Leaf orientation, light interception and stomatal conductance of *Eucalyptus globulus* ssp. *globulus* leaves

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Summary Juvenile and adult leaves of the heteroblastic species *Eucalyptus globulus* Labill. ssp. *globulus* did not show active diurnal orientation toward or away from incident radiation. Juvenile leaves of a late-maturing sapling of a Tasmanian provenance were evenly distributed in all azimuth sectors. In contrast, an early-maturing sapling of the same age from Wilsons Promontory, Victoria had a predominance of adult leaf blades facing east and west. Mid-vein and blade angles of juvenile and adult leaves were non-random with an overall vertical declination of the leaves. Both leaf types intercepted a greater irradiance during the morning than at midday. Sub-horizontal juvenile leaves intercepted 22% more irradiance than vertical adult leaves during the middle of the day. The amphistomatal and isobilateral adult leaves intercepted sunlight equally on both leaf surfaces. Stomatal conductance was variable during the period of measurement but was similar for the Tasmanian juvenile (0.4 to 0.9 cm s^{-1}) leaves and Wilsons Promontory adult (0.5 to 1.2 cm s^{-1}) leaves. Greater light interception by the sub-horizontal juvenile leaves would confer a growth advantage to saplings and regenerating canopies. Reduced light interception and leaf temperature of vertical adult *E. globulus* leaves would assist in water conservation, particularly at high solar angles.

Keywords: azimuth, leaf angle, leaf structure, Myrtaceae, ontogeny, temperature.

Introduction

Eucalyptus globulus Labill. develops strikingly different seedling, juvenile, transitional and adult leaf forms during successive life stages. Broad, thin, blue-grey, glaucous, dorsiventral and hypostomatal juvenile leaves shift to narrow, thick, green, isobilateral and amphistomatal leaves with the ontogenetic development of the tree. It has often been noted that the ontogenetic change from sessile juvenile leaves to petiolate adult leaves is accompanied by a change in leaf orientation from horizontal to vertical (Johnson 1926, Jacobs 1955, Pryor 1976, King 1997, James 1998). However, few quantitative measurements of eucalypt leaf angle and orientation have been made, especially in juvenile and adult leaves within a single species. Leaf angle and orientation control daily integrated radiation, peak irradiance and diurnal distribution of irradiance (Rundel and Gibson 1996). The direct influence of eucalypt leaf angle on light interception and the indirect influence on leaf temperature have not been studied in detail. Similarly, although stomatal conductance of juvenile or adult *Eucalyptus* leaves has often been measured, a comparison of the ontogenetic leaf forms under the same conditions has rarely been undertaken. This study determined the effects of leaf angle and orientation on light interception, leaf temperature and stomatal conductance of juvenile and adult leaves of *E. globulus* ssp. *globulus*.

Materials and methods

The orientation and angle of leaves present on single saplings of *E. globulus* ssp. *globulus* provenances from St. Marys, Tasmania (Tasmanian provenance; CSIRO Forest Research Seedlot Number 16474 CL002) and Wilsons Promontory, Victoria (Wilsons Promontory provenance; 16399 DFC 219; hereafter referred to as Wilsons Prom.) seed sources were measured. Two-year-old saplings of both provenances were grown outdoors in full sunlight, at The University of Western Australia (31°57′ S, 115°52′ E). The saplings were watered daily and supplied with controlled-release fertilizer. Although rooted in containers, the saplings had penetrated the surrounding soil. The canopy of the late-maturing Tasmanian sapling consisted only of leaves of juvenile form (James 1998). The smaller early-maturing Wilsons Prom. sapling had undergone vegetative phase change within the first year of growth, and had a canopy consisting only of the adult leaf form. Because the saplings were shaded in the afternoon by adjacent trees and midsummer cloud cover, measurements were conducted only in the morning and at midday.

Leaf orientation and inclination

Recently matured leaves from the north, east and south-facing axillary branches that were exposed to full sunlight were measured under summer conditions in early January. One hundred juvenile Tasmanian and adult Wilsons Prom. leaves were randomly sampled and marked. The azimuth to which the leaf

blade faced in its natural position was determined with a compass, with north given the value of 0°, east as 90° and south as 180°. The vertical component of leaf angle was measured as the deviation of the mid-vein from horizontal (mid-vein angle) with a clinometer (PM-5/360PC, Suunto Co., Espoo, Finland). The rotation of the leaf blade about the mid-vein (blade angle) was measured by sighting along the leaf blade with a clinometer. The angle of the branch to which leaves were attached was also determined.

