Crown structure and vertical foliage distribution in 4-year-old plantation-grown *Eucalyptus pilularis* and *Eucalyptus cloeziana*

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Abstract Tree growth and form are both influenced by crown architecture and how it effects leaf distribution and light interception. This study examined the vertical distribution of foliage in 4-year-old plantation-grown *Eucalyptus pilularis* Sm. and *E. cloeziana* F. Muell. trees. Leaf area (LA) distribution was determined at two different sites using allometric approaches to determine LA in crown sections and for whole trees. Leaf area was distributed more towards the upper crowns when canopies had been closed for longer. Leaf area was also skewed more towards the upper crowns for *Eucalyptus pilularis* than *E. cloeziana*. These species differences were consistent with differences in vertical light availability gradients as determined by point quantum sensors. Leaf area of individual branches was highly correlated with branch cross-sectional area (CSA) and whole-tree LA was closely related to stem CSA. Branch-level allometric relationships were influenced by site and crown position. However, the general allometric equations between stem size and whole-tree leaf area could be applied across sites. Results from this study suggest that pruning of live branches in these species should follow species-specific guides for the timing and height of pruning to optimise the effects on stem growth and form.

Keywords Leaf area index · Leaf area distribution · Pruning · Crown architecture

Introduction

Crown structure and architecture are closely linked to tree productivity and stem growth. The size of the crown

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determines productivity through its role in radiation interception, and the architecture of the crown influences light penetration (Jarvis and Leverenz 1983) and canopy microclimate (Gary 1974). The spatial distribution of leaf area is a principal element of crown architecture because of its strong influence on light attenuation within the crown and potential to influence tree growth (Xu and Harrington 1998). The quantity of light captured by an individual tree is determined by the amount, distribution and arrangement of foliage within the crown (Linder 1985). An understanding of crown size and structure is required to describe tree growth rates and to develop growth models based on the physical environment and physiological processes that govern growth of individual tree species.

Information about leaf area distributions within tree crowns is also important when developing pruning regimes. Pruning is a silvicultural manipulation that directly removes branches from the base of the crown to a pre-determined height, fixed length of the live crown, or to a desired maximum diameter of the unpruned stem section. The amount of leaf area removed depends on the vertical distribution of foliage at the time of pruning, which varies greatly between species and even between clones (Reis et al. 2004), stand characteristics and stages of stand development (Forrester et al. 2012a). In closed canopy *Eucalyptus maculata* Hook. (Pook 1984) and *Eucalyptus nitens* (Dean and Maiden) Maiden (Medhurst and Beadle 2001; Forrester et al. 2012a), the vertical distribution of foliage was skewed towards the top of the crown, while in many conifers growing in closed stands the leaf area is normally distributed over the length of the live crown (Jarvis and Leverenz 1983). In young *E. nitens* trees, it was shown that the distribution of leaf area prior to complete canopy closure was skewed towards the base of the crown; however, following canopy closure leaf area was skewed towards the top (Pinkard and Beadle 2000). Given the close link between leaf area and tree growth, an understanding of the vertical distribution of leaf area within tree crowns is critical to interpreting growth responses following pruning and to identify pruning regimes that optimise tree growth and form.

Allometric methods have been used successfully to predict both whole-tree leaf area as well as its vertical distribution in a wide range of conifers (Snowdon 1986; Xiao and Ceulemans 2004) and broadleaved species (Pereira et al. 1997; Hunt et al. 1999; Medhurst and Beadle 2001; Forrester et al. 2012a). Whole-tree leaf area has been predicted from variables such as stem diameter or sapwood area. These relationships have been reported to vary with site quality (Montagu et al. 2005), canopy density (Medhurst et al. 1999), tree age (Albrektson 1984), climatic and site conditions (Bancalari et al. 1987; Shelburne et al. 1993; Berninger and Nikinmaa 1997), level of weed infestation (Hunt et al. 1999) and silvicultural treatment (Pinkard and Beadle 1998).

However, site-, treatment- (Medhurst et al. 1999; Forrester et al. 2012a) and age-independent (Pereira et al. 1997) relationships have also been found for branch or whole-tree leaf area allometric equations.

Eucalyptus pilularis Sm. is one of Australia's most important native forest hardwoods (Clarke et al. 2009). In Australia, there are about 20,000 ha of plantations containing *E. pilularis* or *E. cloeziana* F. Muell. (Nichols et al. 2010) and both species have been grown in Africa, Asia and South America (Clarke et al. 2009). In northern New South Wales and southern Queensland, Australia, these species are being cultivated with the aim of producing high-value solid wood products (Bruskin 1999; Dickinson et al. 2000). The two species are often planted at the same site, where *E. cloeziana* is established on upper slopes and ridge positions and *E. pilularis* is planted on mid and lower slopes. These species possess contrasting crown architectures in young plantations. In closed-canopy stands, *E. pilularis* maintains a much shorter live crown than *E. cloeziana* trees of the same age (Alcorn et al. 2007). Currently most plantations in northern New South Wales are managed using natural branch shedding processes to produce high-quality, knot-free timber. Pruning is being considered as an alternative means of controlling branches in order to produce high-quality timber.

The aim of this study was to gain an understanding of the vertical leaf area distribution and within-canopy light environment of the two species with contrasting crown architectures. To assess whether these species properties might be influenced by site factors, the investigations were carried out at two different sites. The objectives were (1) to develop allometric relationships between branch size and leaf area and between stem size and whole-tree leaf area to accurately predict leaf area on standing trees non-destructively at two sites, (2) to characterise and compare the vertical distribution of leaf area in young, 4-year-old, *E. pilularis* and *E. cloeziana* plantations on two sites and (3) to describe the light climate within the crown of both species. Results of this study on vertical distribution of foliage and light attenuation within crowns and how these are influenced by species and site have particular relevance also for other species, where pruning commonly removes live branches.

