Determination of specific leaf area of some commercially useful sub-tropical hardwood species

Mark A. Hunt[1,2,4], Kate E. Murray[1], Michael Battaglia[3,4] and Nicole J. Mathers[4]

[1]Department of Primary Industries and Fisheries, Locked Bag 16, MS 483 Fraser Rd, Gympie 4570, Queensland, Australia
[2]Email: mark.hunt@dpi.qld.gov.au
[3]Ensis, GPO Box 252-12, Hobart 7001, Tasmania, Australia
[4]CRC Forestry, GPO Box 252-12, Hobart 7001, Tasmania, Australia

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Summary

Variability of specific leaf area (SLA) across taxa, sites and crown zones was determined for four sub-tropical hardwood species, *Eucalyptus grandis*, *E. cloeziana*, *E. argophloia* and *Corymbia citriodora* ssp. *variegata*, growing in south-eastern Queensland. Mean SLA values were stable amongst those taxa sampled on dry sites but varied markedly between provenances of *E. grandis* on a moist site. Mean SLA did not vary significantly with crown zone in any of these four sub-tropical eucalypts, which is in contrast to that observed in temperate species, both in Australia and overseas. A provenance of *E. cloeziana* from a moist coastal site exhibited the largest SLA of all taxa studied.

Keywords: leaf area; variation; species differences; provenance; environment; subtropics; models; *Eucalyptus*; Queensland

Introduction

The east coast and sub-tropical eucalypt species in Australia have evolved with soft leaves on warm, moist and sometimes nutrient-rich sites, and such species are candidates for wood production on high-quality sites over short rotations (Kriedemann 1996). In Queensland, Australia, development of a hardwood plantation industry was in its infancy only 5 y ago (Lee *et al.* 2001) with only 5% (about 9000 ha) of the industrial plantation resource planted to hardwoods in south-eastern Queensland (Wood *et al.* 2001). Lee *et al.* (1998) have suggested that large differences in growth rates could be expected between provenances of sub-tropical species at the broad regional level, and within regions, because of the large range of natural environments and, hence, genetic differences due to specific adaptation to these local environments. In temperate/subtropical eucalypt species (*Eucalyptus occidentalis*, *E. camaldulensis* and *E. grandis*), Sefton *et al.* (2002) reported significant differences in leaf morphology and physiology between species growing in common environments. They suggested that leaf traits of eucalypt seedlings were strongly influenced by genetic factors which reflected the species' natural habitats. Unfortunately, little information is widely available on the physiology of sub-tropical species and their provenance variation, particularly from the sub-tropical lowlands of southern Queensland (Linder 1985; Lee *et al.* 1998), except for *E. grandis* (Cromer and Jarvis 1990; Leuning 1990; Leuning *et al.* 1991; Birk and Turner 1992; Cromer *et al.* 1993). Longer-term knowledge of these species is necessary to drive selection and management decisions that at present have little in the way of historical or empirical yield data to suggest limits to survival and/or growth across the potential plantation estate.

Estimates of leaf area are required for predictions of growth, transpiration and light interception (Medhurst and Beadle 2002), and leaf area index (L^*) is one of the sensitive variables that is of most interest to physiologists and process modellers when attempting to predict the productivity of forest stands (Sands 1995; Sands *et al.* 2000). Stand L^* is commonly calculated as the product of foliage mass and specific leaf area (SLA, $m^2\ kg^{-1}$), which is the ratio of fresh foliage surface area to unit dry foliage mass (Landsberg and Gower 1997). SLA is an important link between plant carbon and water cycles because it describes the distribution of plant biomass relative to leaf area within a plant canopy (Pierce *et al.* 1994). Predicting forest productivity on sites not yet established with hardwood plantations will require models to assess the suitability of such sites for different tree species. Two such process-based models are 3-PG (Landsberg and Waring 1997) and CaBala (Battaglia *et al.* 2004). Whereas some models explicitly use L^* as an input parameter, 3-PG and CaBala calculate L^* internally using input parameters of SLA and foliage mass (Sands 1996; Battaglia *et al.* 2004). Such models have been initially parameterised to meet the needs of temperate species, such as *E. globulus* (Battaglia and Sands 1997) or *Pinus radiata* (Landsberg and Waring 1997), but are capable of being parameterised for other species, such as *E. nitens* (Sands *et al.* 2000) and *Picea sitchensis* (Waring 2000). Parameterisation of the process-based productivity models 3-PG and CaBala for site selection and forest productivity of sub-tropical and tropical species requires the specification of an average SLA value. However, inter-specific variance in SLA is unknown in sub-tropical hardwood species, particularly in relation to physiological parameters, such as crown zone, and little information is available in the published literature on SLA or L^* of the sub-tropical hardwoods of Australia (Linder 1985; Lee *et al.* 1998).

The objectives of this study were to:

(a) measure SLA and its variation among species and silvicultural treatments of four sub-tropical eucalypt species

(b) compare the results with those published in the literature for temperate eucalypts

(c) consider the magnitude of the effect that any measured differences in (a) and (b) might have on yield or productivity estimates predicted by the process-based models 3-PG and CaBala.

Materials and methods

Species descriptions

Eucalyptus grandis

Eucalyptus grandis (flooded gum, rose gum) is a tall to very tall forest tree that generally grows to 45–55 m in height and 1.2–2 m diameter at breast height (dbh) (Boland *et al.* 1994). This species is naturally distributed in coastal areas and sub-coastal ranges from Newcastle in New South Wales (NSW) northwards to west of the Daintree in northern Queensland (Brooker and Kleinig 1996). The climate is mostly warm humid, and for the northern areas the temperature ranges for the hottest and coolest months are 29–32°C and 10–17°C, respectively. Mean annual rainfall is in the range of 1000–3500 mm with a distinct summer maximum. *Eucalyptus grandis* occurs on flats or the lower slopes of deep fertile valleys, commonly on the fringes of rainforest, and prefers moist, well drained, moderate to high fertility soils of alluvial or volcanic origin (Boland *et al.* 1994).

