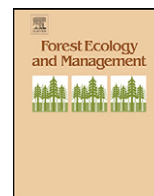




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Within-stand and seasonal variations of specific leaf area in a clonal *Eucalyptus* plantation in the Republic of Congo

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ABSTRACT

Specific leaf area (SLA ; $m^2_{leaf} kg^{-1}_{leaf}$) is a key ecophysiological parameter influencing leaf physiology, photosynthesis, and whole plant carbon gain. Both individual tree-based models and other forest process-based models are generally highly sensitive to this parameter, but information on its temporal or within-stand variability is still scarce. In a 2–4-year-old *Eucalyptus* plantation in Congo, prone to seasonal drought, the within-stand and seasonal variability in SLA were investigated by means of destructive sampling carried out at 2-month intervals, over a 2-year period. Within-crown vertical gradients of SLA were small. Highly significant relationships were found between tree-average SLA (SLA_t) and tree size (tree height, H_t , or diameter at breast height, DBH): SLA_t ranged from about $9 m^2 kg^{-1}$ for dominant trees to about $14–15 m^2 kg^{-1}$ for the smallest trees. The decrease in SLA_t with increasing tree size was accurately predicted from DBH using power functions. Stand-average SLA varied by about 20% during the year, with lowest values at the end of the 5-month dry season, and highest values about 2–3 months after the onset of the wet season. Variability in leaf water status according to tree size and season is discussed as a possible determinant of both the within-stand and seasonal variations in SLA .

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1. Introduction

Specific leaf area (SLA), the ratio of leaf area to leaf dry mass ($m^2 kg^{-1}$), or its inverse, leaf mass per area (LMA) are key ecophysiological parameters, widely used in ecosystem process-based models to derive canopy leaf area from leaf biomass (e.g., Landsberg and Waring, 1997; Sands and Landsberg, 2002; Battaglia et al., 2004; Corbeels et al., 2005), or conversely, to derive leaf biomass from canopy leaf area (Dufrène et al., 2005; Davi et al., 2008). Specific leaf area is also a key attribute influencing photosynthetic capacity (e.g., Niinemets, 1999; Reich et al., 1999; Sefton et al., 2002; Wright et al., 2004; Shipley et al., 2005) and leaf respiration (Meir et al., 2001; Cavaleri et al., 2008),

and is thus often used in canopy gas-exchange models to predict the spatial (i.e., vertical gradients) or temporal variability of photosynthetic parameters (Wilson et al., 2000; Davi et al., 2008). Moreover, SLA is an important trait characterizing plant adaptation to environmental conditions: its plasticity is often seen as a way for plants to increase the efficiency of light-harvesting (e.g., Rozendaal et al., 2006; Sack et al., 2006; Poorter and Rozendaal, 2008), and/or the efficiencies of resource-use (e.g., light, water and nitrogen-use efficiencies; Niinemets, 2001; Sefton et al., 2002).

For woody plants, changes in SLA with leaf or plant age have been reported by several authors (Day et al., 2001; Sefton et al., 2002; England and Attiwill, 2008). Plant water status during leaf development, and/or the amount of photosynthetically active radiation (PAR) absorbed by the leaf during its formation have been identified as important factors influencing the SLA of adult leaves (Le Roux et al., 1999; Niinemets, 2007). Specific leaf area is generally known to decrease from the bottom of the canopy to its top (Le Roux et al., 1999; Marshall and Monserud, 2003; Sellin and Kupper, 2006; Weiskittel et al., 2008; Davi et al., 2008; Cavaleri

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et al., submitted for publication), or from the interior of individual tree crowns to their periphery (Han et al., 2003; Sellin and Kupper, 2006; Weiskittel et al., 2008), and these variations are considered either as an adaptation to a varying light environment within the canopy (e.g., Niinemets, 1997; Kenzo et al., 2006; White and Scott, 2006), allowing optimization of carbon gains (e.g., Rambal et al., 1996; Meir et al., 2002), or as a result of increased leaf water stress (decreased leaf water potential) with height or branch length, due to gravity or path length resistance (Koch et al., 2004; Woodruff et al., 2004; Ryan et al., 2006; He et al., 2008; Du et al., 2008). Height-related variation in SLA is commonly described by exponential functions relating SLA or LMA to the cumulated leaf area index (from the top of the canopy to its bottom), similar to the functions used to model light attenuation inside forest canopies (Rambal et al., 1996; Davi et al., 2008), or by exponential functions relating SLA or LMA to the height above ground level, h (e.g., Koch et al., 2004; Burgess and Dawson, 2007; Ishii et al., 2008):

$$SLA = SLA_{\max} \exp(-kh), \quad (1)$$

where SLA_{\max} is the SLA observed at the bottom of the canopy.

In eucalypt forests, SLA has been related to tree height (H_t) by power functions (England and Attiwill, 2006):

$$SLA = c H_t^d. \quad (2)$$

Specific leaf area of *Eucalyptus* forests or plantations has also been shown to decrease with stand age (Leuning et al., 1991; King, 1999; Sands and Landsberg, 2002; Almeida et al., 2004; Fontes et al., 2006; England and Attiwill, 2006; Pinkard et al., 2007; Paul et al., 2007), and with the shortage of water and nutrients (Bennett et al., 1997; Li et al., 2000; Roderick et al., 2000; Whitehead and Beadle, 2004; Pinkard et al., 2007). The most recent versions of the widely used 3PG model incorporate an equation describing the decrease of SLA with stand age (Sands and Landsberg, 2002; Almeida et al., 2004; Fontes et al., 2006), whereas canopy-average SLA is made dependent on the nitrogen supply to the leaf in the CABALA model (Battaglia et al., 2004), and on the foliar N:C ratio in a recent version of the G'DAY model (Corbeels et al., 2005). However, none of these models accounts explicitly for potential seasonal variations of SLA that may result from seasonal drought, or from seasonality in leaf production, leaf fall, or incoming solar radiation. Neglecting seasonal variation in SLA may affect the model's ability to provide accurate estimates of carbon gains, as suggested by several sensitivity analyses performed on the 3PG model, which showed that simulated LAI , net primary productivity (NPP), and tree growth were highly sensitive to SLA (Esprey et al., 2004; Stape et al., 2004).

Individual tree-based models such as MAESTRO/MAESTRA (Medlyn, 2004) have also been applied to *Eucalyptus* forests for estimating tree and stand carbon assimilation and transpiration (Leuning et al., 1991; Medlyn et al., 2007). They represent the forest canopy as an array of tree crowns, whose dimension, leaf area, and other structural and physiological properties must be specified. For such models, tree-average SLA (SLA_t) is more relevant than stand-average SLA (SLA_s). Accurate estimates of SLA_t are particularly important for model applications where tree leaf area is estimated as the product of tree leaf biomass (obtained from allometric regressions) and SLA (e.g., in Medlyn et al., 2007), rather than directly from allometric equations. However, there is a lack of information on the within-stand variability in SLA_t , and on its dependence on tree size or environmental factors.

