum net photosynthetic rate of $10.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ was the highest yet recorded for a fern. These observations are consistent with the relatively low growth typically observed in *D. antarctica* on sunny, exposed sites and vice versa on cool, humid sites exposed to sunflecks. Favourable water relations maintained under conditions of moderate VPD (2.03 kPa) were probably due to stomatal control. However, inadequate rainfall or high VPD (4.98 kPa) caused water stress, recovery of which was limited by slow water transport through fronds. These observations are consistent with the limitation of *D. antarctica* distribution to sites sheltered from hot winds and with reliable water supply. The funnel-shaped rosette of fronds of *D. antarctica* may harvest rainfall and make it accessible to aerial roots situated at the base of fronds. This process may maintain favourable water relations independently of a subterranean root system. This proposed strategy of water acquisition is unique for a fern species and may eliminate a need for soil moisture competition with surrounding plant species. It is suggested that the ecophysiological characteristics observed in *D. antarctica* in this study may contribute to the ecological niche it occupies, which is characterized by a variable environment.

Key words: photosynthesis, stomatal conductance, vapour pressure deficit, water relations.

INTRODUCTION

Pteridophytes (ferns) inhabit a wide range of terrestrial environments from deserts (Nobel 1978), to shaded forest understoreys (Bannister & Wildish 1982) and rainforest canopies (Hew & Wong 1974; Hietz & Briones 1998). Their ecophysiological characteristics therefore vary widely. Some ferns are tolerant of dehydration. For example, *Polypodium polypoides* is not damaged following loss of 97% of its water content and resurrects its photosynthetic activity 30 min after rehydration (Stuart 1968). Ferns that avoid dehy-

dration tend to have high water storage capacity in fronds and/or long, succulent creeping rhizomes with fronds spaced widely along the rhizome, a high cuticular resistance to transpiration, and stomata sensitive to water loss (Hietz & Briones 1998). Ferns that have a low tolerance to dehydration have high rates of uncontrolled water loss and little or no water storage in leaves or rhizomes, so this restricts them to moist, humid environments (Hietz & Briones 1998).

Ferns inhabiting moist, shaded environments tend to exhibit little or no stomatal response to increasing vapour pressure deficit (VPD) (Nobel 1978; Hollinger 1987; Hietz & Briones 1998) and low stomatal conductance at low VPD (Nobel *et al.* 1984). By contrast, in environments characterized by periods of high incident photosynthetic photon flux density (PPFD > $400 \mu\text{mol m}^{-2} \text{s}^{-1}$) and moderate VPD, ferns may exhibit strong stomatal control of water loss, with high stomatal conductance under moderate evaporative demand and pronounced stomatal closure in response to high VPD (Nobel *et al.* 1984; Hietz & Briones 1998).

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The relationships between the water potential of ferns and factors such as soil water status, stomatal conductance (Nobel 1978; Hollinger 1987), relative water content (RWC) of the foliage and VPD (Tinklin & Bowling 1969; Roberts *et al.* 1984) are highly variable among species (Roberts *et al.* 1980, 1984). This variation is accentuated by differences in the degree of tolerance or avoidance of water stress, between the efficiency of the vascular systems (e.g. Walter & Stadelmann 1974; Nobel 1978) and in gradients of water potential that develop within the plant (Nobel 1978). Direct absorption of water via fronds can restore water potential during the recovery of desiccation-tolerant pteridophytes (Eickmeier 1979; Schwab *et al.* 1989) and, for some species, is essential for recovery (Stuart 1968). However, water absorption for most ferns is thought to occur principally through a subterranean root system or rhizomatous mats in epiphytic ferns (Andrade & Nobel 1997; Hietz & Briones 1998).

Although the ecophysiology of epiphytic ferns (Hietz & Briones 1998) and some ground fern species is reasonably well known (Nobel 1978; Hollinger 1987), few studies (Bannister & Wildish 1982; Nobel *et al.* 1984) have addressed the special case of tree ferns. The Soft Tree Fern, *Dicksonia antarctica*, is a characteristic understorey species of wet sclerophyll and rainforest communities on moist, fertile soils in south-eastern Australia and Tasmania within an altitudinal range from sea level to 1000 m a.s.l. (Neyland 1986). Growth in the stem height of *D. antarctica* may range from 0.5 to 8.8 cm per year (Mueck *et al.* 1996). Maximum height can reach 5–6 m with an apical rosette of fronds 2–6 m in diameter, and an individual may live for

500–1000 years (Mueck *et al.* 1996; Unwin & Hunt 1996). During its relatively long (compared with co-occurring tree species) lifetime, *D. antarctica* may be exposed to a wide range of light regimes, from shaded beneath a dense tree canopy, to high light intensities in a forest gap. The trunk and growing apex of *D. antarctica* are very resistant to damage by fire and the apical rosette of fronds rapidly regenerates after intense wildfires (Hickey 1994). During the period of regeneration of woody species following fire, *D. antarctica* may experience prolonged periods of exposure to high light intensities and dry atmospheric conditions.