Light interception

For each of the 100 marked leaves of the Tasmanian and Wilsons Prom. saplings, instantaneous measurements of incident sunlight were determined from 0730 to 0830 h and 1130 to 1230 h on a cloudless day early in January. These times corresponded to an eastern and northern solar azimuth, respectively. Photosynthetic flux density incident to the adaxial (R_{ad}) and abaxial (R_{ab}) surface of each of the marked leaves was determined with a photometer (LI-188B, Li-Cor Inc., Lincoln, NE) integrating over 1-s intervals with a quantum sensor (LI-190SB, Li-Cor Inc.) placed at the same angle as the natural position of the leaf blade. The adaxial face of the leaves was considered to be the face receiving the most sunlight at the time of measurement.

Available light was determined by facing the light sensor directly toward (R_T) and away from (R_A) the sun at 15-min intervals. The sensor was also placed horizontally upward (R_U) and downward (R_D), and vertically toward the north, south, east and west, and the observed values were expressed as a percentage of R_T. Solar azimuth and inclination above horizontal were measured at the same time. Percentage of incident radiation intercepted by a theoretical, horizontal leaf ($\%R_H$) was determined at each time period as:

$$\%R_H = \frac{(R_U + R_D)}{(R_T + R_A)}\,100.$$

The percentage of irradiance incident to each of the measured leaves ($\%R_{leaf}$) was calculated as:

$$\%R_{leaf} = \frac{(R_{ad} + R_{ab})}{(R_T + R_A)}\,100.$$

The ratio of R_{ad}/R_{ab} was calculated for each juvenile and adult leaf measured.

Categories of mutual shading were subjectively estimated for each of the 100 marked juvenile and adult leaves during the two periods of measurement. Unshaded leaves were given a value of 0; leaves with shade covering $\leq 25\%$ of the leaf blade were recorded as 1, $> 25\%$ to $\leq 50\%$ as 2, $> 50\%$ to $\leq 75\%$ as 3, and $> 75\%$ as 4.

Leaf temperature and conductance

Leaf temperature (T_{leaf}) was determined for the 100 marked juvenile and adult leaves on two cloudless midsummer days in January with an infrared thermometer (Model 3529, Tsuruga

Electric Corp., Osaka, Japan) equipped with a Raytek Raynger IP-K probe (Raytek GmbH, Berlin, Germany). Leaf temperature was determined from 0730 to 0830 h (eastern solar azimuth) and 1130 to 1230 h (northern azimuth). Air temperature was determined at 5-min intervals. The difference between leaf and air temperature (ΔT) was calculated for each leaf.

Stomatal conductance was determined with a leaf diffusion porometer (Mk3, Delta-T Devices, Cambridge, U.K.). The porometer was calibrated every 15 min to encompass changes in air temperature and humidity over the measurement period. Measurements were made on four cloudless days from 0730 to 0830 h and 1130 to 1230 h. Adaxial and abaxial stomatal conductances were determined on opposite sides of the mid-vein of the amphistomatal, adult Wilsons Prom. leaves. Only the abaxial conductance of the Tasmanian juvenile leaves was determined because of the hypostomatal distribution of stomata (James 1998). Between 20 and 30 juvenile and adult leaves under full sun conditions were randomly chosen and measured within each time period. Leaf temperature was simultaneously determined for each measured leaf and ΔT was calculated.

Statistical analysis

The mean and standard error of the mean was determined for each leaf data set with Minitab software (release 10.51, Minitab Inc., State College, PA). Confidence intervals between values were determined by Fisher's least significant difference. Statistical differences between the time of measurement and leaf form were determined by multivariate analysis.

Because solar movement was symmetrical throughout the day and each leaf blade had two opposite faces, the leaves were divided into four azimuth sectors. North (N) encompassed the azimuth angles of 338 to 23° and 158 to 203°; NE encompassed 23 to 68° and 203 to 248°; E encompassed 68 to 113° and 248 to 293°; and SE encompassed 113 to 158° and 293 to 338°. The number of leaves within each category was compared to a uniform distribution by chi-squared (χ^2) analysis. The distribution of leaves within mid-vein and blade angle increments of 10° were also compared by χ^2 analysis. Mid-vein and blade angles, mean percentage of irradiance intercepted, and the ratio of adaxial to abaxial irradiance of the juvenile and adult leaves within the azimuth categories were compared by one-way analysis of variance using Minitab.