Materials and methods

Experimental sites

Two plantations, each containing *E. pilularis* and *E. cloeziana* were selected for this study; 'Woodcock' and 'Southgate'. Woodcock is a commercial plantation located near Beechwood (31°22′S, 152°40′E) and Southgate is an

experimental plantation located near Nana Glen (30°1′S, 153°8′E), both in northeastern New South Wales, Australia. Both sites were ex-pasture prior to plantation establishment. Soils at Woodcock are well-drained brown dermosols and brown kandosols. The average annual rainfall is 1,479 mm (1920–2006) and the elevation is 90–150 m above sea level. Soils at Southgate are deep (1–1.5 m) brown and yellow earths. The average annual rainfall is 1,435 mm (1920–2006) and the elevation is 165 m above sea level.

At both sites, site preparation involved ripping of soils to a depth of 0.7 m and mounding, and the application of pre-plant herbicide, in September 2000. *E. pilularis* (Whian Whian State Forest seedlot) and *E. cloeziana* (Pomona State Park and Mebbin State Forest plantation seedlot) seedlings were planted in late November or December 2000. The initial spacing at Woodcock was 1,136–1,250 trees ha^{-1}; 4 m between rows and 2.2–2.0 m within rows. At Southgate, the initial spacing was 1,250 trees ha^{-1}; 4 m between rows and 2 m within rows. At each site, each seedling was fertilised with 9 and 10 g of elemental N and P, respectively, at the time of planting. Post-planting herbicide was applied twice before age 1 year. At Woodgate, the *E. cloeziana* stand was planted on a moderately steep (8°) upper east facing slope and *E. pilularis* on a moderate lower slope (6°) facing east to southeast. More detail about the sites and seedling establishment is provided in Alcorn et al. (2007, 2008).

Crown architecture, sapwood area and leaf area measurements

In September 2004, 15 *E. pilularis* and 15 *E. cloeziana* trees were selected at Southgate and 13 trees of each species were selected at Woodcock. Selected trees were in the co-dominant or dominant crown class within the stand (Smith et al. 1997), straight and single stemmed, free of visible health defects and surrounded by four immediate neighbours in each direction (within the row and perpendicular in adjacent rows), with at least seven or eight neighbouring trees in all orientations. Sizes and crown dimensions of measurement trees are shown in Table 1. At the Southgate site, *E. cloeziana* trees were larger than *E. pilularis* trees, while the opposite was the case at the Woodgate site.

For each tree, diameter at 1.3 m (DBH) and the diameter at the base of the live crown were measured and these points marked on the stem. Trees were measured for total height and height to the base of the live crown, which was defined as the point of stem insertion of the lowest live branch contained within a geometrically regular crown envelope (Soares and Tomé 2001). Live-crown length (LCL) was calculated as the difference between total height and height to the base of the live crown. The LCL was divided vertically into six height zones of equal length. Commencing at the base of the crown, crown zones of 0–17, 18–33, 34–49, 50–67, 68–83 and 84–100 % LCL

Table 1 Crown and stem characteristics for co-dominant and dominant trees chosen from stands of *E. pilularis* and *E. cloeziana* at two sites to describe crown and branch architecture

	Southgate site		Woodcock site	
	E. pilularis	*E. cloeziana*	*E. pilularis*	*E. cloeziana*
Mean DBH[†] (cm)	11.5 (0.3)*	12.7 (0.3)*	12.0 (0.3)*	9.3 (0.3)*
DBH range (cm)	9.7–13.0	10.4–14.7	10.4–13.9	7.9–11.5
Mean basal area (cm^2)	105.5 (6.1)	128.5 (6.1)	114.1 (4.9)*	69.3 (4.9)*
Mean height (m)	10.4 (0.3)*	11.6 (0.3)*	11.9 (0.2)*	7.9 (0.2)*
Height range (m)	8.9–12.6	9.2–13.3	10.7–12.8	6.5–9.2
Live-crown height (m)	2.3 (0.1)*	1.2 (0.1)*	3.9 (0.2)*	1.3 (0.2)*
Crown length[‡] (m)	8.1 (0.2)*	10.4 (0.2)*	8.0 (0.3)*	6.6 (0.3)*
Live-crown ratio[#]	0.78 (0.01)*	0.90 (0.01)*	0.67 (0.02)*	0.83 (0.02)*
Height to lowest live branch (m)	2.0 (0.1)*	1.1 (0.1)*	2.8 (0.2)*	0.9 (0.2)*
Projected crown area (m^2)	11.5 (0.8)*	14.2 (0.8)*	13.2 (0.8)	13.0 (0.8)
Number of trees	15	15	13	13

Values in parentheses are standard error of the mean

* Significant difference between species means within a site ($P = 0.05$)

[†] Diameter at breast height (1.3 m)

[‡] Crown length (total tree height minus height to base of live crown)

[#] Live-crown length divided by total height

were marked along the stem. Live-crown ratio was calculated as the LCL divided by total tree height. Crown diameter was measured parallel and perpendicular to the rows and used to calculate the projected crown area (PCA).

For all trees, the diameter over bark of all branches along the main stem was measured 30 mm from the stem junction within each crown zone. Branch cross-sectional area (CSA_b) was calculated from branch diameters assuming branches were circular. Five live branches from each crown zone were selected to represent the range of diameters present including the largest, smallest and three intermediate branches spread equally between the minimum and maximum diameter. These branches were sampled from five trees of each species at Southgate (150 branches per species) and three trees per species at Woodcock (90 branches per species). Several studies in *Eucalyptus* plantations (Medhurst et al. 1999; Pinkard and Neilsen 2003; Forrester et al. 2012a) have shown that branch allometric equations do not vary with tree size, age, site quality or silvicultural treatment (pruning, thinning, fertilizer application). All leaves of harvested branches were removed. A sub-sample of 15 leaves was selected from each branch and the projected leaf area measured using a Li-3000A Leaf Area Meter (Li-Cor Inc., Lincoln, Nebraska, USA). The sub-sample and remaining leaves were then dried at 70 °C for a minimum of 72 h or until constant weight was reached, and weighed. The specific leaf area (SLA in m^2 kg^{-1}) of the sub-samples was calculated and used to calculate the total leaf area of the given branch (LA_b). A measure of leaf area display efficiency was calculated as the ratio of branch size to branch leaf area (LA_b: CSA_b) for all branches. Whole-tree leaf area estimates (LA_t) were calculated from the sum of LA_b, which was determined from CSA_b to LA_b relationships described below. Leaf area index (LAI) was calculated as LA_t divided by PCA. LA_t was used to examine relationships between stem CSA at 1.3 m ($CSA_{1.3}$), stem CSA at the base of the live crown (CSA_{lcb}) and sapwood area at 1.3 m ($SapA_{1.3}$).