This study aimed to identify the environmental constraints affecting gas exchange, stomatal conductance and water relations in the Soft Tree Fern, *D. antarctica*. In addition, the study describes how ecophysiological attributes may contribute to the success of *D. antarctica* in an environment highly variable in PPFD, water supply and evapotranspirational demand. Six hypotheses are proposed and tested: (i) that the stomatal conductance of *D. antarctica* will exhibit a strong response to VPD; (ii) that increased VPD will negatively affect maximum net photosynthesis and quantum yield of photosynthesis; (iii) that decreased stomatal conductance will limit photosynthesis; (iv) that photosynthetic rates may be dependent on acclimation to microenvironmental effects during frond development; (v) that water potential and RWC exhibit elasticity in response to moisture availability and VPD changes; and (vi) that morphology of fronds, aerial stem and adventitious roots contribute to the maintenance of favourable water relations in *D. antarctica*.

METHODS

Stomatal conductance

Variation within a frond

Within-frond variation in stomatal conductance was assessed at Liffey Valley (35 km south of Launceston, Tasmania: 146°56'E, 41°40'S). Temperature and humidity were measured by an Assman psychrometer (Lambrecht Instruments, Göttingen, Germany) and incident PPFD by a quantum sensor mounted on a portable steady-state porometer (Licor 1600c, Licor, Nebraska, USA). Conductance was measured under conditions of low temperature (8–14°C), low VPD (0.21–0.63 kPa) and low light intensity (100–300 $\mu\text{mol m}^{-2} \text{s}^{-1}$), on a frond of three randomly selected, 1–2 m-tall sporophytes on 28 July 1993. Measurements were made at each of 12 primary pinna positions (the primary branches within a frond; see Fig. 1) evenly spaced down the length of a

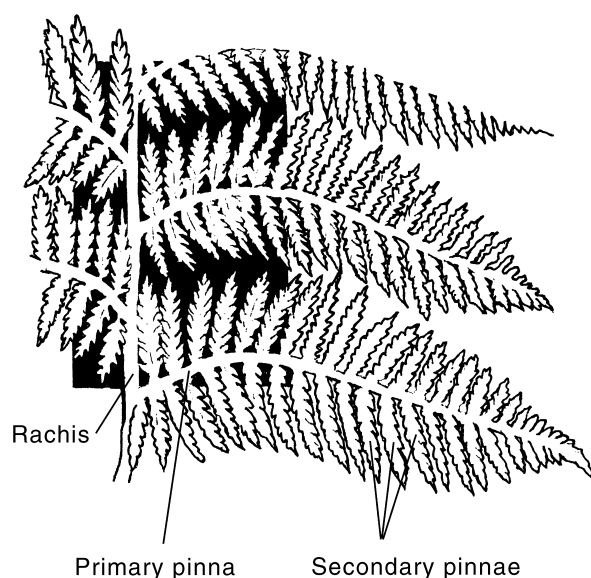


Fig. 1. Frond of *Dicksonia antarctica* indicating the primary pinnae, secondary pinnae, and rachis.

single 1.2-m frond on each sporophyte. At each of the 12 pinnae positions, four records of stomatal conductance were made on six occasions at approximately 1-h intervals between 10.00 and 16.00 hours Australian Eastern Standard Time (AEST). Measurements were restricted to the abaxial surface as fronds were hypostomatous.

Light, temperature and vapour pressure deficit

The response of stomatal conductance of *D. antarctica* to light, temperature and VPD was studied at two sites. Measurements were made on the same sporophytes as those used in the assessment of variation within a frond, under the low ambient PPFD ($100\text{--}300\ \mu\text{mol m}^{-2}\text{ s}^{-1}$) conditions at Liffey (a wet sclerophyll forest understorey site under a dense tree canopy with no exposure to sunflecks – defined as a shady site) on 13 and 14 August, 1993. In the grounds of the University of Tasmania (Hobart, Tasmania: $147^{\circ}15'\text{E}$, $42^{\circ}50'\text{S}$), where *D. antarctica* was present in the understorey of a wet gully dominated by *Eucalyptus obliqua* and *Eucalyptus globulus*, measurements were made on 28 July and 6 August, 1993. In the shade of the tree canopies, PPFD at the University was comparable to that at Liffey (approximately $200\ \mu\text{mol m}^{-2}\text{ s}^{-1}$) but during sunflecks (that occurred often through the sparse, relative to Liffey, canopy) PPFD rose to $1000\ \mu\text{mol m}^{-2}\text{ s}^{-1}$ (this site was defined as sunny). Stomatal conductance was measured at approximately 1.5-h intervals between 10.00 and 16.00 hours AEST on each day using the porometer. At both sites the VPD was approximately 0.2 kPa at 10.00 hours (9°C and 80% relative humidity RH), and approximately 0.7 kPa at 14.00 hours (14°C and 55% RH).