For eucalypts and other woody species, power functions are widely used to relate tree leaf biomass, B_t (kg), to tree diameter (e.g., Landsberg and Waring, 1997; O'Grady et al., 2000; Fontes et al., 2006) or tree leaf area, A_t (m^2), to tree diameter (e.g., O'Grady

et al., 2006; Macfarlane et al., 2007; Grigg et al., 2008):

$$\begin{cases} A_t = a_A DBH^{b_A} \\ B_t = a_B DBH^{b_B} \end{cases} \quad (3)$$

where DBH is the diameter of the tree at breast height (1.3 m), and a_A , b_A and a_B , b_B the parameters to be estimated by regression. Such use of power functions indifferently for leaf area and leaf biomass suggests that SLA_t ($m^2 kg^{-1}$) may also be predicted from DBH with a power function:

$$SLA_t = a_{SLA} DBH^{b_{SLA}}. \quad (4)$$

with

$$a_{SLA} \approx \frac{a_A}{a_B} \text{ and } b_{SLA} \approx b_A - b_B.$$

On the other hand, H_t may also be a good predictor of SLA_t . England and Attiwill (2006) used Eq. (2) to describe the relationship between the average SLA of upper crown leaves of individual trees and H_t , but this equation may also relate SLA_t to H_t , since within-crown vertical gradients of SLA are generally small in eucalypt canopies (King, 1997; Medlyn et al., 2007).

The objectives of this study were (i) to assess the within-stand variability in SLA_t in a 4-year-old clonal *Eucalyptus* stand in Congo; (ii) to test the hypothesis that SLA_t is correlated to DBH and to H_t , and (iii) to assess the seasonality of SLA_s . These issues were addressed by the means of destructive sampling at 2-month intervals, over a 2-year period, including two dry and two wet seasons.

2. Materials and methods

2.1. Study site

The study site ($4^{\circ}47'29''S$, $11^{\circ}58'56''E$, 108 m elevation) is located in the Atlantic coastal zone of the Republic of Congo, in central Africa. It is one of the eddy-covariance sites of the CARBOAFRICA network (http://www.carboaffrica.net/index_e-n.asp). Large *Eucalyptus* plantations (some 40,000 ha) have been managed for pulpwood production around the city of Pointe Noire for about 30 years. The original vegetation was a savannah dominated by the C4 Poaceae species *Loudetia arundinacea* (Hochst.) Steud. and *Hyparrhenia diplandra* (Hack.) (Laclau et al., 2002). The deep sandy soils are classified as Ferralic Arenosols according to the FAO (Food and Agriculture Organization) classification (Trouvé et al., 1994), with high sand (80–90%) and low clay (8–10%) and silt (2–2.5%) contents (Laclau et al., 2005; Nouvellon et al., 2008). These soils are characterized by low water retention, a very low level of organic matter (Epron et al., 2004; D'Annunzio et al., 2008) and a poor cationic exchange capacity (Nzila et al., 2002). The stand considered in this study is a commercial plantation, first afforested with *Eucalyptus* in 1981. After the first harvest in 1988, two subsequent coppices were conducted and harvested in 1995 and 2002. In 2002 the stumps were devitalized and a clone of the hybrid *Eucalyptus urophylla* (S.T. Blake) \times *Eucalyptus grandis* (W. Hill ex Maiden) (currently the most commonly planted clone in Congo) was planted at a stocking density of 800 trees/ha⁻¹ (tree spacing: 3.7 m \times 3.4 m), which is the current (and close to optimum) density applied by the forest company. Each tree received 200 g per plant of NH_4NO_3 fertilizer at planting and weeds were eliminated by several herbicide (glyphosate) applications the first year after planting (see Marsden et al. (2008) for more details).

Climate is characterized by high mean annual air humidity and temperature (85% and 25 °C, respectively), with low seasonal variations (ca. 2% and 5 °C, respectively). Annual precipitation

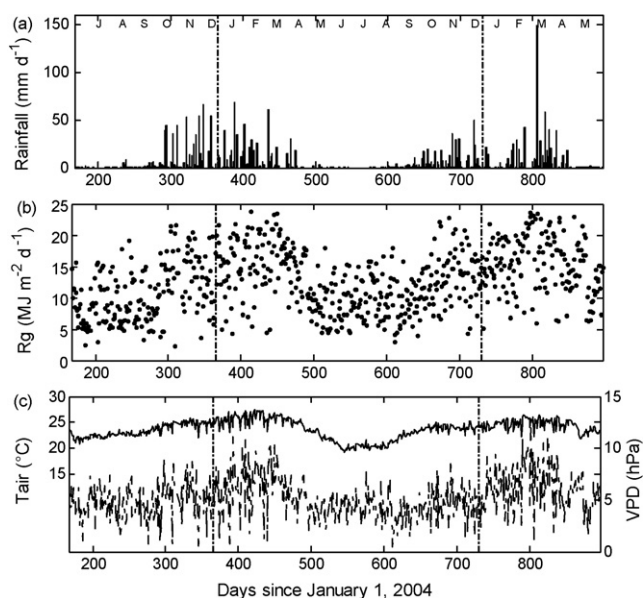


Fig. 1. (a) Daily rainfall (mm day^{-1}), (b) daily incoming global radiation ($\text{MJ m}^{-2} \text{day}^{-1}$), and (c) daily mean air temperature (upper line; $^{\circ}\text{C}$), and vapour pressure deficit (lower line; hPa) recorded at the Kissoko site from June 15, 2004 to June 15, 2006.

(1998–2005) averaged 1274 mm yr^{-1} with a dry season between May and September. Annual rainfall during the experiment (from June 2004 to June 2006) was 1194 mm yr^{-1} . Rainfall distribution, global radiation, air temperature and vapour pressure deficit recorded at this site from June 15, 2004 to June 15, 2006 are shown on Fig. 1. Actual evapotranspiration measured by eddy-covariance over this stand was presented in Fisher et al. (in press).

2.2. Destructive measurements of tree leaf biomass, leaf area, and SLA

Destructive sampling was carried out at two-month intervals over 2 years (11 measurement dates from October 2004 to June 2006). Ten to fifteen trees were sampled at each date. Before each sampling campaign H_t and DBH were measured on six permanent plots which contained 30 tree positions (six rows of five trees). These inventories were carried out (1) in order to ensure that trees for destructive measurements were sampled across the range of tree sizes, and (2) to scale tree leaf area and biomass to the stand level. After the inventory, the diameter distribution was divided into 10–15 classes, and one tree per class was randomly selected outside the permanent plots. For each selected tree, DBH was measured. The tree was then felled and measured for total height (H_t) and height to green crown base (H_b). The green crown length ($L = H_t - H_b$) was divided into three equal-length sections (lower, middle and upper). All leaves of each section were removed, taken to the laboratory, and weighed. Twenty-five leaves were randomly selected in each section, and their fresh mass and area were immediately measured. These leaves were then dried at 65°C to constant weight. The dry weights of these sub-samples were used in conjunction with their measured area to calculate specific leaf area for each crown section. The foliage dry weight of each crown section was calculated from the foliage fresh weight and the dry to fresh weight ratio of the sub-samples. The tree leaf biomass, leaf area, and specific area were then estimated as:

$$B_t = \sum_{i=1}^3 B_i \quad (5)$$

$$A_t = \sum_{i=1}^3 B_i SLA_i, \quad (6) \quad 202$$

$$SLA_t = \frac{A_t}{B_t}, \quad (7) \quad 204$$

where B_i and SLA_i are the foliage dry weight (kg), and SLA ($\text{m}^2 \text{kg}^{-1}$) in the i th crown section. 206
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2.3. Data analysis 208