Eucalyptus cloeziana

Eucalyptus cloeziana (Gympie messmate) is typically a small (10 m) to tall (20–35 m) tree that reaches its best development in the Gympie region, where it can attain heights up to 60 m and 2 m dbh (Boland *et al.* 1994). *Eucalyptus cloeziana* occurs widely across Queensland but in scattered areas, particularly east of Tambo to Mundubbera and Gympie, and from west of Townsville to north-west of Cooktown (Brooker and Kleinig 1996). The climate is warm sub-humid to humid with the mean maximum temperature of the hottest month in the range 29–34°C and the mean minimum of the coldest month around 5–18°C. Up to five light frosts can occur each year through most of the range. The mean annual rainfall varies greatly from 550 to 2300 mm and the best development is on metasediments or loams of volcanic origin of moderate depth. However, *E. cloeziana* does occur on shallow soils over coarse sandstone or on shallow to moderately deep coarse-textured soils derived from granite (Boland *et al.* 1994).

Eucalyptus argophloia

Eucalyptus argophloia (western white gum) is a medium-sized to tall tree reaching 40 m in height and 1 m in dbh. This species is endemic to a small area around 40 km long and 20 km wide north-east of Chinchilla, in southern Queensland, including Burncluith, Pelican and Burra Burri (Boland *et al.* 1994; Brooker and Kleinig 1996). The climate is warm sub-humid, with the mean maximum temperature of the hottest month around 32°C and the mean minimum of the coldest month around 4°C. Some 10–15 frosts may occur each year and the mean annual rainfall is around 700 mm. *Eucalyptus argophloia* grows on the edges of flats in country of low topographic relief where the soils are red loams or grey-brown clays and clay loams of moderate fertility (Boland *et al.* 1994). It is considered vulnerable to extinction (Leigh and Briggs 1992) because much of the habitat has been developed for cropping and pasture, and only about 40 scattered natural populations remain in the area (Norton 1997).

Corymbia citriodora *ssp.* variegata *(formerly* Eucalyptus maculata*)*

Corymbia citriodora ssp. *variegata* (spotted gum) is a medium-sized to tall tree, reaching 35–45 m in height and 1–1.3 m dbh (Boland *et al.* 1994). This species is widely distributed in coastal areas of NSW, and in Queensland it extends northwards to Maryborough and up to 400 km inland. The climate of the natural distribution is warm humid to warm sub-humid and the mean maximum temperature of the hottest month is 25–30°C. The mean minimum of the coldest month is 1–8°C and frosts are few and fairly mild in coastal areas, but up to 60 per year can occur in colder sites. The mean annual rainfall is 750–1750 mm. *Corymbia citriodora* ssp. *variegata* grows on a wide range of soils, the best development being on well-drained and moderately heavy textured soils such as those derived from shales (Boland *et al.* 1994).

Site and stand descriptions

In total, trees in seven pre-existing experiments — two at Toolara and five at Narayan — were sampled to provide data for this study.

Toolara

The two experiments at Toolara were located within the Toolara Forest Reserve in south-eastern coastal Queensland (26°00'S, 152°49'E). The annual rainfall at this site is about 1300 mm.

Toolara 1 — 350 HWD

This was an area of first-rotation slash pine (*Pinus elliottii* ssp. *elliottii*) established in 1950 (Cromer *et al.* 1993). Remnants of native vegetation imply that the freely drained rises were home to open forests and woodlands in which *E. signata* and *E. intermedia* were probably the most common and widely distributed species (Ross and Thompson 1991). The pine plantation was clearfelled during 1986 and the stumps were removed. The site was ploughed and isolation drains separating plots were constructed before being hand-planted with *E. grandis* seedlings in late February 1987. The stocking rate was 1111 stems ha^{-1} (spacing 3.4 m × 2.65 m). A detailed description of site and soil characteristics is provided by Ross and Thompson (1991). Fertilisation and irrigation treatments were established to examine the maximum growth potential by elimination of water and nutrients as limiting growth factors. Two replications of a 2 × 2 × 4 experiment (32 treatments) were laid out as a randomised complete block design, each with 42 trees (6 rows of 7 trees) for each treatment. Fertiliser treatments of (1) zero and (2) luxury (1600 kg N, 480 kg P, 480 kg K, 458 kg Ca, 2138 kg S, 24 kg Cu, 24 kg Zn and 24 kg B per hectare) were applied over the initial 4-y period, with three applications per year. The selected sample plots were irrigated during this time at a watering regime equivalent to 7.75 mm h^{-1}. This was applied to replace the quantity of water corresponding to pan evaporation and transpiration. Irrigation water from a ground-water bore adjacent to the site was applied up to several times per week using under-tree sprays. The site was kept totally weed free for the initial 4-y period by spraying with herbicide, and insects and pathogens were controlled during this period when necessary (Cromer *et al.* 1993).