To take account of the variation within a frond at each time of measurement, 10–12 records were made at different primary pinna positions along each frond over a 5-min period. Although PPFD changed during this 5-min period, VPD and temperature only varied slightly (by a maximum of 0.04 kPa and 0.5°C). To avoid the problem of multiple observations (of VPD) for each sample point (Draper & Smith 1981; White & Kile 1994), statistical analysis of temperature and humidity data was conducted using mean frond stomatal conductance values (mean of the 10–12 records made at each measurement). All data were used in analysis of the relationship between stomatal conductance and PPFD.

Photosynthesis

Photosynthetic photon flux density

Photosynthesis was measured using a portable open gas analysis system (ADC LCA-2; Analytical Develop-

ment Company, Hoddesdon, England) in conjunction with a Parkinson PLC-B leaf chamber. Measurements were made between 10.00 and 16.00 hours on 4 days (29 July, 5 August, 20 September and 21 September 1993) using the same three sporophytes used in the stomatal conductance investigation at Liffey. Measurement was conducted on 4 clear-sky days of similar temperature and humidity. Incident PPFD ($5\text{--}300\ \mu\text{mol m}^{-2}\text{ s}^{-1}$) and VPD (0.21–0.75 kPa) were low.

At the University, on 12–13 July 1993, measurements of photosynthesis were made on three sporophytes that had been transplanted into pots three months earlier and were acclimated to glasshouse conditions. Levels of natural irradiance incident at the frond surface were similar to those at Liffey. Photosynthetic light response curves were generated using a lamp comprising four 150-W Wotan xenon quartz globes attached to the Parkinson PLC-B leaf chamber. Incident photon flux densities less than $750\ \mu\text{mol m}^{-2}\text{ s}^{-1}$ were obtained using neutral density filters. Photon flux densities (PPFD) greater than $750\ \mu\text{mol m}^{-2}\text{ s}^{-1}$ were obtained by increasing power to the lamp. The VPD were low, ranging from 0.34 to 0.78 kPa.

Vapour pressure deficit

At Kingston (12 km south of Hobart, Tasmania: $147^{\circ}20'\text{E}$, $49^{\circ}59'\text{S}$), a single *D. antarctica* sporophyte growing in a high-light environment was studied to determine the photosynthetic light response to VPD. Eight light response curves were obtained under ambient external VPD from 0.9 to 1.5 kPa over 6 days (22 March, and 13, 14, 26, 27 and 28 April 1997). All measurements were made on a single primary pinna. Resampling of a single primary pinna removed any variation attributable to differences between individual pinnae, fronds and positions along a frond. Light response curves were generated as described previously. For each light response curve, four to eight measurements were conducted at each PPFD. In addition to the light response curves, maximum rates of photosynthesis (mean of four to eight measurements) were recorded on the same primary pinna at moderate VPD (0.55–0.9 kPa).

Water relations

At the University, six sporophytes were transplanted into pots and transferred to a glasshouse for 3 months from the beginning of April 1993. Three sporophytes were allocated to each of two microclimate treatments: (i) low VPD = 0.21 kPa, under ambient glasshouse conditions (PPFD $100\ \mu\text{mol m}^{-2}\text{ s}^{-1}$, relative humidity 85% and temperature 12°C); and (ii) moderate

VPD = 2.03 kPa, created using a fan heater and a metal halide lamp (PPFD 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, relative humidity 35% and temperature 25°C). Frond RWC and water potentials were determined on distal portions of pinnae each hour for the 3 h following VPD treatment. The RWC were determined on five replicate secondary pinnae (the secondary branchlets within a branch; see Fig. 1) for each sporophyte each hour and calculated following Turner (1981) using:

$$\text{RWC} = (W_f - W_d)/(W_t - W_d) \times 100$$

where W_f is the fresh weight at the time of sampling; W_t is the turgid weight, obtained after pinnae had been placed at room temperature in a covered Petri dish containing distilled water and illuminated at a PPFD equivalent to the light compensation point for 24 h and blotted dry; and W_d is the dry weight obtained after oven drying for 24 h at 80°C. Water potentials were measured using a pressure chamber (PMS Instrument Co., Corvallis, Oregon; Scholander *et al.* 1965).

Fronds from six *D. antarctica* sporophytes growing in a wet gulley at the University (described earlier) were assessed on 5 August 1997. Fourteen fronds were cut, then recut under water to prevent air entering the xylem. Fronds varied in length from 1.8 to 2.9 m. The fronds were taken to the laboratory and divided randomly into two treatments: (i) four fronds into a low VPD treatment (VPD = 0.59 kPa; ambient laboratory conditions of 15°C and 65% RH); and (ii) 10 fronds into a high VPD treatment (VPD = 4.98 kPa; 36°C and 15% RH in a drying room). The PPFD incident at the frond was approximately 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in both treatments.