Results

Leaf orientation and inclination

Mature juvenile and adult *E. globulus* ssp. *globulus* leaves did not actively orient toward or away from incident radiation throughout the day. Juvenile leaves of the Tasmanian sapling were uniformly distributed within the four azimuth sectors (Figure 1). Blades of adult Wilsons Prom. leaves, however, were not oriented in a uniform azimuth distribution ($x^2 = 31.4$, $P < 0.01$), because half of the leaves were within the eastern sector (Figure 2).
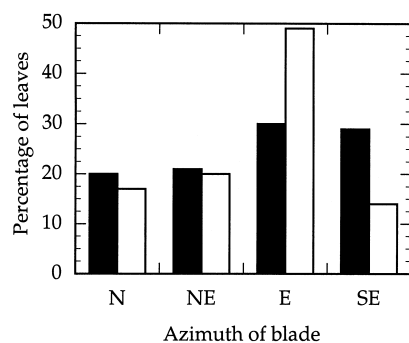
Figure 1. Frequency distribution of juvenile *Eucalyptus globulus* ssp. *globulus* leaves from a Tasmanian (solid bars) sapling, and adult leaves from a Wilsons Prom. (open bars) sapling within four leaf azimuth categories.

Juvenile leaves of the Tasmanian sapling had a lower mean mid-vein angle compared with adult Wilsons Prom. leaves (Table 1). Both mid-vein and blade angles of the juvenile leaves deviated significantly from a uniform distribution (Figure 2A; $x^2 = 17.7$, $P < 0.01$ and $x^2 = 24.4$, $P < 0.01$, respectively). Over half of the juvenile leaves had a mid-vein angle of less than 40° and a blade angle greater than 60° (Figure 2A).

Distribution of mid-vein ($x^2 = 124.3$, $P < 0.01$) and blade ($x^2 = 268.5$, $P < 0.01$) angles of adult Wilsons Prom. leaves

Table 1. Angle of deviation from horizontal of juvenile Tasmanian and adult Wilsons Prom. *Eucalyptus globulus* ssp. *globulus* leaves. Mean branch angles for the Tasmanian and Wilsons Prom. saplings have been included. Values are the means and standard error of the means for 100 leaves and 45 branches. Statistical differences between juvenile and adult leaves have been given as ** = $P < 0.01$ and ns = not significantly different at $P = 0.05$.

Angle (°)	Juvenile	Adult	Significance
Leaf blade	59.3 ± 2.4	81.5 ± 0.8	**
Leaf mid-vein	37.9 ± 2.6	73.7 ± 1.4	**
Branch angle	−4.9 ± 3.8	−8.1 ± 3.7	ns

were also non-uniformly distributed (Figure 2B). Most of the adult leaves had a mid-vein and blade declination of greater than 60°. Mid-vein and blade angles for the juvenile and adult leaves within the N, NE, E or SE azimuth categories were not statistically different. Branches of both saplings were angled slightly below horizontal (Table 1).

Light interception

Light availability increased during the morning as the sun rotated from an eastern to a northern azimuth (Table 2). The percentage of directly overhead incident irradiance also increased from morning to midday because of increasing solar inclination (Table 2).

Both leaf forms intercepted more radiation during the morning than at midday (Table 3). The percentage of available sunlight intercepted by both the juvenile and adult leaves decreased significantly from the morning to midday (Table 3). Juvenile leaves, however, intercepted a greater percentage of sunlight than adult leaves during the middle of the day. Adult
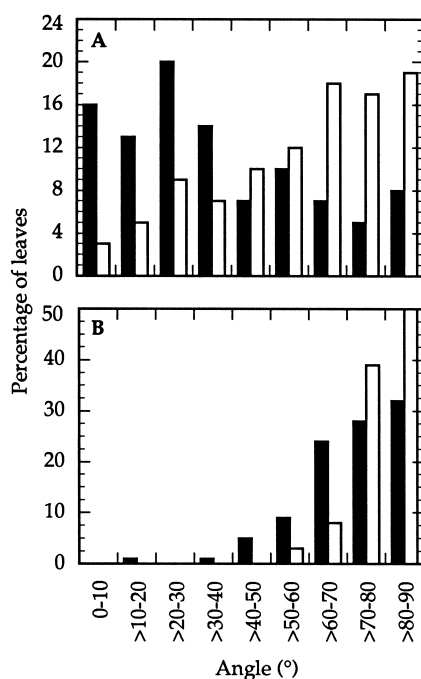

Figure 2. Frequency distribution of mid-vein (solid bars) and blade (open bars) angles for 10° increments from the horizontal for 100 replicate (A) juvenile leaves present on a Tasmanian *Eucalyptus globulus* ssp. *globulus* sapling, and (B) adult leaves present on a Wilsons Prom. *E. globulus* sapling.

