ALLOMETRIC RELATIONSHIPS BETWEEN STEM VARIABLES AND LEAF AREA IN PLANTED *EUCALYPTUS NITENS* AND NATURALLY REGENERATING *ACACIA DEALBATA*

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(Received for publication 22 February 1999; revision 7 May 1999)

ABSTRACT

Allometric relationships between stem variables and leaf area were determined for plantation *Eucalyptus nitens* (Deane et Maiden) Maiden and competing *Acacia dealbata* Link in 8-year-old and 4-year-old stands. Both cross-sectional area and sapwood area were considered at crown break and breast height. Whilst all four stem variables could be used to calculate tree leaf area adequately, proximity of the stem measurement to crown break was found to be more important than the choice of sapwood area or cross-sectional area in determining the closeness of the derived allometric relationship. When the relationship between sapwood area at crown break and leaf area was used, a single equation was suitable for predictive purposes across treatments for each species.

Keywords: allometry; sapwood area; leaf area; *Eucalyptus nitens*; *Acacia dealbata*.

INTRODUCTION

The estimation of tree or stand leaf area is important for interpreting, scaling, and modelling a variety of forest processes and may be undertaken using a range of direct and indirect methods (Campbell & Norman 1989; Goel & Norman 1990). A common method for estimating leaf area at the stand scale uses a combined approach. Destructive sampling of trees is used to develop allometric relationships between leaf area (or leaf mass) and an easily

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measured stem variable for each canopy element that is being examined. These elements may be species, size classes, or crown layers. The allometric relationships are then used in combination with stem measurements to obtain a stand-scale estimate of leaf area (e.g., Battaglia *et al.* 1998).

Sapwood area is the functional variable likely to be most highly correlated with leaf area (Waring *et al.* 1982) and, accordingly, the most common stem variable used for scaling. However, the nature of that relationship is not clear and its acceptance is not universal (Pereira *et al.* 1987). Whilst leaf area is normally considered to be a function of sapwood area (as interpreted by the pipe model *sensu* Shinozaki *et al.* 1964), some studies have indicated that sapwood production in fact may be dependent on foliage area (e.g., Kaufmann & Troendle 1981). Regardless of the direction of causation, the relationship between sapwood area and leaf area is at least functional, and thus should be portable (Lavigne *et al.* 1996). Even so, such relationships are not universal (Gazarini *et al.* 1990) and have been shown to vary with species (Kaufmann & Troendle 1981) and a range of site and stand variables (Brix & Mitchell 1983; Espinosa Bancalari *et al.* 1987; Keane & Weetman 1987; Grier & Running 1977; Mencuccini & Grace 1995).

Cross-sectional sapwood area tapers from breast height to the crown base, due partly to the increase in sapwood allocation to storage with distance from the base of the live crown or crown break (Hillis 1987). Therefore, measurement at crown break should facilitate derivation of a closer relationship with leaf area than measurements from lower in the stem (Maguire & Batista 1996). Such a measure is often impractical on a large scale, particularly where crown lift is marked. Sapwood taper is a non-linear function of crown height (Maguire & Hann 1990; Medhurst *et al.* in press). Thus, variation in the degree of taper between sites (influenced by site and silvicultural factors) may be accounted for in development of allometric relationships by the use of both sapwood area and crown height for their derivation (Medhurst *et al.* in press). These relationships should then be more portable.

For allometric relationships that are developed for a specific site, portability is less important and the utility of a stem scaler is enhanced by its ease of measurement. The measurement of sapwood area may be difficult, particularly in stands where axial or radial distribution of sapwood is uneven (e.g., Hunt & Beadle 1998). In such stands, stem core sampling must be replaced by destructive sampling of trees and the subsequent use of the relationship in scaling exercises is precluded (as it is generally impractical to destructively sample all trees in a stand). Furthermore, the difficulty in delineating functional from non-functional sapwood may cause bias in the measurement. Under such circumstances, basal area may be a more appropriate measure with which to develop stem variable:leaf area allometric relationships.