At the start (10.00 hours AEST) and end (17.30 hours AEST) of the experiment, measurements of water potential and RWC were made as previously described on two fronds in the low VPD treatment. At approximately 11.00, 12.00, 13.00, 14.30 and 17.30 hours AEST, measurements of water potential and RWC were made on two fronds in the high VPD treatment. Each was measured on four primary pinnae spaced evenly along the frond. The RWC was measured at the closest primary pinna on the opposite side of the frond to that measured for water potentials. For each of the chosen primary pinnae, subsamples were taken from the base, middle and apex of the pinna for determination of RWC. In addition, at each of the positions where pinnae were sampled, two segments were cut from the rachis of the frond for determination of RWC.

Water acquisition

Eight sporophytes were transplanted into pots in April 1993 and transferred into the University glasshouse. On July 30, sporophytes were randomly divided into two treatments, a control in which plants had intact

stems, and a treatment in which the stems were severed near the ground and suspended above ground in their natural orientation, using wires attached to the roof of the glasshouse. All sporophytes were watered daily using overhead sprinklers so the stem apex and fronds received water. The mean maximum and minimum temperatures in the glasshouse were 15 and 7°C, respectively. The four potted plants that remained intact were also watered daily at the base to keep the soil moist. The number of new fronds produced, and the time taken for fronds to expand fully was recorded for all plants.

Statistical analysis

Analysis of variance with repeated measures was conducted using the general linear model (GLM) procedure in SAS (1989) to determine the effect of pinna position on stomatal conductance. Boundary line analysis (Jarvis 1976) was used to investigate the relationships of stomatal conductance and net photosynthesis with PPFD. The GLM procedure in SAS was used to investigate the relationship of stomatal conductance with temperature.

Maximum net photosynthesis and quantum yield of photosynthesis were estimated by a non-rectangular hyperbolic function that was used to describe light response curves:

$$Y = 2\alpha X A_x / (\alpha X + A_x) + \sqrt{(\alpha X + A_x)^2 - 4\theta X A_x}$$

where α approximates the efficiency of photosynthesis (quantum yield); A_x gives the light-saturated value of A (maximum net photosynthesis); θ describes the slope of the curve; and Y and X are the assimilation rate (A) and PPFD, respectively (Long & Hällgren 1993). The relationships of maximum net photosynthesis and quantum yield of photosynthesis with VPD were analysed using the GLM procedure in SAS.

Analysis of variance (ANOVA) with repeated measures was conducted using the GLM procedure in SAS to determine the effect of pinna position and time of measurement on the RWC of pinnae and rachis and on the water potential of pinnae. ANOVA was used to compare frond growth between treatments at 4, 8 and 12 weeks.

RESULTS

Stomatal conductance

Vapour pressure deficit, temperature and photosynthetic photon flux density

Variation of stomatal conductance along individual fronds was found to be significant ($P < 0.001$). Therefore the response of stomatal conductance to PPFD,

VPD and temperature was averaged from measurements taken at evenly spaced positions along individual fronds.