Table 2. Orientation of the sun during January at The University of Western Australia and surrounding irradiance during morning and midday. Values of R_T and R_A are the irradiances measured when the quantum sensor faced directly toward and away from the sun, respectively. The terms horizontal and vertical refer to the positioning of the quantum sensor.

	East (morning)	North (midday)
Sun azimuth (°)	90–110	20–340
Inclination above horizontal (°)	35–40	85–90
R_T (μmol m^{-2} s^{-1})	2110–2380	2560–2590
R_A (μmol m^{-2} s^{-1})	160–260	210–250
Surrounding environment (% of R_T)		
Horizontal upward (R_U)	52	97
Horizontal downward (R_D)	5	8
Vertical north	16	33
Vertical south	10	9
Vertical east	91	21
Vertical west	7	7
Interception by a horizontal leaf (% R_H)	53	98

Table 3. Light interception and shading of juvenile Tasmanian and adult Wilsons Prom. *Eucalyptus globulus* ssp. *globulus* leaves with the sun oriented toward the east (E; morning) and north (N; midday). Abbreviations: % R_{leaf} is the proportion of available sunlight intercepted by each leaf; R_{ad} and R_{ab} are the irradiances incident to the adaxial and abaxial leaf surfaces, respectively. Values are mean and standard error of the mean for 100 replicates. Values for shade indicate that 25% (1) to 50% (2) of the leaf blade was in shade. Statistical differences between the leaf forms, times of measurement and the leaf by time interaction have been indicated by ** = $P < 0.01$ and ns as not significant at $P = 0.05$.

	Juvenile		Adult		Significance		
Solar azimuth	E	N	E	N	Leaf	Time	Int.
Light interception							
Actual (μmol m^{-2} s^{-1})	1550 ± 60	1370 ± 63	1430 ± 52	756 ± 35	**	**	**
% R_{leaf}	62.7 ± 2.4	48.6 ± 2.2	59.8 ± 2.1	27.0 ± 1.3	**	**	**
R_{ad}/R_{ab}	13.7 ± 1.0	12.1 ± 0.9	12.5 ± 0.8	5.4 ± 0.5	**	**	**
Shade	1.3 ± 0.1	1.9 ± 0.1	1.3 ± 0.1	1.0 ± 0.1	**	ns	**

leaves reduced their midday light interception to half that intercepted during the morning. Compared with a theoretical horizontal leaf (Table 2), the juvenile leaf form intercepted 10% more radiation in the morning, and 50% less radiation during the middle of the day. Similarly, the adult leaf form intercepted 7% more sunlight in the morning, and 70% less radiation at midday than a theoretical horizontal leaf.

For both juvenile and adult leaves, the ratio of radiation intercepted by the abaxial leaf surface to that intercepted by the adaxial leaf surface was 13:1 when the sun was low in the eastern sky (Table 3). During the middle of the day, the ratio for juvenile leaves was the same, whereas for adult leaves it was significantly reduced. Of the adult leaves sampled, 44% intercepted the majority of incident radiation on the abaxial leaf surface during the two measurement periods. Only 6 and 14% of juvenile leaves sampled intercepted the majority of sunlight on the abaxial surface when the sun had an eastern and northern azimuth, respectively.

Juvenile leaves within each of the four azimuth categories intercepted a similar percentage of maximum sunlight (Figure 3A) and had a similar leaf surface ratio of light interception (Figure 3B). In contrast, adult leaves facing east and south-east intercepted a significantly greater proportion of morning sunlight than leaves with a north facing leaf blade (Figure 3A). Within each azimuth sector, adult leaves intercepted a similar percentage of maximum sunlight and had a similar leaf surface ratio of light interception when the sun was in the northern sky, despite the greater potential sunlight availability for north–south oriented leaves (Table 2).

Adult leaves of the Wilsons Prom. sapling were shaded less than Tasmanian juvenile leaves, particularly during the middle of the day when the sun was directly overhead (Table 3). The majority of adult leaves had less than 50% of the blade shaded during both measurement times (Figure 4). In contrast, juvenile leaves had a majority of leaves with little or no shading during the morning, whereas 40% of leaves had 50 to 75% of the blade shaded during the middle of the day.