Toolara 2

Toolara 2 is situated on the alluvial flats of Tinana Creek and the vegetation remnants indicate that the young alluvia carried wet sclerophyll forest close to the stream consisting of vine scrub species with *E. grandis* emergents (Ross and Thompson 1991). The site was ploughed twice with a Shearer Majestic disc plough and mounds (0.5 m high × 0.8 m wide) were formed with two passes of the plough during December 1986, before being hand-planted with *E. cloeziana* seedlings in March 1987 at a stocking of 1111 stems ha^{-1} (spacing 4 m × 2.25 m). Ross and Thompson (1991) provide a detailed description of site and soil characteristics. An initial fertiliser application at planting and a further seven applications during the 2-y project saw a total of 402 kg N, 121 kg P, 121 kg K, 115 kg Ca, 649 kg S and 6 kg each of Cu, Zn and B applied per hectare. The mounded areas on the site were kept totally weed free by spraying with herbicide.

Narayen

The five experiments at Narayen were located at the Narayen Research Station (formerly managed by CSIRO) near Mundubbera, south-eastern Queensland (25°41'S, 150°52'E).

Narayen 1 — 505b TCA

Narayen 1 was part of a species evaluation trial established in 1992 to compare the performance of 30 tree species, aiming to identify those suitable for planting in the 500–600 mm y^{-1} rainfall zone of southern Queensland. Narayen 1 has a general rolling relief, with a local, gentle (2%) upper slope and a south-western aspect. The soil is decomposed granite, described as a hard pedal, yellow duplex Prairie Soil (yellow podsolic DY242) with a surface pH of 6.5. The topsoil depth is 40–90 cm and the original vegetation was open grassy eucalypt woodland. The vegetation present (grass and herbs) was partially removed by slashing and the site was deep ripped to >30 cm, with a three-tine ripper. Weeds were sprayed with glyphosate in February 1992 and the site was then left fallow for 2 months. *Eucalyptus argophloia*, *E. cloeziana* and *C. citriodora* ssp. *variegata* were established in late March 1992 when they were fertilised with 130 g Crop King 55® ('CK55': 13.2% N, 14.7% P, 13.2% K, 1.5% S). Any dead plants were refilled in May 1992. No irrigation at planting was required and initial spacing was 1250 stems ha^{-1} (4 m × 2 m), which were thinned to 500 stems ha^{-1} in May 1995. All plots were form pruned in April 1994. Fertiliser was applied again in March 1994 with 110 g DAP (18% N, 23% P). The total amounts of nutrients applied were 46 kg N, 55 kg P, 20 kg K and 2.5 kg S per hectare.

Narayen 2 — 517 TCA

Narayen 2 was a weed mat trial conducted for University Partnerships – University of New England, in which five establishment treatments, including weed control, were examined. Species originally included *Casuarina cunninghamania*, *Acacia holosericea* and *E. argophloia*, but only *E. argophloia* remained at the establishment of this experiment. The soil at Narayen 2 is described as a red-yellow podsol, with the original vegetation having been a low open forest. The planting lines were ripped to a depth of about 25 cm with a three-tine ripper in January 1993. The experimental area was completely disc harrowed in late February 1993 and a band 1 m wide down each side of the planting line was kept weed free through applications of glyphosate and simazine herbicides. Stock was planted in late March 1993 and fertilised initially in April 1993 with 150 g of CK55, and re-fertilised with 500 g Custom Blend® (CB) in October 1998. Initially spaced at 1 m × 3 m intervals in line plots, the stand was thinned and ground pruned in August 1998, and minor form pruned and tended in August 1999.

Narayen 3 — 512 TCA

This experiment was originally a species evaluation trial in the 500–700 mm y^{-1} rainfall zone of southern Queensland. A ridge site, the original vegetation was grassy eucalypt woodland, but before establishment it was an improved pasture dominated by *Cenchrus ciliaris* (buffel) and *Chloris guayana* (rhodes) grasses. The soil is described as a soloth with sandy loam topsoil and a medium clay subsoil overlaying decomposed granite at 40–90 cm. Prior to planting with species including *E. argophloia* and *C. citriodora* ssp. *variegata* in late March 1993, the site was sprayed with glyphosate to achieve a weed-free band 2 m wide along planting rows. All stock was fertilised at planting with 150 g stem^{-1} of CK55 (supplying 23 kg N ha^{-1}, 24 kg P ha^{-1} and 20 kg K ha^{-1}). Trees were re-fertilised at 12 months with 20 kg N ha^{-1} and 23 kg P ha^{-1}. Plots were thinned from 1103 to 662 stems ha^{-1} after 2 y, leaving 6 stems per plot. Weed control after planting consisted of glyphosate and simazine applications aimed at maintaining a weed-free zone of 1 m radius around each stem.

Narayen 4 — 528 TCA

This site was planted in August 1997 with *C. citriodora* ssp. *variegata*. After planting, the site was mown and chip hoed, and simazine and glyphosate herbicides were applied. All stock was fertilised at establishment with 30 g stem^{-1} CK55 and re-fertilised with Crop King 88® (CK88) at 30 g stem^{-1} in November 1998. A further 500 g stem^{-1} of CB was applied in October 1998 and at age 12 months the stand was thinned from 2500 to 1500 stems ha^{-1}. All stems retained were ground pruned to 1–1.3 m.

Narayen 5 — John Wilson experiment

Narayen 5 was located on cleared brigalow (*Acacia harpophylla*) country with a mean annual rainfall of 712 mm (Wilson 1998). The soil was a highly fertile dark brown clay with very high total soil N (about 0.6%) and organic carbon content (about 6–7%) in the surface 0–100 mm (Catchpoole 1992; Wilson 1998). The previous vegetation of old (>15 y), sown pasture (mostly green panic, *Panicum maximum*) was originally fertilised with superphosphate at 100 kg ha^{-1} y^{-1}. No fertiliser was applied in the several years preceding or during the experiment and it had never been fertilised with nitrogen. No site preparation occurred, apart from planting *E. argophloia* in January 1989 into holes with roughened sides. At stand establishment, each seedling received 150 g of di-ammonium phosphate fertiliser spiked into a hole 0.12 m deep (about 0.1 m from the stem), and the pasture was slashed 4 months later. The site has been described in detail by Wilson (1998).