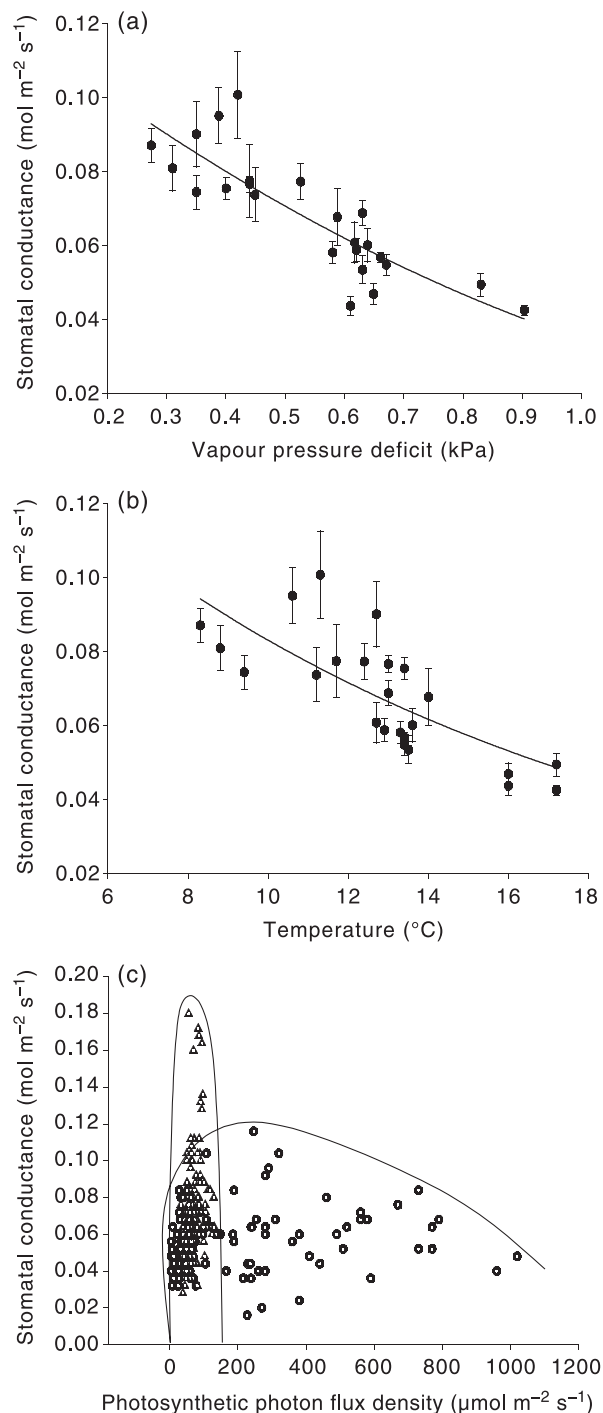


Fig. 2. Relationships of stomatal conductance with (a) vapour pressure deficit, (b) air temperature and (c) photosynthetic photon flux density, for *Dicksonia antarctica* growing in natural stands in the field at Liffey gully and at the University of Tasmania gully in July and August 1993. For (a) and (b), each point is the mean of 10–12 replicate measurements made at each PPFD. For (c) all data points obtained are depicted, (Δ), Liffey; (○), University.

A significant negative curvi-linear relationship existed between stomatal conductance and VPD at low VPD between 0.2 and 0.9 kPa ($Y = 0.134 e^{-1.307x}$, $r^2 = 0.74$, $P < 0.001$; Fig. 2a). Extrapolation of this relationship indicated that stomatal closure might occur when VPD was approximately 1.8 kPa.

A non-significant curvi-linear relationship existed between stomatal conductance and air temperature ($Y = 0.197 e^{-0.085x}$, $r^2 = 0.64$, $P < 0.08$; Fig. 2b).

At Liffey, the boundary between stomatal conductance and PPFD increased steeply to a maximum stomatal conductance of approximately 0.18 mol m⁻² s⁻¹ at a PPFD of 50 μmol m⁻² s⁻¹ and then declined rapidly to around 0.05 mol m⁻² s⁻¹ at PPFDs nearing 200 μmol m⁻² s⁻¹ (Fig. 2c). In contrast, ferns at the University exhibited a similar steep increase in stomatal conductance but to a lower maximum of approximately 0.12 mol m⁻² s⁻¹ at PPFD of approximately 250 μmol m⁻² s⁻¹. At PPFD greater than 250 μmol m⁻² s⁻¹, stomatal conductance steadily declined to approximately 0.05 mol m⁻² s⁻¹ at 1000 μmol m⁻² s⁻¹ (Fig. 2c).

Photosynthesis

Vapour pressure deficit

Maximum net photosynthesis of *D. antarctica* decreased linearly with increasing VPD ($r^2 = 0.99$, $P < 0.0001$; Fig. 3). Extrapolation of the observed relationship indicated that net photosynthesis would approach zero at a VPD of approximately 1.8 kPa. Similarly, quantum yield of photosynthesis linearly decreased with increasing VPD ($r^2 = 0.87$, $P < 0.0001$; Fig. 3).

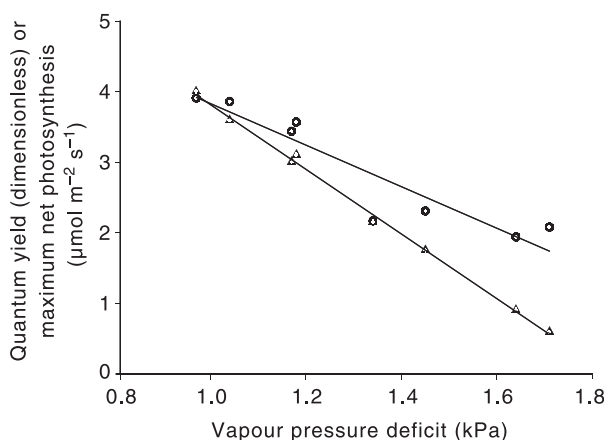


Fig. 3. Relationship of maximum net photosynthesis and quantum yield of photosynthesis ($\times 10^{-2}$) in response to vapour pressure deficit (VPD) of *Dicksonia antarctica* situated on a sunny, exposed site at Kingston, Tasmania. (Δ), Maximum net photosynthesis; (○), quantum yield of photosynthesis.

Photosynthetic photon flux density

A boundary line relationship suggested that 90% light saturation of net photosynthesis occurred at $280 \mu\text{mol m}^{-2} \text{s}^{-1}$ in *D. antarctica* at the University (Fig. 4). The maximum photosynthetic rate of $10.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ was reached at $690 \mu\text{mol m}^{-2} \text{s}^{-1}$. Values of photosynthesis greater than $6 \mu\text{mol m}^{-2} \text{s}^{-1}$ in this relationship invariably coincided with conditions of