Acacia dealbata is an important woody weed in both softwood and hardwood plantations in south-east Australia. In order to investigate the mechanisms and extent of its competitive ability, a study was undertaken in a young *Eucalyptus nitens* plantation with pronounced natural *A. dealbata* regeneration. As part of this study, canopy architecture and structure were studied in mixed *A. dealbata*/*E. nitens* stands of two ages. The aims were to:

(1) Identify the most appropriate stem variable for use in allometric relationships for scaling measurements of tree leaf area to the stand level;
(2) Define species differences in the functional relationship between sapwood area and leaf area; and

(3) Consider the effect of presence or absence of *A. dealbata* competition on allometric relationships for *E. nitens*.

The results are also discussed within the context of the competitive nature of the relationship between the two species.

MATERIALS AND METHODS

Site Description

The study was conducted in a commercial eucalypt plantation at Wyena, in north-east Tasmania, approximately 35 km east of Launceston (lat.41°12′S, long.147°16′E). The plantation occupied the head of a small north-facing valley and comprised approximately 38 ha of *Eucalyptus globulus* Labill. and 560 ha of *E. nitens*. All experimental work was conducted in the *E. nitens* coupes planted at 816 to 1000 stems/ha. It was a moderately wet site, rainfall being predominantly in winter (1000 mm/year) and with generally good but variable drainage. Two experimental sites were established for this study. Site 1 was located in a coupe planted in 1988 on ex-agricultural land and Site 2 in a coupe planted in 1992 on cleared native forest. At Site 2, the stem density of *A. dealbata* was highly variable, enabling sampling at both acacia-free and acacia-infested locations (Plots T and U respectively). Site 1 and Site 2/Plot U experienced very high densities of *A. dealbata* stems, 3200 and 14000 stems/ha respectively. The plantation and experimental sites have been described in detail elsewhere (Hunt *et al.* 1999 refer to Sites 1 and 4 for 1 and 2 above).

Sampling Procedure

The sampling procedure was based on that described by Pinkard & Beadle (1998).

In July/August 1996, five eucalypts and five co-dominant acacias at Site 1 were selected to represent the variation in diameter present at the site. Each tree was felled at ground level with a chainsaw. Diameter at breast height (d) was measured for each tree as were total height (h_t) and height to the base of the crown (h_c), yielding green crown length (l_c). The height above-ground and the diameter-over-bark at 4 cm from the base of each branch were measured for each live branch from the base to the tip of the live crown. The crown was divided into thirds and branches were allocated to crown sections based on the origins at the stem. On the basis of diameter distribution within each third of the crown, five representative branches were selected. Selected branches were excised at the base and removed to the laboratory for processing. Branch diameters were converted to cross-sectional area (csa) for the determination of regression relationships between branch cross-sectional area, branch length, and leaf area per branch which could then be used to estimate leaf area for whole crowns. Foliage was oven-dried to constant weight at 80°C (W_{80}). Additionally, five eucalypts and five acacias were sampled in the same manner from Plot U at Site 2 and a further five eucalypts were sampled from Plot T at Site 2.

Leaf Area Determination

A sub-sample of leaves was used for the determination of specific leaf area (SLA). Ten leaves were selected randomly from each sample branch. Specific leaf area was calculated on a projected leaf area or single-sided basis. Leaves were weighed fresh (W_f) prior to area determination using a flat-bed scanner and image analysis software (Hunt & Hodson in press) and oven-dried to W_{80}. Branch leaf area (A_l) was calculated as the product of total leaf dry weight and specific leaf area. Regression analysis was used to develop relationships between branch cross-sectional area and leaf area, which were used to calculate tree leaf area.

Sapwood Area Determination

Sapwood area (A_s) was determined for breast height (1.3 m) and at the crown base. This was achieved by staining the relevant stem disks with dimethyl yellow, tracing a stencil of the sapwood indicated by the stain, and scanning the stencil for image analysis.

Analysis

Linear regression (SAS GLM) was used to develop relationships between leaf area and stem variables; t-tests (for unpaired data) were used to investigate differences in specific leaf area between species and tree ages. For relationships between basal area and leaf area and between sapwood area (at crown base) and leaf area, a test for equality of regression equations (Rao 1952, pp.112–115) was used to investigate the effects of species, age, and competition.