Leaf temperature and conductance

Juvenile leaves of the Tasmanian sapling had a similar or higher temperature than adult Wilsons Prom. leaves. The dif-

ference between leaf and air temperature (ΔT) was significantly greater ($P < 0.01$) for juvenile leaves than for adult leaves during the middle of the day (Table 4). Although air temperatures were higher at midday, ΔT of juvenile and adult leaves was lower when the sun was overhead ($P < 0.05$). Stomatal conductance was variable over five days of measurement (Table 4), with no consistent differences between juvenile and adult leaves. Conductance values ranged from 0.4 to 0.9 cm s^{-1} for juvenile Tasmanian leaves, and from 0.5 to 1.2 cm s^{-1} for adult Wilsons Prom. leaves. On only one day did stomatal conductance decline significantly ($P < 0.01$) from morning to midday for juvenile (0.86 ± 0.06 cf. 0.53 ± 0.05 cm
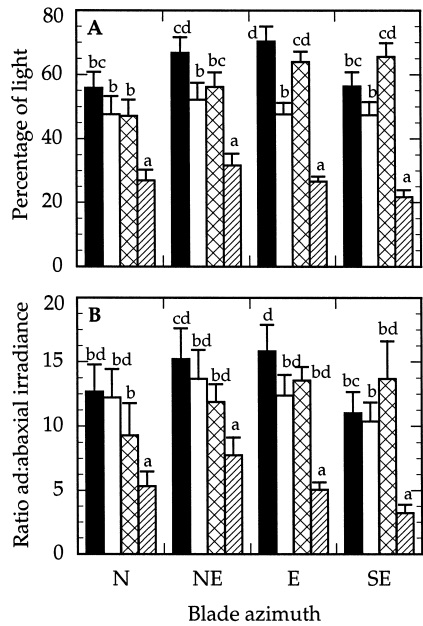
Figure 3. (A) Percentage of maximum sunlight, and (B) ratio of adaxial and abaxial radiation intercepted by juvenile (solid and open bars) and adult (hatched and striped bars) leaves within each azimuth category with an eastern sun orientation (solid and hatched bars) and northern sun orientation (open and striped bars). Bars are means and error bars are the standard error of the mean for 100 replicate leaves. Bars with the same letter are not significantly different at $P = 0.05$.
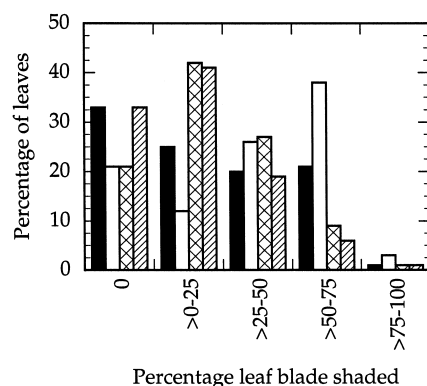
Figure 4. Frequency distribution of leaves within each shade category for juvenile (solid and open bars) and adult (hatched and striped bars) *Eucalyptus globulus* ssp. *globulus* leaves, with the sun in the east (solid and hatched bars) and north (open and striped bars) azimuth.

s^{-1}) and adult (1.16 ± 0.07 cf. 0.75 ± 0.05 cm s^{-1}) leaves.

Discussion

Leaf orientation and angle are determined by light availability and directionality during growth. Eucalypt leaf orientation is established when the leaves are immature. Maturation and sclerification prevent further changes in orientation (Jacobs 1955, Werk and Ehleringer 1984). The phototropic nature of adult *E. globulus* ssp. *globulus* leaves was shown by the non-uniform east–west azimuth distribution of the adult Wilsons Prom. leaf blades. Although juvenile leaves of most species of *Eucalyptus* arise perpendicular to the shoot, variation in the angle of axillary branches results in most leaves being sub-horizontally oriented (Cameron 1970b, King 1997). We found that orientation and angle of the sessile *E. globulus* ssp. *globulus* juvenile leaves was primarily determined by the azi-

Table 4. Range of leaf temperatures and stomatal conductances of juvenile leaves from a Tasmanian sapling and adult leaves from a Wilsons Prom. *Eucalyptus globulus* ssp. *globulus* sapling. The difference between leaf and air temperature (ΔT) was measured on 7 days in January, and stomatal conductance was measured on 5 days. Measurements were taken over a 1-h period when the sun had an eastern or northern azimuth. Values are the mean and standard error of the mean for 20 to 30 leaves. Negative ΔT values indicate leaf temperature was below air temperature.

	Morning (East)	Midday (North)
ΔT (°C)		
Juvenile	-0.8 ± 0.2 to 1.8 ± 0.5	-3.3 ± 0.2 to 2.1 ± 0.3
Adult	-1.3 ± 0.2 to 1.4 ± 0.4	-3.9 ± 0.2 to 0.4 ± 0.4
Stomatal conductance (cm s^{-1})		
Juvenile	0.40 ± 0.03 to 0.86 ± 0.06	0.53 ± 0.05 to 0.81 ± 0.06
Adult	0.48 ± 0.05 to 1.16 ± 0.07	0.55 ± 0.05 to 0.75 ± 0.05

muth and declination of the branch to which the leaf was attached and by internodal twisting of the stem. Juvenile leaf orientation and inclination were secondarily determined by phyllotaxy of the leaf pair, and by the rotation of the leaf blade. Twisting of branches and a long, flexible petiole allowed adult leaves to hang vertically. The azimuth of the adult leaves was determined by the twisting of the petiole and leaf blade.