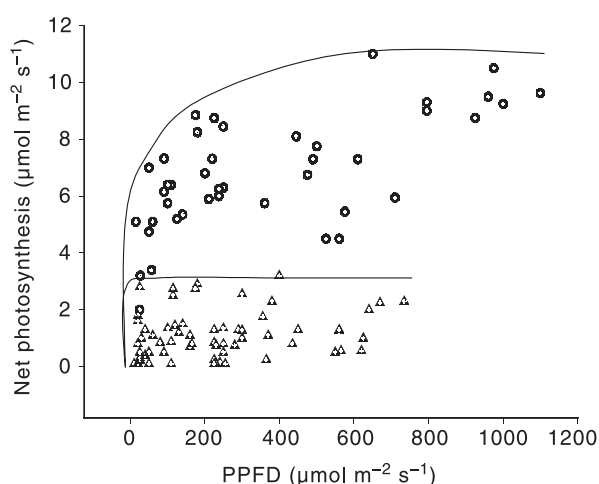


Fig. 4. Relationship between net photosynthesis and photosynthetic photon flux density for *Dicksonia antarctica* acclimated to an environment of high natural illumination in a glasshouse at (○) the University of Tasmania and to an environment of low natural illumination at (△) Liffey gully. Data are pooled for 2 and 4 days of measurement at the University glasshouse and Liffey gully, respectively. Boundary lines are shown (after Jarvis 1976).

low VPD (<0.6 kPa; relative humidity above 77% and temperature $15\text{--}22^\circ\text{C}$). A different boundary relationship existed at a similar VPD for *D. antarctica* sporophytes at Liffey. The maximum photosynthetic rate of $3.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ was significantly less than that obtained at the University (Fig. 4).

Water relations

In glasshouse studies on intact, well-watered sporophytes exposed for 3 h to moderate VPD (2.03 kPa), water potential and RWC remained close to 0.0 MPa and 100%, respectively. However, when fronds were exposed to high VPD (4.98 kPa), a significant decline in water status was observed (Tables 1,2). Exposure of fronds for 6.5 h at a VPD of 4.98 kPa caused RWC of pinnae to fall significantly. By contrast the RWC of the rachis declined less than in pinnae and at the end of the dehydration period, the base of the rachis (86%) had a greater RWC than the apex (41%). Exposure to 7.5 h at low VPD (0.59 kPa) had a similar effect on RWC as 1 h at VPD = 4.98 kPa (Table 1).

Initial water potential was -1.8 MPa in *D. antarctica* sporophytes in the gully at the University (Table 2). Gradients in water potential of approximately 0.3 MPa m^{-1} existed between the apex and the base of the frond. This was maintained for the duration of the study at low VPD (0.59 kPa). After 2 h at high VPD (4.98 MPa), the water potential of all pinnae had declined significantly and smaller pinnae at the base and apex of the frond had lower water potentials than larger pinnae at other positions.

Table 1. Mean percentage relative water content (\pm SE) of pinnae and rachis taken from fronds of *Dicksonia antarctica* exposed to two desiccation treatments, low vapour pressure deficit (VPD) (0.59 kPa) and high VPD (4.98 kPa)

Time (h)	Treatment	Tissue	Apex	Position on frond		
				1/3	2/3	Base
0.0	Low	Pinna	98 ± 1	98 ± 1	98 ± 1	96 ± 2
		Rachis	100 ± 0	98 ± 1	97 ± 0	97 ± 2
1.0	High	Pinna	81 ± 2	83 ± 2	79 ± 2	71 ± 2
		Rachis	84 ± 4	90 ± 1	91 ± 1	94 ± 0
2.0	High	Pinna	70 ± 0	66 ± 3	59 ± 4	52 ± 4
		Rachis	80 ± 2	87 ± 3	90 ± 3	92 ± 2
3.0	High	Pinna	43 ± 5	52 ± 8	43 ± 10	37 ± 4
		Rachis	54 ± 10	83 ± 2	90 ± 0	93 ± 2
4.5	High	Pinna	38 ± 1	46 ± 5	45 ± 5	37 ± 3
		Rachis	44 ± 6	78 ± 4	85 ± 2	91 ± 1
6.5	High	Pinna	26 ± 3	37 ± 6	25 ± 3	13 ± 2
		Rachis	41 ± 2	74 ± 2	82 ± 0	86 ± 2
7.5	Low	Pinna	80 ± 5	87 ± 1	82 ± 2	73 ± 3
		Rachis	87 ± 7	91 ± 1	89 ± 1	94 ± 2

Four segments of pinnae and rachis were sampled from positions evenly distributed along two fronds at times 0, 1, 2, 3, 4.5, 6.5 and 7.5 h.

Water acquisition

There was no significant difference in the number of fronds produced, or in the average time taken for new fronds to fully unfurl, between sporophytes that were intact and growing in pots and those that had been cut just above ground level and suspended from the roof of the glasshouse.

DISCUSSION

The results of this study indicate: (i) that *Dicksonia antarctica* exhibits a strong response to VPD; (ii) that increasing VPD negatively affects maximum net photosynthesis and quantum yield of photosynthesis; (iii) that low stomatal conductance limits photosynthesis; (iv) that photosynthetic capacity may depend on climatic conditions during frond development; (v) that water relations become unfavourable at a VPD of 4.98 kPa; and (vi) that the morphology of fronds may provide moisture and maintain water relations in *D. antarctica* from rainfall. The effects of the various environmental variables studied on the photosynthesis and the water relations of *D. antarctica* also indicate a capacity of the species to inhabit an ecological niche characterized by a wide range of light, moisture and temperature conditions.