Stem discs were taken at 1.3 m height to estimate sapwood area. Only five trees of each species could be sampled for sapwood area at Southgate due to the need for limited destructive harvesting for ongoing experiments at this site. All 13 trees of each species at Woodcock were sampled. To identify the sapwood area, discs were stained with 5 % dimethyl orange in ethanol solution immediately after harvesting and placed in plastic bags. The outline between the heartwood and sapwood boundary was traced using tracing paper, the sapwood outline was cut out and the sapwood area determined using a Li-3000A Leaf Area Meter (Li-Cor Inc.).

Light attenuation measurements

To quantify the vertical light environment within crowns of *E. cloeziana* and *E. pilularis* trees at Southgate, light transmission within the crown was determined on two vertical transects from above the canopy to below the canopy in the northern (within row) and eastern (between row) aspect of eight trees of each species selected the same way as the destructively sampled trees and following the light measurement procedure used by Bauhus et al. (2004). All measurement trees were located more than 50 m from the edge of the stand. Measurements of photosynthetic photon flux density (PPFD) were made vertically in the middle of the six vertical crown zones (defined above). A silicon diode quantum sensor (LI-COR) mounted on a 15 m telescopic height pole and connected to a LAI-2000 (LI-COR) data logger was used to obtain measurements at a horizontal distance of 1 m from the stem on the northern and eastern aspect. Percent PPFD was calculated as the ratio between the instantaneous measurement made with the quantum senor in the canopy and a simultaneous PPFD measurement recorded by a second quantum sensor connected to a LAI-2000 Data Logger, which recorded every 15 s. This second sensor was erected at 1.3 m above the ground in a 5 ha clearing and was located no more than 500 m from the below-canopy sensor. Measurements were taken under diffuse light conditions during dawn and dusk, following the methodology proposed by Messier and Puttonen (1995). All sensors were calibrated in the laboratory using a light meter with attached quantum sensors (Skye Instruments Ltd, Wales, UK).

Statistical analyses

Site, species or crown zone effects on tree or crown dimensions, SLA, mean leaf area or LAI were examined using residual maximum likelihood (REML). Post-hoc least significant difference tests were used to identify which groups of data were different from each other. The effects of site, species or crown zone effects on branch-level relationships between CSA_b and LA_b, as well as tree-level relationships between LA_t and stem cross-sectional area ($CSA_{1.3}$) at breast height (1.3 m) over bark, stem cross-sectional area at the base of the live crown (CSA_{lcb}) over bark and sapwood area at breast height ($SapA_{1.3}$), were also tested using maximum likelihood analysis, with each of these variables ln transformed. The bias introduced by back-transforming logarithmic models was accounted for by calculating a bias correction-factor for each model. Generalised allometric leaf area models (independent of site and crown zone) were also developed for each species to allow comparisons with the site- and crown zone-specific allometric leaf area models. The bias correction factor was calculated as the ratio of the actual sample mean to the mean of the back-transformed predicted values from the regression (Snowdon 1991). All statistical analyses were

performed using Genstat (VSN International 2004, Hemel Hempstead, Herts, UK).

Results

Stem and crown characteristics

Mean DBH and height of *E. pilularis* trees were significantly smaller than *E. cloeziana* trees at Southgate but at Woodcock mean values of *E. cloeziana* trees were significantly smaller than those of *E. pilularis* trees (Table 1). Also, the PCA was significantly larger in *E. cloeziana* than in *E. pilularis* at Southgate but not different at Woodcock. On both sites, *E. cloeziana* trees exhibited a lower live crown and higher live-crown ratio than *E. pilularis*.

Leaf characteristics

At both sites, SLA in *E. pilularis* was consistently lower than in *E. cloeziana* (Table 2). Within each site, SLA varied significantly with crown zones and species. With the exception of *E. pilularis* at the Woodcock site, mean SLA generally decreased with increasing height in the crown and the change in mean SLA between the highest and lowest crown zone was smaller in *E. pilularis* than *E. cloeziana*.

Branch leaf area

The specific allometric leaf area equations developed between ln CSA_b and ln LA_b were dependent on crown zone and site. The slope and intercept varied significantly between crown zone and site for both *E. pilularis* and *E. cloeziana* (Table 3). The coefficient of determination of the model between actual versus predicted LA_b of

harvested branches was 0.89 for *E. pilularis* and 0.94 for *E. cloeziana*. The correction coefficients for the back-transformation bias for *E. pilularis* and *E. cloeziana* were 1.01 and 1.03, respectively, for specific models, and 1.11 and 1.05 for the general models where all branches were combined.

Vertical distribution of leaf area within crown

To examine the proportions of leaf area in different crown zones, branch leaf area (determined from zone-specific equations) was modelled and summed for each of the six crown zones for all trees. Mean leaf area was significantly higher in the mid-crown zone (51–67 %) than all other crown zones in both species at the Southgate site (Fig. 1a). At Woodcock, however, mean leaf area decreased from the base of the crown to the top in *E. cloeziana*, with a significantly higher leaf area in the lowest crown zone (0–17 %) than in all other crown zones (Fig. 1c). In *E. pilularis*, mean leaf area was also highest in the lower crown (18–33 %), but this was not significantly different from all other crown zones in the lower half of the crown.

Mean LA_b:CSA_b ratio was highest in the mid-crown (51–67 % crown zone) of both species at Southgate (Fig. 1b). At Woodcock, mean LA_b:CSA_b ratio was highest at the base of the crown (0–17 % crown zone) in both species but not significantly different from the 18–33 % crown zone in *E. pilularis* (Fig. 1d). In all species on either site, the leaf area to branch size ratio was lowest in the upper most crown zone.