Foliar sampling

Foliage was sampled from four tree species in two campaigns during 1999 (see Table 1).

- *Eucalyptus grandis* (Coffs Harbour and Pomona provenances) and *E. cloeziana* (Woondum provenance). Each species was sampled in a separate experiment at Toolara. Both experiments, planted in 1987, were sampled during July–August 1999.
- *Corymbia citriodora* ssp. *variegata* (Presho and St Mary provenances), *E. cloeziana* (Coominglah provenance) and *E. argophloia* (Nudley provenance only). These three species were sampled in 1999 across varying numbers of the five experiments of varying age (2–10 y old) at Narayen.

For each selected tree, leaves were sampled from the upper, middle and lower crown zones. Designation of crown zone was based on equal vertical divisions of the foliage. Within each crown zone, foliage was sampled from fully expanded leaves in the northern aspect of the outer crown. In every case, each sample contained ten leaves, severed at the base of the leaf, leaving the petiole on the branch. All samples were stored and transported to the laboratory in a portable refrigerator in sealed plastic bags.

Specific leaf area

Specific leaf area (SLA) was measured using a Delta-T Devices Ltd Area Meter Mk 2, (Cambridge, UK) with a reading frame of about 450 mm × 300 mm and a resolution of 50 dpi. Measurements were made of a single-sided leaf (area reported in m^2 kg^{-1}) on the basis of oven-dry weight at 75°C (W_{75}). The instrument was calibrated according to the manufacturer's instructions prior to use and subsequently at 30-min intervals.

Statistical analysis

Statistical analysis (analysis of variance, ANOVA) was undertaken using Genstat V9 (Laws Agricultural Trust 2007) and SigmaStat V3.1 (Systat Software 2004). When investigating within-crown variation in SLA, crown zones were treated as subplots within trees (as plots) in a split-plot ANOVA model. Differences amongst provenances where more than one taxon was planted at a site were investigated using one-way ANOVA, and fertiliser × provenance effects were investigated using two-way ANOVA. Due to the confounded nature of much of the data, the use of ANOVA was restricted to only a subset of the data and we have relied on presentation of means and standard errors for many of the comparisons.

Results

All species

Average SLA for all sites, species and provenances are shown in Table 2.

There was little variation in SLA among crown zones for any of the species or provenances considered in this study, though there was marked variation between provenances in some cases. Figure 1 indicates that in all crown zones *E. cloeziana* displayed the greatest SLAs (7.3, 6.9 and 6.9 m^2 kg^{-1} for the lower, middle and upper crown zones, respectively — means of two provenances) while *E. argophloia* and *C. citriodora* ssp. *variegata* exhibited the lowest SLA in all crown zones (4.7, 4.3 and 4.4 m^2 kg^{-1} and 4.5, 4.7 and 4.9 m^2 kg^{-1}, respectively). When the SLAs within each crown zone were analysed for individual provenances at each site, only two provenances displayed any variation with crown zone. These were the Coffs Harbour provenance of *E. grandis* (at Site 1) and Woondum provenance of *E. cloeziana* (at Site 2). In the Coffs Harbour *E. grandis* the larger leaf areas were measured in the lower crown zones of both fertilised and unfertilised trees but this variation in SLA was not statistically significant. However, in the Woondum provenance the SLA of the lower crown zone was significantly different from that of both the upper ($P<0.05$) and middle ($P<0.01$) crown zones.

Table 1. The number of sample trees in the matrix of species, provenances and experiments

Species	Provenance	Seedlot	Location	Location and experiment						
				Toolara		Narayen				
				1	2	1	2	3	4	5
E. grandis	Coffs Harbour* (NSW)	15641	30°18'S, 153°08'E	12						
E. grandis	Pomona* (Qld)	Unknown	26°23'S, 152°52'E	12						
E. cloeziana	Woondum*	14425	26°18'S, 152°48'E		10					
E. cloeziana	Coominglah#	7	25°00'S, 151°00'E			6				
C. citriodora ssp. *variegata*	St Mary*	179	25°45'S, 152°29'E			4				
C. citriodora ssp. *variegata*	Presho#	178	25°11'S, 149°10'E					6	8	
E. argophloia	Nudley#	46	26°31'S, 151°00'E			4	2	6		2

* Moist coastal provenance
\# Dry inland provenance

Table 2. Mean specific leaf area (SLA) (± standard deviation) for all sites, species and provenances

