



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

Yann Nouvellon<sup>a,b,\*</sup>, Jean-Paul Laclau<sup>a,c</sup>, Daniel Epron<sup>d,e</sup>, Antoine Kinana<sup>b</sup>, André Mabiála<sup>b</sup>, Olivier Roupsard<sup>a,f</sup>, Jean-Marc Bonnefond<sup>g</sup>, Guerric le Maire<sup>a</sup>, Claire Marsden<sup>a,d,e</sup>, Jean-Daniel Bontemps<sup>h</sup>, Laurent Saint-André<sup>a</sup>

<sup>a</sup> CIRAD, Persyst, UPR80, TA10/D, 34398, Montpellier Cedex 5, France

<sup>b</sup> UR2PI, BP 1291, Pointe-Noire, People's Republic of Congo

<sup>c</sup> USP, ESALQ, Av. Pádua Dias, 11, Piracicaba, SP, 13418-900, Brazil

<sup>d</sup> Nancy Université, Université Henri Poincaré, UMR1137 Ecologie et Ecophysiologie Forestières, BP 239, F-54506, Vandoeuvre les Nancy, France

<sup>e</sup> INRA, UMR1137 Ecologie et Ecophysiologie Forestières, F-54280, Champenoux, France

<sup>f</sup> CATIE, 7170, Turrialba, Costa Rica

<sup>g</sup> INRA, UR1263 EPHYSE, F-33140, Villenave d'Ornon, France

<sup>h</sup> AgroParisTech, ENGREF, 14 rue Girardet, F-54000, Nancy, France

### ARTICLE INFO

#### Article history:

Received 24 February 2009

Received in revised form 18 May 2009

Accepted 19 May 2009

#### Keywords:

Specific leaf area

Leaf mass per area

*Eucalyptus*

Tree size

Allometric relationship

Model comparison

Water constraint

### 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  $SLA$ .

© 2009 Elsevier B.V. All rights reserved.

### 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 (Dufrêne 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

\* Corresponding author at: Departamento de Ciências Atmosféricas, IAG, Universidade de São Paulo, Rua do Matão, 1226, Cidade Universitária, São Paulo, SP, Cep 05508-900, Brazil. Tel.: +55 11 30912786; fax: +55 11 30914714.

E-mail address: [yann.nouvellon@cirad.fr](mailto:yann.nouvellon@cirad.fr) (Y. Nouvellon).

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 cumulative 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):

$$SLA = cH_t^d. \quad (2)$$

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<sup>2</sup>), 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<sup>2</sup> kg<sup>-1</sup>) 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°47'29"S, 11°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.carboafrica.net/index\\_e-n.asp](http://www.carboafrica.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) × *Eucalyptus grandis* (W. Hill ex Maiden) (currently the most commonly planted clone in Congo) was planted at a stocking density of 800 trees ha<sup>-1</sup> (tree spacing: 3.7 m × 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<sub>4</sub>NO<sub>3</sub> 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

Download English Version:

<https://daneshyari.com/en/article/88450>

Download Persian Version:

<https://daneshyari.com/article/88450>

[Daneshyari.com](https://daneshyari.com)