To examine the change in vertical leaf area distribution (determined from the zone-specific models) with increasing height in the crown, the cumulative leaf area with increasing LCL were plotted for both species at Southgate and Woodcock (Fig. 2a, c). The distribution of leaf area within the live crown of trees at Southgate was skewed

Table 2 Mean specific leaf area (SLA; m^2 kg^{-1}) of leaves removed from branches in six vertical crown zones of *E. pilularis* and *E. cloeziana* trees at two sites

| Crown zone (% live-crown length)	SLA (m^2 kg^{-1}) Southgate site		SLA (m^2 kg^{-1}) Woodcock site	
	E. pilularis	*E. cloeziana*	*E. pilularis*	*E. cloeziana*
0–17	8.5 (0.2)[a]	13.1 (0.2)[a]	5.9 (0.2)[a]	10.3 (0.2)[a]
18–33	8.0 (0.2)[b]	11.5 (0.2)[b]	5.5 (0.2)[a]	8.8 (0.2)[b]
34–50	7.6 (0.2)[bc]	9.9 (0.2)[c]	5.5 (0.2)[a]	8.9 (0.2)[b]
51–67	7.8 (0.2)[bc]	9.7 (0.2)[d]	5.9 (0.2)[a]	9.1 (0.2)[b]
68–83	7.5 (0.2)[c]	9.6 (0.2)[d]	5.8 (0.2)[a]	8.4 (0.2)[b]
84–100	6.6 (0.2)[d]	9.0 (0.2)[e]	5.6 (0.2)[a]	7.2 (0.2)[c]
Mean	7.7	10.5	5.7	8.8

Letters a to e indicate significant differences between crown zones within a site ($P < 0.05$). Within a zone, *E. cloeziana* always had higher ($P < 0.05$) SLA than *E. pilularis*, at both sites. Sectioning of crown zones starts with 0 % at the base of the crown and moves to 100 % at the tree top. Values in parentheses refer to standard errors of mean. For each mean within a specific crown zone $n = 25$

Table 3 Linear regression equations to predict the natural logarithm of branch leaf area (LA_b in m^2) in six vertical crown zones and two sites using the natural logarithm of branch-cross-sectional area (CSA_b in mm^2)

Species	Site	Zone (%)	Equation
E. pilularis	Southgate	0–17	$\ln(LA_b) = -11.510 + 1.934 \times \ln(CSA_b)$
		18–33	$\ln(LA_b) = -9.231 + 1.652 \times \ln(CSA_b)$
		33–50	$\ln(LA_b) = -7.741 + 1.462 \times \ln(CSA_b)$
		51–67	$\ln(LA_b) = -6.149 + 1.256 \times \ln(CSA_b)$
		68–83	$\ln(LA_b) = -5.883 + 1.051 \times \ln(CSA_b)$
		84–100	$\ln(LA_b) = -7.672 + 1.304 \times \ln(CSA_b)$
	Woodcock	0–17	$\ln(LA_b) = -9.668 + 1.792 \times \ln(CSA_b)$
		18–33	$\ln(LA_b) = -8.018 + 1.510 \times \ln(CSA_b)$
		33–50	$\ln(LA_b) = -7.026 + 1.320 \times \ln(CSA_b)$
		51–67	$\ln(LA_b) = -6.013 + 1.114 \times \ln(CSA_b)$
		68–83	$\ln(LA_b) = -5.158 + 0.909 \times \ln(CSA_b)$
		84–100	$\ln(LA_b) = -6.880 + 1.162 \times \ln(CSA_b)$
E. cloeziana	Southgate	0–17	$\ln(LA_b) = -6.803 + 1.217 \times \ln(CSA_b)$
		18–33	$\ln(LA_b) = -6.898 + 1.288 \times \ln(CSA_b)$
		33–50	$\ln(LA_b) = -6.245 + 1.197 \times \ln(CSA_b)$
		51–67	$\ln(LA_b) = -5.325 + 1.071 \times \ln(CSA_b)$
		68–83	$\ln(LA_b) = -5.794 + 1.145 \times \ln(CSA_b)$
		84–100	$\ln(LA_b) = -7.061 + 1.314 \times \ln(CSA_b)$
	Woodcock	0–17	$\ln(LA_b) = -7.464 + 1.472 \times \ln(CSA_b)$
		18–33	$\ln(LA_b) = -8.141 + 1.542 \times \ln(CSA_b)$
		33–50	$\ln(LA_b) = -7.604 + 1.452 \times \ln(CSA_b)$
		51–67	$\ln(LA_b) = -6.717 + 1.325 \times \ln(CSA_b)$
		68–83	$\ln(LA_b) = -7.098 + 1.400 \times \ln(CSA_b)$
		84–100	$\ln(LA_b) = -7.961 + 1.427 \times \ln(CSA_b)$
E. pilularis	All branches combined		$\ln(LA_b) = -7.1 + 1.31 \times \ln(CSA_b)$
E. cloeziana	All branches combined		$\ln(LA_b) = -6.8 + 1.3 \times \ln(CSA_b)$

Sectioning of crown zones starts with 0 % at the base of the crown and moves to 100 % at the tree top. For each crown zone equation $n = 25$ at Southgate and $n = 15$ at Woodcock. For the equations with all branches combined $n = 240$