Species	Provenance	Site	Experiment	Fertilised	Age (y)	Crown zone SLA ($m^2\ kg^{-1}$)		
						Lower	Middle	Upper
E. grandis	Coffs Harbour	Moist coastal	Toolara 1	No	12	7.00 ± 0.74	6.69 ± 0.39	6.09 ± 0.75
E. grandis	Coffs Harbour	Moist coastal	Toolara 1	Yes	12	6.89 ± 0.96	6.16 ± 0.52	6.39 ± 1.03
E. grandis	Pomona	Moist coastal	Toolara 1	No	12	5.10 ± 0.88	5.45 ± 0.65	5.01 ± 0.36
E. grandis	Pomona	Moist coastal	Toolara 1	Yes	12	4.87 ± 0.58	5.15 ± 0.43	5.13 ± 0.44
E. cloeziana	Woondum	Moist coastal	Toolara 2	Yes	12	9.66 ± 1.56	8.70 ± 1.18	8.81 ± 1.10
E. cloeziana	Coominglah	Dry inland	Narayen 1	Yes	7	4.87 ± 0.18	4.99 ± 0.34	5.00 ± 0.34
E. argophloia	Nudley	Dry inland	Narayen 1	Yes	7	4.63 ± 0.57	4.53 ± 0.49	4.44 ± 0.59
E. argophloia	Nudley	Dry inland	Narayen 2	Yes	6	4.48 ± 0.65	4.20 ± 0.53	4.02 ± 0.71
E. argophloia	Nudley	Dry inland	Narayen 3	Yes	6	4.95 ± 0.94	3.99 ± 0.99	4.49 ± 1.29
E. argophloia	Nudley	Dry inland	Narayen 5	Yes	10	5.29 ± 0.56	4.67 ± 0.04	5.10 ± 0.56
C. citriodora ssp. *variegata*	St Mary	Dry inland	Narayen 1	Yes	7	4.81 ± 0.34	4.91 ± 0.29	5.19 ± 0.31
C. citriodora ssp. *variegata*	Presho	Dry inland	Narayen 3	Yes	6	4.72 ± 0.42	4.65 ± 0.32	4.47 ± 0.45
C. citriodora ssp. *variegata*	Presho	Dry inland	Narayen 4	Yes	2	4.26 ± 0.29	4.55 ± 0.56	4.68 ± 0.66

Eucalyptus grandis

When *E. grandis* was analysed separately from the other three species, there was a highly significant difference ($P < 0.001$) in the SLA of the two provenances (Coffs Harbour and Pomona) (Fig. 2) but no difference was detected between fertiliser treatments. Similarly, SLA did not vary significantly amongst crown zones. Figure 2 indicates that the Coffs Harbour provenance exhibited a greater mean SLA in all crown zones (6.9, 6.4 and 6.2 $m^2\ kg^{-1}$ for the lower, middle and upper crown zones, respectively) than the Pomona provenance (SLA values of 5.0, 5.3 and 5.0 $m^2\ kg^{-1}$ for the lower, middle and upper crown zones, respectively).

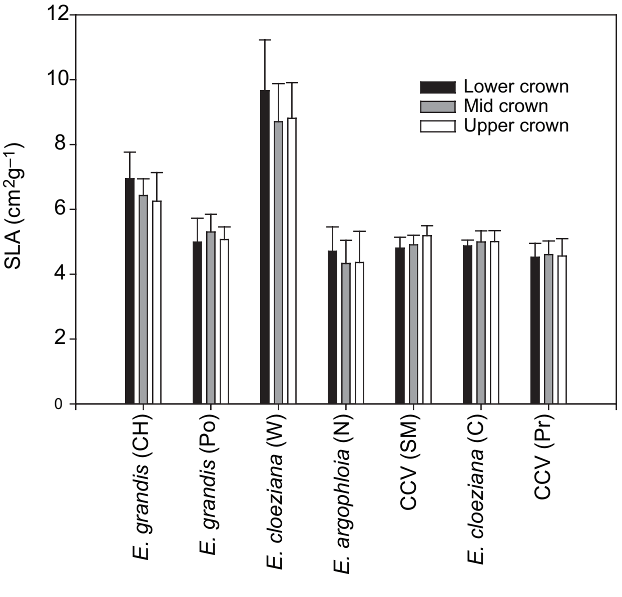

Figure 1. Specific leaf area (SLA) ($m^2\ kg^{-1}$) of each crown zone for the seven taxa sampled (CH = Coffs harbour; Po = Pomona; W = Woondum; N = Nudley; CCV (SM) = *C. citriodora* ssp. *variegata* St Marys; C = Coominglah; Pr = Presho). Means are presented with standard deviation for each crown zone.

Dry vs moist sites

Within species and provenances, SLA differed markedly between the moist and dry sites (Table 2). Notably there were large differences in *E. cloeziana* SLA. Trees on moist sites exhibited a greater mean SLA (6.8 $m^2\ kg^{-1}$) than those species on dry sites (4.7 $m^2\ kg^{-1}$) However, age and provenance variation prevented significance testing and meaningful interpretation of these differences.

Moist sites: Eucalyptus grandis *vs.* Eucalyptus cloeziana

Both provenances of *E. grandis* and the Woondum provenance of *E. cloeziana* were situated on the coastal (moist) sites in the Toolara Forest Reserve. At the species level, *E. cloeziana*

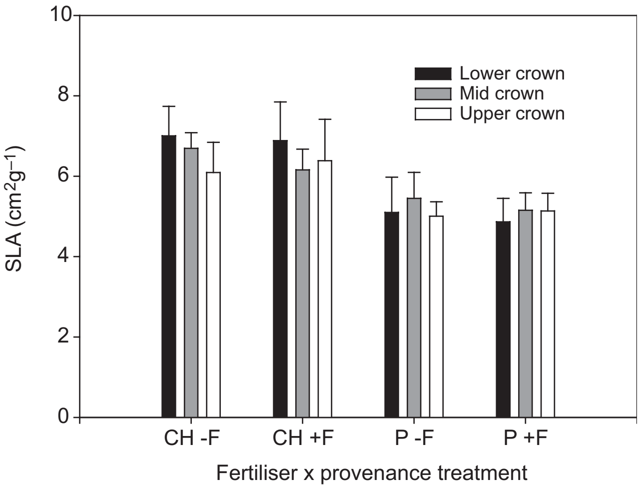

Figure 2. Specific leaf area (SLA) of *E. grandis* in relation to provenance and fertiliser treatment (CH = Coffs Harbour, P = Pomona; -F = non-fertilised, +F = fertilised). Means for each crown zone are shown with standard deviation.

exhibited a much greater SLA (9.7, 8.7 and 8.8 m^2 kg^{-1} for the lower, middle and upper crown zones) than *E. grandis* (5.8, 5.8 and 5.5 m^2 kg^{-1}) in all crown zones (Table 2).