The orientation and angle of juvenile and adult *E. globulus* ssp. *globulus* leaves were within the range of values found for other eucalypt species (Thomas and Barber 1974, Ashton 1976, Pereira et al. 1987, Borralho et al. 1989, Ögren and Evans 1992, James and Bell 1996). In similar studies, juvenile leaves represented the greatest proportion of *E. globulus* ssp. *globulus* leaves with an angle between 65 and 72° (Borralho et al. 1989), and 75% of adult *E. globulus* leaves had a leaf inclination of greater than 80° from horizontal (Pereira et al. 1987). An increase in leaf angle with ontogenetic development occurs in seedlings of *E. camaldulensis* Dehnh., resulting in increased verticality from the seedling to the juvenile and transitional leaf forms (James and Bell 1996). Increased verticality of successive ontogenetic leaf forms with increasing irradiance has been noted for *E. fastigata* H. Deane & Maiden (Cameron 1970a), *E. regnans* F. J. Muell. (Ashton and Turner 1979) and *E. globulus* ssp. *globulus* (James and Bell 1999a).

Within a canopy, leaf temperature is related directly to radiation absorption, and indirectly to incident radiation, leaf orientation, shading and leaf position (Miller 1967). Vertical leaf orientation is usually regarded as an adaptation that reduces radiation load at high solar angles, but is also beneficial for sunlight interception during winter months with low solar angles (James and Bell 1996). Among leaves fixed in any given orientation, horizontal leaves generally have the greatest daily light interception (Nobel et al. 1993, Jurik and Akey 1994), and have a large peak of incident irradiance at noon (Ehleringer and Werk 1986). As a result, horizontal leaves have a higher daily water loss than leaves in other orientations (Werk and Ehleringer 1984, Smith and Ullberg 1989, Jurik et al. 1990). We found that juvenile and particularly adult *E. globulus* ssp. *globulus* leaves exhibited a reduction in light interception during the middle of the day, and increased light interception in the morning compared with a theoretical horizontal leaf. Greater interception of solar radiation during the early morning and later afternoon hours, when the vapor pressure deficit is lower, allows vertical leaves to have a higher water-use efficiency than horizontal leaves (Forseth and Ehleringer 1983, Körner and Cochrane 1985, Ehleringer and Werk 1986, Ehleringer and Comstock 1987). Although sub-horizontal juvenile leaves showed a lower light interception than a theoretical horizontal leaf, light interception was still greater than that of vertical adult leaves. As a consequence, juvenile leaves had a higher leaf temperature, particularly during the middle of the day, than adult leaves. The non-random east–west orientation of adult *E. globulus* leaves also resulted in peaks of intercepted radiation during the morning and afternoon, and reduced intercepted radiation at noon. Such orientation would increase carbon exchange and transpiration rates of

these leaves early and late in the day (see Werk and Ehleringer 1984, Ehleringer and Werk 1986, Smith and Ullberg 1989, Jurik et al. 1990).

The narrow, pendulous adult *E. globulus* ssp. *globulus* leaves utilize convective cooling and reduce transpirational water loss by hanging vertically, having increased leaf movement, and a reduced leaf dimension (see Ladiges 1974, Gates 1980, Miller 1983). Broader sub-horizontal juvenile leaves, by contrast, rely more on transpiration for leaf cooling. Vertical adult *Eucalyptus* leaves may have been selected to reduce midday heat loads, and increase water-use efficiency and carbon gain under conditions of reduced water availability (Jacobs 1955, King 1997). Increased leaf angle has been associated with habitat aridity for several species and communities (Geller and Smith 1982, Ehleringer and Werk 1986, Ehleringer and Comstock 1987, Ehleringer 1988, Gibson et al. 1991, Smith et al. 1998).

The waxy coating on the juvenile *E. globulus* ssp. *globulus* leaves would be expected to increase diffuse reflectance, and reduce leaf absorptance and heat load (Hall et al. 1965, Howard 1966, Pearman 1966, Cameron 1970*b*, Thomas and Barber 1974, Charles-Edwards et al. 1986, James and Bell 1996). The importance of reflectance in reducing light absorption and leaf temperature is unclear for the juvenile *E. globulus* ssp. *globulus* leaves, because they were warmer than the green adult leaves. However, we note that the juvenile leaves intercepted 3% more light and were about 0.5 °C warmer than adult leaves in the morning, but intercepted 22% more light and were only 1.8 °C warmer than adult leaves at midday. Given the similar stomatal conductances of juvenile and adult leaves, this difference may indicate that the reflectivity of the glaucous juvenile leaves has a substantial effect on energy balance, and may offset the greater boundary layer resistance of the broader juvenile leaves.