Fig. 1 Vertical distribution of leaf area (m^2, **a**, **c**) and ratio of mean branch leaf area (LA_b in m^2, **b**, **d**) to branch cross-sectional area (CSA_b in cm^2) ratio (LA_b:CSA_b) in six vertical crown zones for *E. cloeziana* and *E. pilularis* trees at the Southgate and Woodcock sites. Sectioning of crown zones starts with 0 % at the base of the crown and moves to 100 % at the tree top. *Error bars* represent the standard error of mean for each species. At Southgate $n = 15$ for each species, and at Woodcock, $n = 13$ for each species
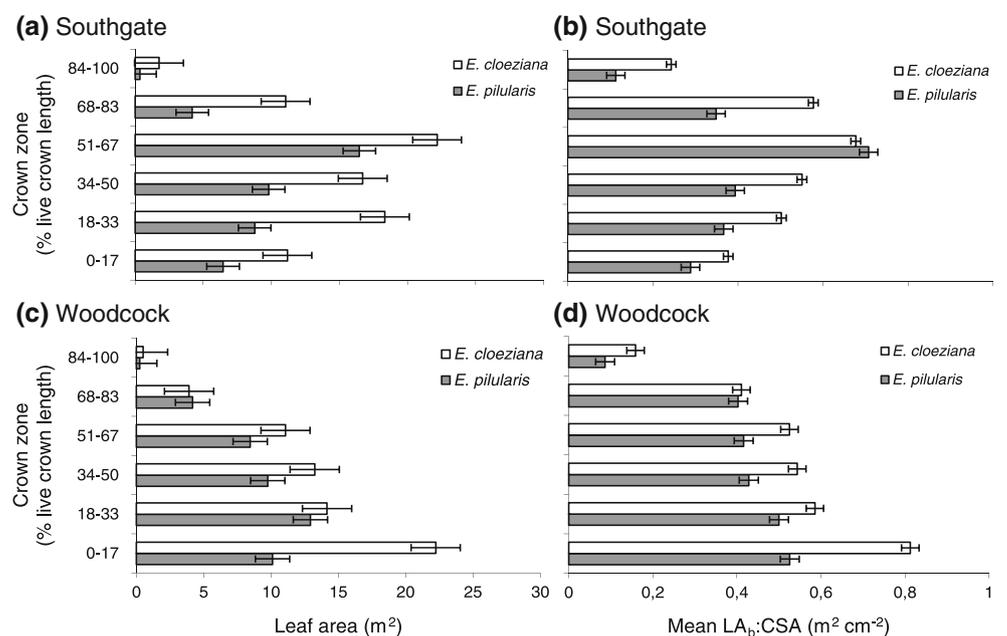
slightly downwards, with 55 and 57 % of total leaf area within the lower half of the crown of *E. pilularis* and *E. cloeziana* crowns, respectively. At Woodcock, the distribution was strongly skewed downward, with over 71 and 76 % in the lower half of *E. pilularis* and *E. cloeziana* crowns, respectively.

Fig. 2 Cumulative leaf area by percent live-crown length and percent stem length for *E. pilularis* and *E. cloeziana* at the Southgate (**a**, **b**) and Woodcock (**c**, **d**) sites. Sectioning of the crown and stem starts with 0 % at the base of the crown or stem and moves to 100 % at the tree top. *Error bars* are standard errors of mean. At Southgate $n = 15$ for each species, and at Woodcock, $n = 13$ for each species
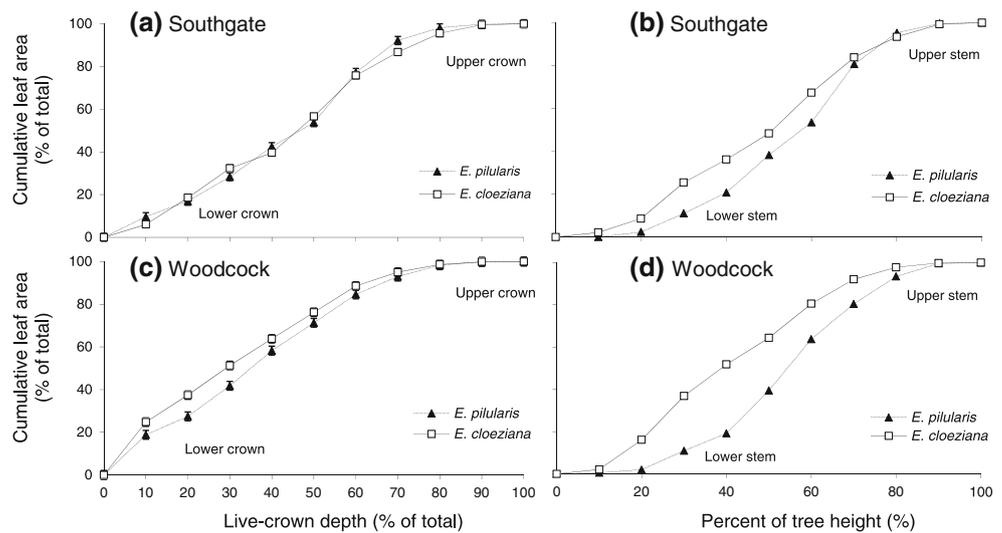
The patterns of cumulative leaf area increase with height differed between sites (Fig. 2). At Southgate, there was almost a linear increase in cumulative leaf area with increasing height along the live crown from the bottom up to 40 % in both species (Fig. 2a). Between 40 and 70 % LCL, the rate of increase in cumulative leaf area was proportionally greater than the increase in height along the live crown. Above 70 % LCL, the rate of increase in cumulative leaf area was less than the increase in height along the live crown. At Woodcock, there was a steep increase in cumulative leaf area with increasing height up to 10 % above the ground in both species (Fig. 2c). Between 10 and 60 %, LCL the rate of increase in cumulative leaf area was slightly greater than the increase in height along the live crown. Above 60 % live-crown depth, the rate of increase in cumulative leaf area was less than the increase in live-crown depth.

Vertical distribution of leaf area along stem

To examine the change in the vertical distribution of leaf area along the entire tree stem, mean leaf area (determined from the zone-specific models) was calculated for 10 % intervals of tree height for both species at either site (Fig. 2b, d). Leaf area distribution along the entire stem was skewed upwards for *E. pilularis* at both sites, with a mean of 38 and 39 % of the total leaf area distributed in the lower half of the stem. For *E. cloeziana* at Southgate, leaf area was approximately equally distributed between the upper and lower stem, with a mean of 48 % of the total leaf area in the lower half of the tree. However, leaf area distribution in *E. cloeziana* at Woodcock was strongly skewed downward with 64 % of the total leaf area within the lower half of the stem. For *E. pilularis* at both sites, almost no leaf area was present on the lower 10 % of stem.