Differences in SLA_t between sampling dates were tested using PROC MIXED of the SAS software (SAS Institute, 1999). The model was constructed by considering the following points: (i) data are basically cross-sectional data since 10–15 trees were felled at each sampling date (by opposition to longitudinal data where the same trees are observed at each date), (ii) trees were selected to cover the whole range of the diameter distribution expressed as a continuous variable, (iii) observations were assumed to be uncorrelated among the sampled trees because they were cut far from each other in a 40 ha plot, (iv) the crown sections were nested in a given tree. There was no repetition by tree \times cross-section level at a given date. The model was then an analysis of covariance using tree DBH (continuous data), sampling date and crown section (categorical data) as fixed effects and an additional random effect on the intercept at the tree level. A compound symmetry with separate intercept for each tree was used for the random covariance structure. Interactions (e.g., date \times DBH , crown section \times DBH) as well as a tree random effect on the slope were also tested using the AIC criterion but did not improve the model accuracy. The total number of observation was 342 corresponding to 11 sampling dates, 10–15 trees per sampling date and three crown sections per tree. Original values were log-transformed to normalize the distributions. The probability level used to determine significance was $P < 0.05$. When significant effects between sampling dates and between cross-sections were found, the means were compared with the Tukey–Kramer’s multiple comparison tests using the Lsmmeans/Pdiff option. The decomposition of the variance between the fixed effects, the tree random effect and the residuals was performed according to Hervé (1999). Relationships between SLA_t and H_t , and between SLA_t and DBH were investigated by non-linear regression. For the relationship between SLA_t and H_t , two functions were tested and compared. The first equation was the power function used by England and Attiwill (2006) to relate SLA to H_t in *Eucalyptus regnans* forests (Eq. (2)). The second equation was derived from Eq. (1), which is widely used to describe the decrease of SLA with height above ground level (a.g.l.) in forest canopies, as a result of increasing light availability or increasing water constraint. SLA_t can be estimated from this equation after integration over the crown length:

$$SLA_t = \frac{1}{L} \int_{H_b}^{H_t} SLA_{\max} \exp(-kh) LAD(h) dh, \quad (8) \quad 249$$

where h is the height a.g.l., and LAD is the leaf area distribution function (characterizing the vertical distribution of tree leaf area). An analytical solution of this integral can be obtained if a uniform leaf area distribution within the crown is assumed: 250
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$$SLA_t = \frac{SLA_{\max}}{k H_t C_r} \{ \exp(-k H_t) [\exp(k H_t C_r) - 1] \}, \quad (9) \quad 254$$

where C_r is the crown ratio (L/H_t ; e.g., Soares and Tomé, 2001; Pinkard and Neilsen, 2003) which was estimated at 0.56 ($r^2 = 0.34$, $n = 114$). Although leaf area is unlikely to be uniformly distributed within the crown, this assumption is often made in applications of 255
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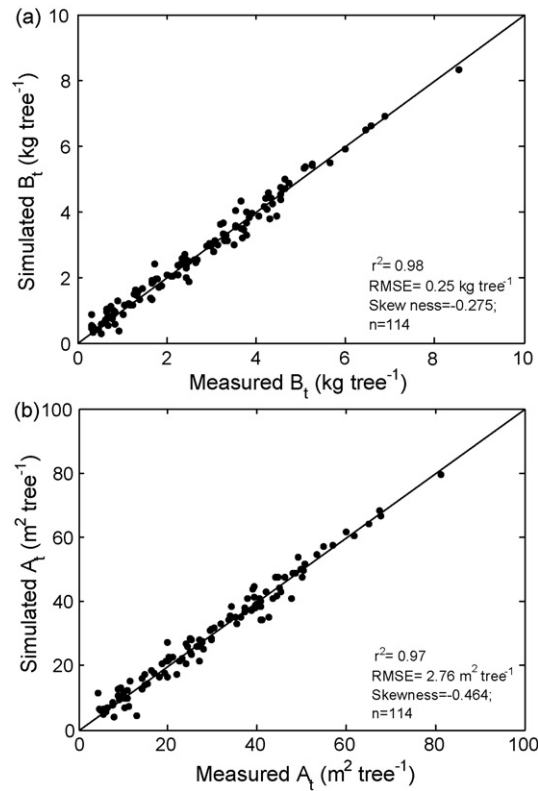


Fig. 2. Comparison of simulated and measured (a) tree leaf biomass (B_t ; kg), and (b) tree leaf area (A_t ; m^2). Leaf area and leaf biomass were estimated from Eq. 3a, and 3b, respectively.

individual tree-based models (e.g., Medlyn et al., 2007), and other ecophysiological models (e.g., Battaglia et al., 2004).

To obtain stand level estimates of leaf biomass (B_s ; $kg\ m^{-2}$), leaf area index (LAI ; $m^2\ m^{-2}$), and SLA (SLA_s), strong allometric relationships (r^2 of about 0.98, very low root mean square errors, and skewness close to zero; see Fig. 2) between B_t and DBH (Eq. 3b), and between A_t and DBH (Eq. 3a) were established for each date, and applied to DBH measurements of the six inventory plots:

$$B_s = \frac{\sum_{i=1}^n a_B DBH_i^{b_B}}{A_p} \quad (10)$$

$$LAI = \frac{\sum_{i=1}^n a_A DBH_i^{b_A}}{A_p} \quad (11)$$

$$SLA_s = \frac{\sum_{i=1}^n a_A DBH_i^{b_A}}{\sum_{i=1}^n a_B DBH_i^{b_B}} \quad (12)$$

where n is the number of trees in the six inventory plots (163 trees), DBH_i is the measured DBH of the i th tree, and A_p is the total area covered by the six plots. We checked that we obtained very similar SLA_s as those computed from Eq. (12) by using allometric relationships between SLA_t and DBH (Eq. (4)), and between B_t and

DBH (Eq. 3b), i.e.,:

$$SLA_s = \frac{\sum_{i=1}^n [a_B DBH_i^{b_B} a_{SLA} DBH_i^{b_{SLA}}]}{\sum_{i=1}^n a_B DBH_i^{b_B}} \quad (13)$$

3. Results

3.1. Tree leaf biomass and leaf area

From the first measurement date (October 11, 2004) to the last (June 7, 2006), mean H_t increased from 14.7 to 21.1 m, and mean DBH increased from 0.11 to 0.15 m (Fig. 3). Despite the genetic homogeneity of this clonal plantation, there were large within-stand variations in H_t and DBH , as shown by the standard deviations on Fig. 3. In October 2004, H_t ranged from 7.3 to 17.7 m, and DBH from 0.05 to 0.14 m, and at the last measurement date, H_t varied from 8.7 to 23.5 m, and DBH from 0.05 to 0.19 m. Tree leaf biomass and leaf area were even more variable: across all measurement dates, mean B_t of the smallest and biggest sampled trees were about 0.48 and 5.50 kg, corresponding to mean A_t of about 6.4 and 57.0 m^2 , respectively. Therefore, the biggest sampled tree had, on average, 11.3 times more leaf biomass and 8.9 times more leaf area than the smallest tree.

For all measurement dates, Eq. 3b and 3a accurately represented the changes in B_t or A_t with tree size (Fig. 2 and Table 1). The root mean square errors (RMSE) were low, the r^2 were high (about 0.98 for B_t and 0.97 for A_t), and the distributions of the residuals were not skewed.