Within the canopy, leaf shading reduces light capturing efficiency, and so the effect of leaf orientation is less apparent (Miller 1967, Takenaka 1994). The vertical and alternate leaf positioning of the adult Wilsons Prom. *E. globulus* ssp. *globulus* leaves resulted in less mutual shading compared with the Tasmanian juvenile leaves. Because the leaves measured were at the terminus of branches, the shading of juvenile leaves within the canopy during the middle of the day was underestimated. In contrast, the adult canopy was open in structure, with most leaves being exposed to full sunlight. The greater length to width ratio and longer petiole of the adult leaves would improve light capture by reducing the leaf area aggregated around the stem (Takenaka 1994). The decussate phyllotaxis of the juvenile leaves, in contrast, would increase leaf overlap and mutual shading, particularly during the middle of the day. Pendulous adult leaves allow significant penetration of overhead light within the canopy, but obstruct light at low solar angles (Lamb 1968, Ashton 1976, Pryor 1976, Pereira et al. 1987).

Stomatal conductances of juvenile and adult leaves of comparable age were similar and within the range of other conductance values published for the ontogenetic leaf forms of

Eucalyptus species (see review by James 1998). Chalmers (1992) also found that juvenile and adult leaves of Wilsons Prom. *E. globulus* ssp. *globulus* seedlings had similar stomatal conductance values. Vapor pressure deficit would be greater for the warmer, more light-exposed juvenile leaves than for the adult leaves, resulting in a greater transpirational water loss at the same stomatal conductance. The verticality of the adult leaf form would be advantageous in lowering transpirational water loss by reducing light interception during the middle of the day, but allows photosynthesis to continue by maintaining a high stomatal conductance.

Horizontal leaves receive a substantially higher irradiance on the upper surface, but a lower irradiance on the lower surface compared with vertical leaves. Palisade cells tend to occur at the leaf surface with the greatest incident light, and function to propagate light deeper into the leaf (Gates et al. 1965, Charles-Edwards et al. 1986, DeLucia et al. 1991, Smith et al. 1997). Correspondingly, horizontal leaves are typically dorsiventral in structure, with palisade mesophyll cells located beneath the upper, adaxial epidermis. Isobilateral leaves have palisade mesophyll cells on both sides or throughout the leaf, and tend to have a vertical orientation. Leaves with horizontal orientation also tend to be hypostomatous, whereas vertical leaves tend to be amphistomatous (Poulson and DeLucia 1993, Smith et al. 1998). Although steeply inclined, the greatest proportion of sunlight was incident on the adaxial surface of the juvenile *E. globulus* ssp. *globulus* leaves, reflecting the dorsiventral, hypostomatous structure of the leaves (James 1998). Adult leaves were oriented such that either the adaxial or abaxial leaf surface intercepted the majority of incident radiation, with the two leaf surfaces intercepting more equal amounts of sunlight throughout the day than the juvenile leaves. Adult *E. globulus* leaves have an isobilateral and amphistomatous structure (James 1998), enabling equal utilization of sunlight by both leaf surfaces. Studies have indicated that vertical leaves have a similar photosynthetic capacity on both adaxial and abaxial leaf surfaces (DeLucia et al. 1991, Evans et al. 1993, Ögren and Evans 1993, Poulson and DeLucia 1993, Terashima and Hikosaka 1995, Myers et al. 1997). Horizontal leaves, in contrast, have a greater photosynthetic capacity on the adaxial surface, which intercepts the greater proportion of solar radiation. Efficient light processing by the abaxial leaf surface of the vertical adult leaves may reduce the potential for decreased net carbon gain and growth caused by the reduced interception of sunlight, particularly during the middle of the day.

As the angle of radiation incident on a leaf increases, reflection is increased and irradiance is reduced to below the photosynthetic saturation point, allowing more efficient utilization (Kriedemann et al. 1964, Howard 1966, Pearman 1966). *Eucalyptus globulus* ssp. *globulus* juvenile and adult leaves saturate photosynthetically at 700 and 800 µmol m^{-2} s^{-1}, respectively (Battaglia et al. 1996). Even during the middle of the day when sunlight interception was minimized, the irradiance incident on the juvenile and adult *Eucalyptus globulus* ssp.

globulus leaves was close to or above that required for photosynthetic saturation (see Körner and Cochrane 1985).