Stem size and whole-tree leaf area relationships

Mean whole-tree leaf area (LA_t) estimates were not significantly different between the two sites but were significantly different between species (Table 4). Whole-tree leaf area for *E. pilularis* ranged from 32 to 68 m^2 at Southgate and 34 to 66 m^2 at Woodcock, while leaf area in *E. cloeziana* trees ranged from 33 to 128 m^2 at Southgate and from 37 to 119 m^2 at Woodcock. Relationships between LA_t and stem cross-sectional area at breast height ($CSA_{1.3}$) were weaker than those between LA_t and cross-sectional area at the base of the live crown (CSA_{lcb}) or between LA_t and $SapA_{1.3}$ at both Southgate and Woodcock (Fig. 3; Table 5).

Individual LAI values for the trees described in Table 1 ranged from 2.8 to 6.7 and 3.9 to 8.2 m^2 m^{-2} for *E. pilularis* and *E. cloeziana* at the Southgate site, respectively, and from 2.6 to 4.8 and 3.8 to 7.0 m^2 m^{-2} for *E. pilularis* and *E. cloeziana* at the Woodcock site, respectively. Mean tree LAI was significantly higher for *E. cloeziana* than *E. pilularis* trees but not significantly different between

Table 4 Whole-tree leaf area (LA_t in m^2) and leaf area index (LAI) for *E. pilularis* and *E. cloeziana* trees at two sites

Variable	Southgate		Woodcock	
	E. pilularis	*E. cloeziana*	*E. pilularis*	*E. cloeziana*
LA_t	50 (9.8)[a]	73 (9.8)[b]	48 (9.8)[a]	72 (9.8)[b]
LAI	4.1 (0.6)[a]	5.7 (0.6)[b]	3.8 (0.6)[a]	5.3 (0.6)[b]

Standard errors of mean are shown in parentheses

Means sharing the same letters are not significantly different from other means ($P > 0.05$)

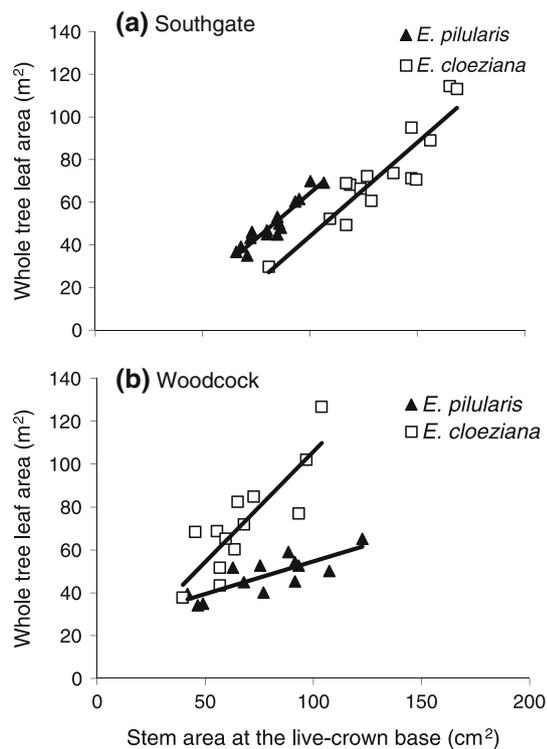For each species at Southgate $n = 15$ and for each species at Woodcock $n = 13$

Fig. 3 Relationship between cross-section area at the base of the live crown (CSA_{lcb} in cm^2) and whole-tree leaf area (m^2) for *E. pilularis* and *E. cloeziana* at the **a** Southgate and **b** Woodcock sites

sites (Table 4). LAI was only weakly correlated with both stem cross-sectional areas at the base of the live crown and at stem height at both sites.

Relationships between stem size variables (CSA_{lcb}, $CSA_{1.3}$, $SapA_{1.3}$) and LA_t determined using models where branches from all crown height zones were combined (general models) produced very similar levels of goodness of fit values to those produced using specific models for each crown height zone (Table 5). Similarly, the relationships between CSA_{lcb} and LAI and between $CSA_{1.3}$ and LAI generated using the general models yielded the same statistical significance and very similar goodness of fit and co-efficients as the specific model relationships.

Light transmission

Light transmission decreased non-linearly with depth in the crown on both the northern and eastern aspects for both species (Fig. 4). The rate at which transmission of relative light availability decreased was similar in the upper and lower crown zones for both species in both aspects. However, relative light availability decreased faster in the mid-crown of *E. cloeziana* than in *E. pilularis* in both aspects. In both species, relative light availability in the lower half of the tree crown was fairly constant. Total transmission was <10 % for *E. pilularis* and <5 % for *E. cloeziana*, of the total above-canopy light availability.

Discussion

The vertical distribution of leaf area along tree stems changes with stand development. The most marked

Table 5 Regression equations developed to predict whole-tree leaf area (LA_t in m^2) from stem cross-sectional area at the base of the live crown (CSA_{lcb} in cm^2), stem cross-sectional area at breast height ($CSA_{1.3}$ in cm^2) and sapwood area at breast height ($SapA_{1.3}$ in cm^2) for *E. pilularis* and *E. cloeziana* at two sites