Dry sites

The three dry-site taxa at Site N1 (*E. cloeziana* Coominglah, *E. argophloia* and *C. citriodora* ssp. *variegata* St Mary) did not display a significant difference in SLA amongst the three crown zones (Fig. 3). Neither were the SLA values for the three taxa significantly different from one another. The two dry-site taxa at Site N3 (*E. argophloia* and *C. citriodora* ssp.*variegata* Presho provenance) similarly did not exhibit significant differences either amongst crown zones or between taxa (Fig. 4).

Whilst it was not possible to statistically compare the two *C. citriodora* ssp. *variegata* provenances (as they were planted at different sites), the St Mary provenance exhibited a consistently greater SLA than Presho provenance in all crown zones (Table 2).

E. argophloia *and* C. citriodora variegata

E. argophloia was planted at four of the dry site experiments (Table 1). SLA was not significantly different amongst crown zones or between sites (Fig. 5). Similarly, where *C. citriodora* ssp. *variegata* was considered at two sites, no differences amongst crown zones or sites were detected (Fig. 6).

Discussion

Eucalyptus grandis

E. grandis has been, by far, the most studied of the sub-tropical eucalypts considered 'viable' for commercial use in southern

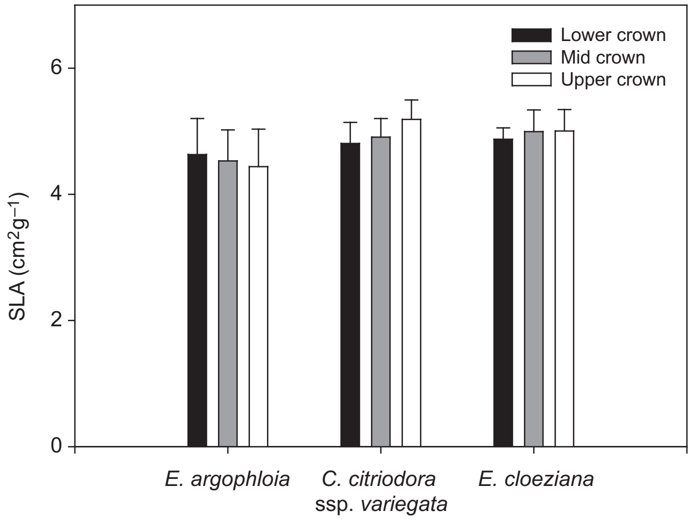

Figure 3. Specific leaf area (SLA) of the three taxa (*E. argophloia*, *C. citriodora* ssp. *variegata* Coominglah and *E. cloeziana* St Mary) planted at Site N1, a dry inland site. Means are plotted with standard deviation.

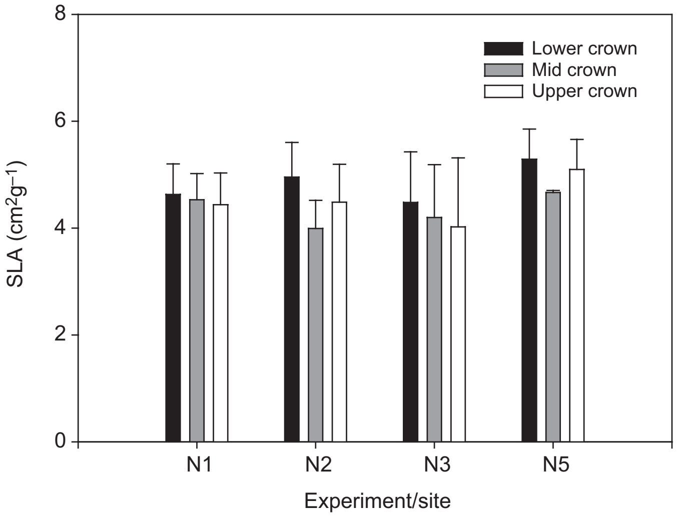

Figure 5. Variation in specific leaf area (SLA) among crown zones for *E. argophloia* at Sites N1, N2, N3 and N5, all dry inland sites. Means are shown with standard deviation.

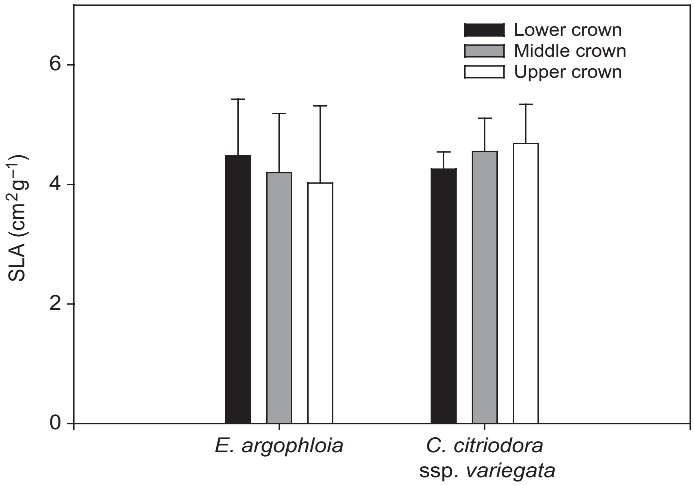

Figure 4. Variation in specific leaf area (SLA) between crown zones for two species planted at Site N3, *E. argophloia* and *C. citriodora* ssp. *variegata* Presho. Means are shown with standard deviation.