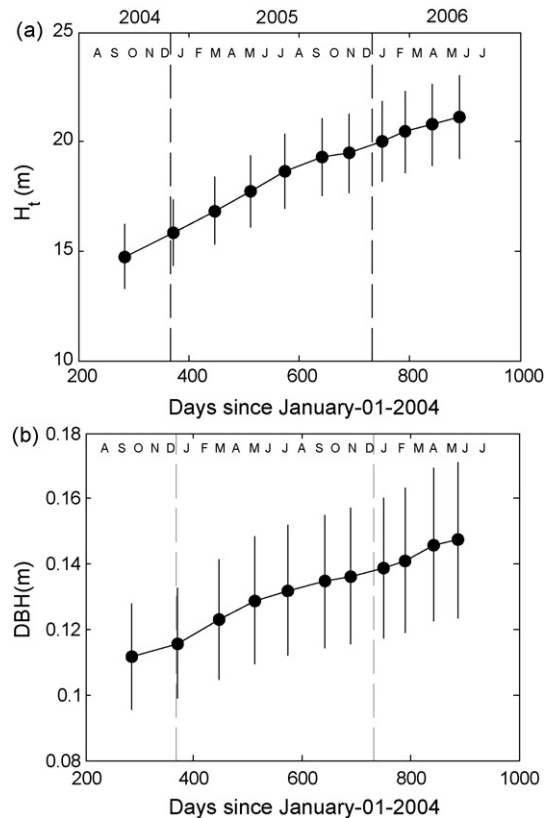


Fig. 3. Changes in (a) tree height (m), and (b) DBH (m) from October 2004 to June 2006 (mean values and standard deviations; $n = 163$ trees) at the permanent inventory plots.

Table 1

Parameter values for Eq. 3b and 3a adjusted for each sampling date; B_t : tree leaf biomass (kg); A_t : tree leaf area (m^2); DBH : diameter at breast height (m); n : number of sampled trees. Coefficient of determination (r^2), root mean square error (RMSE), and skewness are also given.

Date	$(3b)B_t = a_B DBH^{b_B}$						$(3a)A_t = a_A DBH^{b_A}$				
	n	a_B	b_B	r^2	RMSE	Skewness	a_A	b_A	r^2	RMSE	Skewness
11 October 2004	9	487.8	2.394	0.983	0.171	0.019	3050.7	2.167	0.987	1.408	0.343
05 January 2005	10	972.6	2.803	0.966	0.225	0.644	6976.3	2.546	0.952	3.115	0.817
23 March 2005	10	462.4	2.378	0.969	0.264	-0.556	4819.0	2.329	0.975	2.669	-1.542
26 May 2005	10	682.0	2.627	0.989	0.169	-0.069	4260.0	2.338	0.992	1.450	-0.158
27 July 2005	10	194.6	2.053	0.968	0.242	0.647	1458.1	1.856	0.971	2.365	0.724
03 October 2005	10	215.6	2.104	0.993	0.110	0.001	1592.3	1.950	0.988	1.406	-0.687
21 November 2005	15	244.2	2.178	0.958	0.283	-0.926	1913.2	2.020	0.958	2.799	-0.884
20 January 2006	10	928.5	2.886	0.993	0.157	-0.028	7680.2	2.707	0.988	2.287	0.071
01 March 2006	10	472.6	2.488	0.974	0.311	0.307	3282.0	2.255	0.963	3.709	0.088
21 April 2006	10	1099.3	2.893	0.978	0.373	-0.142	5828.6	2.543	0.970	4.060	-0.508
07 June 2006	10	844.9	2.877	0.982	0.283	-0.944	3819.2	2.482	0.964	3.380	-1.310

303

Table 2

Results of the analysis of covariance using tree DBH, sampling date and crown section as fixed effects and an additional random effect on the intercept at the tree level; sample size = 342 (see text).

Factors	Num DF	Den DF	F value	Pr > F	% of variability explained
DBH	1	314	87.88	<0.0001	28
Date	10	314	23.74	<0.0001	26
Crown part (fixed)	2	314	30.98	<0.0001	6
Part of the fixed effects due to the covariance between factors					3
Tree effect (random on the intercept)					3
Residual					34

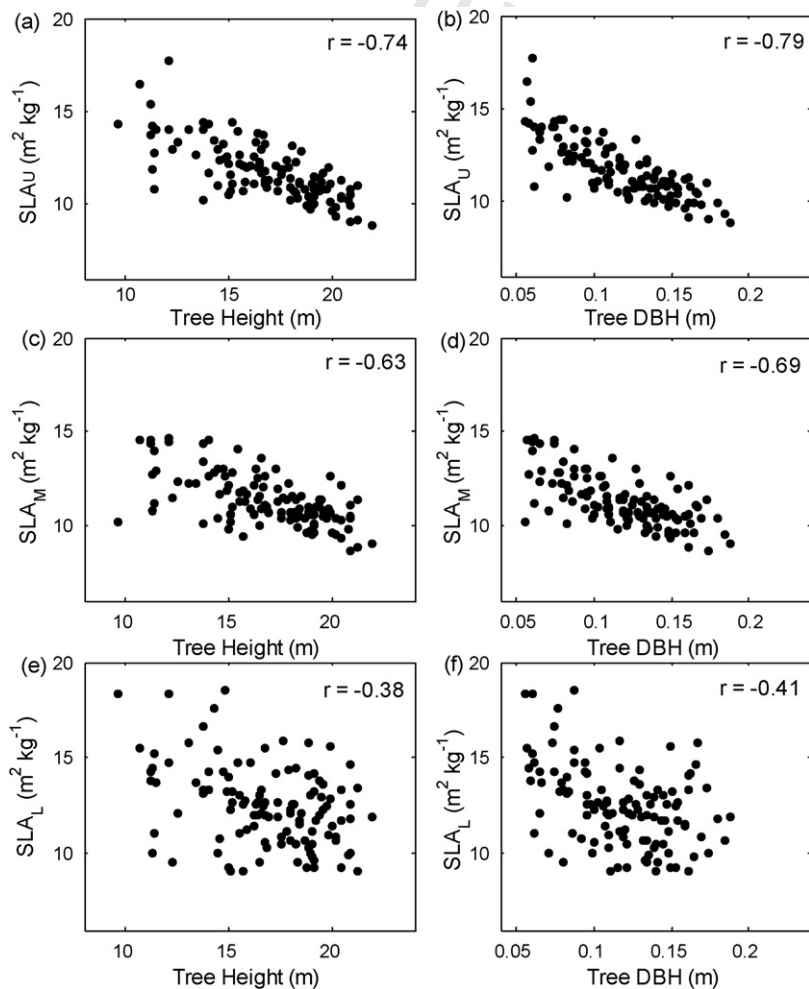


Fig. 4. Specific leaf area of upper (SLA_U), middle (SLA_M), and lower crown (SLA_L) sections of all sampled trees ($n = 114$), versus tree height (a, c, e) or DBH (b, d, f).

303 Equations 3a and 3b imply that A_t scales with B_t following a
 304 power function whose exponent $\alpha \approx b_A/b_B$. Using our fitted b_A and
 305 b_B coefficients (Table 1), α was always smaller than one, indicating
 306 that A_t increased at a lower pace than B_t with increasing tree size. In
 307 others words, the ratio of A_t and B_t , SLA_t , is expected to decrease
 308 with increasing tree size, since $b_B > b_A$.