RESULTS

Specific Leaf Area

Variation in specific leaf area was small for both species (57–75 cm^2/g for *E. nitens* and 48–69 cm^2/g for *A. dealbata*) and differences between ages within each species (across and within crown zones) were not significant ($p > 0.05$; t-tests). Neither was specific leaf area significantly different between eucalypts growing in the presence or absence of *A. dealbata* at Site 2. *Eucalyptus nitens* from stands of both ages had higher specific leaf area than associated *A. dealbata* (Table 1). Specific leaf area increased with crown depth (i.e., from upper crown foliage to lower crown foliage) for trees of both species and in stands of both ages, except for *E. nitens* at Site 1.

TABLE 1–Mean specific leaf area (SLA, cm^2/g) for upper, middle, and lower crown thirds by species, treatment, and age.

Species	Planting date	Site/Plot	Upper crown 1996	Middle crown 1996	Lower crown 1996
E. nitens	1988	1	67	60	65
E. nitens	1992	2/U	57	64	71
E. nitens	1992	2/T	59	64	75
A. dealbata	1988	1	48	51	69
A. dealbata	1992	2/U	50	55	64

Leaf Area *v.* Sapwood Area/Basal Area

Branch cross-sectional area was more closely correlated with branch leaf area than either branch length or branch length and cross-sectional area combined for all treatments. Accordingly, cross-sectional area was used as the scaling variable for leaf area (Table 2).

TABLE 2–The slopes and intercepts of the regression relationships between branch cross-sectional area and branch leaf area. All data were log (*e*) transformed. All equations are significant at the 0.001 level.

Species	Planting date	Site/Plot	Crown zone	Slope	Intercept	r^2
E. nitens	1988	1	Upper	1.90	1.32	0.79
E. nitens	1988	1	Middle	2.38	0.92	0.89
E. nitens	1988	1	Lower	2.23	0.90	0.75
E. nitens	1992	2/U	Upper	2.54	0.52	0.72
E. nitens	1992	2/U	Middle	2.13	1.38	0.85
E. nitens	1992	2/U	Lower	2.19	1.17	0.72
E. nitens	1992	2/T	Upper	0.88	1.93	0.5
E. nitens	1992	2/T	Middle	1.26	2.32	0.7
E. nitens	1992	2/T	Lower	2.30	1.08	0.78
A. dealbata	1988	1	Upper	1.86	1.25	0.87
A. dealbata	1988	1	Middle	2.22	0.84	0.75
A. dealbata	1988	1	Lower	2.48	0.05	0.55
A. dealbata	1992	2/U	Upper	1.49	1.54	0.59
A. dealbata	1992	2/U	Middle	2.67	1.18	0.92
A. dealbata	1992	2/U	Lower	2.59	0.46	0.89

Highly significant regression relationships were found between leaf area and basal area of *A. dealbata* and *E. nitens* in both 4-year-old (Fig. 1a) and 8-year-old (Fig. 1b) trees. Regression relationships were also developed between leaf area and sapwood area at breast height (Fig. 1c and 1d), cross-sectional area at the crown base (Fig. 1e and 1f), and sapwood area at the crown base (Fig. 1g and 1h). For eucalypts at Site 1 (8 years old) and at Site 2/Plot T (4 years old), the consideration of these stem variables did not return significantly better relationships than basal area.

Regression equations describing the relationship between basal area and leaf area, and between sapwood area (at crown base) and leaf area, for *A. dealbata* at Site 2/Plot U and at Site 1 were not significantly different. The same result was returned for a comparison of these relationships in *E. nitens* in the acacia-free (Plot T) and the acacia-infested (Plot U) 4-year-old stands at Site 2. However, separate regression equations were significantly better descriptors of the relationships when species comparisons were made at both ages (i.e., at Site 1 and at Site 2/Plot U). Similarly, regression equations describing the relationships between basal area and leaf area for *E. nitens* at Site 1 (8 years old) and Site 2/Plot U (4 years old) were significantly different. A single equation was adequate for description of the relationship between sapwood area (at crown base) and leaf area for *E. nitens* trees of both ages (Table 3).

The mean ratio of leaf area to sapwood area (A_l:A_s) was calculated for the five treatments (Table 4). *Acacia dealbata* exhibited significantly lower ($p < 0.05$; t-test) A_l:A_s ratios than *E. nitens* in stands of both ages. Differences within species among treatments were not significant.