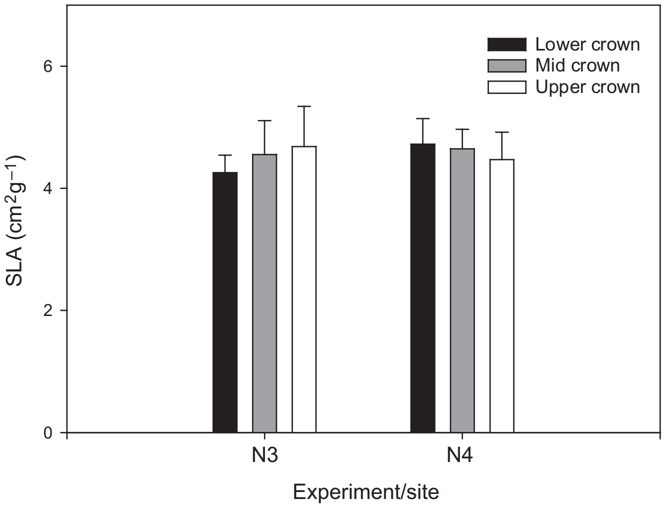

Figure 6. Specific leaf area (SLA) differences (means with standard deviation) among crown zones for *C. citriodora* ssp. *variegata* (Presho) planted at Sites N3 and N4, both dry inland sites.

Queensland. Cromer *et al.* (1993) reported that high productivity of *E. grandis* was dependent on maintaining a high L^* to intercept a high proportion of the available solar radiation, and for plants that are high in nitrogen (N), SLA becomes very important. Cromer and Jarvis (1990) demonstrated that SLA and leaf nutrient concentrations of *E. grandis* increased as the rate of N uptake increased. In the study by Cromer *et al.* (1993), SLA was initially higher in those trees that had been fertilised compared with those that had not, but declined over the first 2 y to 10 $m^2 kg^{-1}$, indicating that values of SLA tend to be high in seedlings and to decline with age. Linder (1985) also found a decline in SLA from over 20 $m^2 kg^{-1}$ when trees were <3 months old to about 5 $m^2 kg^{-1}$ when they were >12 months old. The great changes in SLA of eucalypts observed during the sapling stage result from pronounced differences in juvenile and adult foliar morphology (Leuning *et al.* 1991).

In the current study, SLA was determined for 12-y-old *E. grandis* stands that were fertilised and irrigated (or not) during the first 4 y of establishment. For the Coffs Harbour provenance there were no significant differences in SLA between crown zones in either the fertilised or non-fertilised trees, and there were no significant differences between fertiliser treatments. The Coffs Harbour provenance exhibited greater mean SLA in all crown zones than the Pomona provenance (Fig. 2), but SLA did not differ significantly with crown zone for either fertilised or non-fertilised trees in the Pomona provenance. Coffs Harbour proved to be the better provenance within this region, and this would most likely be due to poor seed stock possibly including in-breeding in the Pomona provenance. Both provenances, however, displayed little variation in SLA with crown zone in the canopy.

The lack of variation of SLA with fertiliser treatment for both provenances within this 12-y-old *E. grandis* stand supports the view of Cromer *et al.* (1993) that changes in SLA due to nutrition were an important determinant of growth rate in seedlings and young trees, but that this influence declined rapidly as the trees approached canopy closure. SLA also did not differ significantly with crown zone in this study, which contrasts sharply with the significant differences in SLA observed with crown zone for other eucalypt species (Pierce *et al.* 1994; Pinkard and Beadle 1998; Medhurst and Beadle 2002). The study by Pinkard and Beadle (1998) indicated that SLA of an *E. nitens* plantation increased with depth in the crown, reflecting changes in the light environment. Medhurst and Beadle (2002) also reported that SLA of an *E. nitens* plantation varied significantly with crown zone, with the lower zone having a significantly higher SLA ($P<0.01$) than the middle and upper zones.

Eucalyptus cloeziana

Eucalyptus cloeziana (Woondum) exhibited the greatest mean SLA of all the species in this study, most probably due to its better adaptation to the Gympie region where it was planted, while the Coominglah provenance displayed values similar to those reported for *E. grandis* by Cromer *et al.* (1993) and the values obtained for the Pomona provenance in the current study. The large differences observed between the two *E. cloeziana* provenances could be a direct result of site conditions (dry vs. moist) but could also be due to higher levels of inbreeding or poorer quality seed parents in the Coominglah provenance (Lee *et al.* 1998), even though it has performed well in trials overseas (Moura *et al.* 1993). Dickinson *et al.* (1996) have reported that 3.5 y after establishment Woondum provenance (southern Queensland) trees survived, grew and resisted defoliation as well as or better than a Cardwell provenance (northern Queensland), and provenances from lower-rainfall sources (≤ 1300 mm) generally had lower growth potential. Pierce *et al.* (1994) state that species grown in water-limiting environments typically have reduced SLA in comparison to the same species grown in non-water-limiting environments, and the data from this study certainly support that contention. As the Coominglah provenance was grown on dry sites, its much lower SLA than the Woondum provenance could be a direct result of it being planted in the water-limiting environment at Narayen Research Station.

Eucalyptus argophloia and *Corymbia citriodora* ssp. *variegata*

Eucalyptus argophloia exhibited the lowest mean SLA values in this study (particularly for the middle and upper crown zones). This species, however, may prove to have greater growth potential on water-limited sites than the other three species considered. This is because reduced SLA can indicate an adaptation to water-limiting environments (Pierce *et al.* 1994) and in its natural range *E. argophloia* experiences a mean annual rainfall of only 700 mm. Improvement of this species (by selection of specific traits) to grow in water limiting, drought environments may also improve its status as 'vulnerable to extinction'. As with the other species studied, the mean SLA values for *E. argophloia* did not vary significantly between crown zones.