309 3.2. Within-crown and between-crown variation in SLA

310 SLA values were significantly different ($P < 0.01$) in the three
 311 crown sections (Table 2). The mean SLA (across all dates and all
 312 sampled trees; $n = 114$) of the upper (SLA_U), middle (SLA_M), and
 313 lower (SLA_L) crown sections were 11.7, 11.3 and 12.5 $m^2 kg^{-1}$,
 314 respectively. SLA_U , SLA_M , SLA_L , and crown-average SLA (SLA_t) varied
 315 considerably with tree size (Figs. 4 and 5 and Table 2), from values
 316 of about 9 $m^2 kg^{-1}$ for the biggest trees, to values higher than 14
 317 $m^2 kg^{-1}$ for the smallest trees. The SLA of all crown sections were
 318 more negatively correlated to DBH than to H_t , and the absolute
 319 value of the correlation coefficients decreased from the upper to
 320 the lower crown sections (Fig. 4). The SLA of all crown sections
 321 were negatively correlated to the absolute leaf height (i.e., the
 322 center point of the crown sections; data not shown), but the
 323 strength of the correlations was similar (upper crown section), or
 324 lower (middle and lower crown sections) to the strength of the
 325 correlations between SLA and H_t ($r = -0.75, -0.57; -0.23$ for the
 326 relationships between SLA and absolute leaf height, for upper,
 327 middle and lower crown sections, respectively, and $-0.74, -0.63$
 328 and -0.38 for the relationships between SLA and H_t for the same
 329 crown sections (Fig. 4)).

When applied to the whole dataset, Eqs. (9) and (2) showed
 similar performances, and explained about 49% of the variation in
 SLA_t (Fig. 5a and b). Better results were obtained with Eq. (4) which
 explained about 60% of the variation in SLA_t (Fig. 5c and d). When
 applied to each sampling date, Eqs. (9) and (2) explained about 86%
 of the variations in SLA_t , with RMSE of about 0.55 $m^2 kg^{-1}$ (Fig. 6a
 and b and Table 3). Eq. (4), which uses DBH as the driving variable,
 was more accurate for estimating SLA_t . About 90% of the variation
 in SLA_t was explained with this model (Fig. 6c and Table 3), the
 RMSE were low (about 0.47 $m^2 kg^{-1}$), and the residual distribu-
 tions were not skewed.

Significant differences in SLA_t were found between sampling
 dates (Fig. 7): over the 2-year period, SLA_t was lowest at the end of
 the dry season (10.8 and 10.2 $m^2 kg^{-1}$ in October 2004 and October
 2005, respectively), and peaked about 3 months after the start of
 the wet season (13.0 and 12.5 $m^2 kg^{-1}$ in January 2005 and January
 2006, respectively).

337 3.3. Stand leaf biomass, LAI and SLA 347

Over the 2-year study period, B_s ranged from 0.164 $kg m^{-2}$ in
 January 2005 to 0.303 $kg m^{-2}$ in April 2006 (Fig. 8a). In 2005, B_s
 showed little variation from March till the end of the year.

Leaf area index exhibited a clear seasonal trend (Fig. 8b), with
 lowest values at the end of the dry season (e.g., 1.84 $m^2 m^{-2}$ in
 October 2004), and highest values about 1 or 2 months before the
 end of the wet season (e.g., 3.10 $m^2 m^{-2}$ in March-April 2006).
 These seasonal variations were due to changes both in SLA_s (Fig. 8c)
 and in B_s .

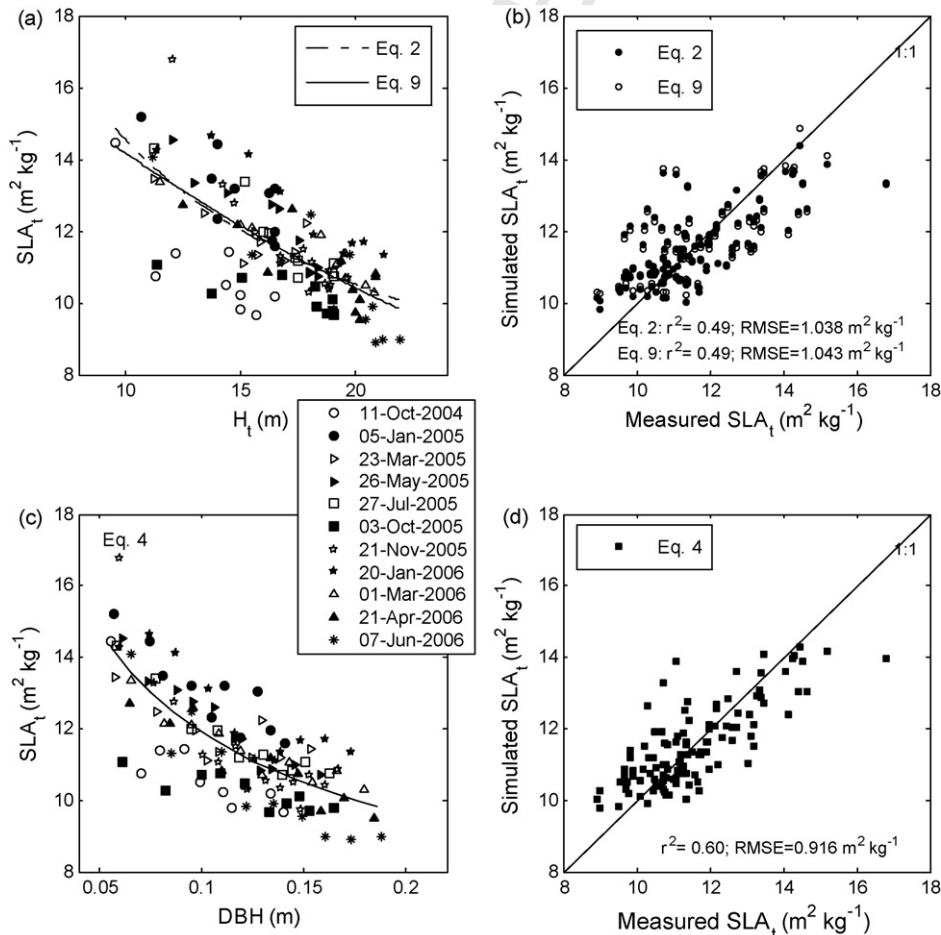


Fig. 5. Tree-average SLA (SLA_t) versus tree height (a), or DBH (c), and simulated SLA_t versus measured SLA_t (Fig. 5b for Eqs. (2) and (9), and Fig. 5d for Eq. (4)). These equations were adjusted over the whole data set (all sampled trees of all measurements dates; $n = 114$). Corresponding parameter values for these equations are reported in Table 3.

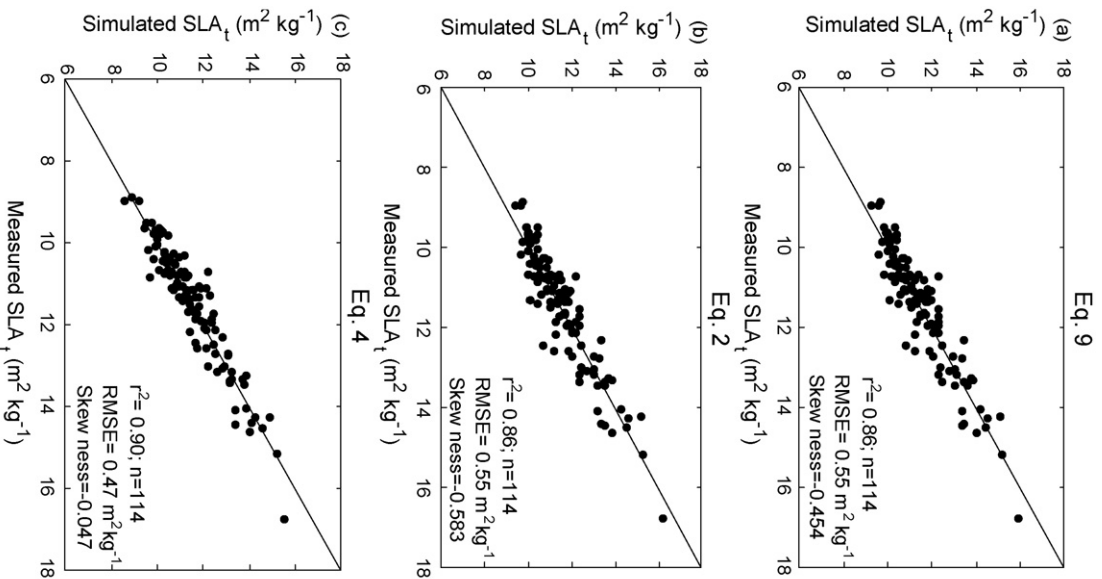


Fig. 6. Simulated versus measured tree-average specific leaf area (SLA_t) after model calibration for each sampling date: (a) Eq. (9); (b) Eq. (2); and (c) Eq. (4). Corresponding parameter values for these equations are reported in Table 3.