Site	Allometric model type	Equation for *E. pilularis*	Predictor area range (cm^2)	r^2	Equation for *E. cloeziana*	Predictor area range (cm^2)	r^2
Southgate	Specific	$LA_t = -35.5 + 0.99 \times CSA_{lcb}$	66–107	0.86	$LA_t = -35.5 + 0.99 \times CSA_{lcb}$	81–169	0.82
	General	$LA_t = -51.5 + 1.17 \times CSA_{lcb}$	66–107	0.87	$LA_t = -65.2 + 1.17 \times CSA_{lcb}$	81–169	0.82
Woodcock	Specific	$LA_t = 19.3 + 0.37 \times CSA_{lcb}$	42–123	0.76	$LA_t = 3.9 + 0.95 \times CSA_{lcb}$	40–104	0.74
	General	$LA_t = 19.5 + 0.34 \times CSA_{lcb}$	42–123	0.78	$LA_t = 6.9 + 0.74 \times CSA_{lcb}$	40–104	0.77
Southgate	Specific	$LA_t = -12.2 + 0.56 \times CSA_{1.3}$	74–133	0.44	$LA_t = 9.8 + 0.56 \times CSA_{1.3}$	85–170	0.44
	General	$LA_t = -17.4 + 0.60 \times CSA_{1.3}$	74–133	0.35	$LA_t = 13.4 + 0.60 \times CSA_{1.3}$	85–170	0.37
Woodcock	Specific	$LA_t = 16.4 + 0.29 \times CSA_{1.3}$	85–152	0.23	$LA_t = -1.9 + 1.01 \times CSA_{1.3}$	49–104	0.75
	General	$LA_t = 10.7 + 0.31 \times CSA_{1.3}$	85–152	0.35	$LA_t = 3.03 + 0.78 \times CSA_{1.3}$	49–104	0.76
Southgate	Specific	$LA_t = -52.8 + 1.33 \times SapA_{1.3}$	66–89	0.91	$LA_t = -48.2 + 1.60 \times SapA_{1.3}$	54–80	0.82
	General	$LA_t = -43.7 + 1.21 \times SapA_{1.3}$	66–89	0.88	$LA_t = -73.9 + 2.06 \times SapA_{1.3}$	54–80	0.85
Woodcock	Specific	$LA_t = -9.3 + 0.76 \times SapA_{1.3}$	55–99	0.71	$LA_t = -18.9 + 2.15 \times SapA_{1.3}$	29–60	0.73
	General	$LA_t = -8.9 + 0.72 \times SapA_{1.3}$	55–99	0.81	$LA_t = -10.4 + 1.67 \times SapA_{1.3}$	29–60	0.75

A regression equation is shown for whole tree estimates determined using a specific allometric branch leaf area equations for each crown height zone (specific) and a general branch leaf area equation where branches from all zones were combined (General). All equations were significant ($P < 0.05$)

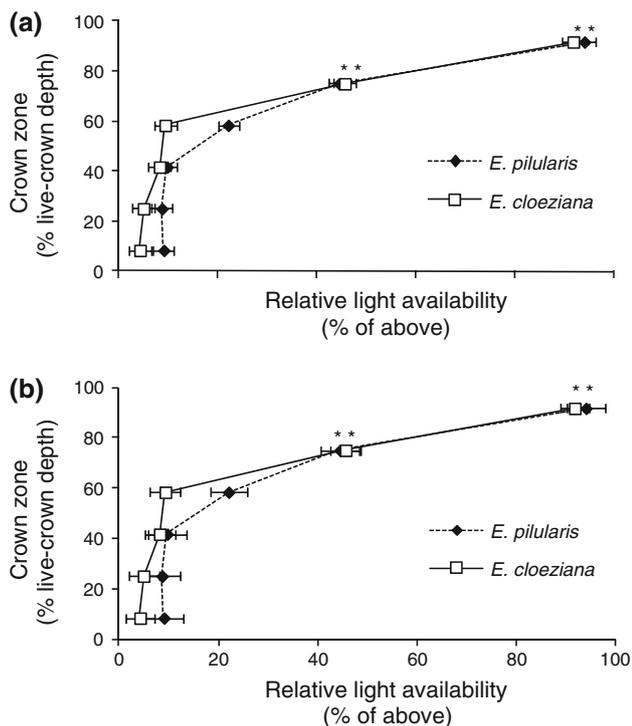For each species at Southgate $n = 15$ and at Woodcock $n = 13$ for each species

Fig. 4 Attenuation of relative light availability (% of total PPFD above the canopy) measured in the middle of six, equally spaced, vertical crown positions in the northern aspect (a) and eastern aspect (b) of *E. pilularis* and *E. cloeziana* trees at Southgate site. Sectioning of crown zones starts with 0 % at the base of the crown and moves to 100 % at the tree top. *Error bars* represent the standard error of mean for each species. *Asterisk* indicates significantly different mean relative light availability from all other crown positions at the 0.05 significance level. *n* = 8 for each species

changes occur at canopy closure as the amount of available light at the canopy base declines (Beadle 1997) resulting in a loss of leaf area from the lower crown and a redistribution of foliage toward the top of the crown (Mäkelä and Vanninen 1998; Medhurst and Beadle 2001; Forrester et al. 2012a). Leaf area distributions of *E. cloeziana* were skewed much more towards the lower crowns at the Woodcock site, consistent with the later canopy closure at that site; canopies of both species closed prior to sampling at Southgate and for *E. pilularis* at Woodcock, but for *E. cloeziana* at Woodcock canopies closed after sampling. The upward shift in vertical leaf distribution at the Southgate site is likely to be a response of increasing crown competition following canopy closure (Maguire and Bennett 1996; Xu and Harrington 1998; Forrester et al. 2012a). The Woodcock site was also steeper, which would have allowed more light to reach the lower crowns.

The vertical leaf area distributions also varied between species, particularly prior to canopy closure, such that distributions of *E. pilularis* were skewed more towards the upper crowns than those of *E. cloeziana*. This is probably related to differences in shade tolerance. The LAI of

E. cloeziana was about 40 % higher than that of *E. pilularis*, and a higher proportion of photosynthetically active radiation was intercepted by *E. cloeziana* crowns. *E. cloeziana* also had lower live-crown heights and slower rates of crown rise than *E. pilularis*, a trend that has been found for these species across a wide range of site qualities in northeastern New South Wales, Australia (Alcorn et al. in press). The higher LAI and light interception by *E. cloeziana* stands were not only associated with changes in leaf display but also with differences in leaf morphology. The SLA was higher for *E. cloeziana* (7.2–13.1) compared with *E. pilularis* (5.5–8.6), and both ranges are comparable to other sub-tropical eucalypt species (at similar ages) such as *E. grandis* (6–15, Almeida et al. 2004; Nouvellon et al. 2010), but higher than those reported for temperate eucalypt species such as *E. globulus* (3.5–5.6, Close et al. 2004) or *E. nitens* (3.5–6.0, Medhurst et al. 1999; Medhurst and Beadle 2005; Forrester et al. 2012b). The higher SLA indicates a lower carbon investment per unit of light intercepted by *E. cloeziana* compared with *E. pilularis* (Whitehead and Beadle 2004).