Pook (1984a,b, 1985) studied the canopy dynamics of a regenerated 16-y-old stand of pole and sapling *E. maculata* (now *C. maculata* — see McDonald and Bean (2000) regarding classification of these taxa) in NSW. An average SLA value of 5.1 $m^2 kg^{-1}$ was reported by Pook (1984b) for mature leaves and the L^* was found to decrease from 4.3 to 0.8 after a 7-month drought, but these values recovered after the break of the drought to pre-drought values (Pook 1985). The SLA values determined for *C. citriodora* ssp. *variegata* in this study were again quite low compared to those of *E. grandis* and *E. cloeziana* (Woondum), but this could be a direct result of site conditions as *C. citriodora* ssp. *variegata* was grown on water-limited, inland sites. *C. citriodora* ssp. *variegata*, like all other species, showed no variation in mean SLA with crown zone, but the canopy-average SLA of *C. citriodora* ssp. *variegata* in this study (4.7 $m^2 kg^{-1}$) was still greater than the default eucalypt SLA value of 3.5 $m^2 kg^{-1}$, which is used as an input value for the process-based models 3-PG and ProMod when no experimental data are available. The mean SLA values for the St Mary provenance were larger than those for the Presho provenance in all crown zones, but there was no indication of a relationship between canopy depth and SLA. These values were also very similar to those reported by Pook (1984b) for *E. maculata*. The canopy-average values of SLA (across all three crown zones) for *C. citriodora* ssp. *variegata* in this study were 4.97 $m^2 kg^{-1}$ for the St Mary provenance and 4.56 $m^2 kg^{-1}$ for the Presho provenance, which were once again greater than the default value used for eucalypts in models.

Comparison with temperate species

Leaf areas peak relatively early in the life of forest stands — at a level greater than the final equilibrium value (Ryan *et al.* 1997) — but decline relatively quickly after canopy closure. SLA can vary with species, leaf age, position in the canopy and nutrients (Beadle 1997), and values determined in this study indicate that sub-tropical hardwoods can also have variability between and within species. Yet little variation in SLA was found between canopy regions (crown zones) in these sub-tropical hardwoods, which is in contrast to observations in temperate species, such as *E. nitens* (Pierce *et al.* 1994; Pinkard and Beadle 1998; Hunt *et al*. 1999; Medhurst and Beadle 2002). In most temperate studies referred to above, the plantations considered were thinned or under heavy intraspecific competition and therefore experienced substantial variation (with crown position) in light environment during development. Canopy light environment in the present study was much more uniform. Consequently, the present study does not satisfactorily inform us as to whether ontogenetic/developmental causes driven by silviculture or inherent physiological/morphological characteristics determined by genetics are accounting for the differences apparent between the temperate and the subtropical taxa. Regardless, the observed differences exist and they may have considerable implications for parameterisation of the process-based models 3-PG and CaBala for these particular sub-tropical species. Because little variation occurs in mean SLA among the three crown zones, the selection of an average SLA value for model input would be much simpler, but the allometric equations used in the two models may have to be altered slightly to reflect this lack of variation and differences in the incoming light attenuation of the sub-tropical eucalypts. The input required to describe site conditions and climate, particularly rainfall, could become much more important for models predicting growth productivity than SLA or L^* for these four sub-tropical eucalypt species.

Landsberg *et al.* (2003) evaluated the generality of the 3-PG model by analysing data from sites that ranged from sub-tropical Africa and Australia to northern Europe, including *E. grandis*, *E. globulus*, *Pinus radiata*, *Picea abies* and *Pinus taeda*. Little is reported on the *E. grandis* experimental plantations from Gympie, Australia, except that the model demonstrated it could provide good descriptions of virtually any good quality data set for forest growth. This may not apply to the less productive species or on less productive sites. The SLA values used for model input for *E. grandis* in the study by Landsberg *et al.* (2003) were taken from Cromer *et al.* (1993) as 5 $m^2\,kg^{-1}$ or the default value was used, which is 3.5 $m^2\,kg^{-1}$ for eucalypts. This default value of SLA is lower than the canopy-average SLA values determined in this study and is similar to the SLA values reported by Linder (1985) for *E. globulus* (2.7 and 3.7 $m^2\,kg^{-1}$ for control and fertilised trees, respectively) and *E. nitens* (3.9 $m^2\,kg^{-1}$). The current default SLA value of 3.5 $m^2\,kg^{-1}$ used for model input would not be appropriate for the four sub-tropical species evaluated in this study. The lowest canopy-average SLA was 4.23 $m^2\,kg^{-1}$ for the 6-y-old *E. argophloia* stand at the dry Narayen 2 site, while the most productive species, *E. grandis*, had canopy-average SLA values of 6.54 $m^2\,kg^{-1}$ and 5.12 $m^2\,kg^{-1}$ for the Coffs Harbour and Pomona provenances, respectively. The large difference in canopy-average SLA between the two *E. cloeziana* provenances (9.05 and 4.95 $m^2\,kg^{-1}$ for Woondum and Coominglah, respectively) would also make the selection of a single SLA value for this species impractical as an input parameter for both 3-PG and CaBala without considering its nutrient status and site conditions. The lack of variation observed in mean SLA with crown zone in these four sub-tropical eucalypts suggests that crown architecture and canopy development in sub-tropical plantations may be inherently different to that in temperate eucalypts, and the statement by Landsberg (1997, p. 71) that ‘there is no reason to expect leaf area and canopy development in tropical plantations to vary significantly from those observed in any other system’ may need further study.

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