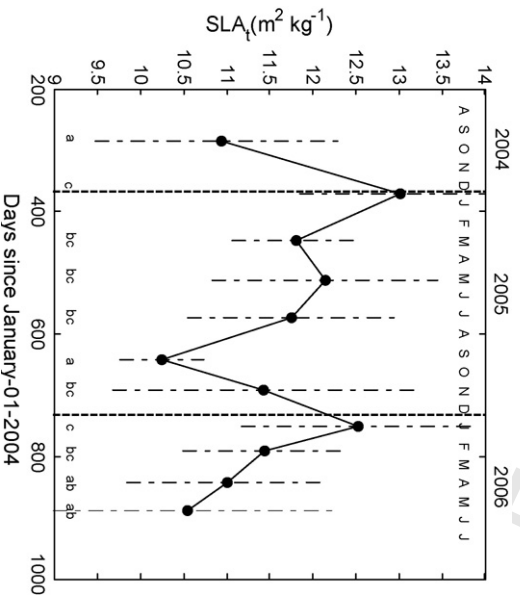


Fig. 7. Time course of SLA_t (mean values and standard deviations; 9–15 sampled trees depending on the sampling date). Different letters at the bottom of the graph indicate significant differences between sampling dates ($P < 0.05$).

Table 3

Parameter values for Eqs. (9), (2), and (4) adjusted over the whole data set, or for each sampling date; SLA_t : tree-average specific leaf area ($m^2 kg^{-1}$); n : number of sampled trees; H_t : tree height (m); C_t : crown ratio (crown length/ H_t); DBH_t : diameter at breast height (m). Coefficient of determination (r^2), root mean square error (RMSE), and skewness are also given.

Date	n	Eq. (9) $SLA_t = \frac{SLA_{max}}{kH_t C_t} \{ \exp(-kH_t) [\exp(kH_t C_t) - 1] \}$					Eq. (2) $SLA_t = cH_t^d$					Eq. (4) $SLA_t = a_{SLA} DBH_t^{b_{SLA}}$				
		SLA_{max}	k	r^2	RMSE	Skewness	c	d	r^2	RMSE	Skewness	a_{SLA}	b_{SLA}	r^2	RMSE	Skewness
All dates	114	19.4	0.044	0.492	1.038	0.071	42.9	-0.469	0.487	1.043	0.043	5.8	-0.312	0.604	0.916	0.167
11 October 2004	9	21.3	0.069	0.692	0.763	0.268	55.2	-0.622	0.731	0.714	0.390	4.4	-0.381	0.756	0.679	0.564
05 January 2005	10	22.5	0.052	0.636	0.668	-0.061	49.0	-0.492	0.634	0.669	-0.148	6.9	-0.276	0.830	0.457	-0.459
23 March 2005	10	17.1	0.033	0.546	0.477	-0.481	30.6	-0.348	0.591	0.453	-0.500	8.0	-0.174	0.645	0.422	-0.033
26 May 2005	10	24.3	0.060	0.880	0.431	-0.500	69.9	-0.631	0.864	0.460	-0.579	5.7	-0.334	0.943	0.297	0.177
27 July 2005	10	22.5	0.055	0.879	0.400	-0.793	56.8	-0.562	0.863	0.425	-1.169	6.1	-0.301	0.954	0.247	0.207
03–Oct–05	10	12.9	0.019	0.605	0.294	-0.307	18.2	-0.205	0.586	0.300	-0.416	7.8	-0.124	0.664	0.271	0.080
21–Nov–05	15	35.0	0.093	0.899	0.537	-0.200	194.3	-0.997	0.927	0.459	-0.099	4.3	-0.460	0.838	0.681	-0.440
20 January 2006	10	21.3	0.043	0.845	0.512	0.014	47.0	-0.465	0.806	0.573	-0.174	6.8	-0.280	0.823	0.547	0.306
01 March 2006	10	17.8	0.035	0.898	0.289	-0.702	34.7	-0.386	0.881	0.311	-0.579	6.8	-0.246	0.932	0.236	0.590
21 April 2006	10	18.6	0.041	0.633	0.667	-0.585	42.4	-0.468	0.617	0.682	-0.693	6.0	-0.282	0.828	0.457	-0.617
07 June 2006	10	22.4	0.057	0.771	0.783	-1.190	63.7	-0.618	0.746	0.825	-1.283	4.0	-0.451	0.914	0.480	0.357

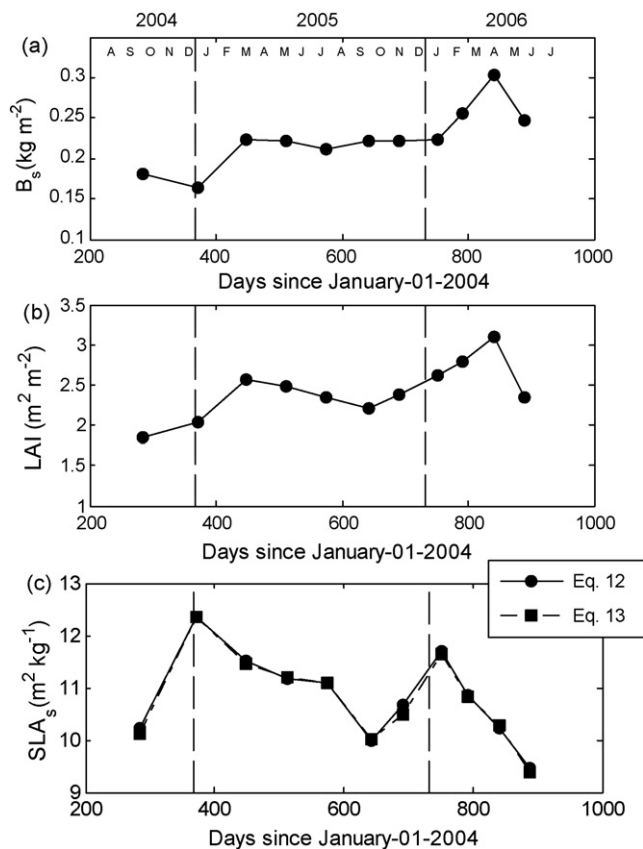


Fig. 8. Seasonal course of stand leaf biomass (B_s ; Eq. (10); (a)), leaf area index (LAI; Eq. (11); (b)), and stand-average specific leaf area (SLA_s ; Eqs. (12) and (13); (c)).