Specific leaf area also increased towards the lower crown zones, where light availability was lower, a trend that is consistent with findings in other tree species including *E. nitens* (Pinkard and Beadle 1998; Hunt et al. 1999; Medhurst et al. 1999), *Acacia dealbata* (Hunt et al. 1999), *Pseudotsuga menziesii* (Bartelink 1996), *Fagus sylvatica* (Bartelink 1997), *Quercus ilex* (Gratani 1997). This trend indicates the importance of canopy stratification when whole-tree leaf area is estimated from leaf mass. The pattern of decreasing SLA with increasing height is a morphological response to light availability (Smith 1991; Larcher 1995; Beaudet and Messier 1998), where less carbon is invested per unit light intercepted (Beadle 1993), to increasing resistance to hydraulic conductivity (Koch et al. 2004) and/or a consequence of leaf ontogeny (Ashton and Turner 1979). A vertical gradient of leaf ontogeny from immature to mature foliage was observed in *E. cloeziana*, which is common in young eucalypt crowns (Florence 1996). No ontogenetic differences between leaves were observed in crowns of *E. pilularis*, which may partly explain the larger vertical difference in SLA throughout the crown of *E. cloeziana* than *E. pilularis*.

The differences in crown architecture between sites and species have implications for pruning regimes in managed plantations. For the stands in this study, pruning to remove the lower 50 % of the LCL will remove about 55–57 % of the leaf area from both species after canopy closure. This lower crown zone intercepts less than 10 % of the photosynthetically active radiation, compared to the upper half of the LCL that intercepts more than 80 %. However, in stands in which the canopy has recently closed or is just prior to canopy closure, 71 or 76 % of the leaf area would

have been removed from *E. pilularis* and *E. cloeziana* crowns, respectively, and may therefore have a greater impact on the growth of the trees.

The relative transmission of diffuse PPFD used to characterise the light environment within the canopy in this study were similar to those in unthinned *E. nitens* trees. Medhurst and Beadle (2005) reported fractions of PPFD in the outer region of the upper, middle and lower crown zones of 0.51, 0.22 and 0.09, respectively. Estimates of the fractions of light in the upper, middle and lower third of the crown from Fig. 4 would be approximately 0.60, 0.15 and 0.10, respectively, for *E. pilularis* and 0.60, 0.10 and 0.08, respectively, for *E. cloeziana*. The greater rate of decrease in light availability with depth in the crown in *E. cloeziana* than *E. pilularis* at Southgate can be attributed to higher amounts of leaf area in the upper crown (Fig. 4). The low relative light availability in the lower crown is consistent with findings by Henskens et al. (2001), who reported very low levels (<10 %) of available light at the base of *E. globulus* canopies.

The strong relationships observed between branch cross-sectional area and branch leaf area for *E. pilularis* and *E. cloeziana* is consistent with other studies of young eucalypts (*E. nitens*, White et al. 1998; Hunt et al. 1999; Medhurst et al. 1999; Medhurst and Beadle 2001, 2002; Forrester et al. 2012a) (*E. globulus*, White et al. 1998) (*E. obliqua* L' Herit., Attiwill 1962) and other species (Whitehead et al. 1990; Bandara et al. 1999; Fernández and Norero 2006). For a given species, the relationships developed in this study varied between crown zones. This is likely related to processes of leaf senescence in the lower crown as also found in *E. nitens* plantations, where different equations were required for each zone (Medhurst and Beadle 2001) or degree of branch senescence (Forrester et al. 2012a).

This was illustrated by the high ratio or branch leaf area to branch cross-sectional area in the mid-crown, which is likely related to the development of branches at that level such that leaf area per branch increases until a maximum level before leaves are shed owing to self-shading from above. In unpruned *E. nitens* trees that had just reached canopy closure, a higher $LA:CSA_b$ ratio was reported for the mid-crown (50–70 % crown zone) than for the lower half of the tree (0–50 %) (Pinkard and Beadle 1998). In another *E. nitens* plantation, the leaf area density (m^2 leaf area per m^3 crown volume) declined towards the lower crown (Forrester et al. 2012a). Similar trends were found in both species at Southgate in this study. Higher maximum $LA:CSA_b$ ratios were recorded for both species at Southgate and *E. cloeziana* at Woodcock than for unthinned *E. nitens*. The lower LA:CSA ratio in the lower crown when compared to the mid-crown, suggests the beginning of leaf senescence due to shading at Southgate. This is

consistent with trees having reached canopy closure and commencement of the lift of the live crown. This also appears to be the case for *E. pilularis* at Woodcock, where leaf senescence appears to have occurred within the lower and mid-crown, as maximum LA:CSA ratios are lower than in all other crown zones and species. These vertical gradients in branch characteristics show the importance of stratifying sampling either by zone or branch characteristics.

Stronger relationships existed between whole-tree leaf area and stem area at the base of the live crown than with stem area at breast height (Table 5). Functionally, the stem area at the base of the live crown is more likely to reflect the water conduction requirements of the tree (Shinozaki et al. 1964a, b), which might explain the closer relationship observed in this study and other studies (Medhurst et al. 1999).

Management implications

The timing of pruning to remove branches before the live crown rises above the ground is considered desirable for most eucalypts to avoid pruning dead branches, which may affect future wood quality (Montagu et al. 2003). *E. cloeziana* had a higher LAI and live-crown ratio than *E. pilularis*, suggesting that *E. cloeziana* can be pruned later than *E. pilularis*. The retention of lower foliage in *E. cloeziana* at age 4 years may be the result of higher shade tolerance or more efficient use of carbon in low light environments as indicated by its higher specific leaf area. However, the exact timing of pruning also depends on the desired size of the central knotty core of the stem, the maximum diameter of branches considered for pruning and stem height to which pruning will occur (Alcorn et al. in press).

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