Leaf structure and photosynthetic potential can change among plants of a given habitat and, in the case of *E. globulus* ssp. *globulus*, within a single individual. A model of leaf structure and function in relation to light environment and stress was developed by Smith et al. (1998) (Table 5). The model was largely based on the association between leaf structure, orientation, sunlight exposure and aridity for species within five plant communities from Western Australia. Smith et al. (1998) found that a decrease in annual precipitation and an increase in total daily sunlight corresponded to the proportion of species with more inclined or thicker mesophyll leaves. Leaf bicoloration was associated with horizontal leaf orientation, with the adaxial leaf surface intercepting a greater proportion of sunlight than the abaxial leaf surface. Amphistomatous and isobilateral leaf structure was positively correlated with leaf inclination and the ratio of sunlight incident to the two leaf surfaces (Table 5) (Smith et al. 1997, 1998). Plant species with leaves possessing a high photosynthetic capacity occurred in high-light, low-stress environments. Such species had a horizontal leaf orientation and structural features such as thick leaves with multiple layers of palisade mesophyll. As sunlight and stress increased, leaves became inclined and symmetrical in structure, with sunlight incident to both leaf surfaces (Table 5). Low-light, low-stress leaves had a dorsiventral and hypostomatous leaf structure with limited palisade development, resulting in a low photosynthetic potential.

Characteristics of the juvenile *E. globulus* leaves correspond to those of the high-light and low-stress, or high-water availability category leaves of the Smith et al. (1998) model (Table 5). The adult leaf form, in contrast, has characteristics of leaves found under conditions of high sunlight and limited water availability (James 1998, James and Bell 2000). A higher photosynthetic potential of the high specific leaf area juvenile leaves (James 1998, James and Bell 2000) would provide *E. globulus* with a growth advantage, particularly with a reduction in leaf area and transpiration after defoliation or fire (see Doley 1982, Beadle et al. 1989, King 1997, James 1998). The adult leaf form, in contrast, would be advantageous for water conservation.

In conclusion, the higher leaf temperature of juvenile *E. globulus* ssp. *globulus* leaves compared with adult leaves is primarily a result of the greater light interception of the sub-horizontal juvenile leaves. Adult leaves have a more vertical leaf orientation than juvenile leaves, which reduces light interception. Steep leaf angles and mutual shading, combined with transpiration, assist in reducing *E. globulus* leaf temperature below air temperature. Even though the two ontogenetic leaf forms had similar stomatal conductances under comparable conditions, the juvenile Tasmanian sapling had a higher leaf temperature and greater leaf dimension and, therefore, may have greater total transpirational water loss. The faster growth rate of trees with a juvenile canopy may be a result of their greater light interception. The greater interception of irradiance by individual juvenile leaves suggests that this leaf form is more adapted to high incident light than the more vertical adult leaves that avoid high irradiances during the middle of the day.

Acknowledgments

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Table 5. Juvenile (high light/low water stress environment) and adult (high light/high water stress environment) leaf characterisitics of *Eucalyptus globulus* ssp. *globulus* compared with characteristics predicted by the Smith et al. (1998) model.

Characteristic	Juvenile		Adult	
	Predicted	Observed	Predicted	Observed
Orientation	Horizontal	Horizontal	Vertical	Vertical
Adaxial/abaxial PAR	> 3.5	> 3.5	< 2.0	< 2.0[1]
Thickness (μm)	> 600	< 600	400–600	400–600
Thickness/width ratio	< 0.1	< 0.1	> 0.1	< 0.1
Symmetry	Dorsiventral	Dorsiventral	Isobilateral	Isobilateral
Morphology	Large laminar broadleaf	Large laminar broadleaf	Small and cylindrical[2]	Large laminar broadleaf
Stomatal distribution	Hypo/amphistomatal	Hypo/amphistomatal	Amphistomatal	Amphistomatal
Coloration	Bicolored	Bicolored	Not bicolored	Not bicolored
Palisade distribution	Multiple adaxial layers	Multiple adaxial layers[4]	Adaxial and abaxial	Adaxial and abaxial
Photosynthetic potential[3]	1	1	2	2

[1] As 44% of adult leaves intercepted maximum irradiance on the abaxial surface, and inclination results in equal light interception by the two leaf surfaces when integrated over the day, adult leaves are believed to conform to the model.

[2] Width > 0.1 largely applies to small, cylindrical needle leaves, the extreme form of the high sun, high stress leaf category.

[3] Relative ranking: 1 is greatest.

[4] In high light.

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