Stand-average SLA (SLA_s ; Fig. 8c) showed a marked seasonal pattern similar to the one depicted on Fig. 7 for the sampled trees, with peaks of SLA_s occurring around January, about 2–3 months after the beginning of the wet season, followed by a steady decrease till the onset of the next wet season (around October). There was little difference between SLA_s computed from Eq. (12) and SLA_s computed from Eq. (13) (Fig. 8c). Stand-average values of SLA differ from the values presented on Fig. 7, since they were obtained by weighting the SLA_t of the trees of different size by their relative contribution to total leaf biomass (Eq. (13)), whereas SLA values presented on Fig. 7 are simple (non-weighted) averages of the SLA_t of sampled trees. Since big trees have smaller SLA_t than small trees, and contribute more to stand leaf biomass, stand-average SLA were lower than the mean SLA_t of sampled trees: SLA_s ranged from 10.2, 10.0 and $9.45 \text{ m}^2 \text{kg}^{-1}$ in October 2004, October 2005, and June 2006, respectively, to 12.3 and $11.7 \text{ m}^2 \text{kg}^{-1}$ in January 2005 and January 2006, respectively. Therefore, SLA_s varied by about 20% throughout the year.

4. Discussion

4.1. Within-crown variation in SLA

In contrast with the steep within-crown vertical gradients of SLA reported in several studies for both coniferous (e.g., Ishii et al., 2002; Marshall and Monserud, 2003; Koch et al., 2004; Xiao et al., 2006) and broad-leaf tree species (e.g., Bartelink, 1997; Kenzo et al., 2006; Sellin and Kupper, 2006; Holdaway et al., 2008), we found little difference in SLA between-crown sections (mean SLA in the lower crown section was only 8% higher than that of the two others). Small within-crown vertical gradients of SLA were also reported for 6–13 year-old *E. nitens* stands in Tasmania (Medhurst

et al., 1999; Medhurst and Beadle, 2002). Canopies of eucalypt forests are generally more open than other forest types: pendulous leaves and low LAI (as in this study: $\sim 2.5 \text{ m}^2 \text{m}^{-2}$) allow more light to reach the lower parts of the canopy, and this more uniform light distribution within the canopy may partly explain the low vertical gradients of SLA (King, 1997; Whitehead and Beadle, 2004; Burgess and Dawson, 2007; Medlyn et al., 2007). Furthermore, in fast-growing canopies, the foliage developed in the upper part of the crown under high light environment rapidly becomes shaded by new developing foliage. The capacity of older leaves to re-acclimate to lower irradiance is limited by anatomical constraints (Niinemets, 2007). Therefore, the anatomy and SLA of older leaves in the middle and lower parts of the crown might be only weakly related to current light environment, and this might contribute to dampen the vertical within-crown gradients of SLA .

4.2. Within-stand variations in SLA_t

Unlike the low within-crown vertical variations in SLA , we found strong tree size related variations in SLA_t , with lower SLA_t for dominant trees ($\sim 9 \text{ m}^2 \text{kg}^{-1}$) than for suppressed trees (~ 14 – $15 \text{ m}^2 \text{kg}^{-1}$). Similar tree size related differences in SLA have been reported for other tree species (e.g., Niinemets, 1997; Holdaway et al., 2008; Niklas and Cobb, 2008), but it is still unclear if these differences are mostly driven by ontogenic changes (e.g., Day et al., 2001), differences in light-environment (e.g., White and Scott, 2006), or increased water limitation with tree size (e.g., Woodruff et al., 2004; Cavaleri et al., submitted for publication).

Crowns of dominant trees are exposed to higher levels of irradiance than those of suppressed trees. Such differences in crown light environment may contribute to the variability in SLA_t , since SLA is known to be negatively correlated with the level of irradiance experienced by the leaf during its development (e.g., Le Roux et al., 1999; O'Grady et al., 2008). However, in *Eucalyptus* plantations, crown leaf area density ($\text{m}^2 \text{leaf m}^{-3}$ crown; not measured in this study) was reported to increase with tree size (Medhurst et al., 1999), leading to greater self-shading within larger trees (Binkley et al., 2002), and lower light interception per unit of leaf area with increasing tree size (Binkley et al., 2002). Therefore, differences in light environment are unlikely to be the major determinant of the observed variability in SLA_t , which probably results from other factors such as differences in water limitations between dominant and suppressed trees. The decrease in SLA with increasing H_t reported by England and Attiwill (2006) for *E. regnans* leaves sampled in outer branches of the upper crown of dominant trees in several even-aged stands ranging from 6 to 240 years of age could obviously not be attributed to differences in light environment since all sampled leaves were sun leaves exposed to similar levels of ambient sun light. Instead, England and Attiwill (2006) suggested that the observed decreases in SLA with increasing tree age and height may result from (1) increasing leaf water stress (more negative water potential), due to gravity and/or increased path length resistance; and (2) a hypothetical age effect, i.e., "some inherent genetic factor that slows growth of older trees, thereby reducing carbon demand, which reduces carbon export from the leaves, and therefore increases dry mass accumulation in the leaf" (England and Attiwill, 2006).

In even-aged stands, leaves of dominant trees may experience increased water limitation compared to those of suppressed trees, owing to (1) increased path length and gravitational resistance to the flow of water from the soil to the leaves; and (2) increasing wind speed and vapour pressure deficit, and thus evaporative demand, with increasing height (e.g., Rijkers et al., 2000; Aranda et al., 2004). Increasing water limitation with increasing tree size

was presented as the possible cause for larger investments in leaf structural carbon (e.g., thickening of cell walls), increased leaf tissue density, and lower SLA in large trees (Niinemets, 1997).

In our study, H_t explained a large part of the variability in SLA_t , but an even larger proportion of that variability was explained by DBH : among the three equations tested, the power function relating SLA_t to DBH (Eq. (4)) was the most accurate. This suggests that other factors, such as the tree's sapwood area, or the ratio of leaf area to sapwood area, which was shown to increase with increasing DBH in several *Eucalyptus* plantations (e.g., Medhurst and Beadle, 2002) may also contribute to the observed tree size related variation in SLA_t .

Eq. (2) was proposed by England and Attiwill (2006) to relate the SLA of sun leaves sampled at the top of the crown of *E. regnans* trees to H_t : it predicted 52% of the variability in SLA for trees ranging from ≈ 10 to ≈ 90 m in height. In our study, Eq. (2) explained about 49% of the variability in SLA_t when applied to the whole data set, and 59–93% of the variability when applied to each measurement date (Table 3).

No improvement was obtained using Eq. (9), an integrated form of Eq. (1), which has been used in numerous studies to predict the vertical profiles of SLA within canopies or within individual tree crowns (e.g., Koch et al., 2004; Burgess and Dawson, 2007; Ishii et al., 2008). Leaf height depends on tree height, and on the position of the leaf within the crown. In our study, within-crown vertical gradients of SLA were low, but the SLA of each crown section was strongly correlated with H_t (Fig. 4), thus explaining the relatively good performance of Eq. (9) (49% of the variability in SLA_t explained when Eq. (9) was applied to the whole data set, and about 86% of that variability explained when the model was applied to each sampling date; Figs. 5 and 6 and Table 3). Our fitted value of the coefficient k (0.044 m^{-1} for the whole data set; see Table 3) is higher than the values obtained for *Sequoia sempervirens* trees in different locations in California: 0.026 m^{-1} (Koch et al., 2004), 0.027 – 0.031 m^{-1} (Burgess and Dawson, 2007), and 0.016 m^{-1} (Ishii et al., 2008).