Stomatal conductance of *D. antarctica* was highly responsive to VPD, a curvi-linear decrease occurring at VPD > 0.25 kPa. This response is atypical of ground ferns and herbaceous understorey plants, which generally exhibit little or no stomatal response to VPD (Nobel 1978; Hollinger 1987; Hietz & Briones 1998; Franks & Farquhar 1999). For example, the ground ferns *Osmunda regalis* and *Pteridium esculentum* exposed to VPD of 1.0 and 2.0 kPa at 30°C exhibited declines in stomatal conductance from 0.28 to 0.19 and 0.31–0.22 mol m⁻² s⁻¹, respectively (Franks & Farquhar 1999). The strong stomatal response to VPD exhibited by *D. antarctica* in this study is more consistent with a plant adapted to exposed, sunny environments (Nobel *et al.* 1984; Hollinger 1987; Hietz &

Briones 1998). The relationships of temperature (that was not significant) and PPFD with stomatal conductance observed here may be due to an effect on VPD, given the sensitivity of *D. antarctica* to VPD. Weaker relationships of temperature and PPFD with stomatal conductance are consistent with this. Although the response of stomatal conductance to VPD reported here is more typical of an overstorey than an understorey fern (Hollinger 1987; Franks & Farquhar 1999), this is entirely consistent with the ecological niche of *D. antarctica*. Following wildfire or when forest gaps are formed, *D. antarctica* may be exposed to high VPD, temperatures and PPFD for prolonged periods before successional processes modify the microclimate.

The decrease in maximum net photosynthesis and quantum efficiency with VPD may be because of stomatal closure, given the strong response of stomatal conductance to VPD. The form of the relationship was consistent with cessation of net photosynthesis at approximately 1.8 kPa, the estimated value of VPD at which stomata would close. A low photosynthetic efficiency and low photosynthetic rate at high VPD may contribute to the low growth rates of *D. antarctica* in sunny exposed conditions relative to that of individuals in humid understoreys (Hickey 1994). Conversely, the high photosynthetic rates observed in the glasshouse at high PPFD and low VPD (analogous to conditions in the understorey during periods of sunflecks; Pearcy 1988) demonstrate a high potential capacity for carbon assimilation and growth of *D. antarctica* in humid understoreys.

Net photosynthesis of fronds developed under a high-light environment was significantly greater at PPFD > 50 µmol m⁻² s⁻¹ compared with that developed under a low light environment. This observation is typical of sun versus shade leaves (Demmig-Adams & Adams 1992) and indicates a strong capacity of the photosynthetic systems of *D. antarctica* to acclimate to the prevailing environmental conditions. Acclimation of tree ferns to light environment has been reported previously (Bannister & Wildish 1982).

The maximum measure of stomatal conductance of 0.19 mol m⁻² s⁻¹ (at a VPD of 0.3 kPa, 80% relative

Table 2. Mean water potential (MPa; ± SE) were measured on pinnae excised from fronds of *Dicksonia antarctica* exposed to two treatments, low vapour pressure deficit (VPD) (0.59 kPa) and high VPD (4.98 kPa)

Time (h)	Treatment	Apex	Position on frond		
			1/3	2/3	Base
0.0	Low	-1.8 ± 0.1	-1.6 ± 0.1	-1.4 ± 0.1	-1.2 ± 0.1
1.0	High	-2.4 ± 0.2	-2.6 ± 0.2	-2.5 ± 0.3	-1.3 ± 0.1
2.0	High	-3.0 ± 0.2	-2.7 ± 0.2	-2.8 ± 0.1	-3.1 ± 0.1
4.5	High	-4.0 ± 0.0	-2.6 ± 0.5	-2.5 ± 0.0	-4.0 ± 0.0
7.5	Low	-1.9 ± 0.1	-2.0 ± 0.1	-1.7 ± 0.1	-1.3 ± 0.1

Four segments of pinnae and rachis were sampled from positions evenly distributed along two fronds at times 0, 1, 2, 3, 4.5, 6.5 and 7.5 h.

humidity) was almost double that reported for the same species at a VPD of 0.7 kPa (Nobel *et al.* 1984). Nobel *et al.* (1984) observed conductances greater than $0.06 \text{ mol m}^{-2} \text{ s}^{-1}$ at a VPD of 2.75 kPa, which, according to our results, caused stomatal closure. These apparent inconsistencies may be because of different acclimation states of the plant material used. Nobel *et al.* (1984) used fronds that had developed in a glasshouse at high PPFD (approximately $1000 \mu\text{mol m}^{-2} \text{ s}^{-1}$), high temperature (diurnal range of 20–27°C), and moderate humidity (average humidity of 55% during the day) leading to comparatively high daytime VPD (approximately 2 kPa). These conditions are markedly different from those reported here. Acclimation state is clearly important in determining the stomatal (and thus photosynthetic and potentially growth) response of *D. antarctica*.