DISCUSSION

Tree leaf area was significantly related to all stem variables measured and stem cross-sectional area was found to be a comparable predictor of leaf area to sapwood area (either

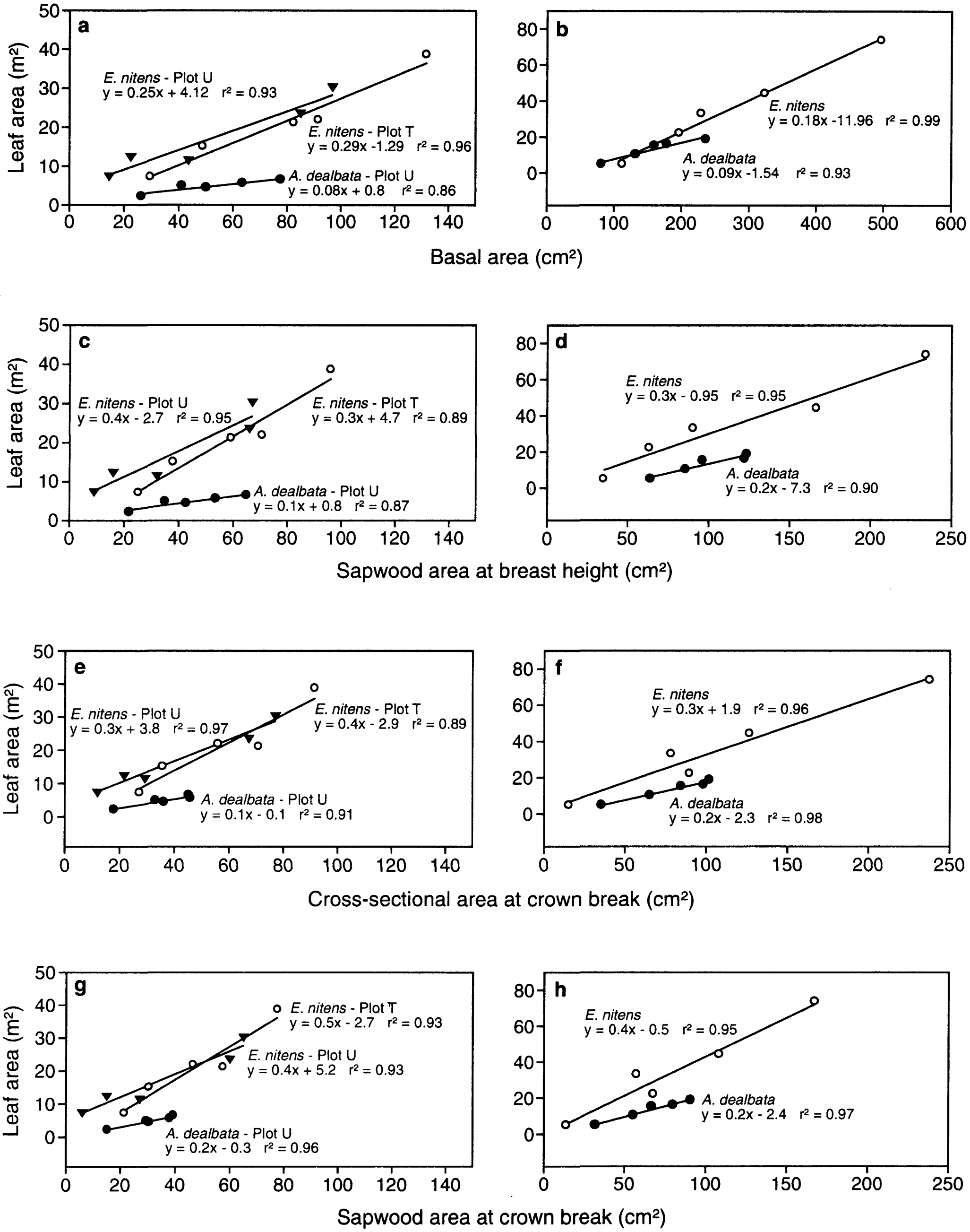

FIG. 1–Relationship between basal area (a,b), sapwood area at breast height (c,d), cross-sectional area at crown break (e,f) or sapwood area at crown break, and tree leaf area for *E. nitens* and *A. dealbata* in (a,c,e,g) 4-year-old acacia-infested (U) and acacia-free (T) stands at Site 2 and (b,d,f,h) an 8-year-old acacia-infested stand at Site 1.