Power functions (Eqs. 3a–b and (4)) made it possible to predict accurately A_t , B_t , and SLA_t from DBH . As reported in two recently published studies (Holdaway et al., 2008; Niklas and Cobb, 2008), we found that A_t increased non-isometrically with B_t : for increasing tree size, A_t increased more slowly than B_t ($b_A < b_B$), thus explaining the decreases in SLA_t with increasing DBH ($\alpha < 1$, and $b_{SLA} < 0$). Our mean α value (0.91; Table 1) was similar to the mean value (0.90) found by Holdaway et al. (2008) for several *Nothofagus solandri* stands in New Zealand. Our mean b_{SLA} value (-0.31) was higher than the mean value (≈ -0.37) reported by Niklas and Cobb (2008) for several tree species. Such a b_{SLA} value of -0.31 indicates that a 4-fold increase in DBH (which corresponds to the range of DBH observed in our stand) would result in a 35% decrease in SLA_t .

Such strong within-stand variations in SLA_t need to be taken into account for an accurate estimation of stand leaf area index. Ignoring differences in SLA_t between trees of different sizes (e.g., Vertessy et al., 1995; Roberts et al., 2001; Medlyn et al., 2007) may lead to an overestimation of the leaf area of big trees and an underestimation of that of small trees. Using constant SLA_t in individual tree-based models like MAESTRA (Medlyn, 2004) could lead to misestimation of crown transpiration or photosynthesis and could explain observed discrepancies between simulated crown transpiration and measured sap flow (Medlyn et al., 2007).

4.3. Seasonal variations of stand-average specific leaf area

Our mean value of SLA_s ($10.8 \text{ m}^2 \text{ kg}^{-1}$) is similar to the values estimated by Dovey and Du Toit (2006) in *E. grandis* stands in South Africa (10.8 and $9.4 \text{ m}^2 \text{ kg}^{-1}$, for 2-year-old and 3-year-old stands,

respectively), and by Leuning et al. (1991) in 19-month-old *E. grandis* stands in Australia (10 and $9 \text{ m}^2 \text{ kg}^{-1}$ in fertilised and non-fertilised stands, respectively). It is higher than the values reported by Dye et al. (2004) for *E. grandis* × *amaldulensis* hybrid clones (7.1 to $8.1 \text{ m}^2 \text{ kg}^{-1}$ for 3-year-old stands), or by Sands and Landsberg (2002) for *Eucalyptus globulus* stands in Australia (9 and $4 \text{ m}^2 \text{ kg}^{-1}$ for 2-year-old stands and 4-year-old stands, respectively).

Specific leaf area of eucalypts grown in plantations is generally higher than in their native environment (Whitehead and Beadle, 2004), and usually decreases sharply during the first 3–4 years after planting, e.g., from 11 to $4 \text{ m}^2 \text{ kg}^{-1}$ in *E. globulus* and *Eucalyptus nitens* stands in Australia (Sands and Landsberg, 2002), or from 10.5 to $7 \text{ m}^2 \text{ kg}^{-1}$ in *Eucalyptus grandis* stands in Brazil (Almeida et al., 2004). In 3-PG, a function has been introduced in order to account for this age-related trend in SLA_s (Sands and Landsberg, 2002). Our results (e.g., Fig. 5) suggest that this “age-related” trend in SLA_s may simply result from an increase in stand-average tree size as the stand ages.

We found large seasonal variations in SLA_s , with a magnitude of about $2.2 \text{ m}^2 \text{ kg}^{-1}$ ($\approx 20\%$ of the year round average of SLA_s ; Fig. 8c). Seasonal changes in SLA and other leaf traits have often been reported for deciduous species (e.g., Wilson et al., 2000; Xu and Baldocchi, 2003; Simioni et al., 2004; Grassi et al., 2005). For evergreen species, seasonality was thought to be small, but recent studies have reported large seasonal or inter-annual variations in SLA (e.g., Misson et al., 2006), especially in evergreen forests prone to seasonal drought (Sala et al., 1994; Faria et al., 1998; Prior et al., 2004; Prior et al., 2005; Turner et al., 2008). Variations in SLA in evergreen forests may result from seasonal changes in light or water availability (Turner et al., 2008), seasonal changes in the ratio of young to old leaf biomass (Sala et al., 1994), selective retention of leaves with low or high SLA (Ishii et al., 2002), or variation in the leaf nutrient or non-structural carbohydrate contents (Misson et al., 2006), due to retranslocation processes (Sala et al., 1994).

Specific leaf area in *Eucalyptus* species exhibits considerable phenotypic plasticity (Roderick et al., 2000; Sefton et al., 2002; Warren et al., 2006), and commonly decreases with decreasing soil water availability (Medhurst et al., 1999; Roderick et al., 2000; Turner et al., 2008), a trend we also observed at our study site: SLA_s was lowest at the end of the dry season, and increased after the onset of the wet season. Decreases in SLA between wet and dry seasons were also reported for *E. tetradonta* in Australia (Prior et al., 2004) and *E. globulus* in Portugal (Faria et al., 1998). In a study involving 43 *Eucalyptus* species and 24 sites located along a rainfall gradient in Australia, Turner et al. (2008) found that SLA of leaves produced in a wet year were higher than those produced during the previous drier year. Similarly, Warren et al. (2006) measured leaf traits on 29 species (35 ecotypes) of 16-year-old *Eucalyptus* at a productive (rainfall of 1200 mm yr^{-1}), and unproductive (600 mm yr^{-1}) common garden: SLA was $\approx 20\%$ greater at the productive site than at the unproductive site, a difference that is similar in range to the variation observed at our site between the dry and the wet season. Depressive effects of water deficit on SLA were also reported for cuttings or seedlings of various *Eucalyptus* species subjected to experimental drought conditions (e.g., Li et al., 2000; Pita and Pardos, 2001; Costa e Silva et al., 2004).

At our study site, water availability may also indirectly affect SLA_s by modifying the ratio of young to old leaf biomass, since SLA of old leaves is generally lower than SLA of young leaves (England et al., 2007; Laclau et al., 2009). This ratio is determined by the rates of leaf production and leaf shedding, which are both influenced by water availability (Pook, 1984). In *Eucalyptus* stands in Congo, leaf turnover is high (≈ 2 ; Laclau, 2001) and leaves are produced all year round, but their production rate is seasonal and strongly correlated with available soil water (unpublished data). In

woody plants, both the leaf appearance rate (Lebon et al., 2006), and the leaf expansion rate (Tardieu et al., 1999) are sensitive to soil water deficit, and SLA was shown to decrease when environmental conditions have a greater depressive effect on the leaf expansion rate than on photosynthesis, and to increase in the opposite case (Tardieu et al., 1999). Variability in the leaf and plant sink:source relationships, according to tree size (Sala and Hoch, 2009) and season (Korner, 2003) may therefore contribute to both the within-stand and seasonal variation in SLA, as observed in this study.

These aspects should not be overlooked, since the seasonality and the magnitude of carbon fluxes are strongly influenced by the temporal changes in SLA and related physiological parameters, in both deciduous (e.g., Wilson et al., 2001; Marron et al., 2003) and evergreen forests (e.g., Misson et al., 2006).

5. Conclusions

This study has demonstrated that in these young, fast-growing, clonal *Eucalyptus* plantations specific leaf area can be accurately simulated at the tree level from DBH and that the relationship between DBH and SLA_t can further be used to estimate SLA at the stand level. We observed low intra crown vertical variability of SLA but large inter crown variability (big trees having smaller SLA than small trees) that should be taken into account for estimating crown transpiration or photosynthesis using individual tree-based models.

Further studies are required to better understand the factors and mechanisms causing temporal variations in SLAs, owing to their importance in predicting seasonality of both water and carbon fluxes at the ecosystem level.

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