This capacity to acclimate to microclimatic conditions may be a selective advantage for *D. antarctica* following environmental disturbance. Thus, the developing fronds can adjust their ecophysiological characteristics to match a new microenvironment. In this way, during the lifetime of a single *D. antarctica* sporophyte (to a maximum of 500–1000 years; Mueck *et al.* 1996), the rosette of fronds developed under particular environmental conditions has the capacity to function in either cool, humid and shaded conditions beneath a dense tree canopy or warm, dry and high PPFD conditions in a forest gap or following wildfire.

The maximum photosynthetic rate of $10.8 \mu\text{mol m}^{-2} \text{ s}^{-1}$ observed in *D. antarctica* acclimated to high PPFD under low VPD conditions at the University is the highest recorded for a pteridophyte. Previously, maxima of $8.3 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (*D. antarctica*; Nobel *et al.* 1984), $9.8 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (*Pteridium aquilinum*; Hollinger 1987) and $9.7 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (*Cheilanthes persica*; Grant *et al.* 1998) have been reported.

The water use of *D. antarctica* was extremely conservative, unlike that previously described for some fern species (Franks & Farquhar 1999). The water potential and RWC of fronds of *D. antarctica* remained close to 0.0 MPa and 100%, respectively, for well-watered sporophytes in the University glasshouse exposed to moderate VPD (2.03 kPa). This high water status was probably linked to the strong stomatal response to VPD observed in this study. However, sporophytes deprived of moisture developed water stress (water potential of -1.8 MPa) and had gradients in water potential of approximately 0.3 MPa m^{-1} . Water gradients remained despite exposure to low VPD (0.59 kPa) conditions for up to 7.5 h. Further, results of water potential and RWC in fronds exposed to high VPD (4.98 kPa) conditions indicated that water losses exceeded supply and that RWC of the pinnae decreased much more quickly than that of the rachis. Thus, while strong stomatal control maintains favourable water relations under con-

ditions of moderate VPD and adequate moisture availability, limited moisture availability and/or high VPD lead to water stress and water uptake into fronds occurs only slowly. Thus, although *D. antarctica* may maintain favourable water relations during short periods of high VPD, these ecophysiological characteristics may limit the distribution of the species to sites sheltered from hot, dry winds and where moisture is regularly available.

Slow water transport has been reported previously for pteridophytes (Walter & Stadelmann 1974). The primitive anatomy of their tracheid conductive elements in vascular strands causes high hydraulic resistance and low rates of water transport within the fronds. Nobel (1978) reported a 10-MPa m^{-1} water potential gradient along the stipe of *Notholaena parryi*. Great hydraulic resistance was hypothesized to occur because of the small conducting area in the xylem. Further, Nobel (1978) suggested that the production of short fronds ($<0.6 \text{ m}$) was due to a limitation to water transfer against a steep potential gradient. In contrast to *N. parryi*, *D. antarctica* has long fronds (1–3 m). Maximum stomatal conductance and rates of photosynthesis of *D. antarctica* occur only under conditions of low VPD, conditions conducive to low transpiration rates. The strong response of stomatal conductance to VPD may therefore operate to maintain favourable water relations under the variable environmental conditions prevalent across the natural distribution of *D. antarctica*.

Growth processes, particularly cellular expansion, require positive turgor (Tyree & Jarvis 1982). The water relations and the initiation and unfurling of fronds in the present experiment were unaffected by severing the stem near the ground and suspending it above the ground in its natural orientation for 8 weeks, provided water was supplied to the apex of the plant. Reports from horticulturalists (N. Pike, pers. comm., July 1993), and observations of ferns cut during the clearing of walking tracks, indicate that *D. antarctica* may survive for years in this condition. The funnel-like morphology of the rosette of fronds may facilitate the harvesting of rainfall, which collects in the stem apex and may hydrate the aerial adventitious roots present at the base of each frond. This characteristic of *D. antarctica* is unusual as water absorption occurs mainly through a subterranean root system or rhizomatous mat in epiphytic ferns (Andrade & Nobel 1997; Hietz & Briones 1998). However, desiccation-tolerant pteridophytes have been shown to rehydrate via direct absorption of water through the frond (Eickmeier 1979; Schwab *et al.* 1989). Stuart (1968) noted that *Polypodium polypodioides* will not rehydrate without direct application of moisture to the fronds. Thus, *D. antarctica* may maintain favourable water relations for growth through the interception of rainfall by fronds. This strategy may eliminate a need for soil

moisture competition with surrounding tree species. In conclusion, this study has reported a number of eco-physiological characteristics that may contribute to the success of *D. antarctica* in an environment highly variable in light, water supply and evapotranspirational demand, allowing the species to occupy a broad ecological niche.

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