TABLE 3–Coefficients of determination (r^2) for regression relationships between stem variables and leaf area.

Species	Site/Plot	Planting date	Basal area	Cross-sectional area (crown base)	Sapwood area (breast height)	Sapwood area (crown base)	Average
A. dealbata	2/U	1992	0.86	0.91	0.87	0.96	0.90
A. dealbata	1	1988	0.93	0.98	0.90	0.97	0.95
E. nitens	2/U	1992	0.93	0.97	0.95	0.94	0.95
E. nitens	2/T	1992	0.96	0.90	0.95	0.93	0.94
E. nitens	1	1988	0.99	0.96	0.96	0.95	0.97
Average			0.93	0.94	0.93	0.95	

TABLE 4–Mean leaf area (m^2) to mean sapwood area (cm^2) ratio (A_l:A_s).

Species	Site/Plot	A_l:A_s	Standard error (n=5)
A. dealbata	2/U	0.11	0.02
A. dealbata	1	0.13	0.03
E. nitens	2/T	0.35	0.05
E. nitens	2/U	0.56	0.23
E. nitens	1	0.29	0.09

at breast height or crown base) for both species in all stands. Taken across stands and species, sapwood area at the crown base was the best predictor of leaf area, followed by cross-sectional area at the crown base. Basal area and sapwood area at breast height were of equal value.

Although sapwood area is functionally related to leaf area and cross-sectional area is not, there are several reasons why sapwood area is not always a better predictor of leaf area and why the measurement of sapwood area may not be as useful. When sapwood area is determined from cores, any irregular shape of the heartwood reduces the accuracy of the measurement. For instance, Baldwin (1989) reported a minimum of two cores being necessary to account for the ellipsoid shape of the heartwood of *Pinus taeda* L. Furthermore, when sampling of sapwood is required several times during a growing season or in successive growing seasons, sapflow may be disrupted. The heartwood boundary in the present study was irregular in most trees sampled, and more so in *E. nitens* in acacia-infested plots than acacia-free plots, in older than in younger stands, and in *A. dealbata* than in *E. nitens*. Even stained discs may not yield a reliable estimate of conducting sapwood area. Sapwood can provide a sink storage for carbohydrates in the stem (Kramer & Kozlowski 1979) and the differentiation between conducting and non-conducting sapwood may be difficult. The functional relationship between sapwood area and leaf area is further confounded by within-stem variation in a range of variables including sapwood permeability (Pothier *et al.* 1989; Shelburne *et al.* 1993) and hydraulic conductance (Coyea & Margolis 1994). These variables further complicate the establishment of strong predictive relationships between leaf area and sapwood area.

The general utility of the allometric relationships developed in this study is similar to that of a range of recent studies conducted in both hardwoods and softwoods (e.g., Gilmore *et al.* 1996; Pereira *et al.* 1997). Relationships between leaf area and each stem variable were specific to species, but within each species a single regression relationship predicting tree leaf area from sapwood area at the crown base was an adequate descriptor across treatments. Greatest application of a crown base measure has been found not only when transporting relationships between stands of different densities but also in particularly dense stands (Maguire & Hann 1990). This may be because variation in lifting of crowns at high stem densities (within populations) or variation in density itself (among populations) influences the degree of stem taper between breast height and crown height. In the present study, there were very large differences in stand density between Plots T and U. However, a single regression equation was suitable for describing the relationship between the basal area and leaf area in the two stands and recourse to a sapwood area measure or a measure at crown break was unnecessary. Competition was likely to have been heaviest among *A. dealbata* stems (rather than between *A. dealbata* and *E. nitens* or among *E. nitens* – *see* Hunt *et al.* 1999). Consequently, variations in crown base and stem taper were more pronounced among *A. dealbata* within and between populations (*sensu* Maguire & Hann 1990) and sapwood area at crown base was the most accurate predictor of leaf area for acacias. Nevertheless, *A. dealbata* in stands of two ages with very different stem densities were described as well by a single regression equation as by separate equations.

Specific leaf area of *E. nitens* was consistently and significantly higher than *A. dealbata,* though the magnitude of variation was not marked. The values for both species fell within the range reported elsewhere for *E. nitens* (Cherry *et al.* in press). Concurrent studies indicated that the light environment in the lower canopy in acacia-infested stands is markedly reduced compared to that in acacia-free stands (Hunt 1998) but this was not associated with higher specific leaf area for *E. nitens* in Plot U compared to Plot T, even in the lower third of the crowns. This result indicates a low capacity for *E. nitens* to morphologically respond to light at the foliar level (*sensu* Givnish 1987). Therefore, the trend of reducing specific leaf area with crown depth (which was consistent at Site 2 regardless of acacia presence or absence) may be related more to leaf age than to morphological plasticity.

The ratio A_l:A_s differed markedly between the two species. Although published values are unavailable for *A. dealbata*, Beadle & Mummery (1990) and White *et al.* (1998) both reported values for *E. nitens* similar to those reported in this study. The reduction in A_l:A_i from 0.56 to 0.29 between 4-year-old and 8-year-old trees for *E. nitens* in the acacia-infested stands is consistent with the reduction in this ratio with age reported by Beadle & Mummery (1990). Such a reduction has been hypothesised as associated with an increase in allocation of sapwood to storage with distance from the crown base (Hillis 1987). A_l:A_s of *E. nitens* in the 4-year-old *A. dealbata* stand more closely reflected that for the older trees at Site 1 than the acacia trees of the same age. White *et al.* (1998) demonstrated that an increase in A_l:A_s may result from water limitation due to a rationalisation of the sapwood required to meet the hydraulic needs of foliage with reduced stomatal conductance. Thus, *E. nitens* in acacia-infested Plot U may have experienced greater water limitation than in acacia-free Plot T. However, as sapwood measurements used to calculate the ratio were taken at breast height, and as eucalypts in Plot U exhibited much more crown lift than those in Plot T, the between-site difference may simply be due to the lack of consideration in the ratio of sapwood taper from breast height to crown break (*sensu* Hillis 1987).

In order to model leaf area across the range of treatments for each species in this study, the variation in sapwood characteristics between breast height and the crown base was considered. The relationship between sapwood area measured at the crown base and leaf area has been found to be independent of site for *E. nitens* (White *et al.* 1998; Cherry *et al.* in press; Medhurst *et al.* in press). Similar site independence of tree allometry has been identifed for *Pseudotsuga menziesii* (Mirb.) Franco (Bartelink 1996) and *Fagus sylvatica* L. (Bartelink 1997). Whilst the measure at crown base has been demonstrated as particularly useful for predicting leaf area (e.g., Maguire & Batista 1996), stem taper can be accounted for by using crown height as a covariate of a basal measurement, thus enabling greater application of the method for routine sampling (e.g., Long & Smith 1988, 1989; Medhurst *et al.* in press).

For scaling, the choice of sapwood area or basal area or cross-sectional area is dependent on the experimental objectives. The measurement of sapwood area (or volume) is particularly useful in studies where productivity modelling is important. Sapwood volume may be used as a correlate of respiration with leaf area a correlate of productivity, and thus the relationship between the two may provide an estimate of stand growth efficiency (Ryan 1989, 1990; Ryan & Waring 1992). However, for experiments where an estimate of stand leaf area (or its distribution) is the objective, little advantage is gained by using sapwood area instead of basal area (Dean & Long 1986; Shelburne *et al.* 1993). Basal area is the most easily measured tree dimension, has a strong practical role in scaling for tree size (Tucker *et al.* 1993; Shi & Cao 1997), and has been shown to be suitable for both *E. nitens* and *A. dealbata* in this study.

CONCLUSION

Sapwood area may be a better predictor of leaf area of *E. nitens* and *A. dealbata* than cross-sectional area but differences were small and the additional sampling required to obtain sapwood area is not warranted. Should tighter relationships be desired, additional sampling effort should better be directed to diameter measurement at the crown base for conversion to cross-sectional area. When sapwood area at crown base was used to model leaf area, the sample size was insufficient to determine statistically significant different regressions on the basis of age or presence of competition for either species. However, interspecific differences in the relationship between stem variables and tree leaf area precluded the use of a general model to satisfactorily describe both species.

ACKNOWLEDGMENTS

We thank Boral Timber Tasmania for use of the plantation and Dr Don White, Mr Michael Hong, and two anonymous reviewers for valuable comments on the manuscript.

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